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Effects of inter-stimulus interval on perceived locations of successively flashed perisaccadic stimuli

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Abstract

We investigated the perceived locations of two stimuli flashed successively near the time of saccade execution in a dark room. The inter-stimulus interval (ISI) between the flashes ranged from 80 to 240 ms. The results show that when the ISI was 120 ms or shorter, perceived locations of the flashes interacted with each other so that the perceived distance between them was equal to the distance between these flashes on the retina. When the ISI was 240 ms, this interaction was weak. These results suggest two hypotheses. Firstly, the relation of retinal locations of flashes is a strong cue for perceiving the flash locations when the ISI is shorter than about 120 ms.

Secondly, the process of perceiving or memorizing a flash location requires some time. Therefore, the perceived location of the succeeding flash affects that of the preceding flash when the ISI as shorter than about 120 ms.

Keywords: Saccade; Location perception; Egocentric; Retinotopic; Inter-stimulus interval

1. Introduction

When we make a saccade while viewing objects, the retinal locations of object images change quickly. However, we usually do not perceive any illusory change of object location at that time. This fact indicates that the human visual system perceives object locations in a way unaffected by saccade execution. One such way is to represent object locations with respect to any part of the observer's body that does not move during saccade. We shall refer to this way of perceiving object locations as "egocentric localization". Egocentric localization is achieved by integrating information about retinal location of object images and eye position in the orbit (Holst, 1954; Mateeff, 1978; Matin, 1972).

Theoretically, there should not be any illusory perception of object locations produced by saccade execution if egocentric localization works perfectly. However, it has been reported that a flash presented in a dark before, during or after saccade execution was erroneously located (Honda, 1989, 1990, 1991; Mateeff, 1978; Matin, 1965; Matin, Matin, & Pearce, 1969; Matin, Matin, & Pola, 1970). In these studies, the subject made a saccade in the dark and a flash was presented at nearly the same time as the saccade onset. The subject was requested to report the location of the flash. The difference between perceived and actual location of the flash was analyzed. The results of these studies showed that the size and direction of the error depended on the difference between onset time of the flash and saccade. This illusion indicates that egocentric localization is incomplete near the time of saccade execution. Then, why does saccade execution not cause an illusory change in object location even though a perisaccadic flash in the dark is erroneously located? Concerning this problem, previous studies such as Honda (1993, 1999) and Dassonville, Schlag, and Schlag-Rey (1995) showed that presentation of other visual stimuli reduced size of localization error of a perisaccadic flash. These results indicate that the human visual system uses the relationship of object locations in the retinal image to perceive their locations. For simplicity, we shall refer to this relation as "retinotopic relation". We must understand how egocentric localization and retinotopic relation are integrated in the human visual system to answer why saccade execution does not cause illusory change in object location.

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On using retinotopic relation to perceive locations of visual stimuli, one of the most obvious constraints is that using retinotopic relation is valid only when the stimuli are simultaneously presented on the retina. However, Irwin, Brown, and Sun (1988) reported that the human visual system violates this constraint under a certain condition. They presented a horizontal array of five letters briefly before saccade and then a bar above one letter in the array after the saccade. The subject judged which letter the bar was presented above. The result showed that the judgment depended on the inter-stimulus interval (ISI) between these stimuli. That is, the relation of the letter array and bar location was correctly perceived when the letter array was presented about 200 ms before saccade onset and bar was presented 40 ms after saccade onset. However, the bar was perceived above the letter having the same retinal location as the bar when the letter array was presented immediately before saccade onset and bar was presented 40 ms after saccade onset. This result indicates that the human visual system uses retinotopic relation to perceive locations of stimuli successively flashed with a short ISI even when a saccade was executed during the ISI. This phenomenon raises several questions about the use of retinotopic relation. Firstly, it is not clear how the use of retinotopic relation depends on the length of the ISI between presaccadic and postsaccadic stimulus. Irwin et al. examined only two conditions where the ISI was about 40 or 240 ms. How is the relation of presaccadic and postsaccadic stimulus perceived when the ISI is intermediate between 40 and 240 ms? Secondly, when the relation of presaccadic and postsaccadic stimuli is perceived on retinotopic relation, at least one of these stimuli must be perceived at an erroneous location. However, the experiment of Irwin et al. did not deal with this problem because their subject only reported the relation of the presaccadic and postsaccadic stimuli. Where are these stimuli actually perceived when relation of these stimuli is perceived in retinotopic relation? Although these questions are important to understand how egocentric localization and retinotopic relation are integrated in the perception of perisaccadic flashes, no study has directly dealt with these questions.

In this paper, we will report an experiment that directly examined these questions. The subject was requested to make a saccade in the dark, and two flashes presented successively near the time of the saccade execution. We systematically changed the ISI between these flashes and asked the subject to point to the perceived location of the flashes. With this method, it is easier to control the ISI than in the method of Irwin et al. (1988) where the onset of the bar was determined with respect to the saccade onset. In addition, this method can directly deal with the perceived location of the flashes. Based on the results of this experiment, we will discuss how the human visual system uses egocentric localization and retinotopic relation to perceive perisaccadic flashes.

2. Methods

Three male subjects, HS, MM and TN participated in the experiment. HS was an author of this paper. All subjects had normal or corrected-to-normal visual acuity. The experiment contained two conditions, referred to as the "double-flash" condition and "single-flash" condition.

