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Perception of relation of stimuli locations successively flashed before saccade

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Abstract

Based on localization error for a single perisaccadic flash, eye position signal is supposed to change more slowly than physical eye position. Nevertheless, a flicker is not perceived as moving in accordance with localization error for a single flash. We carried out two experiments to investigate this problem. Experiment 1 examined how a single flash or a flicker presented before saccade was perceived. The results showed that the flicker was not perceived as moving, although mislocalization for the single flash increases gradually before saccade. Experiment 2 was a vernier test of two stimuli successively flashed before the saccade. The results showed that the point of subjective equality shifted in accordance with the mislocalization for a single perisaccadic flash when the interstimulus interval (ISI) was about 2 s; however, it did not shift when the ISI was 78 ms. Comparison between these results and previous studies suggests that the relation of the locations of successive flashes before saccade is perceived exocentrically when the ISI and stimulus onset asynchrony between flashes was short. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Saccade; Mislocalization; Vernier; Egocentric; Exocentric

1. Introduction

When we rotate eyes while surrounding objects remain stationary, the retinal images change their location. Nevertheless, we usually do not perceive any motion of the objects. This property of the human visual system is called 'visual stability'. One of the most accepted explanations of visual stability is that any motion of images on the retina is cancelled by signals representing the position of the eyes (Holst, 1954). This concept insists that the perceived location of an object is determined by the algebraic summation of the retinal image location and the information about eye position (eye position signal: EPS). Thus, this explanation is called 'subtraction theory' (Mateeff, 1978).

To elucidate the nature of EPS, researchers have studied various illusory perceptions of stimulus location. A frequently referred illusion is that a brief light stimulus flashed just before, during or just after voluntary saccade is mislocated. The size of localization error depends on the time when the stimulus is flashed relative to saccade onset (Matin, 1965; Matin, Matin, & Pearce, 1969; Matin, Matin, & Pola, 1970; Mateeff, 1978; Honda, 1989, 1990, 1991, 1993).

This illusion is considered evidence that EPS does not represent the physical eye position correctly near the time of saccade execution. Under the assumption of the subtraction theory, we can estimate the time course of EPS. That is, because the perceived location of the flash (P) is determined by summation of its retinal location (R) and EPS, EPS can be calculated by $EPS = P - R$ (Mateeff, 1978). Fig. 1 shows an example of the time course of EPS estimated with this equation. Many experimental results show that this curve looks like a 'damped' version of the physical eye position (Matin, 1972; Mateeff, 1978; Honda, 1990, 1991). This consideration leads us to a model that EPS changes slowly compared with the physical eye position when we execute a saccade. We call this model 'Damped-EPS model'.

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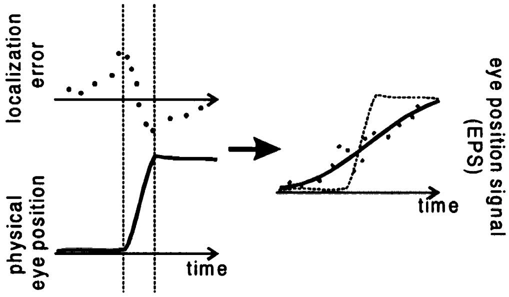

Fig. 1. Time course of mean localization error and EPS estimation. Left top panel: Typical time course of mean localization error for a perisaccadic flash. The abscissa indicates the difference between the stimulus and the saccade onset. The ordinate represents mean localization error. Right panel: Estimated EPS. Under assumption of the subtraction theory, we obtained the estimated EPS curve from the time course of mean localization error and the physical eye position (left bottom panel).

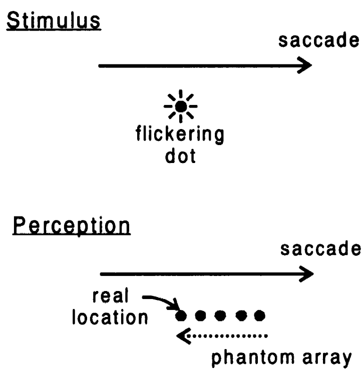

Fig. 2. Phantom array. When we make a saccade across a flickering dot, an array of dots is perceived. This array is perceived as if it is drawn from the neighborhood of the saccade endpoint to its physical location, i.e. in the direction opposite to the saccade.

