Vision Res. Vol. 33, No. 5/6, pp. 709–716, 1993
Printed in Great Britain

0042-6989/93 $6.00 + 0.00
Pergamon Press Ltd

Saccade-Contingent Displacement of the Apparent Position of Visual Stimuli Flashed on a Dimly Illuminated Structured Background

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Received 21 May 1992; in revised form 27 August 1992

Subjects were required to perceptually judge the location of flash targets presented at the time of a saccade at various positions scattered two-dimensionally on a dimly illuminated structured background. The saccade-contingent mislocalization was shown only in the direction parallel to the saccade, and not in the direction perpendicular to the saccade. In addition, the mislocalization under the "illuminated background" condition was different in several respects from that observed when targets were presented in the dark. It was suggested that the mislocalization is successfully explained by assuming three physiological and cognitive processes: a sluggish activity of the extraretinal eye position signal, visual cues from the visible background, and selective inattention to image displacements.

Saccade Visual localization Visual stability Eye position signal

Under normal illumination, image displacements on the retina, which are caused by saccadic eye movements, do not bring about an apparent displacement of the corresponding perceived object. A predominant explanation for this visual stability, first suggested by Helmholtz (1866), is the cancellation theory which explains that visual information about image displacements is compared with an internal (extraretinal) signal about eye movements, and that a mismatch is generally perceived as movement of the object in the world.

Several psychophysical studies have been conducted to examine this explanation. Matin *et al.* asked their subjects to report the visual direction of a brief flash presented in the dark at various times before, during, or following a voluntary saccade (Matin, Matin & Pearce, 1969; Matin, Matin & Pola, 1970). The direction of the flash was judged relative to the location of a fixation target viewed and extinguished before the saccade. Using this procedure, they demonstrated that a shift of visual direction occurred even when the flash was presented before the beginning of the saccade. Similar results were obtained when a subject reported the position of a brief flash presented in the dark by moving a probe stimulus to the position where the flash appeared (Honda, 1989, 1990, 1991). In these latter studies, the detailed time–course of visual mislocalization was examined. When subjects made a saccade, a visual target flashed immediately before or at the beginning of the saccade was mislocalized in the same direction as the saccade, whereas when the target was flashed at the end or immediately after the saccade the subject mislocalized it in the opposite direction to the saccade. These results, as well as those reported by Matin *et al.*, indicate that visual stability does not occur at least for a target briefly presented in the dark, and further that extraretinal eye position signals (EEPSs) postulated in the cancellation theory do not inform the actual position of the eye during saccades. Indeed, Honda (1990, 1991) estimated the time–course of the EEPS based on the psychophysical data on perceptual mislocalization, and showed that the EEPS does not reflect the actual position of the eye.

A similar mislocalization has been reported when a flash target is presented during a saccade on an illuminated background. In Bischof and Kramer's (1968) and Mateeff's (1978) experiments, a flash target was presented on a horizontal scale with divisions, and their subjects were asked to verbally report the scale division above which they had seen the target. Clear mislocalization was shown in these experiments. Mislocalization was demonstrated also in O'Regan's (1984) experiment, in which the subjects indicated the position where they saw the flash target by moving a cursor controlled by a potentiometer knob. According to O'Regan, the mislocalization effect is mainly caused by complicated retinal events caused by movement of the visual scene across the retina. This explanation is consistent with the finding that mislocalization occurred when the background was

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moved rather than the eye (MacKay, 1970; O'Regan, 1984).

Thus, it is evident that mislocalization occurs under both the "dark" and the "illuminated background" conditions. Under the "dark" condition, the mislocalization is not explained as a result of saccade-related retinal events, because there is no visible background which may smear on the retina during saccades. Therefore, the EEPS seems responsible for the mislocalization. Under the "illuminated background" condition, on the other hand, the background scene smears on the retina, and therefore, saccade-related retinal effects may have an important role in producing mislocalization (Bischof & Kramer, 1968; O'Regan, 1984). Thus, there is a possibility that the origin of the mislocalization is quite different between these two background conditions.

