



Visual Mislocalization Produced by a Rapid Image Displacement on the Retina: Examination by Means of Dichoptic Presentation of a Target and its Background Scene

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The time course of visual mislocalization produced by a rapid retinal image displacement was examined in moving-background and saccadic eye movement experiments. In both experiments, the target for localization task and its background scene were dichoptically presented: they were presented separately to the different eyes. The error curves of mislocalization shown in the dichoptic viewing condition were the same as those in monocular viewing (in the moving-background experiment) and binocular viewing conditions (in the saccadic eye movement experiment), indicating that in both experiments the neural interaction responsible for generating mislocalization took place at a site after the lateral geniculate nucleus in the visual system, not at the retinal level. Two possible explanations for mislocalization, one neurophysiological and the other cognitive, were proposed. Furthermore, it was established that the error curves of mislocalization are substantially different between the moving-background and the saccadic eye movement experiments: in the saccadic eye movement experiment, the error curves changed with the actual target position, but not in the moving-background experiment. This was interpreted as showing that the basic mechanism for mislocalization is not the same between the two experimental situations.

Visual localization Retinal image displacement Saccade Visual integration Dichoptic viewing

This paper reports on two experiments that were conducted to explore the mechanism responsible for visual mislocalization produced by a rapid retinal image displacement. When a visual target is briefly presented during rapid displacements of its background visual scene, the target's position is sometimes misperceived. Such mislocalizations have been assumed to be produced by a complex interaction between the neural signals generated by the target and its background scene (MacKay, 1970). The first experiment attempted to explore where in the visual system the two types of visual (neural) signals were integrated. For this purpose, mislocalization was compared between the monocular and dichoptic viewing conditions. In the dichoptic viewing condition, a visual target and its background scene were separately projected on the different eyes, whereas in the monocular viewing condition both were projected on the

same one eye. In the second experiment, the same examination was attempted for saccade-related mislocalization.

EXPERIMENT 1: MISLOCALIZATION BY A RAPID DISPLACEMENT OF THE BACKGROUND SCENE

Sperling and Speelman (1965) reported that the position of a visual stimulus flashed during a rapid shift of background scene was misperceived at a different position from its actual position. This finding was later confirmed by MacKay (1970). In MacKay's experiment, a scale pattern was moved horizontally in the visual field, and a small flash stimulus was presented at various points in time near the displacement of the scale pattern. The subjects were asked to report the position on the scale that the flash target appeared to occupy. According to MacKay, the flash was mislocalized in the direction opposite to the scale displacement. The mislocalization occurred from about 50 msec before the onset of the

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displacement and continued during the displacement, the error curve rising to maximum at time of onset.

How then are such mislocalizations to be explained? MacKay explained as follows. "The location of a flash target relative to its background involves an interaction between the neural signals generated by each, which interaction takes an appropriate time to complete. If during this time the retinal image of the background shifts to a new position, the integrative process will have two different background signals to cope with, each making its own contribution to the total weight of evidence with respect to flash location. The later the flash comes, before the moment of transition, the greater will be the weight attached to the new scale-position as compared with the old" (MacKay, 1970, p. 732). Thus, the target's apparent position changes depending on the temporal relationship between the target and its background movement. It should be noted here that MacKay's explanation suggests that visual localization during rapid image displacements involves a relatively higher cognitive computational process in the brain.

On the contrary, mislocalization may be explained as a result of complex retinal events produced by a rapid shift of the image of the background scene across the retina, because neurons at this level also interact each other possibly via a horizontal and amacrine cells. Bischof and Kramer (1968) investigated saccade-related visual mislocalization and, in explaining their results, attached great importance to such an activation process on the retina.

Experiment 1 was conducted to decide where in the visual system mislocalization of visual targets is generated when its background scene is rapidly displaced. In both explanations described above, it is assumed that mislocalization is caused by an interaction of neural signals for the target and its background scene. However, MacKay's (1970) explanation implies that this interaction may take place at a more central level of the visual system. On the other hand, we cannot entirely exclude the possibility that such an interaction occurs at the retinal level. In order to make this point clear, I replicated MacKay's experiments under two viewing conditions of visual stimuli, i.e. dichoptic and monocular conditions. In the dichoptic condition, a target and its background were presented separately to the different eyes. In the monocular condition, both the target and its background were presented to the same one eye. If the integration process responsible for mislocalization only takes place at the retinal level, no mislocalization will be observed in the dichoptic condition, because in this condition neural signals for the target and its background scene cannot interact until they leave the lateral geniculate nucleus (LGN). On the contrary, if mislocalization is shown in the dichoptic condition, this implies that the integration process takes place at the level after the LGN.