Although the Damped-EPS model is widely accepted, some counterarguments have been presented. One such counterargument concerns the perception of a stimulus that is flickering in the dark when we made a saccade across the stimulus. If we apply the Damped-EPS model to this situation, this flickering stimulus should be perceived moving in accordance with the time course of localization error shown in Fig. 1. However, Hershberger and colleagues showed that this is not the case (Hershberger, 1987; Hershberger & Jordan, 1992). They asked their subjects what was perceived when they made a saccade across a stimulus flickering at 200 Hz (1 ms on/4 ms off). Most of their subjects reported that the stimulus (a small dot) initially jumped in the direction of the saccade, then ran in the direction opposite to the saccade, and finally stopped near the physical location of the stimulus. The stimulus did not appear to run in the direction of the saccade (Fig. 2). This illusory array of dots is called the 'phantom array'. Hershberger argued that this result indicated that EPS does not change gradually but discretely in advance of saccade onset. According to their explanation, the reason that the time course of localization error changes gradually is not that EPS is damped, but that the time when EPS jumps varied between trials. Consequently, the time course of mean localization error results in a smooth curve (Hershberger, 1987; Hershberger & Jordan, 1992). We shall call this model the 'Discrete-EPS model'.

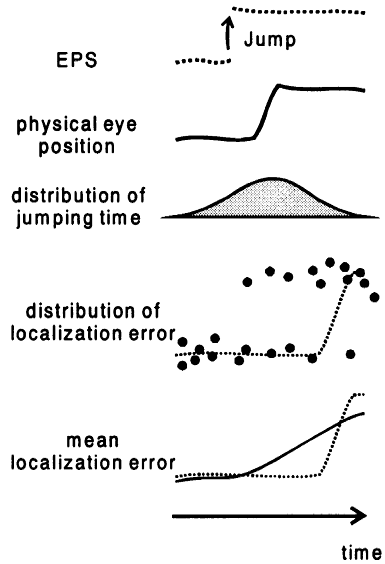

Fig. 3. Discrete-EPS model. This model assumes that EPS discretely changes before saccade onset and that the time when EPS 'jumps' is varied between trials. The model can naturally explain perception of a flickering dot when we make a saccade across it (Fig. 2). Because the time when EPS jumps varied between trials, mean localization error is thought to change gradually.

The Discrete-EPS model also has problems. At first, according to the Damped-EPS model, two phantom arrays (i.e. in the same and the opposite direction as the saccade) are overlapped in a very short period of time under the experimental condition of Hershberger (1987). Therefore, the result of Hershberger and colleagues may only show that the latter part of the phantom array (in the direction opposite the saccade) masked the beginning part of the phantom array (in the direction of the saccade). To avoid this possibility, a condition where a flickering stimulus is presented only before saccade onset must be examined. However, Hershberger and colleagues did not test this condition (Hershberger, 1987; Hershberger & Jordan, 1992; Jordan & Hershberger, 1994; Hershberger, Jordan, & Lucas, 1998). The second problem with the Discrete-EPS model is the explanation of the gradual increase in localization error before saccade onset. If their explanation is correct, localization error of each trial must distribute around zero and the value equal to the amplitude of the following saccade (Fig. 3). However, there are no data supporting this prediction.

Although the Discrete-EPS model would be incorrect, we should not dismiss Hershberger's question regarding the Damped-EPS model. In this paper, we examine perception of stimuli successively flashed before saccade onset. Based on these results, we discuss why the phantom array in the direction of saccade is not perceived.

2. Experiment 1

The most important advantage of the Discrete-EPS model over the Damped-EPS model is that it can naturally explain why we do not perceive a phantom array in the direction of saccade when a flicker was presented immediately before saccade. However, there is no report that directly examines what is perceived when such a stimulus is presented. In Experiment 1, we examined the perception of a brief flickering stimulus presented before or during saccade, and compared the result with the time course of mislocalization for a single perisaccadic flash.