2.1. Double-flash condition

The subject sat on a chair with the head stabilized by a dental bite board. Horizontal movement of the left eye of the subject was recorded by an Ober2 eye recording system (Permobil Meditech). Sixteen green light emitting diodes (LED: 0.2° in diameter and 25 cd/m^2 in luminance) and eight yellow LEDs were placed at a distance of 57 cm from the subject. These LEDs formed three rows as shown in Fig. 1. The middle row was at the subject's eye level and contained two green LEDs and eight yellow LEDs. The right green LED in the middle row was the fixation point at the beginning of a trial (F). The left green LED in the middle row was the saccade target (T). The top and the bottom row contained seven green LEDs, respectively. A pointer was placed in front of these LEDs and the subject could move it horizontally. The location of the pointer was recorded by a potentiometer. The pointer had two green LEDs and a

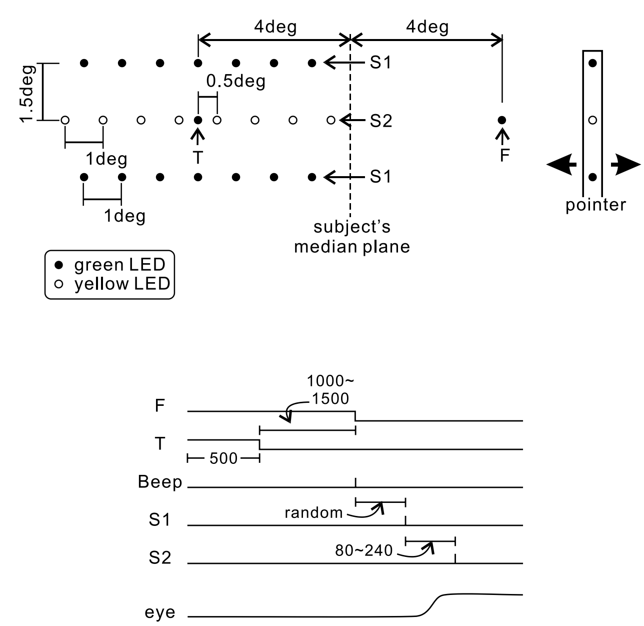

Fig. 1. Stimulus and procedure.

yellow LED on its head. The pointer was painted black so that the subjects could not see it in the dark unless the LEDs were turned on. A keybox was placed in front of the subject. These apparatuses were controlled by a PC/AT compatible computer with a digital I/O board and a timer board.

The experiment was performed in a completely dark room. One experimental session included 48 trials. A session was started when the subject moved the pointer more than 15° right from the median plane of the subject and pressed the button on the keybox. At the beginning of each trial, a warning buzzer (2000 Hz, 20 ms) sounded and F and T were turned on. After a delay of 500 ms, T was turned off. The subject remembered the location of T and maintained fixation on F. After a delay of 1000–1500 ms after the offset of T, F was turned off and a warning buzzer sounded. The subject made a saccade to the location where T had been presented as soon as the buzzer sounded. In addition to F and T, one of vertically aligned pairs of green LEDs in the top and bottom rows was flashed for 2 ms. We call this stimulus S1. After offset of S1, one of the yellow LEDs in the middle row was flashed for 2 ms. We called this stimulus S2. The ISI between S1 and S2 was fixed to 80, 120, 160, 200 or 240 ms throughout a single session. The locations of S1 and S2 were randomly changed in each trial. Onset time of S1 and S2 were adjusted so that either S1 or S2 was flashed near the time of saccade onset. The task of the subject was to point to the location of S1 and S2 using the pointer. Three seconds after the beginning of the trial, either green LEDs or a yellow LED on the pointer was turned on. If the green LEDs were turned on first, the subject pointed to the location of S1 and pressed the button on the keybox. Then the yellow LED was turned on, and the subject pointed to the location of S2 and pressed the button. If the yellow was turned on first, the subject pointed the location of S2 and then S1. Which color LED was turned on first was randomly changed in each trial. After pointing to S1 and S2, the subject moved the pointer to the right. When the pointer was moved more than 15° right from the median plane of the subject, the next trial was started. Forty successive trials were performed in one session. To avoid fatiguing the subject, the number of sessions was restricted to less than six per day. Sessions on the first day of the experiment were practiced and not used for subsequent analyses. The experiment was continued until sufficient data were obtained for all ISI conditions to plot the time course of localization error of S1 and S2 (see Section 3). This took about two weeks for each subject.

2.2. Single-flash condition

The procedure for the single-flash condition was the same as that for the double-flash condition except that either S1 or S2 alone was flashed in each trial.

3. Results

Output of the eye recorder was analyzed off-line to determine saccade onset. Saccade onset was defined as the time when angular velocity of horizontal eye rotation exceeded 40°/s. Trials in which latency of the saccade was more than 350 ms, the subject made rightward saccades, the subject made another saccade before S2 onset, or the subject could not detect S1 or S2 were omitted from further analyses.

Table 1 shows mean and standard deviation of amplitude, duration and latency of saccades selected on these criteria. The differences of amplitude of the saccades between conditions reached about 3° at maximum (subject TN).

Fig. 2 shows the results of the single-flash condition (only the result for MM is shown here). The time course of localization error was similar to that in previous studies (Honda, 1990, 1991). To confirm that the distribution of localization errors was independent of stimuli (S1 or S2), we split the data in 20 ms interval and applied a two-way ANOVA (stimulus × stimulus-saccade onset difference) separately for each subject. The ANOVA showed that only the effect of stimulus-saccade onset difference was significant for all subjects (Table 2). Therefore, we assumed in the following analyses that the time course of localization error did not depend on which of S1 or S2 flashed.

