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Perisaccadic perception of continuous flickers

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Abstract

To realize perceptual space constancy, the visual system compensates for the retinal displacement caused by eye movements. It has been reported that the compensation process does not function perfectly around the time of a saccade—a perisaccadic flash is systematically mislocalized. However, observations made with transient flash stimuli do not necessarily indicate a general perisaccadic failure of space constancy. To investigate how the visual system realizes perisaccadic space constancy for continuous stimuli, we examined the time course of localization for a perisaccadic 500 Hz flicker with systematic variation of the onset timing, the offset timing and the duration. If each flash in the flicker is localized individually in the same way as a single flash, the apparent position and length of the flicker should be predicted from the time course of mislocalization of a perisaccadic flash. However, the results did not support this prediction in many respects. A dot array (of half the length of the retinal image) was perceived when the flicker was presented during a saccade, while only a single dot was perceived when the flicker was presented only before or after the saccade. A flash in a flicker was localized at a different position, depending on the onset timing, the offset timing and the duration of the flicker, even if the flash was presented at the same timing to the saccade. In general, our results support a two-stage localization in which the local geometrical configuration is first generated primarily based on the retinal information, and then localized as a whole in the egocentric or exocentric space. The localization is based on the eye position signal sampled at a time temporally distant from the saccade, which enables precise localization and space constancy for continuous stimuli.

Keywords: Saccade; Localization; Space constancy; Flicker; Continuous light

1. Introduction

Human observers frequently make eye movements to see surrounding environments with the central sensitive area of the retina. Although the eye movements shift the location of stationary objects on the retina, the observers do not normally perceive the displacement of the objects. The visual system compensates for the retinal displacement in some way and realizes perceptual space constancy. A widely-accepted account of this compensation is the cancellation theory (Sperry, 1950; von Holst, 1954; von Holst & Mittelstaedt, 1950), which states that the perceived location of an object is determined by the summation of the retinal location of the object and the internal information about the eye position, namely, that the retinal displacement by the eye movement is canceled by the internal eye position signal (EPS). It has been reported that the compensation process does not function perfectly around the time of a saccade. When a briefly flashed stimulus is presented before, during, and after a saccade, the perceived position of the stimulus is systematically mislocalized (Bockisch &

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Miller, 1999; Boucher, Groh, & Hughes, 2001; Dassonville, Schlag, & Schlag-Rey, 1995; Honda, 1989, 1990, 1991; Mateeff, 1978; Matin, Matin, & Pearce, 1969; Matin, Matin, & Pola, 1970; Matin & Pearce, 1965; Schlag & Schlag-Rey, 1995). Single flashes presented in darkness before saccades were mislocalized toward the direction of saccade, while those presented after saccades were mislocalized in the opposite direction (examples of the time courses are shown in Fig. 2). These errors have been interpreted through the cancellation theory as a result of a mismatch between the actual eye position and the sluggishly changing EPS. Additionally, when measured in relation to visual references, the error indicates a non-uniform mislocalization across the visual field, which resembles a compression of visual space around the saccadic target (Awater & Lappe, 2004; Honda, 1993; Kaiser & Lappe, 2004; Lappe, Awater, & Krekelberg, 2000; Matin & Pearce, 1965; Morrone, Ross, & Burr, 1997; Ross, Morrone, & Burr, 1997).

Perisaccadic space constancy has been studied by mainly using single flashes, but it is debatable whether the mislocalization of a single flash indicates a general failure of perisaccadic space constancy. In typical environments, almost every object continues to exist before and after the saccade, and the visual system may exhibit more robust space constancy in such a continuous environment. Furthermore, a flash stimulus should not be regarded as a general probe for perceptual localization, since it is known that transient stimuli like a flash and a stimulus onset are mislocalized in various ways by the presence of retinal motion (Eagleman & Sejnowski, 2000a, 2000b, 2000c; Kerzel, 2002; Nijhawan, 1994; Purushothaman, Patel, Bedell, & Ogmen, 1998; Schlag, Cai, Dorfman, Mohempour, & Schlag-Rey, 2000; Whitney & Cavanagh, 2000; Whitney & Murakami, 1998). The localization error for a flash presented near the time of a saccade may also include some effects specific to the transient stimulus rather than indicating the general function of realizing the space constancy.