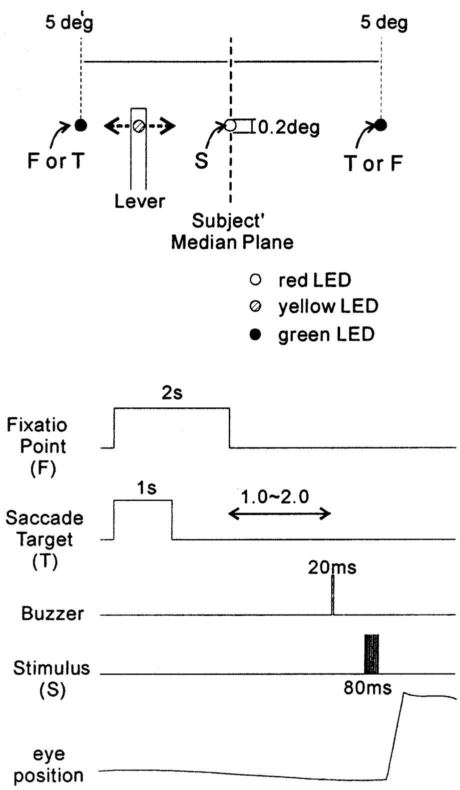

Fig. 4. Arrangement and time courses of the stimuli in Experiment 1. Top panel: Arrangement of the stimuli. Bottom panel: Sequence of stimuli presentation in the direction-discrimination test. Either the left or the right green LED was randomly chosen as the fixation point (F) trial by trial. T and S indicate the saccade target and flicker probe, respectively. See text for detail.

2.1. Method

Two male subjects, HS, and MM participated in this experiment. Both had normal visual acuity. HS was an author of this paper and knew the purpose of the experiment. MM did not know the purpose.

The experiment was performed in a completely dark room. The subject sat on a chair with the head stabilized by a dental bite board. A red light-emitting diode (LED: 0.2° in diameter, 20 cd/m^2) was placed at the subject's eye level at the subject's median plane. The distance from the subject to the LED was 57 cm. Green LEDs (0.2° in diameter, subjectively equal in luminance to the red LED) were placed 5° left and 5° right of the red LED (Fig. 4). A lever, which the subject could move horizontally, was placed in front of these LEDs. This lever had a yellow LED on its head. The lever was painted matt-black so that the subject could not see it in the dark unless the LED on the tip was turned on. A keybox with three buttons was handed to the subject. These buttons were placed horizontally. These appliances were controlled by a PC/AT compatible computer with a digital I/O board and a timer board. Horizontal movement of the subject's left eye was measured by an Ober2 eye recording system (Permobil Meditech).

The experiment consisted of two tests. The first test was a direction-discrimination test of phantom array. This test examined how a flickering stimulus presented tens of milliseconds before saccade onset was perceived. The second test was called a localization test. This test confirmed that the subjects showed localization errors similar to those reported in previous studies.

2.1.1. Direction-discrimination test

At the beginning of each trial, a warning buzzer (2000 Hz, 20 ms) was given and the two green LEDs were turned on. After a delay of 1 s, one of the two was turned off. The disappearing LED was the target of the subsequent saccade (T) and the other LED was the fixation point (F). Which LED disappeared was randomly decided in each trial, therefore the required direction of saccade was randomly changed between trials. F was turned off 1 s after the offset of T. Then after a 1.0–2.0 s blank, a buzzer (2000 Hz) was sounded for 20 ms. The subject was asked to make saccade to the location where T was presented as soon as the buzzer was given. After a random interval from the buzzer onset, the red LED was flickered at 200 Hz (1 ms on, 4 ms off) for 80 ms (S). Duration of the interval was adjusted so that S should be presented immediately before, or during the saccade. The task asked of the subject was to judge whether S was perceived as a horizontal array of dots or not. If the subject perceived a horizontal array drawn from the right to the left, he reported this by pressing the left