Earlier studies have shown that a perisaccadic flash was mislocated toward the target of the saccade as if

Table 1
Mean amplitude, duration and latency of saccades in the double- and single-flash conditions

Condition (ISI)		HS		MM		TN	
80	*A*	9.7	(3.6)	7.0	(1.5)	7.9	(3.1)
	D	47.4	(12.5)	37.3	(6.8)	40.0	(12.0)
	L	214.6	(25.5)	181.4	(23.8)	199.2	(21.0)
120	*A*	7.8	(2.0)	7.2	(1.2)	8.5	(2.3)
	D	43.2	(9.5)	37.0	(6.7)	41.9	(10.0)
	L	221.4	(27.5)	171.7	(17.6)	188.1	(20.3)
160	*A*	8.8	(3.3)	7.2	(1.2)	7.5	(2.2)
	D	47.7	(15.2)	36.4	(6.8)	39.1	(9.7)
	L	209.2	(23.3)	190.0	(33.0)	209.8	(35.3)
200	*A*	9.1	(2.0)	6.1	(1.9)	9.2	(2.6)
	D	46.1	(9.6)	34.1	(7.5)	43.0	(10.0)
	L	234.7	(27.5)	172.3	(22.6)	181.8	(29.5)
240	*A*	7.8	(2.5)	7.21	(1.5)	7.2	(1.6)
	D	45.1	(9.8)	38.9	(7.8)	39.7	(8.2)
	L	232.3	(28.5)	191.0	(24.7)	210.0	(34.0)
Single flash	*A*	8.0	(4.5)	7.4	(1.4)	10.7	(3.1)
	D	51.5	(9.9)	36.5	(5.9)	51.7	(11.8)
	L	224.7	(42.6)	191.5	(38.1)	187.7	(27.9)

Number in parenthesis is the standard deviation. *A*: amplitude, *D*: duration, *L*: latency.

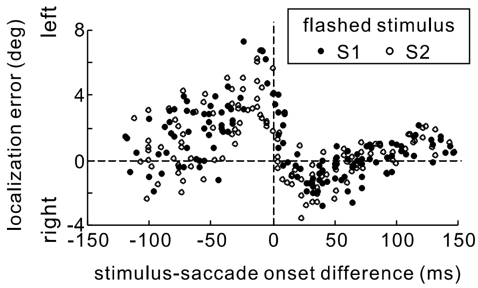

Fig. 2. Results of the single-flash condition (subject = MM). Abscissa represents the difference between the flash and saccade onset. A negative value indicates that flash onset was before saccade onset. Filled and open circles represent the results for S1 flash and S2 flash, respectively. The distributions of filled and open circles were well overlapped.

visual space was "compressed" (Morrone, Ross, & Burr, 1997; Ross, Morrone, & Burr, 1997). If this compression of visual space occurred in our data, we must separately analyze the localization error of each stimulus location. However, we do not anticipate compression occurring in our data because Lappe, Awater, and Krekelberg (2000) showed that the compression effect required the presence of stable visual references. In our experiments, there was no stable visual reference presented. To confirm this expectation, we examined whether this compression effect could be observed in our data before analyzing the effect of ISI in the double-flash condition. Fig. 3 shows the mean perceived locations of S1 and S2 in the double-flash condition when the ISI was 120 ms, separately calculated for each presentation location (average of three subjects). If compression of visual space occurred in our data, intervals between neighboring curves in these graphs should become narrower near the time of saccade execution. However, Fig. 3 seems to indicate that the intervals were unchanged rather than became narrower. To examine this point more quantitatively, we calculated mean of the intervals between perceived locations of the stimuli that were presented at neighboring locations. Here, the interval was defined as $(x+1)^* - x^*$ where x represents actual location of the stimuli and x^* represents perceived location of the stimulus that was presented at x. Defining the median plane of the subject 0.0°, x ranges 1.0, 2.0,..., 6.0 for S1 and 0.5, 1.5,..., 6.5 for S2 (see Fig. 1). If relationship of $(x+1)^*$ and x^* was reverse of that of $x+1$ and x, the interval was a negative

Table 2
Effects of flashed stimulus and stimulus-saccade onset difference in the single-flash condition

Subject	Timing	Stimulus	Timing × stimulus
HS	$F(14,260) = 24.06$[a]	$F(1,260) = 0.10$	$F(14,260) = 1.43$
MM	$F(12,236) = 20.63$[a]	$F(1,236) = 1.69$	$F(12,236) = 0.56$
TN	$F(13,235) = 22.81$[a]	$F(1,235) = 0.02$	$F(13,235) = 0.62$

Timing: effect of stimulus-saccade onset difference.
[a] $p < 0.05$.