Methods

A horizontal luminous scale with divisions was used as a background scene (Fig. 1). Its image [white

(12 cd/m²) on a dark ground (5 cd/m²)] was rear projected on a screen (50 × 75 cm) placed 57 cm from the subject's eye. A mirror mounted on a galvanometer was placed between the screen and the projector. The background scene was moved horizontally by driving the galvanometer.

The subject was seated with the head fixed by a chin and forehead rest. Horizontal eye movements of the right eye were recorded by a photo-electrical (iris-sclera reflection) method. On each trial, a buzzer warning signal was given, and then a fixation point (red LED, 0.3 deg in diameter, 20 cd/m²) appeared at the zero scale division. The duration of the fixation point varied from trial to trial between 1.0 and 2.0 sec. The subject was asked to binocularly keep watching the fixation point. 200 msec after the offset of the fixation point, the background scene was rapidly displaced horizontally 8 deg to the left. (The 200 msec interval was chosen for its equivalence to normal saccade latencies.) The duration of the background displacement was 30 msec, approximately equal to the average duration of 8 deg saccades. At various points in time before, during, or after the background displacement, a vertical rectangular visual stimulus (0.3 × 1.5 deg), which was illuminated by an electric flash tube (Nisshin, HD-100), was presented at the -4, +4, or +12 scale division, and used as a target for visual localization. The target also was projected through the movable mirror that was used to displace the background scene. Therefore, the target's position relative to the scale did not change irrespective of the background displacement. The subject verbally reported the scale division on which the target appeared.

In the dichoptic condition, the background scene and the target were presented to the right and left eyes, respectively, while, in the monocular condition, both were presented to the left eye only. The viewing conditions were set up by making use of a polaroid film.

Two subjects participated in this experiment. Subject HH was the author and subject KN was a male university student. Each served as a subject for 3 days for each of the two viewing conditions. On each day, the target position was restricted to one of the three positions (-4, +4, and +12 on the scale), and 128 trials were conducted dividing into 8 sessions. The timing of the target's presentation was randomized within each session.



FIGURE 1. A background scene used in this study. The horizontal length of the scale (from the -8 to the +16 scale division) was 24 deg when it was projected on the screen.

Results

Eye movements

Eye movements were analyzed by a high-speed digital storage scope (Iwatsu, DS-6121A). In both dichoptic and monocular conditions, the subjects kept watching the position of the original fixation point during the background displacement. Usually, the eye moved toward the apparent target's position more than 200–300 msec after the movement of the background.

Visual localization

Figure 2 shows the results obtained during fixation in the dichoptic and monocular conditions. Although there were relatively large differences in the offset level of the error curves (i.e. the accuracy level when the targets were presented well before or after the displacements) between as well as within subjects, the two subjects showed approximately the same pattern of mislocalization, which did not essentially differ among the three target positions. The more important finding is that the error curves were approximately the same between the two viewing conditions. That is, when a target was presented just before the background displacement, it was mislocalized in the direction opposite to the background displacement. The error reached its maximum at the time the background began to move. On the other hand, when a target was presented at the end of the background displacement, large errors in the same direction as the background displacement were observed. The findings that mislocalizations are shown in the dichoptic condition and that the error curves were the same as those in the monocular condition suggest that visual mislocalization occurs without the target and its background being projected on the same retina of the eye.

EXPERIMENT 2: MISLOCALIZATION AT THE TIME AROUND SACCADE EYE MOVEMENTS

In Experiment 1, the rapid shift of the retinal image was produced by moving the background scene during fixation, and visual mislocalization was observed in both dichoptic and monocular viewing conditions, suggesting that mislocalization was generated at the higher central level. Experiment 2 was conducted to explore what would happen when the retinal image displacement was produced by a voluntary saccadic eye movement instead of moving the background scene. It has been shown by many researchers that a visual stimulus is mislocalized when it is flashed at the time near a saccadic eye movement (Bischof & Kramer, 1968; Honda, 1989, 1990, 1991; Kennard, Hartman, Kraft & Glaser, 1971; Matin, Matin & Pearce, 1969; Matin, Matin & Pola, 1970; Mateeff, 1978; O'Regan, 1984). Although this phenomenon has often been interpreted as reflecting inaccurate neural signals for the position of the eye in the orbit (i.e. corollary discharge in Sperry's term; see Grusser, 1986, for a historical review), MacKay (1970) claimed that saccadic eye movements were not a prerequisite for mislocalization and that what was important was the