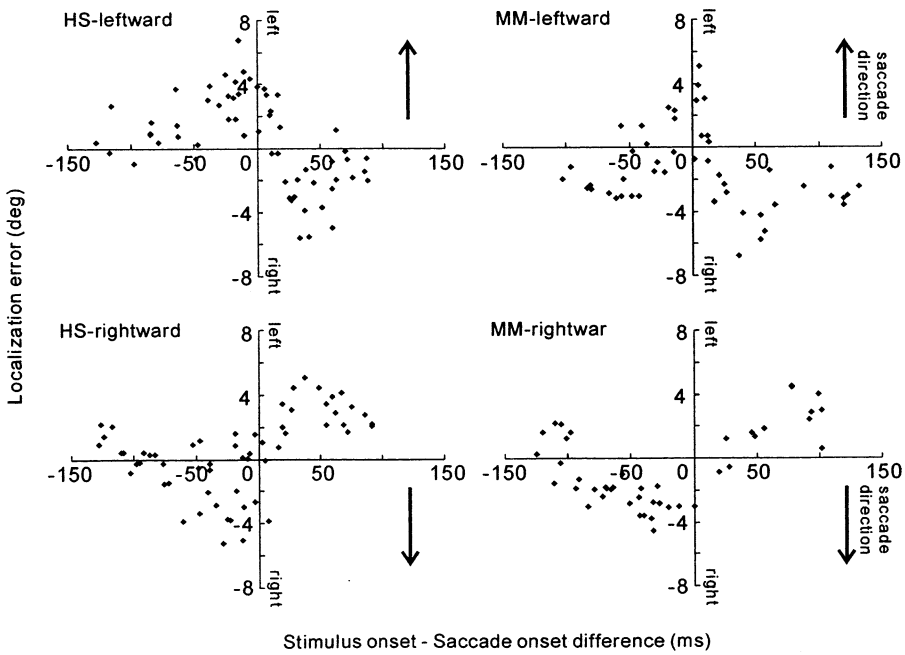

Fig. 5. Performance of the localization test in Experiment 1. Each dot represents the result of each trial. The abscissa indicates the difference between saccade onset and onset of S. A negative value means that the onset of S was before saccade onset. The ordinate represents localization error. A positive value indicates that the location indicated by subject was to the left of the actual location of S.

button on the keybox, and vice versa. If he perceived only one dot or several dots that were not perceived as a horizontal array, he pressed the center button on the keybox. When the subject pressed one of the buttons, one trial was finished. A 2-s interval was inserted before the beginning of the next trial. Thirty-six successive trials were performed in one session. HS performed four sessions and MM performed five sessions.

2.1.2. Localization test

The test consisted of two conditions, the test and the control condition. Each trial of the test condition began with a warning buzzer (2000 Hz, 20 ms), and one of two green LEDs was turned on (F). After a random delay of 1.25–2.0 s, F was turned off and the other green LED was flashed (T) for 20 ms. Simultaneously with the flash of T, a buzzer was given. The subject was asked to make a saccade where T was presented (T was so brief that T disappeared before the onset of the saccade) as soon as T was flashed. After the flash of T, the red LED (S) was flashed for 2 ms so that S was flashed before, during or after the onset of subject's saccade. After a delay of 3 s from the offset of F, the yellow LED on the lever was turned on. Because the saccade latency is normally up to 300 ms in our subjects, the saccade was already finished 3 s after the offset of F. The subject indicated the perceived location of S by adjusting the location of the yellow LED on the lever. Successively 24 trials were performed in one session.

The control condition was the same as the test condition except that the subject was told to fixate on F and not to make a saccade until the yellow LED on the lever was turned on. Localization error was defined as the difference between the perceived location and the actual location of S. Mean localization error in the control condition was considered the response bias, so this value was subtracted when calculating localization error under the test condition.

2.2. Results

Output of the eye tracker was passed through a low-pass filter (cut-off frequency: 100 Hz) analyzed off-line to determine saccade onset. Saccade onset was defined as the time when angular velocity of horizontal eye rotation exceeded 40 deg/s.

Fig. 5 shows the result of the localization test. Clearly, localization error depends on the difference in the onset times similar to that in previous studies (Honda, 1990). The distribution of the localization error changed gradually rather than separating around zero and a value equal to saccade amplitude.