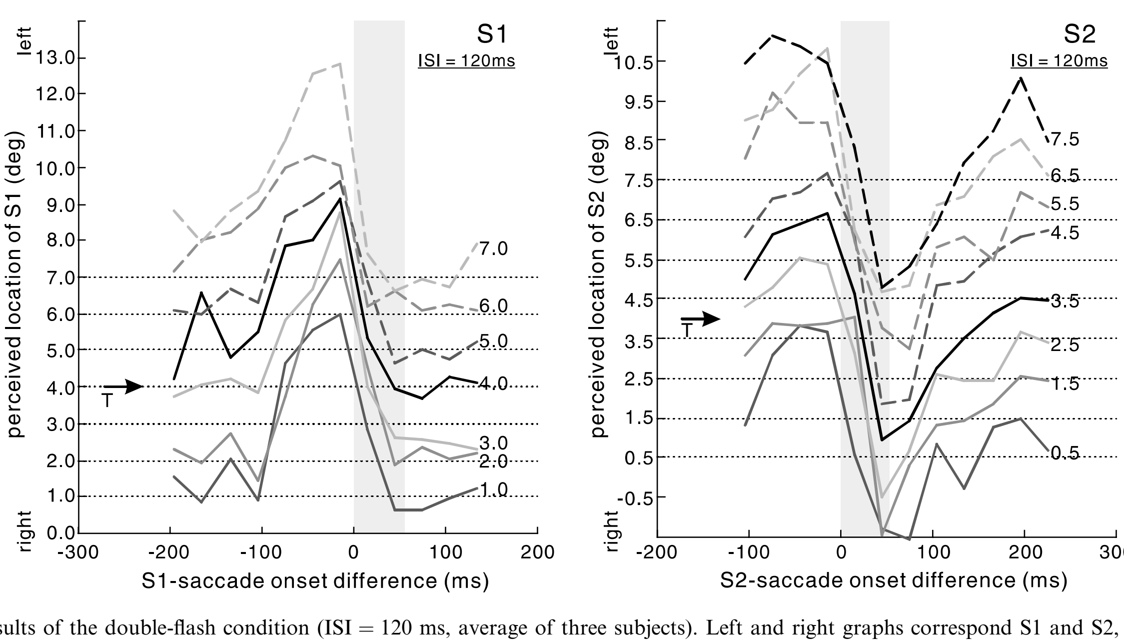

Fig. 3. Results of the double-flash condition (ISI = 120 ms, average of three subjects). Left and right graphs correspond S1 and S2, respectively. Abscissa represents the difference between the flash and saccade onset. The origin of ordinate corresponds to the median plane of subject. An arrow tagged with "T" indicates the location of the saccade goal. A number at right end of each curve represents actual location of the stimulus.

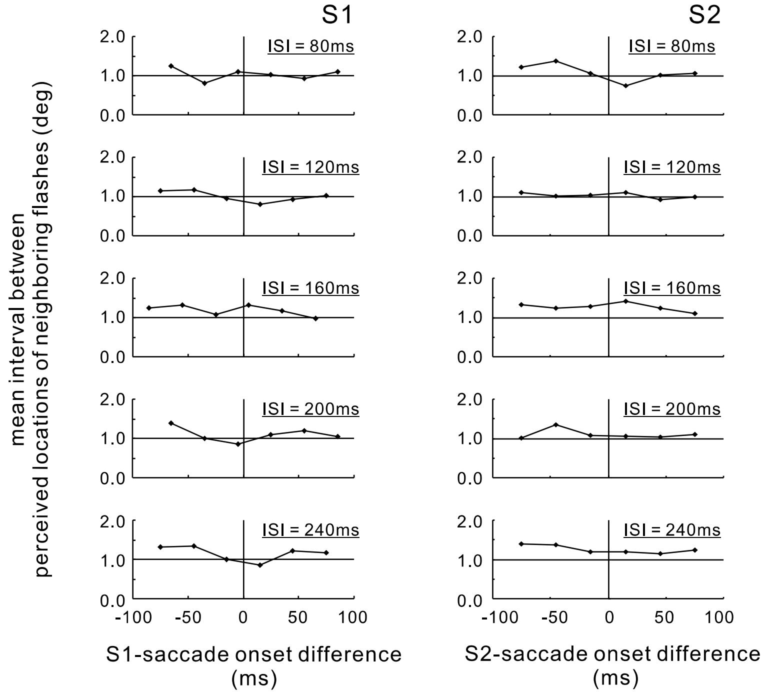

Fig. 4. Mean interval between perceived locations of the stimuli that were presented at neighboring locations. Left and right column correspond to S1 and S2, respectively. If compression did not occur, this value is expected to be 1.0.

value. Fig. 4 shows the mean intervals when the stimuli were presented near the time of saccade execution. As we can see from this figure, the mean intervals were about 1° for all ISI conditions and stimuli. Because actual intervals between neighboring stimuli locations were 1°, this means that the compression effect was insignificantly small in our data. Therefore, we do not deal with the compression effect in further analyses.

Now let us analyze the perceived location of S1 and S2 in the double-flash condition. At first, we examined an error in "signed" distance from S2 to S1, which is defined by following equation

$$D = (S_1^* - S_2^*) - (S_1 - S_2). \tag{1}$$

S_1 and S_2 represent the actual location of S1 and S2. S_1^* and S_2^* represent the perceived location of S1 and S2. "Signed" means that D is positive when S1 was located too far left with respect to S2 compared with the actual relationship of S1 and S2. Black curves with open circles in Fig. 6 show D calculated from the data.

If S1 and S2 were located egocentrically, the perceived distance from S2 to S1 should be predictable from the results of the single-flash condition. Suppose that $\varepsilon(t)$ represents the localization error in the single-flash condition when the difference between stimulus and saccade onset is t. Using $\varepsilon(t)$, perceived location of S1 and S2 can be written as $S_1^* = S_1 + \varepsilon(t_1)$ and $S_2^* = S_2 + \varepsilon(t_2)$ respectively. Here, t_1 and t_2 represent the S1- and S2-saccade onset with respect to saccade onset. Substituting them for S_1^* and S_2^* in Eq. (1), we obtain

$$D_{\text{ego}} = \varepsilon(t_1) - \varepsilon(t_2). \tag{2}$$

Green curves with filled circles in Fig. 6 show D_{ego}. To evaluate differences between D_{ego} and D, we calculated the confidence interval using the law of propagation of uncertainty and student-t distribution. The Welch–Satterthwaite formula was used to calculate the effective degree of freedom of t distribution (Taylor & Kuyatt, 1994, see Appendix A). Large open circles in Fig. 6 indicate that D differed significantly from D_{ego} at those points. These graphs show that D_{ego} does not explain the time course of D well. Based on the results of Irwin et al. (1988), we suspected D differed with D_{ego} because the retinotopic relation between S1 and S2 affected the perceived locations. If perceived relationship between S1 and S2 location coincided with their retinotopic relation, perceived location of S1 can be written as