movement of the retinal image, not the movement of the eye. Therefore, there is a possibility that the primary source of mislocalization may be the complex retinal events caused by rapid image displacements contingent upon saccadic eye movements. In Experiment 2, I examined whether the saccade-related mislocalization also would be shown when the target and its background were dichoptically presented.

Methods

The background scene was the same as that used in Experiment 1 (Fig. 1). On each trial, a buzzer warning signal was given, and then a fixation point (red LED, 0.3 deg in diameter, 20 cd/m²) was presented for 1.0–2.0 sec at the zero scale division. The subject was asked to keep watching the fixation point. At the offset of the fixation point, a small visual cue stimulus for eliciting a saccade was presented for 20 msec, at the position of 8 deg right of the fixation point, i.e. at the eight scale division. The visual cue consisted of two vertically arranged rectangular red LEDs (0.1 × 0.3 deg, 18 cd/m²), the distance between the center of the LEDs being 0.4 deg. The subject was asked to make a saccade toward the visual cue. At various points in time before, during, or after the saccade, a visual target (yellow LED, 0.4 deg in diameter, 30 cd/m²) was presented for 2 msec at the -4, 4, or 12 scale division. The subject verbally reported the scale division on which he had seen the target. The fixation point and the visual cue for saccade were set on a blackboard placed at a different position from the screen, and seen by the subject through a half-silvered mirror set before the subject's eye. By this, these stimuli were presented as an optical image against the background scene. Horizontal eye movements of the subject's right eye were monitored by a photo-electric (iris-sclera reflection) method. To present the target during or after the saccade, the output from the eye movement monitor apparatus was fed into a differential circuit that triggered the target. Targets before the saccade were presented by presetting a shorter time-interval than normal saccade latencies (200 msec) between the target and the visual cue for eliciting the saccade.

The subject always observed the fixation point and the cue stimulus for saccade with the two eyes. The background scene and the target were viewed binocularly (binocular condition) or dichoptically (dichoptic condition). In the dichoptic condition, the subjects observed the visual background scene and the target with the right and the left eyes, respectively.

In addition to the saccade condition described above, localization was examined also in a condition in which the target was presented when the eye remained still. In this control condition, either the fixation point or the cue for saccade was presented for 1.8 sec, and the subject was asked to keep watching these stimuli. Just after the offset of these stimuli, a flash target was presented. The subject made a saccade to the target, and reported its apparent position.

The author (HH) and a male university student (MM) served as subjects. Each subject participated for 4 days