On this point, however, there are two questions which should be answered before we draw a conclusion. First, what role does the EEPS play in localization when the flash target is presented under the "illuminated background" condition? It seems unreasonable to think that under this condition the EEPS have nothing to do with the localization of targets. Rather, it seems that the EEPS contributes at least in part to localizing targets presented in the "illuminated background" condition. Secondly, does the illuminated background produce only a degenerative effect on localization by moving across the retina? Rather, it seems that the visible background functions as a visual frame of reference especially when a target was presented before or after the saccade, and gives the subjects useful visual cues for judging the actual position of the target.

The present study was conducted to investigate these questions. For this purpose, in the present study, the flash target was presented on a dimly illuminated structured background, and the role of the EEPS and that of the visible background were investigated by comparing the results with those shown in the "dark" condition where only the EEPS was responsible for producing mislocalization because of the absence of saccade-related retinal events such as movements of the background across the retina. In addition, the flash targets were presented at various positions scattered two-dimensionally over the background visual field because there has been no attempt to investigate the two-dimensional errors, i.e. errors in both the horizontal and the vertical directions, in localizing targets presented at positions far from the path scanned by the saccade.

METHOD

A subject was seated with the head fixed by a dental bite board and a forehead rest. Horizontal movements of the subject's right eye were monitored by a photoelectric method. The subject's right eye was illuminated by an i.r. light-emitting diode (Toshiba, TLN101), and the reflected light from the two points of the lower limbus (iris–sclera boundaries in 4 o'clock and 8 o'clock positions) was collected by a pair of fiber optic bundles. A phototransistor (Toshiba, TPS601) was attached to the end of each fiber optic bundle, and horizontal eye movements were monitored by recording the difference between the two phototransistor outputs.

A dimly illuminated screen (a dark-blue plastic sheet) was set 57 cm in front of the subject. As shown in Fig. 1, a map of Japan was drawn on the screen with white ink, and used as a structured background visual field on which visual stimuli were presented. It was expected that this type of structured background constructed from a familiar map would give the subject an effective visual frame of reference for judging the position of visual targets. The luminance levels of the dark-blue and the white line-drawing parts were about 0.5 and 2 cd/m^2, respectively. On each trial, a buzzer warning signal was given, and then a fixation point (red

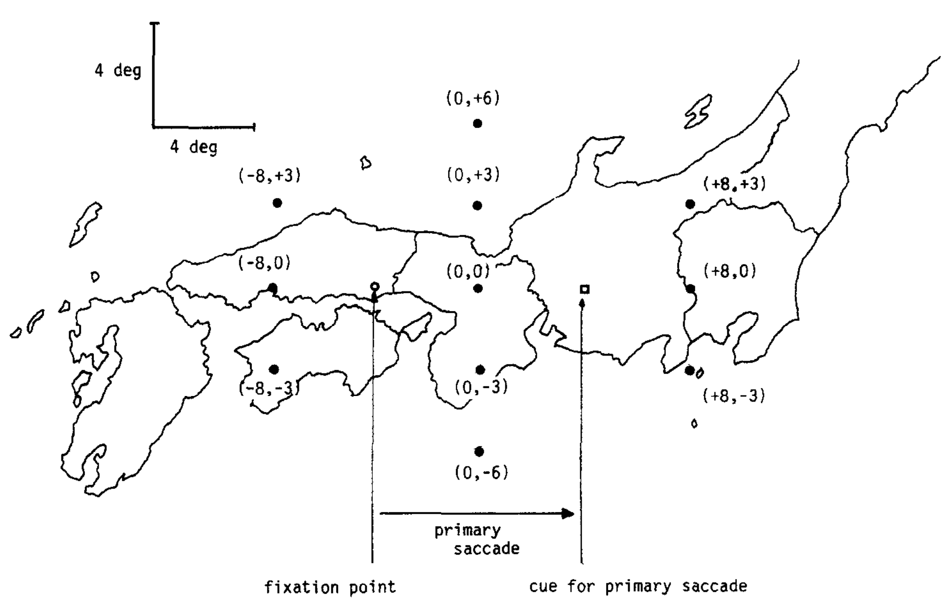

FIGURE 1. The background visual field and the positions of the fixation point, the cue stimulus for the primary saccade and the flash targets.