Indeed, previous studies reported several cases where the time course of mislocalizations measured with single flashes do not agree with those measured with less transient stimuli. Schlag and Schlag-Rey (1995) reported that when a dot was continuously presented immediately before a saccade, although apparent displacements of single flashes predicted the perception of a motion streak, subjects veridically saw a single dot (see also Campbell & Wurtz, 1978; Holly, 1975; Mateeff, 1978; Sogo & Osaka, 2001). The streak was found to be visible only when there was an actual stimulus movement on the retina. As an elegant extension of this finding, Cai, Pouget, Schlag-Rey, and Schlag (1997) showed that when a single flash was presented at the offset of the continuous light stimuli, the flash was mislocalized relative to the continuous stimuli. Hershberger and his colleagues reported that, just as a continuous light presented during a saccade produces a motion streak, a rapidly flickering stimulus produces the perception of a dot array, which they called a 'Phantom Array' (Hershberger, 1987; Hershberger & Jordan, 1992; Hershberger, Jordan, & Lucas, 1998; Jordan & Hershberger, 1994). They showed that the dot appeared to move in the opposite direction of the saccade, and that the length of the perceived dot array was about half the length of the retinal image. In addition, a dot flashed within 80ms before the saccade was seen as spatially coincident with the first flash of the dot array, which is inconsistent with the time course of single-flash mislocalization (Jordan & Hershberger, 1994). More recently, Sogo and Osaka (2002) found an interaction between the apparent locations of successively presented two flashes. Specifically, when the inter-stimulus interval was 120ms or shorter, the apparent distance between the two flashes did not coincide with the time course of the perisaccadic mislocalization, but was coincident with their retinal distance. These findings suggest that perisaccadic localization of intransient stimuli is a complex phenomenon that cannot be simply predicted from localization of single flashes.

To gain further insight into the principle and mechanism underlying space constancy in natural environments, the present study examined the time course of localization for a continuous stimulus, and compared the data with those obtained with a single flash. The stimulus we mainly used was a 500Hz flicker. Considering the temporal response of early visual mechanisms, a 500Hz flicker is indistinguishable from a physically continuous light to the visual system as long as the eye is stationary. We also repeated some experiments with a physically continuous light (see Expts. 2 and 3). A merit of using a high-frequency flicker is that it potentially produces different appearances for two possible types of perceptual spreads. One is caused by retinal painting during saccadic eye movement. In this case, since the eye movement is very fast, the flicker should be seen as an array of dots. The other type is a dot spread potentially observed before or after a saccade, caused by extra-retinal localization errors. If this spread in fact occurs, the flicker that stimulates the same retinal location should be seen as a continuous light spread, rather than a dot array. As described below, however, we never observed the dot spread of the latter type.

In the experiments, we systematically varied the parameters that previous findings (e.g., Schlag & Schlag-Rey, 1995; Sogo & Osaka, 2001, 2002) suggested to be potentially important: the onset timing, the offset timing and the duration. Depending on the timing of eye movements, a flickering LED was perceived either as a single dot or a dot array. We asked subjects to point to the position of either the dot or the left and right ends of the dot array, so as to estimate both the apparent locations and the apparent length. In the first experiment, the time course of localization for a briefly flashed stimulus was measured. The data formed the basis for comparing the time course with the data from subsequent experiments. In the second experiment, we presented a flickering stimulus long before a saccade onset, and systematically changed the offset timing. In the third experiment, we systematically changed the flicker onset time, and presented the stimulus until long after a saccade onset. In the fourth experiment, we systemically changed both the duration and onset/offset timing of the flicker presented around the time of a saccade. Consistent with the previous report, our results showed that perisaccadic mislocalization of continuous flickers was incompatible with the time course of single-flash localization. Further analysis of the pattern of mislocalization led us to a two-stage localization process—the local geometrical configuration is first generated based on the retinally-painted image, then localized as a whole in the egocentric or exocentric space.