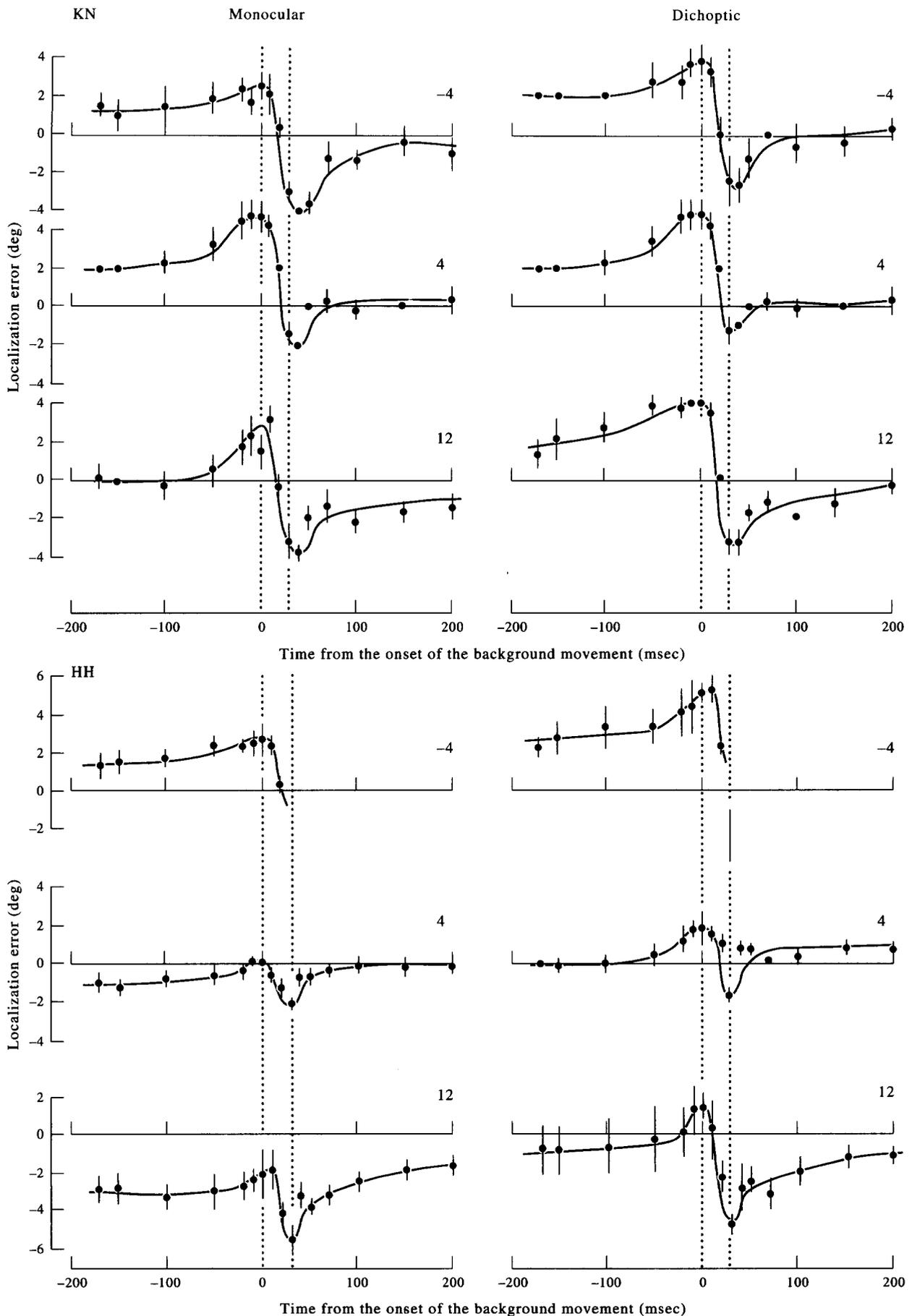


FIGURE 2. The time course of mislocalization in monocular (left) and dichoptic (right) conditions in Experiment 1. The results are shown separately for each actual target position (-4, +4, and +12). The abscissa indicates the time interval (msec) between the beginning of background movements and the target presentation. A minus sign in the abscissa shows that targets were presented before the background movement. Vertical dotted lines show the movement time of the background. The ordinate shows mislocalization (deg). A plus sign in the ordinate shows mislocalization in the direction opposite to the background displacement (rightward). Each dot indicates the average error (and the SD) of 8 trials. The error curves were fitted by eye based on the average errors (dots). The partial lack of data (subject HH) is due to the target being projected on the blind spot.

for each of the two viewing conditions. On each day, 96 trials of the experimental (saccade) condition and 24 trials of the control condition divided into 6 sessions were conducted. The position of the target (the -4 , $+4$, and $+12$ scale division) and the timing of its presentation were randomized within each session.

Results

Eye movements

The subjects sometimes made a saccade with extremely short (< 50 msec) or long (> 300 msec) latencies. In these cases, the target was not presented. When a target was presented immediately after the presentation of the cue stimulus for saccade, the eye sometimes moved directly to the target: a saccade to the visual cue stimulus did not occur. On the remaining trials, the expected primary saccade to the visual cue stimulus was observed. Table 1 shows the mean of the amplitude, the latency and the duration of the primary saccade observed in binocular and monocular conditions separately for each subject. Subject HH slightly overshoot the saccade goal in both viewing conditions, whereas subject MM showed small undershooting in the binocular condition.