LED, 0.3 deg in dia and 20 cd/m^2 in luminance) was presented for 1–1.8 sec at the position of 4 deg left of the center on the visual field. The subject was asked to binocularly keep watching the fixation point. At the offset of the fixation point, a cue stimulus for saccades was presented for 20 msec, 8 deg to the right of the fixation point. The cue consisted of two vertically arranged rectangular red LEDs (0.1 deg × 0.3 deg, 10 cd/m^2), the distance between the centers of the LEDs being 0.4 deg. The subject was asked to make a horizontal saccade (primary saccade) toward the visual cue. Because the duration of the visual cue was too short (20 msec), it disappeared before the beginning of the primary saccade. At various points in time before, during, or after the primary saccade, a flash target (yellow LED, 0.3 deg in dia, 40 cd/m^2) for visual localization was presented for 2 msec. 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 onset of the target. Targets before the saccade were presented by presetting a shorter time interval than the normal saccade latency between the target and the visual cue for eliciting the saccade. When the latency of the primary saccade was shorter than 80 msec or longer than 400 msec, the target was never presented. The position of the target was randomly selected from eleven positions scattered two-dimensionally over the background visual field. In Fig. 1, the numbers in parentheses show the horizontal (x-axis) and the vertical (y-axis) positions of each target. For instance, (0, 0) shows the center of the visual field, and (−8, +3) indicates the position 8 deg left and 3 deg above the center of the visual field. In reality, all LEDs used as visual stimuli (the fixation point, visual cue for primary saccade, and targets) were set on a black board placed at a different position from the background visual field, and seen by the subject through a silver half-mirror set before the subject's eye. By this method, these stimuli were presented as an optical image on the background. Therefore, the visual stimuli were seen only when they were turned on. The subject was asked to move the eyes to where the target had disappeared and to maintain fixation. About 1.4 sec after the target disappearance, a probe stimulus (a spot of laser beam, 0.2 deg in dia, about 40 cd/m^2) was presented for 7 sec. The subject could move the horizontal and the vertical positions of the probe by moving a knob by the right hand. The subject reported the apparent position of the target by moving the probe to that position.

In addition to the saccade condition described above, localization was also examined in a condition in which the target was presented when the eye remained still. Under this control condition, either the fixation point or the visual cue for primary saccade was presented for 1.8 sec, and the subject was asked to fixate these stimuli. Just after the offset of these stimuli, a target was presented for 2 msec. The subject made a saccade to the target and reported its apparent position by moving a probe stimulus.

The position of the probe stimulus on the background visual field was recorded with a video-camera system, and later the localization errors in the horizontal and the vertical directions were measured with an accuracy of 0.5 deg.

Two subjects participated in this experiment. Subject HH was the author and subject MM was a university student who had no experience in eye-movement experiments and, therefore, had no knowledge about the purpose of this experiment. Each subject participated in the experiment for 6 days. On each day, 88 experimental (saccade) trials, divided into 6 sessions and 2 sessions of 11 control trials, were performed by each subject.

RESULTS

Primary saccade

The subject's eye movement was analyzed by a high-speed digital storage scope (Iwatsu, DS-6121A). Out of a total of 528 trials of the experimental (saccade) condition, in 17 trials (3.2%) with subject HH and in 100 trials (18.9%) with subject MM, the target was not presented because of the extremely shorter (<80 msec) or longer (>400 msec) latencies of the primary saccade. When the target was presented immediately after the presentation of the visual cue for primary saccade, the eyes sometimes moved directly to the target without eliciting the expected primary saccade. This was observed in 68 trials (12.9%) and 116 trials (22.0%) in subject HH and MM, respectively. In the remaining trials, the primary saccade was observed. The means of the amplitude, the latency, and the duration of the primary saccades were 8.7 deg (SD = 1.1), 185 msec (SD = 47), and 33 msec (SD = 3.6), respectively, in subject HH, and 8.3 deg (SD = 1.1), 223 msec (SD = 101), and 30 msec (SD = 3.7) in subject MM.

Visual localization

Error in the horizontal direction. Figure 2 shows separately for each target's actual position the localization errors in the horizontal direction as a function of the time interval between the start of the primary saccade and the occurrence of the flash target. The results from the two subjects were quite similar. It is evident from Fig. 2 that the size and the direction of the error were dependent on the position in which the targets were presented.