$$S_1^* = S_2^* + (R_1 - R_2), \tag{3}$$

where R_1 and R_2 represent the retinal location of S1 and S2 respectively. To estimate R_1 and R_2 we used a coordinate system defined in Mateeff (1978). According to this definition, actual location of a flash (S) is a sum of the eye position (E) and the retinal location of the flash (R) (Fig. 5). Therefore, we can estimate the retinal location of the flash by $R = S - E$. Substituting Eq. (3) for S_1^* in Eq. (1), we obtain

$$D_{\text{retino}} = (R_1 - R_2) - (S_1 - S_2). \tag{4}$$

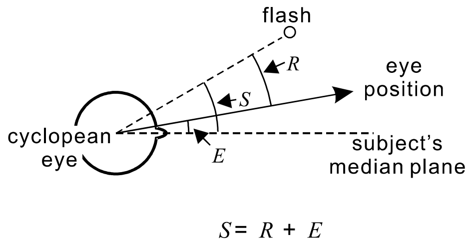

Fig. 5. Definition of the coordinate system (Mateeff, 1978). Leftward rotation (counterclockwise in this figure) was defined as positive.

If perceived relationship between S1 and S2 location based on their retinotopic relation, D should coincide with D_{retino}. Red curves in Fig. 6 show D_{retino}. We can see from these graphs that D_{retino} fit D well when the ISI was 80–120 ms. And D became closer to D_{ego} as the ISI increased. To evaluate whether D was closer to D_{retino} or D_{ego}, we calculated following δ_D for each subject and ISI.

$$\delta_D = E[(D_{retino} - D)^2 - (D_{ego} - D)^2]. \quad (5)$$

Here $E[\ldots]$ denotes taking the mean. δ_Ds are shown at the top right of each plot in Fig. 6. We can see from Fig. 6 that δ_D was positive in all subjects when the ISI was 80 or 120 ms. This means that D was closer to D_{retino} at these ISI conditions in all subjects. D became closer to