Table 1 summarizes the result of the direction-discrimination test. 'Before' shows the result of trials in which S disappeared 50–0 ms before saccade onset. 'During' shows the result of trials in which S was presented during the saccade. Table 1 shows that an array in the direction of the saccade was not perceived when S disappeared before saccade onset. HS scarcely perceived an array in the direction opposite the saccade when S disappeared before saccade, however, such perception was obtained only when S disappeared 10–0 ms before saccade onset. This was probably an artifact due to the use of a low-pass filter and the definition of saccade onset.

2.3. Discussion

The Discrete-EPS model explains the gradual increment of localization error before saccade onset, "The gradual increase may merely reflect a gradual increase in the probability that a discrete shift will have occurred by that time..." (Jordan & Hershberger, 1994, pp. 664–665). According to this explanation, localization error in the localization test should distribute around zero and a value equal to saccade amplitude before saccade onset. However, Fig. 5 shows this is not the case. Other results also showed the distribution of localization error is not bimodal before the saccade (Dassonville, Schlag, & Schlag-Rey, 1995; Miller, 1996). Therefore, the discrete-EPS model is inappropriate for explaining localization error reported in the localization test. Table 1 shows that no phantom array was perceived before saccade onset even if no stimulus was presented during and after the saccade. Therefore, it is not due to masking that a phantom array in the direction of the saccade was not perceived in the experiment of Hershberger and colleagues (Hershberger, 1987; Hershberger & Jordan, 1992).

Why is no phantom array is perceived although localization error for a presaccadic single flash gradually increases? We think that there are two possibilities. At first, the perceived location of a stimulus continuously presented at the same retinal location may not be updated even if EPS started to change before saccade onset. Such a mechanism can maintain the stable visual world regardless of a temporary mismatch between EPS and the actual eye position before saccade onset. In our experiment as well as Hershberger's, the same retinal location was repeatedly stimulated at 200 Hz. This frequency is so high that the flicker is perceived as a continuous stimulus (Van De Grind, Grüsser, & Lunkenheimer, 1973). Consequently, no phantom array may be perceived. The second possibility is that the relation of the locations of stimuli flashed at a short interstimulus interval (ISI) may be perceived based on the retinal locations of these stimuli. The direction-discrimination test of our experiment can be considered as a special case that all flashes were presented at the same retinal location.

Table 1
Subjective direction of phantom array[a]

Saccade	Subject	Before		During	
		'Left'	'Right'	'Left'	'Right'
Leftward	HS	0.00	0.10	0.00	0.95
	MM	0.00	0.00	0.00	0.67
Rightward	HS	0.09	0.00	0.68	0.00
	MM	0.00	0.00	0.75	0.00

[a] The number in each cell represents the ratio of each response ('left', 'right' or 'neither') to all three responses.

The difference between these hypotheses is whether stimulating the same retinal location is necessary or not. If stimulating the same retinal location is necessary to suppress phantom array, the stimuli successively flashed at the different retinal locations were separately mislocated in the same way as a single perisaccadic flash.

This prediction is consistent with the result of Matin et al. (1970), which showed that vernier judgement of two successive flashes was erroneous in accordance with typical localization error when ISI between two flashes was 300–350 ms. However, there are no data obtained at an ISI shorter than 300 ms. In the next experiment, we investigated whether vernier judgement of two successive flashes was erroneous even if the ISI between flashes was much shorter.

3. Experiment 2

In Experiment 2, we examined whether vernier judgement of two stimuli flashed at an ISI of 78 ms would be erroneous in accordance with typical localization data for a single flash. An ISI of 78 ms is shorter than that in the experiment by Matin et al. (1970) and long enough to allow increases in localization error during the interval.

3.1. Methods

Four male subjects, HK, HS, MM and TN participated in this experiment. HS and MM were the subjects of Experiment 1. HK and TN did not know the purpose of the experiment and had normal visual acuity. Before the experiment, we confirmed that HK and TN showed localization error similar to that of HS and MM on the localization test in Experiment 1.