At the target positions (−8, +3), (−8, 0), and (−8, −3), i.e. on the left side of the fixation point, the subjects mislocalized the targets to the saccade direction when they were presented before the saccade onset. When the targets were presented at the end of the saccade, in contrast, the subjects mislocalized the targets in the direction opposite to the saccade's direction. In both subjects, mislocalization occurred at about 50 msec before the saccade onset, and disappeared immediately after the end of the saccade. Similar mislocalization was observed when the targets were presented at the

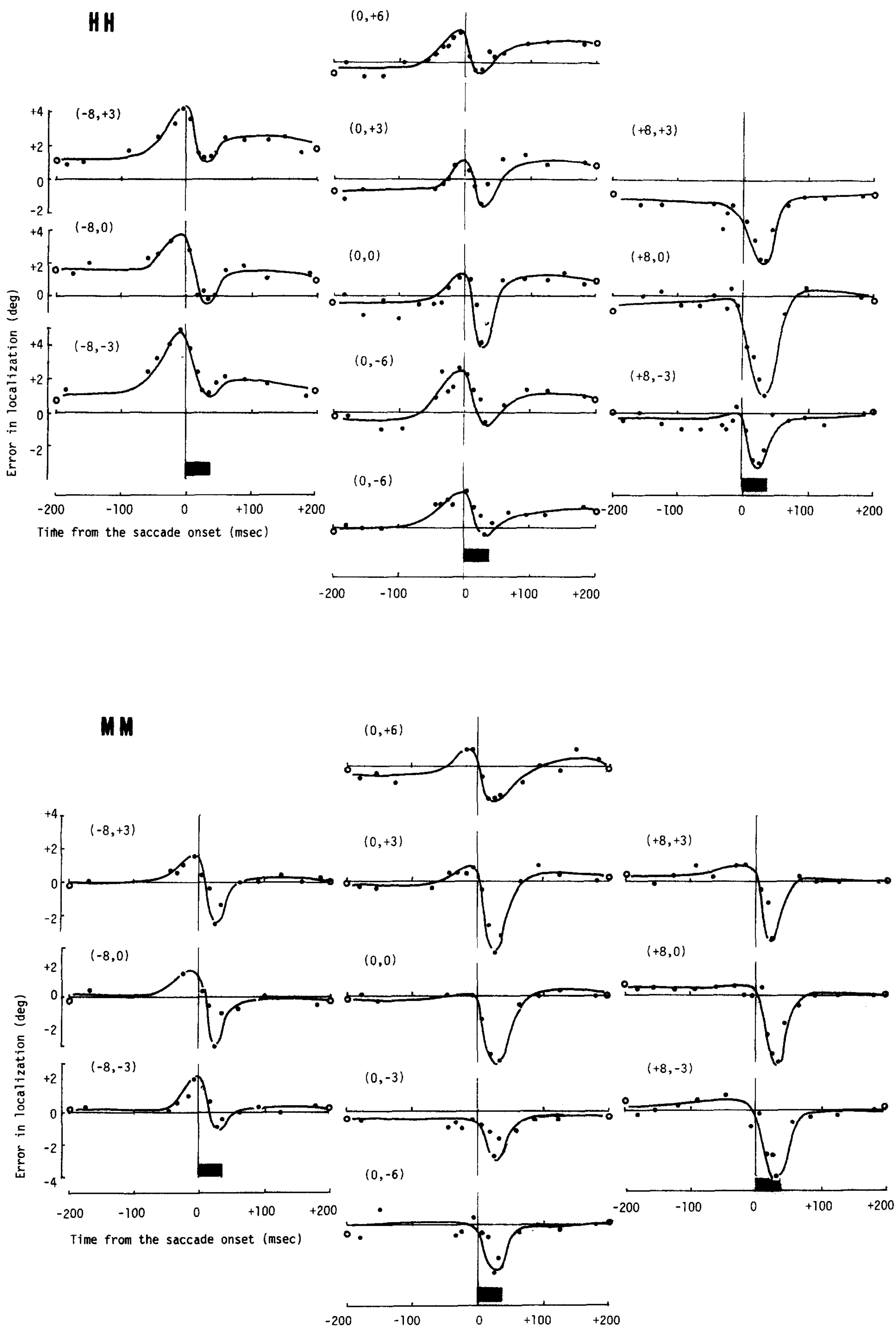
HH
(0,+6)
(-8,+3)
(0,+3)
(+8,+3)
(-8,0)
(0,0)
(+8,0)
(-8,-3)
(0,-6)
(+8,-3)
(0,-6)
+4
+2
0
-2
Error in localization (deg)
-200 -100 0 +100 +200
Time from the saccade onset (msec)
MM
(0,+6)
(-8,+3)
(0,+3)
(+8,+3)
(-8,0)
(0,0)
(+8,0)
(-8,-3)
(0,-3)
(+8,-3)
(0,-6)
+4
+2
0
-2
-4
Error in localization (deg)
-200 -100 0 +100 +200
Time from the saccade onset (msec)