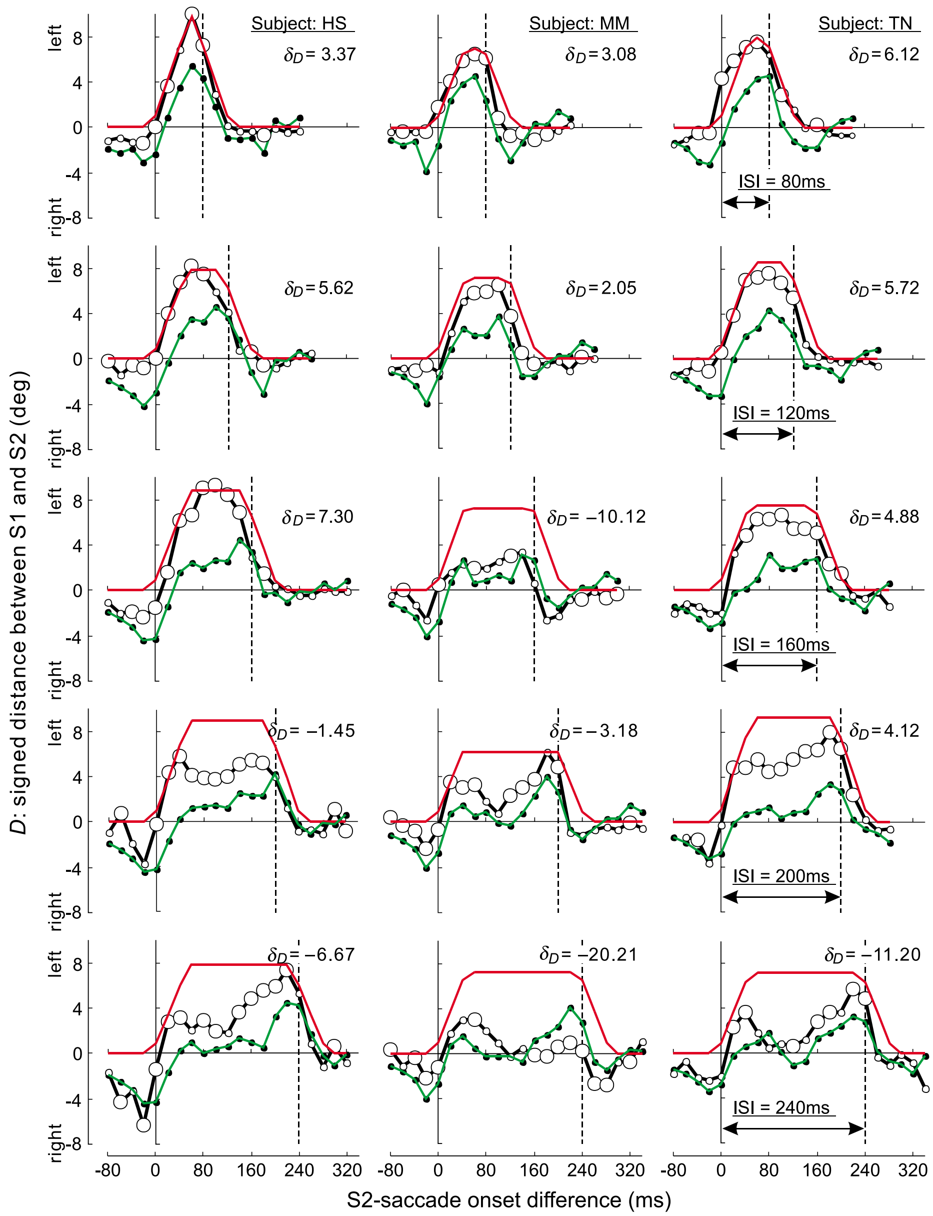

Fig. 6. Time course of D (black curves with open circles), D_{retino} (red curves) and D_{ego} (green curves with filled circles). Abscissa of each plot represents difference between S2 onset and saccade onset. A negative value indicates that S2 was flashed before saccade onset. Each column corresponds to one subject. Large open circles on the black curves indicate that D and D_{ego} was significantly different at that period ($p < 0.05$). δ_D indicates which of D_{retino} or D_{ego} was closer to D. Positive δ_D indicates D is closer to D_{retino} than D_{ego}.

D_{ego} as the ISI became longer, and then δ_D was negative in all subjects when the ISI was 240 ms. Based on these analyses, we conclude that the perception of S1 and S2 location mainly relied on their retinotopic relation when the ISI was 80 or 120 ms. The effect of retinotopic relation became weaker as the ISI became longer, and all of our subjects mainly relied on egocentric localization rather than retinotopic relation when the ISI was 240 ms.

Using the retinotopic relation of perisaccadic flashes to perceive their locations leads us a question: where are the stimuli actually perceived when the saccade is executed during the ISI? To analyze this point, we directly compared localization error of S1 and S2 in the double-flash condition with those in the single-flash condition. Fig. 7 is an example of such comparison (subject = HS, ISI = 120 ms for the double-step condition). This graph suggests that the perceived location (localization error) of S1 shift to the left, while that of S2 shift to the right in the double-flash condition compared with those in the single-flash condition. In addition, the absolute amount of the shift from the result of the single-flash condition seems roughly equal for S1 and S2. To examine this speculation strictly, we use following equation

$$M = \frac{1}{2}((S_1^* + S_2^*) - (S_1 + S_2)). \quad (6)$$

M represents the "signed" difference between the perceived and physical midpoint between S1 and S2. Positive M indicates that the perceived midpoint is left of the physical midpoint. Let us represent the shift of perceived location of S1 and S2 in the double-flash condition from those in the single-flash condition by k_1 and k_2. Because perceived location of S1 and S2 in the single-flash condition can be expressed by $S_1 + \varepsilon(t_1)$ and $S_2 + \varepsilon(t_2)$ respectively, perceived location of S1 and S2 in the double-flash condition are

$$S_1^* = S_1 + \varepsilon(t_1) + k_1, \quad (7)$$

$$S_2^* = S_2 + \varepsilon(t_2) + k_2. \quad (8)$$

Substituting Eqs. (7) and (8) in Eq. (6), we obtain

$$\frac{1}{2}(\varepsilon(t_1) + \varepsilon(t_2) + (k_1 + k_2)). \quad (9)$$

Based on the speculation described above, we assume that the absolute value of k_1 and k_2 are equal but their signs are opposite. That is, $k_1 + k_2 = 0$. Substituting this in Eq. (9), we obtain a prediction of M under our assumption (we shall indicate this by M_p).

$$M_p = \frac{1}{2}(\varepsilon(t_1) + \varepsilon(t_2)). \quad (10)$$

Fig. 8 shows M (black curves) and M_p (green curves). As in Fig. 6, large open circles represent M and M_p significantly differed at that period ($p < 0.05$). We can see from these graphs that M_p explains the time course of M well. This suggests that our assumption that k_1 and k_2 have the same absolute value but the opposite signs is appropriate. Based on these analyses, we conclude that the perceived locations of S1 and S2 in the double-flash condition shifted from those in the single-flash condition so that their relation coincided with their retinotopic relation without changing the midpoint between them.

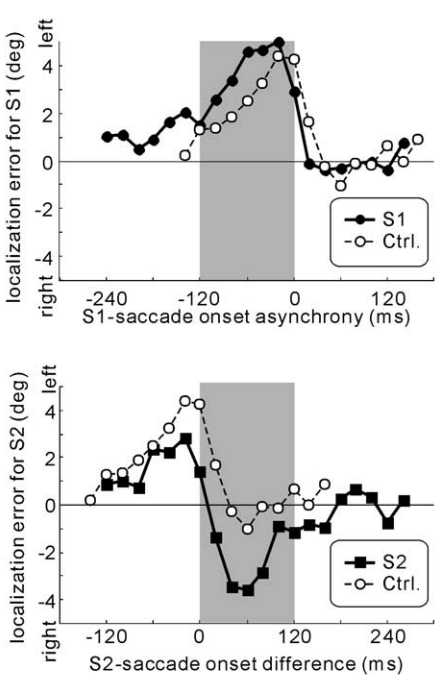

Fig. 7. Comparison between localization errors of S1 and S2 in the double-flash condition and those in the single-flash condition (subject = HS, ISI = 120 ms). Solid curves in the upper and lower plot indicate localization error of S1 and S2 respectively. Dashed curves are the results of the single-flash condition. Shaded area represents where S1 flashed before saccade onset and S2 flashed after saccade onset.