The apparatus used in Experiment 2 was the same as that of Experiment 1, except the arrangement of LEDs. The arrangement of the LEDs is shown in Fig. 6. One red LED, two green LEDs and six yellow LEDs were placed at a distance of 57 cm from the subject. The left green LED was the target of saccade (T) and the right green LED was the fixation target (F). The red LED (S1) was placed at the midpoint between T and F, and six yellow LEDs (S2) were placed around the S1. The task was to discriminate whether S2 was flashed at the

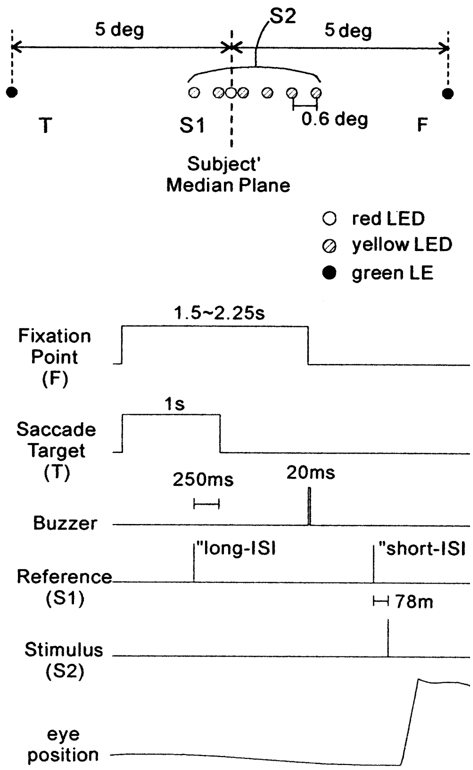

Fig. 6. Arrangement and time courses of stimulus in Experiment 2. Top panel: Arrangement of the stimuli. Unlike Experiment 1, the left green LED was always T (saccade target) and the right green LED was F (fixation point). Bottom panel: Sequence of stimuli presentation in short-ISI and long-ISI conditions. Note that S1 was flashed only one time in each trial. 'Short-ISI' and 'long-ISI' in the figure indicate the time S1 was flashed under each condition. See text for details.

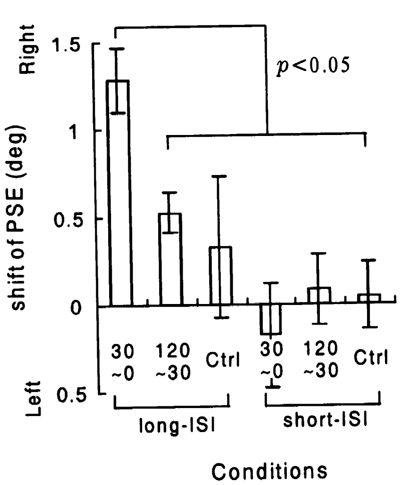

Fig. 7. PSEs in each condition of Experiment 2. Error bars represent the S.E. of the PSE. '30–0': S2 was flashed 30–0 ms before saccade onset. '120–30': S2 was flashed 120–30 ms before saccade onset. Ctrl, control trials.

left or right of S1 when S1 and S2 were flashed before saccade onset. The experiment consisted of two conditions, referred to as 'short-ISI' and 'long-ISI'.

3.1.1. Short-ISI condition

At the beginning of each trial, a warning buzzer (2000 Hz, 20 ms) was given. Simultaneously F and T were turned on. T was presented for 1 s. After a delay between 500 and 1250 ms following the disappearance of T, F was turned off and the buzzer (2000 Hz) was given for 20 ms. The subject was asked to make a saccade to the location where T was presented as soon as the buzzer was given. After a random interval from the buzzer onset, S1 was flashed for 2 ms. Successively, one of S2s was flashed for 2 ms. The ISI between S1 and S2 was fixed at 78 ms. The flashed S2 was randomly chosen in each trial. Duration of the interval between the buzzer and S1 was adjusted so that S2 would be presented immediately before saccade onset. The subject indicated the location of S2 relative to S1 by pressing the left or right button on the keybox. One trial was finished when the subject pressed either key. A 2-s interval was inserted before the beginning of the next trial. Forty-eight successive trials were performed in one session.