FIGURE 2

positions (0, +6), (0, +3), (0, 0), (0, −3), and (0, −6), i.e. at the positions between the fixation point and the visual cue stimulus for the primary saccade. However, at these target positions, mislocalization toward the saccade direction observed before the saccade onset sometimes reduced or disappeared, and mislocalization in the direction opposite to the saccade increased. Finally when the targets were presented on the right side of the goal of the saccade, i.e. at the positions (+8, +3), (+8, 0), and (+8, −3), mislocalization in the saccade direction disappeared, and large mislocalization in the direction opposite to the saccade was observed. It should be noted that at all target positions, the mislocalization disappeared immediately after the end of the saccade. Another interesting finding was that the extent of the mislocalization, i.e. the amplitude of the mislocalization curve, was relatively small when the targets were presented at the positions far from the trajectory scanned by the saccade: the extent of the error shown at the positions (0, +6) and (0, −6) was smaller than that shown at the position (0, 0).

The results obtained under the "illuminated background" condition were different from those shown when the targets were presented in the dark. Figure 3 shows the results of a supplementary experiment in which the targets were presented in the dark at five positions arranged along the path of an 8 deg horizontal saccade. The results in the supplementary experiment were very consistent with those already reported for horizontal (Honda, 1990) and vertical saccades (Honda, 1991). As shown in Fig. 3, the size and the direction of the localization error did not differ among the five target positions. The mislocalization began at about 100 msec before the saccade onset, and continued even after the end of the saccade. In addition, the extent of the error was generally large in comparison with that shown under the "illuminated background" condition (Fig. 2).

Error in the vertical direction. Localization error in the vertical direction was shown in Fig. 4. In subject HH, small downward errors were observed at the target positions (0, +6) and (0, +3). However, this was not the case in subject MM. At the remaining target positions, both subjects localized the target at its actual position. Therefore, it is evident that when targets are flashed at the time of a saccade, mislocalization does not occur in the direction perpendicular to the saccade direction.