Visual localization

Figure 3 shows the results obtained in dichoptic (right) and binocular (left) conditions. The two subjects showed approximately the same pattern of mislocalization. In contrast to Experiment 1, the error curves changed with the actual target position. When the target was presented at the position beyond the saccade goal (on the $+12$ scale division), a large error in the direction opposite to the saccade was observed. On the other hand, when the target was presented at the position opposite to the saccade goal (on the -4 scale division), mislocalization toward the saccade goal was observed. Despite the differences due to the target's actual position, however, the error curves were the same between the two viewing conditions. This indicates that the saccade-contingent mislocalization also takes place without the target and its background being projected on the same retina of the eye.

DISCUSSION

Implications of the results in the dichoptic viewing conditions

The primary objective of this study was to explore where in the visual system mislocalization due to rapid

retinal image displacements originates. For this purpose, mislocalization in a dichoptic condition was examined: the target for localization and its background scene were separately projected on the different eyes. The results were clear-cut. Experiment 1 showed that the error curves of mislocalization produced by a rapid displacement of the background scene were the same between dichoptic and monocular conditions. The same results were obtained in Experiment 2 for visual mislocalization of targets presented around the time of a saccadic eye movement. That is, mislocalization observed in the dichoptic viewing condition was approximately the same as that in the normal binocular viewing condition.

In the monocular viewing condition of Experiment 1, the neural interaction between the signals for the target and its background scene could take place at the retinal and/or more central level of the visual system. In the dichoptic viewing condition, on the other hand, the neural interaction never occurred before the signals had left the LGN. The finding that the same error curves were shown in the monocular and dichoptic conditions strongly supports the idea that the neural interaction responsible for mislocalization occurred at higher levels, not at the retinal level, because it is unreasonable to think that the neural interaction occurs again at the more central level after the same processing has been made at the retinal level. Note here, however, that this conclusion does not exclude the possibility that the neural signals for the target and/or its background are distorted at the retinal level to yield false information about the exact location of these visual stimuli and relayed to higher levels. In this case too, interactions between the signals at the central level are nevertheless needed to cause mislocalization in the moving-background experiment. It should also be noted here that if the error curves were distinctively different between the two conditions, there would be a possibility that the neural interaction took place differentially at the retinal and central levels of the visual system. The present study shows, however, that this was not the case.

Why are the targets mislocalized?

At present, it is difficult to state definitely the mechanism responsible for generating mislocalization in the moving-background experiment (Experiment 1). In this section I propose two possible explanations; the first is based on neurophysiological evidence and the second is a cognitive explanation.

Neurophysiological basis of mislocalization. At what level of the visual system do the neural signals for the

TABLE 1. Means and SDs of latencies (msec), durations (msec), and amplitudes (deg) of the primary saccades in binocular and dichoptic conditions

	Binocular			Dichoptic			
	Latency	Duration	Amplitude	Latency	Duration	Amplitude	
HH (<i>N</i> = 272)	183.9 (23.7)	32.7 (3.6)	8.5 (0.8)	HH (<i>N</i> = 270)	176.8 (17.8)	33.0 (3.7)	8.6 (0.9)
MM (<i>N</i> = 206)	210.4 (62.0)	27.8 (3.5)	7.6 (1.0)	MM (<i>N</i> = 233)	182.6 (41.4)	27.8 (3.2)	7.8 (1.0)