4. Discussion

The first question that we raised is how the use of egocentric localization and retinotopic relation depends on the ISI between stimuli. Our results showed that the perceived relation between stimuli mainly relied on egocentric localization when ISI was 240 ms. This was consistent with the results of Irwin et al. (1988), which showed that the perceived relation of the presaccadic letter array and the postsaccadic bar was correctly perceived. In addition, there were two new findings. Firstly, the perceived relation of the stimuli mainly relied on the retinotopic relation when the ISI was up to 120 ms for all subjects. Secondly, the perceived relation of the stimuli was an intermediate of the predictions by egocentric localization and retinotopic relation when the ISI was 160 and 200 ms though there was individual variation. The second finding is interesting because it suggests that the use of retinotopic relation does not obey an "all-or-none" rule but is a process like a weighted average of egocentric localization and retinotopic relation. In our speculation, the weight of this averaging

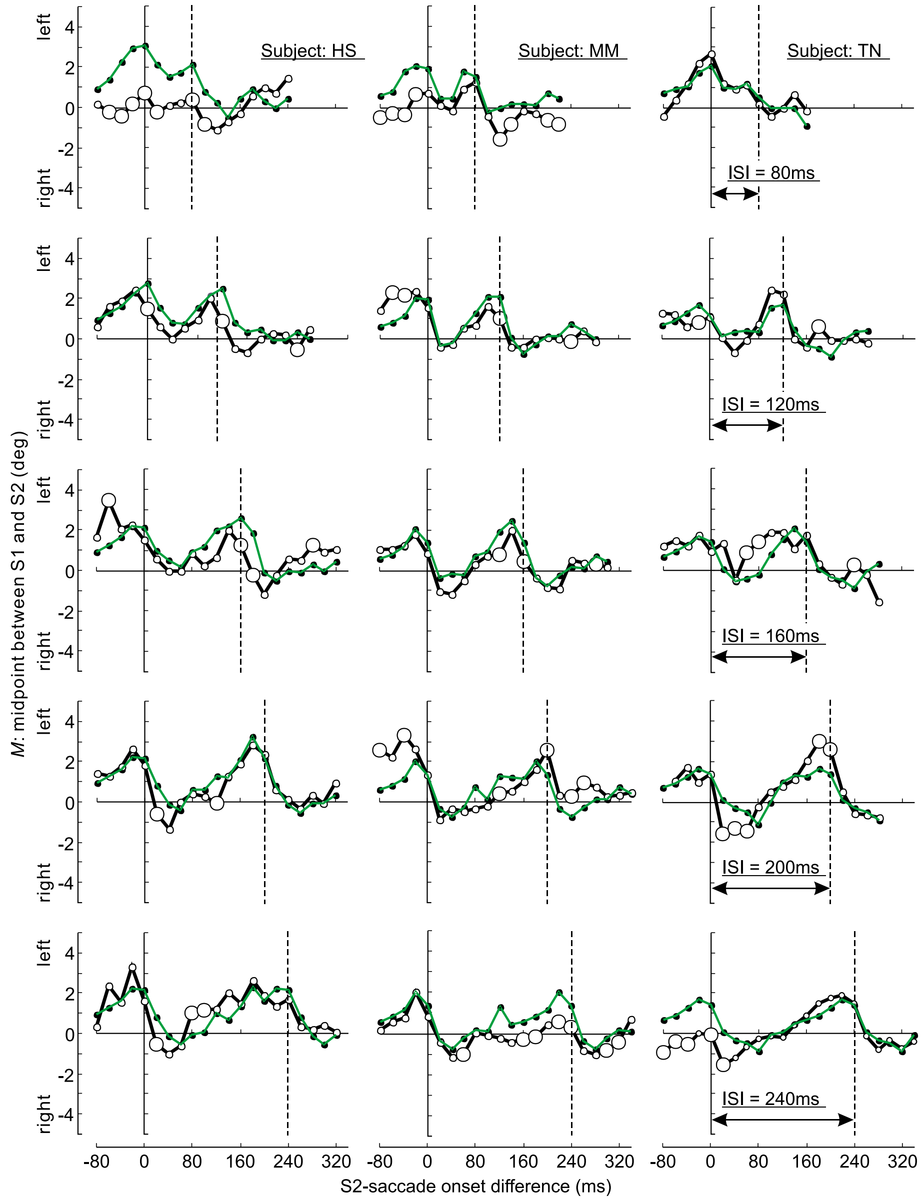

Fig. 8. Time course of M (black curves with open circles) and M_p (green curves with filled circles). The abscissa of the plots are the same as those in Fig. 6. Large open circles on the black curves indicate that M and M_p was significantly different at that period ($p < 0.05$).

process would be a function of the ISI and there would be individual variations in this process. What we want to stress here is that when we say that perceived relation of perisaccadic flashes relied on retinotopic relation, we do not mean that egocentric cues were ignored. To establish perception of the stimuli locations in space, egocentric localization is essential regardless of the ISI. Retinotopic relation is only "taken into account" when the ISI is short.