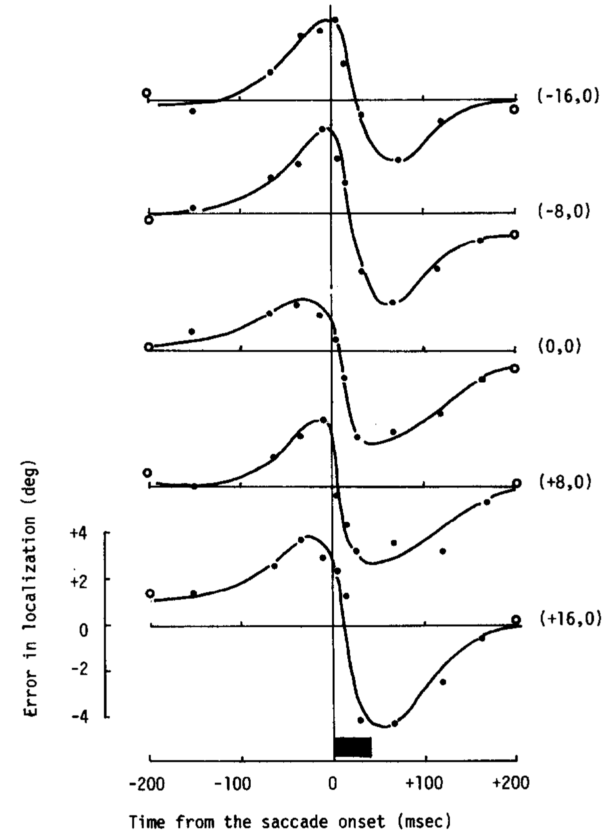

FIGURE 3. Results in the supplementary experiment ("dark" condition), in which targets were presented at one of the five positions arranged horizontally along the path of the primary saccade. The dots in the figure shows the average errors calculated for each of the predetermined time intervals of 10–40 msec. The number of observations per each data point is 5–20.

DISCUSSION

In this study, a flash target was presented at the time of a saccade at various positions scattered two-dimensionally on a dimly illuminated structured background, and the main new findings are as follows. (i) Visual mislocalization of the target occurred only in the direction parallel to the saccade, but not in the direction perpendicular to the saccade direction. (ii) The size and the direction of the errors were different in several respects from those reported for targets presented in the dark. First, when the targets were presented on an illuminated background, the time-course of the mislocalization largely depended on the actual target position, whereas under the "dark" condition the same pattern of mislocalization was observed at all target positions. Secondly, under the "illuminated background" condition, mislocalization occurred shortly (about 50 msec) before the saccade onset, and returned to correct localization immediately after the end of the saccade. In contrast, under the "dark" condition, mislocalization was observed from about 100 msec before the

FIGURE 2 (opposite). Mislocalization in the horizontal direction shown separately for each target's actual position. The abscissa indicates the time interval between the saccade onset and the target presentation. The ordinate indicates the size of mislocalization. Plus sign in the ordinate shows mislocalization in the saccade direction (rightward), and minus sign mislocalization in the direction opposite to the saccade (leftward). The mislocalization curves were fitted by eye based on the average errors (dots) calculated for each of the predetermined time intervals of 10 or 30 msec. The number of observations per each data point is usually five. Sometimes, the data point was not obtained because of lack of observation within the predetermined time intervals. Open circles indicate the results on control trials in which the subjects kept watching the original fixation point (left circle) or the cue for eliciting a saccade (right circle). The mean duration of the saccades was shown as a horizontal bar.