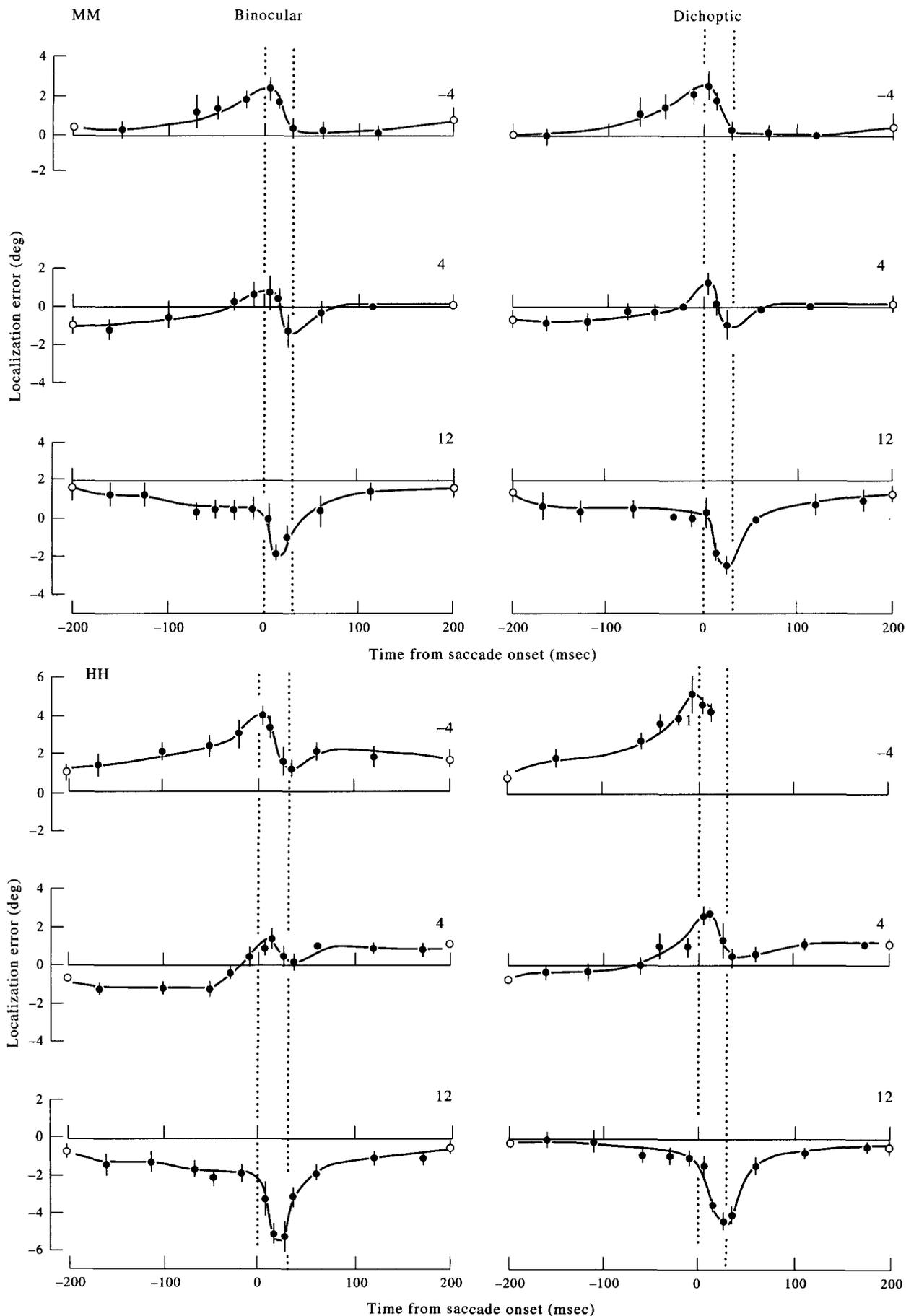


FIGURE 3. The time course of mislocalization in binocular (left) and dichoptic (right) conditions in Experiment 2. Notations are the same as in Fig. 2 except for the following. The abscissa indicates the time interval between the saccade onset and the target presentation. A minus sign in the abscissa indicates that target were presented before saccade onset. Vertical dotted lines show the mean duration of the saccades. A plus sign in the ordinate shows mislocalization in the saccade direction (rightward). Each dot is the average of 5–25 trials. Open circles indicate the results on control trials in which the subjects kept watching the fixation point (left circle) or the visual cue for saccade (right circle).

target and the background scene interact? Before answering this question, let us consider the visual processing which was needed when the subject conducted the localization task in the moving-background experiment. In that experiment, visual targets were flashed around the time of a rapid movement of the background scene, and, therefore, there were at least three visual attributes which must have been processed in the brain; the movement and shape of the background scene and the location of the target. (The shape of the target was not important for localization task.) It seems that mislocalization was produced as a result of a complex cross-talk between concurrent processing of such visual attributes.

It is well known that the structures of visual processing are arranged in a hierarchy that includes at least 10 stages of cortical as well as several subcortical stages (Van Essen & Deyoe, 1995). It is also known that visual attributes such as movement, shape, and location are predominantly processed at various stages after the intermediate cortical level; they are processed and interact at the level beyond the VI area of the cortex.