The second question that we raised is where the perisaccadic stimuli were perceived when their perceived relation was based on retinotopic relation. Concerning this question, we found that presenting a perisaccadic flash caused a shift in perceived location of the preceding flash when the retinotopic relation between the two was used. This finding suggests that the process of perceiving the location of a perisaccadic flash requires a certain period, and that other information obtained during this period can interfere in this process. Though the length of this period remains unknown, our results suggest that the length would be about 120 ms or longer because the perceived relation of the perisaccadic flashes based on their retinotopic relation in all subjects when the ISI was 120 ms. If our hypothesis is appropriate, it is expected that perceived location of the first flash is less affected by presentation of the second flash when the onset times of these flashes are sufficiently separated. This expectation is consistent with an earlier experiment

(Cai, Pouget, Schlag-Rey, & Schlag, 1997). Cai et al. asked their subjects to judge the relationship of the locations of three perisaccadic flashes. The top and bottom dot were vertically aligned and visible from the beginning of the trial. The middle dot was briefly presented before saccade onset, and the top and bottom dot disappeared at the same time as the offset of the middle dot. The subjects reported whether the middle dot was left or right of the other dots. The results showed that the relationship of these dots was not perceived retinotopically but the middle dot shifted in the direction of the saccade relative to other dots. The reason the relationship of these dots was not perceived retinotopically would be probably that the location of the top and bottom dots had already been "established" in the human visual system when the middle dot was presented. Thus, the human visual system had to deal with the conflict between egocentric and retinotopic cues to determine the location of the middle dot. As a result, perceived location of the middle dot would fall into an intermediate location between egocentric and retinotopic localization. Because the experiment of Cai et al. (1997) only showed that the relationship of three dots was not perceived retinotopically, it may be argued that whether the perceived location of the middle dot was an intermediate of egocentric and retinotopic localization. However, we think that earlier studies, which examined localization of perisaccadic flash under presence of stable background stimuli, support our hypothesis (e.g., Dassonville et al., 1995; Honda, 1993, 1999). These studies showed that the presence of a stable background did not eliminate but only reduced the localization error of perisaccadic flash. This fact indicates that the perceived location of the perisaccadic flash was not based on either pure egocentric or retinotopic localization but rather on their intermediate.

Finally, we discuss the relationship between result described by Morrone et al. (1997) and ours. Morrone et al. (1997) sequentially presented two collinear vertical bars ($1.8^\circ \times 25^\circ$) in the perisaccadic period; one was displayed from the middle to the top, the other from the middle to the bottom of a $70^\circ \times 50^\circ$ screen. The task of the subjects was to report the apparent separation of these bars. The ISI between these bars was about 70 ms and the duration of presentation of each bar was 8.3 ms. Because this condition is similar to our double-flash condition with an ISI of 80 ms, our result suggests the apparent separation of these bars should be equal to that of their retinal locations. However, the result described by Morrone et al. showed that separation of these bars was not perceived retinotopically but could be predicted from localization error of a single perisaccadic vertical bar (this would correspond to localization error in the single-flash condition in our experiment). This result seems inconsistent with our conclusion. We think that this inconsistency derives from the existence of background. In the experiment by Morrone et al., the stimuli were presented on a visible, stable red illuminant screen, which could function as a stable background. Therefore, the human visual system would use not only retinotopic relation between two collinear bars but also retinotopic relation between these bars and the background in the experiment by Morrone et al. This factor may affect the perceived relationship between bars. Moreover, the results of Morrone et al. exhibited strong compression of visual space, which would be produced by the background (Lappe et al., 2000). This means that the background in Morrone et al. had a certain effect on the process of perceiving the location of perisaccadic flashes. This effect was absent in our experiment. It is necessary to study how the existence of a stable background affects perception of the location of perisaccadic flashes.

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Appendix A. Law of propagation of uncertainty and the Welch–Satterthwaite formula

In the text, we tested the difference between D and D_{ego} and between M and M_{p}. Because these variables were not directly measured, we estimated variance of these variables by the law of propagation of uncertainty (Taylor & Kuyatt, 1994). Suppose a stochastic variable Y can be expressed as a function of stochastic variables X_i $(i = 1, 2, \ldots, N)$.

$$Y = f(X_1, X_2, \ldots, X_N). \tag{A.1}$$

When first-order Taylor series of f gives a good approximation of f around the mean of X_i, variance of Y can be expressed by following equation

$$u^2(y) = \sum_{i=1}^{N} \left(\frac{\partial f}{\partial x_i}\right)^2 u^2(x_i) + 2\sum_{i=1}^{N-1} \sum_{j=i+1}^{N} \frac{\partial f}{\partial x_i} \frac{\partial f}{\partial x_j} u(x_i, x_j). \tag{A.2}$$

Here $u^2(y)$ and $u^2(x_i)$ denotes variance of Y and X_i respectively, and $u(x_i, x_j)$ denotes covariance between X_i and X_j. Eq. (A.2) is called the law of propagation of uncertainty (Taylor & Kuyatt, 1994).

Concerning comparison of D and D_{ego}, our null hypothesis (H_0) was $D - D_{\mathrm{ego}} = 0$. Using Eq. (2), H_0 can be expressed as $D - (\varepsilon(t_1) - \varepsilon(t_2)) = 0$. Because D, $\varepsilon(t_1)$ and $\varepsilon(t_2)$ were directly measured, we can test H_0 by using Eq. (A.2) (we assumed that D, $\varepsilon(t_1)$ and $\varepsilon(t_2)$ were independent). To obtain confident interval of H_0, distribution of H_0 has to be specified. Taylor and Kuyatt (1994) recommends using t distribution whose degree of freedom is given by Welch–Satterthwaite formula. Welch–Satterthwaite formula is given by following equation

$$\nu_{\mathrm{eff}} = \frac{u^4(y)}{\sum_{i=1}^{N} \left(\frac{\partial f}{\partial x_i}\right)^4 \frac{u^4(x_i)}{\nu_i}}. \tag{A.3}$$

Here ν_{eff} denotes degree of freedom of x_i. Degree of freedom of t distribution is given as a maximum integer that does not exceed ν_{eff}. Concerning comparison of M and M_{p}, the null hypothesis was $M - M_{\mathrm{p}} = 0$. This can be expressed as $M - 1/2(\varepsilon(t_1) + \varepsilon(t_2)) = 0$.

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