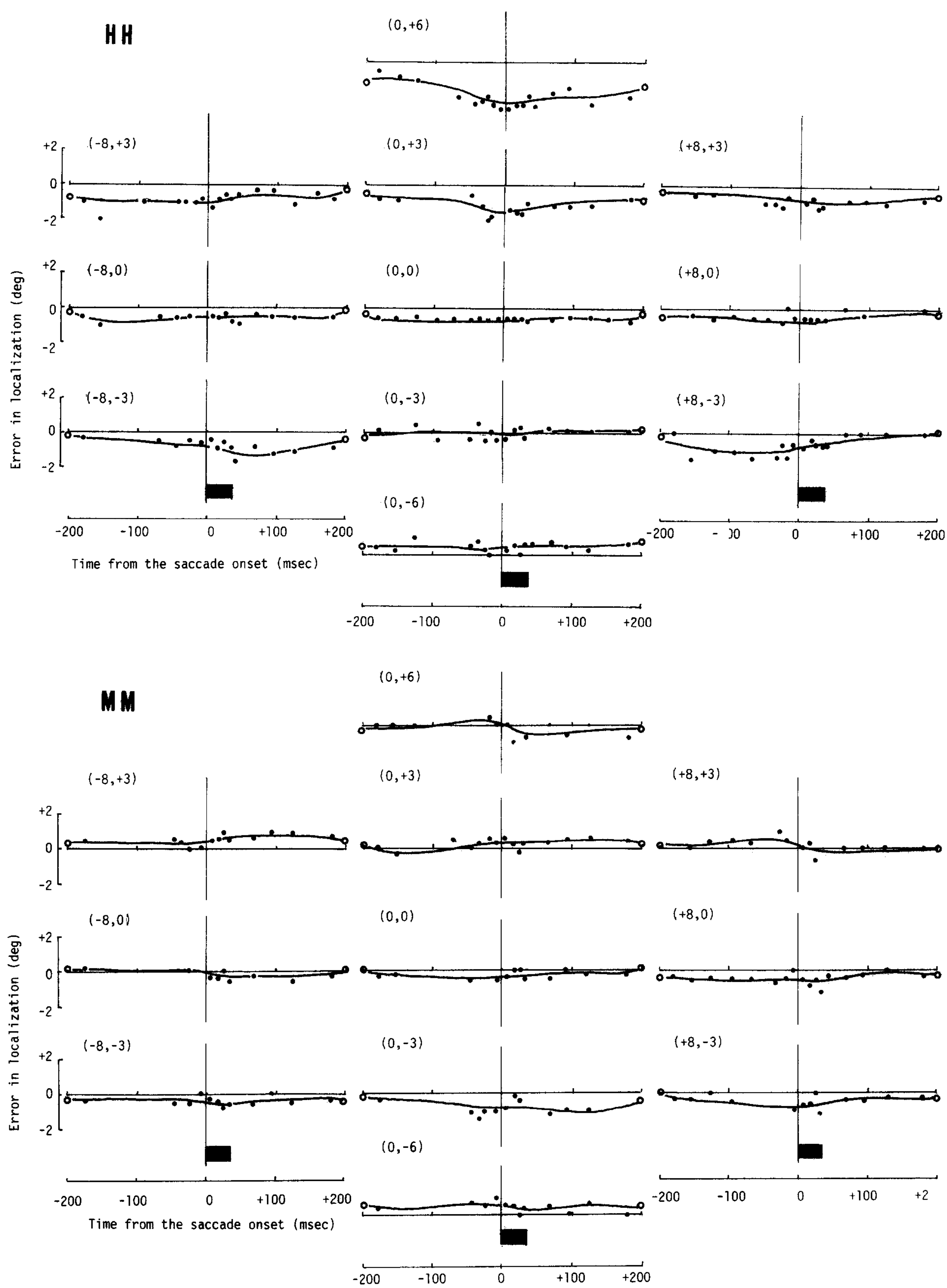

FIGURE 4. Mislocalization in the vertical direction. Plus sign in the ordinate shows mislocalization in the upward direction, and minus sign mislocalization in the downward direction.

saccade onset and continued even after the completion of the saccade. Thirdly, the extent of mislocalization was, in general, smaller under the "illuminated background" condition, than that under the "dark" condition.

How can we explain the findings summarized above? As has already been mentioned, the results shown under the "dark" condition are well explained by the fact that there is a discrepancy between the actual eye position and the EEPS during saccades. In his review on influence of the EEPS on reports of visual direction, Matin (1976) stated that the time-course of the EEPS does not parallel that of the actual saccadic eye movements. Recently, I attempted to estimate the detailed time-course of the EEPS at the time of horizontal and vertical saccades, and demonstrated that, irrespective of the direction of the saccade (i.e. horizontal vs vertical), the EEPS begins about 100 msec before the saccade onset, but it develops so slowly that it cannot catch up with the movement of the eye until more than 50 msec after the end of the saccade (Honda, 1990, 1991).

At the present time, there is no clear-cut explanation for the mislocalization shown under the "illuminated background" condition. However, it seems that a large part of the results is explained by a combination of the following three assumptions. (i) Mislocalization in the "illuminated background" condition is primarily produced by a failure in cancelling the shift of images on the retina by the EEPS. This assumption is supported by a fact that the pattern of mislocalization shown in this study, is *essentially* the same as that reported for the "dark" condition. That is, in both the "illuminated background" and the "dark" conditions, mislocalization to the saccade direction was usually observed before the saccade onset or during the saccade, while mislocalization in the direction opposite to the saccade's direction occurred only after the saccade's onset. Because the EEPS is exclusively responsible for mislocalization in the "dark" condition, this finding weakens the O'Regan's (1984) suggestion that mislocalization may be due almost entirely to visual factors while the influence of the EEPS is minimal. (ii) The illuminated background functions as a visual frame of reference, and provides visual cues for judging the position of the targets, especially when they were presented before or after the saccade, that is, when the retinal image of the background remains still. During the saccade, however, the background moves across the retina, and therefore, cannot function as a visual frame of reference. This means that, during the saccade, the illuminated background cannot effectively correct the mislocalization which is mainly produced by a sluggish activity of the EEPS. (iii) Mislocalization is small at the positions far from the subject's line of sight in comparison with that at the positions observed by the fovea because the subjects are inattentive (or insensitive) to the image displacement at the periphery.