To examine the effect of the difference between S2 and saccade onset, we selected trials where S2 was flashed 120–30 ms before saccade onset and 30–0 ms before saccade onset. We repeated this procedure until at least 10 data were obtained for each S2 location and timing of S2. Most blocks contained 20–30 data. At the end of these sessions, the subject performed two control sessions. The procedure for the control session was the same as described above except that the subject was asked to continue fixating on F and not to make saccades.

3.1.2. Long-ISI condition

The purpose of the long-ISI condition was to confirm that vernier judgement was erroneous when the ISI between S1 and S2 was long (Matin et al., 1970).

The procedure for the long-ISI condition was the same as that for the short-ISI condition except for the onset time of S1. In the long-ISI condition, S1 was flashed 250 ms before the disappearance of T. Onset of S2 was adjusted so that S2 would be presented immediately before saccade onset as in the short-ISI condition.

3.2. Results and discussion

We applied probit analysis to estimate the points of subjective equality (PSEs). PSE was defined as the location of S2 where the probability of the response of 'S2 was right to S1' was 50%. Fig. 7 shows the PSE of each condition and timing of S2 onset. A 2 × 3 (ISI × timing of S2 onset) ANOVA showed that the effect of ISI ($F(1,18) = 8.79$, $P < 0.01$) and interaction between the two factors ($F(2,18) = 5.18$, $P < 0.05$) were significant. Post-hoc tests showed the PSE obtained when S2 was flashed 30–0 ms before saccade onset in the long-

ISI condition significantly shifted to the right compared with other PSEs ($P < 0.05$). Differences between other pairs of PSEs were not significant.

Based on typical time course localization error for a single perisaccadic flash (Matin et al., 1970; Mateeff, 1978; Honda, 1990), the perceived location of S2 would be expected to shift to the left (the direction of the saccade) when was S2 flashed 30–0 ms before saccade onset. Therefore, the PSEs were expected to shift to the right. The result of the long-ISI condition was consistent with this prediction. However, that of the short-ISI condition was not. It may be argued that the 78 ms ISI was so short that localization error did not change sufficiently within the interval. However, this explanation has difficulty in explaining why the PSEs were significantly different when S2 was flashed 120–30 and 30–0 ms before saccade in the long-ISI condition.

In summary, the results show that the shift of the PSE depended on the ISI between S1 and S2. When the ISI was 78 ms, the relative location between S1 and S2 was mainly judged by retinal location of these stimuli and the effect of saccade execution was not observed. This suggests that stimulating the same retinal location is not essential but the timings of flashes are important to suppress illusory shifts in successive flashes (such as phantom array) before saccade onset.

4. General discussion

The damped-EPS model is proposed to explain mislocalization for a single perisaccadic flash. Against this model, Hershberger argued that the damped-EPS model could not explain the reason why there was no phantom array perceived in the direction of saccade. This argument is grounded on the assumption that each flash of the flicker should be mislocated in the same way a single perisaccadic flash is mislocated. However, the present study showed that perceived locations of successive flashes presented before saccade onset were based on their retinal location when ISI was short. This result suggests that the fact that there was no phantom array perceived in the direction of saccade is not evidence EPS jumps discretely before saccade onset. Therefore, we conclude that perception of the phantom array is not evidence against the damped-EPS model.