2. Experiment 1: Localization of a briefly flashed stimulus

In a completely dark room the subject localized the perceived position of a perisaccadically flashed stimulus.

2.1. Methods

2.1.1. Subjects

Three naïve male subjects with normal visual acuity whose age ranged from 22 to 24 (referred to as Y.I., Y.A. and K.F.), participated in all four experiments.

2.1.2. Apparatus

A fixation point (FP), a target point (TP) and a probe stimulus (S) were arranged as shown in Fig. 1a. The FP and TP were red light emitting diodes (LED) (diameter: 0.25 deg, luminance: 16 cd/m^2). The subject was asked to make a saccade from the FP to the TP. The distance between the FP and TP was 8 deg in visual angle. The S was a green LED (diameter: 0.1 deg) and located at the center of the FP and TP. The luminance of the S was 10 cd/m^2 (one subject, K.F., was also tested with 1.6 cd/m^2, which was the luminance of flicker stimuli used in the following experiments). The distance from the subject's right eyeball to the S was 150 cm. The eyeball, FP, TP and S were arranged at same vertical level. The subject sat in a chair with the head stabilized by a chin rest. The subject's left eye was covered with an eye patch. Horizontal movement of the subject's right eye was measured at 600 Hz by an EMR-600 (NAC Inc.) with a resolution of 0.17 deg. The output of analog voltage by EMR-600 and the flash timing of the FP, TP, and S were recorded by a digital I/O of an AT PC. A micro IC (PIC16F877 microchip inc.) was used to control the flash timing of the LEDs. All experiments were performed in a completely dark room.

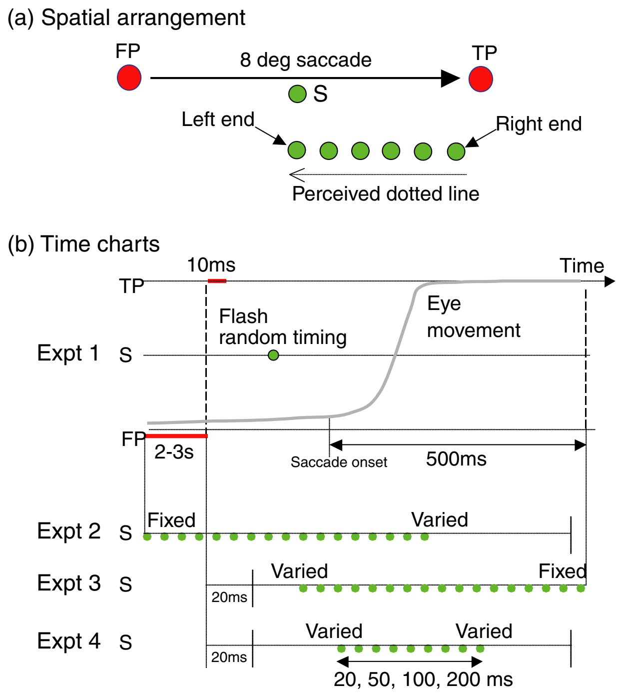


Fig. 1. (a) Spatial arrangement and (b) time charts of experiments. A fixation point (FP), target point (TP) and stimulus (S) were respectively located at −4, 4, and 0 deg away from the front of the right eyeball of the subject. The subject was asked to make an 8 deg saccade from the FP to TP. At the beginning of a trial, the FP was turned on. The subject moved his gaze to the FP. After a random duration (2–3 s), the FP disappears. Immediately after the disappearance of the FP, the TP turned on for 10 ms. The subject had to make a saccade to the TP as quick as possible. In Expt. 1, the S was presented for 2 ms at a random time from 10 ms to 600 ms after the offset of the TP (i.e., from about 200 ms before to about 400 ms after the onset of a saccade). In Expt. 2, the S started to flicker as the FP turned on. The duration of the S was varied so that the termination time was set between 10 ms and 600 ms after the offset of the TP. In Expt. 3, the S started to flicker at a random time from 10 ms to 600 ms after the offset of the TP, and its disappearance time was fixed to 700 ms after the offset of TP (about 500 ms after the saccade offset). In Expt. 4, the presentation time of the flicker was also set between 10 ms and 600 ms after the offset of the TP, and its duration was selected among 20, 50, 100 and 200 ms. In all experiments, the subject was asked to point to the perceived location of the S. When the subject perceived a dot, he localized it using one laser pointer, and when a dot array was perceived, he localized the left and right ends of the dot array using two laser pointers at the same time.