The third assumption was drawn from the cognitive explanation for space constancy proposed by Bridgeman (1983). He observed that when his subjects inspected Escher prints which were displaced synchronously with the subjects' saccade, a majority of the subjects saw a motion of the "figure" part rather than the "ground" part of the prints. Similar observation was that a displacement of the world produced by pushing with a finger on the outer canthus of the eye was more in the center of than in the periphery of the line of sight. From these observations, Bridgeman suggested that the basis of space constancy is an adaptation to retinal displacement during saccades, in other words, a selective inattention to a range of image displacement, rather than a cancellation or subtraction of the incoming visual signal. In the explanation presented below, it is assumed that the adaptation (or inattention) occurs in the image displacement on the *cognitive* level, not in the image displacement on the *retina*, and further that, as a result of the above mentioned selective inattention, the visual scene appears more stable in the periphery. The latter assumption fits in well with the result of the present study that mislocalization was actually smaller in the periphery. In addition, this finding relates well with the Bridgeman and Fisher's (1990) finding that saccadic suppression of displacement is strongest in central vision. It seems that the visual system needs to strongly suppress the large mislocalization in the central area of vision (Bridgeman, 1992, personal communication).

A tentative explanation I propose for the results of the "illuminated background" condition (Fig. 2) is as follows. When a target is flashed on an illuminated background *before the saccade's onset*, the target position is mislocalized in the saccade direction as is the case under the "dark" condition, because there is a discrepancy between the actual eye position and the EEPS. Under the "illuminated background" condition, however, the mislocalization is reduced in size and delayed about 50 msec in its occurrence because of the presence of the stable visible background which functions as a frame of reference for judging the target's actual position. In addition, at the target positions far from the subject's fixation, i.e. at positions (+8, +3), (+8, 0), and (+8, −3), the subject is inattentive to the image displacement produced by the mismatch between the EEPS and the actual eye position, and the target position is mainly judged on the basis of the seemingly stable visual background, resulting in accurate localization.

When a target is presented *during a saccade*, the target's position is mislocalized because of the sluggish EEPS activity. The mislocalization is prominent especially at the positions near the saccade's destination, to which the subject's attention is directed. It should be noted here that the extent of the errors was larger at the target positions near the subject's line of sight than that shown at the positions in the periphery: position (0, 0) vs positions (0, +6) and (0, −6), position (+8, 0) vs positions (+8, +3) and (+8, −3). This finding also is consistent with the third assumption described above.

Finally when a target is presented *after the end of a saccade*, there is still a possibility that mislocalization is brought about by the sluggish EEPS. However, localization is rather accurate, because the image of the background is stable on the retina, and therefore the subject can make use of it as a frame of reference for determining the target position.

I don't think that the explanation proposed here is satisfactory. There are still some problems concerning the saccade-contingent mislocalization observed in the presence of an illuminated background. MacKay (1970), for example, demonstrated that visual mislocalization occurred when the background visual field was suddenly displaced instead of moving the eye. This finding suggests that mislocalization is caused also by retinal image displacements which are not necessarily contingent upon saccadic eye movements. It is not clear, however, how the MacKay's finding relates to the results shown in the present study, because, as described above, it is possible to explain the mislocalization under the "illuminated background" condition without referring to retinal events caused by saccade-free image displacements. Therefore, there is a possibility that mislocalization observed in the MacKay's "background shift" and the "saccadic eye movements" conditions was each caused by distinctively different mechanisms, and a further investigation would be needed for this matter.

In conclusion, the present study demonstrated that the saccade-contingent mislocalization under the "illuminated background" condition was quite different in several respects from that observed under the "dark" condition. In addition, it was suggested that the mislocalization is successfully explained by assuming three physiological and cognitive processes: a sluggish EEPS activity, visual cues from the visible background, and selective inattention to image displacement.

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