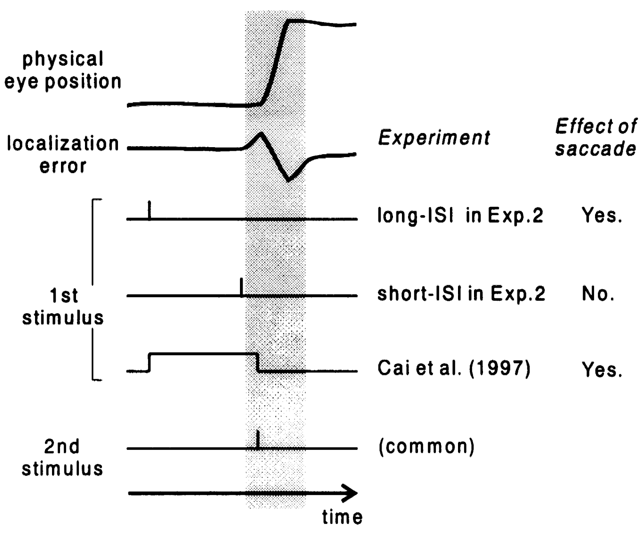

Fig. 8. Time course of stimulus presentation of experiments discussed in the text. Shading represents the period within which a single flash would be mislocated. The second stimulus was common in these experiments, but the first stimulus was varied between experiments. 'Effect of Saccade' indicates whether the result was consistent with localization error for a single perisaccadic flash.

The controversy between the damped-EPS and discrete-EPS models shows us the importance of the effect of relation of the stimuli locations on the retina on perception of the flashes successively flashed before saccade. For simplicity, we call a strategy to perceive locations of stimuli based on the relation of their retinal locations as 'exocentric' localization, and that based on the retinal location and EPS as 'egocentric' localization (Dassonville et al., 1995). The results of Experiment 2 suggest that the length of the ISI between stimuli determine whether egocentric or exocentric localization is used. If this conclusion is correct, a perisaccadic flash is expected to be located correctly when a structured background is continuously presented during a trial (i.e. ISI = 0). However, several studies showed that such a background did not extinguish localization error for perisaccadic flash but only moderately reduced it (Honda, 1993, 1999; Dassonville et al., 1995). This suggests that the short ISI promotes the use of exocentric localization but there must be other determinants.

To consider determinants of the use of exocentric localization, the result of the first experiment of Cai, Pouget, Schlag-Rey, and Schlag (1997) is considered. The task of their experiment was similar to our Experiment 2. However, the reference points (corresponding to our S1) were continuously presented until offset of the target point (our S2). Fig. 8 summarizes the time course of presentation in their experiment and our Experiment 2. The result of Cai et al. showed that the psychometric curve shifted when the target point was flashed 100–0 ms before saccade onset in accordance with localization error for a single flash. The length of the ISI again cannot explain the difference between the results of Cai et al. and the long-ISI condition. However, these results seem to be explained if we assume that the short stimulus onset asynchrony (SOA) between stimuli also promotes the use of exocentric localization. That is, in the long-ISI condition, both the ISI and SOA were so long that the relation of the stimuli locations would be perceived egocentrically. Consequently, the PSE would shift in accordance with the mislocalization for a single perisaccadic flash. In the short-ISI condition, both the ISI and SOA were short. In this condition, the relation of the stimuli locations would be almost based on exocentric localization. Consequently, vernier judgement of the stimuli was based on the relation of their retinal locations. Finally, in the experiment of Cai et al., the ISI was short but the SOA was long. Inferring from the results of Cai et al. (1997), Dassonville et al. (1995) and Honda (1993, 1999) described above, the perceived relation of stimuli locations seems to be an intermediate between egocentric and exocentric localization in this condition. Presenting a continuous stimulus would reduce localization error for a perisaccadic flash by promoting the use of exocentric localization. However, the localization error was not completely extinguished (Honda, 1993, 1999 Dassonville et al., 1995). Consequently, vernier judgement between a continuous stimulus and a flash presented before saccade would shift in the direction of saccade (Cai et al., 1997). In summary, perception of the relation of the locations of the stimuli flashed before saccade would be based on exocentric localization when the ISI and SOA between flashes are short. The use of egocentric and exocentric localization would not be exclusive but fused with each other when the SOA between stimuli becomes longer.

It was perception of relation of locations of stimuli flashed before saccade that we discussed in this paper, not perception of locations of the stimuli. Our results showed that relation of the locations of stimuli flashed before saccade was perceived mainly on exocentric localization when the ISI and SOA between stimuli is short. However, egocentric localization must be used to perceive the location of the stimuli. We will have to examine directly the perceived locations of stimuli flashed near saccade execution to understand how egocentric and exocentric localizations are integrated near saccade execution.

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