Next what types of cells are responsible for producing mislocalization? The cells in the middle temporal (MT) and medial superior temporal (MST) areas of the cortex of a monkey are known to be sensitive to the movement of the visual stimulus field, and are thought to be associated with motion perception (e.g. Newsome, Britten & Movshon, 1989). At the same time, the cells in areas MT and MST increase their activity during eye movements (Komatzu & Wurtz, 1988; Newsome, Wurtz & Komatzu, 1988). Furthermore, these areas connect with the area 7a where exist cells which selectively respond to a particular position of the eye (Sakata, Shibutani & Kawano, 1980). These findings suggest that these cell are closely related with both motion perception and eye movements.

Consider what happened for these cells during the localization task in the moving background experiment. The cells in the areas MT and MST must have been activated by a rapid movement of the background scene, because the range of the optimal stimulus velocity to which these cells respond is known to be very wide, up to about 250 deg/sec (Maunsell & Van Essen, 1983), very similar to the velocity of the moving-background employed in this study (about 260 deg/sec). At the same time, these cells are associated with eye movements as well as motion perception. Therefore, I speculate that the rapid background movement activated also the voluntary eye movement system as well as the perceptual system, and the associated efferent signals for eye position was generated without actual movements of the eye, resulting in mislocalization of the target presented around the time of the background movement.

Although the above mentioned explanation is still a matter of speculation, it should be noted here that Leibowitz and his colleagues proposed a similar explanation for illusory motion and displacement phenomena associated with visual fixation during ego motion. They argued, for example, that when an observer and a fixated light source undergo the same rotary acceleration, the

voluntary pursuit system is activated to oppose the vestibulo-ocular reflex which may occur to prevent loss of fixation, and then the associated efferent motion signal results in illusory movement of the fixated light (Leibowitz, Post & Sheehy, 1986; Post & Leibowitz, 1985).

Cognitive explanation. MacKay (1970) claimed that the decision of the target position was made on the basis of the two different background signals and that these background signals made their own contribution to the total weight of evidence with respect to the target position being dependent on the temporal relationship between the target and the background movement. MacKay's explanation, therefore, suggests that the target's apparent position is determined by the background scene before and after its displacement, not by the background during displacement. This idea was later established by Sperling (1990). In one of his experiments, the background scene was extinguished during its displacement. Even in this condition without image smearing on the retina, mislocalization was observed.

Then, how are the error curves shown in the present study explained? Suppose that a target was flashed, for instance at the +4 scale position, immediately before the background displacement of 8 deg to the left. After the background displacement, the absolute position of the target shifts on the scale to the right to the same extent as the background displacement, and now corresponds to the +12 division on the scale. Therefore, if the perceptual decision of the target's position is made partly on the basis of the signal for the background after the displacement as well as that before displacement, the target will be mislocalized in the direction opposite to the background displacement. Conversely, in the same way, the target flashed immediately after the end of the background displacement will be mislocalized in the same direction as the background displacement because, in this case, the signal for the background before the displacement is thought to be used as well. In any case, the relative contribution of the signals for the background before and after the displacement is thought to change with the timing of the target presentation relative to the background displacement. The error curves shown in Fig. 2 fit very well with this account.

[Localization in the saccadic eye movement experiment (Experiment 2), on the other hand, is thought to be achieved by a combination of the inaccurate representation of the eye position in the brain (Dassonville, Schlag & Schlag-Ray, 1990, 1992; Honda, 1990, 1991) and several cognitive processes. Further discussion about the origin of the saccade-related mislocalization has been presented elsewhere (Honda, 1993).]

Comparison of the moving-background and saccadic eye movement experiments

The present study confirmed my previous finding that the time course of visual mislocalization was different between the moving-background and the saccadic eye movement experiments (Honda, 1995). In the moving-background experiment (Experiment 1), the error curves

were essentially the same across the three actual target positions (i.e., -4 , $+4$, $+12$ on the scale). That is, at all target positions, a bipolar pattern of mislocalization was shown: mislocalization in the direction opposite to the background displacement was observed when the target was presented immediately before the displacement, whereas mislocalization in the same direction as that of the background displacement was shown when the target was presented at the time near the end of the background displacement. On the other hand, in the saccadic eye movement experiment (Experiment 2), localization errors varied with the actual target position: when the target was presented on the -4 scale division mislocalization in the saccade direction was observed, whereas mislocalization in the direction opposite to the saccade was observed at the target position of the $+12$ scale division. The discrepancy of error curves between the moving-background and the saccadic eye movement experiments seems to suggest that the exact mechanisms responsible for generating visual mislocalization were different between these two experiments.

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