2.1.3. Procedure

Each block of the experiments began with a calibration procedure, in which the subject sequentially fixated upon one of five dots located at −8, −4, 0, 4, or 8 deg on the same level as the FP, TP and S. The eye position was calculated linearly based on the measurements for the five positions. The time charts of the experiments are shown in Fig. 1b. At the beginning of each trial, the FP was turned on, and the subject moved his gaze to the FP. After a random duration (2–3 s), the FP disappeared, and the TP (saccade target) turned on immediately for 10 ms. The subject made a saccade to the TP. The S was presented for 2 ms at a random time from 10 ms to 600 ms after the offset of TP (i.e., from about 200 ms before to about 400 ms after the onset of a saccade). The subject was asked to point to the perceived location of the S with a red laser pointer (diameter: 0.08 deg, laser: class II), which was fixed on the table in front of the subject, and could move only horizontally. The plane where the FP, TP and S were attached was covered with graph paper (resolution 1 mm), and the experimenter read the value from the location of the laser beam. We asked the subject to point to the perceived location immediately to avoid potential memory distortion of the perceived location (Sheth & Shimojo, 2001). The measured value of the perceived location was not told to the subject. In all experiments, each experimental block consisted of 50 trials, and each subject ran five blocks.

2.1.4. Data analysis

The same analysis of eye position data was performed in all experiments. Since the subjects were to make an 8 deg saccade, all data samples in which the amplitude of the saccade was over 10 deg or under 5 deg, or the duration was over 70 ms or under 20 ms, or the latency was over 300 ms or under 60 ms, were excluded. Before analyzing the data, a linear low pass filter (cut-off frequency 100 Hz) was applied to eliminate noise. The onset of a saccade was defined as the time when the velocity of the eye movement exceeded 40 deg/s for the first time, and the offset of a saccade was defined as the time when it became less than 40 deg/s for the first time after the saccade onset.

2.2. Results

Table 1 describes the number of trials, amplitudes, durations and latencies of saccades for all subjects in all experiments. These data indicate that stable saccades were achieved. The localization data of Expt. 1 are shown in Fig. 2. The amount of mislocalization was tightly related to the time when the stimulus was flashed. For all subjects, the displacement in the same direction of the saccade began at least 200 ms before the onset of the saccade and reached a maximum at the onset. Soon after the onset, the mislocalization in the opposite direction emerged, and persisted until about 200–400 ms after the offset of the saccade. The mislocalization of Y.I. (Fig. 2a) continued slightly longer than the other subjects. In the data of Y.A. (Fig. 2b), the mislocalization in the same direction apparently began more than 200 ms before the saccade onset, and the mislocalization in the opposite direction after the saccade was not clearly visible. In some trials of K.F. (Fig. 2c), mislocalization in the same direction occurred even after the saccade. The last subject (K.F.) was tested also with a darker S (1.6 cd/m^2, Fig. 2d), but the result was nearly the same as the result with 10 cd/m^2. Besides minor differences between individuals, the general tendencies of

Table 1
Number of trials, amplitudes, durations and latencies of performed saccades in all experiments

		Trials	Mean amplitudes (deg)	Duration (ms)	Latency (ms)
Y.I.	Expt. 1	185	7.69 (1.18)	40.6 (5.8)	220.2 (25.4)
	Expt. 2	181	7.65 (1.43)	40.8 (6.4)	207.7 (31.9)
	Expt. 3	221	7.46 (1.16)	39.4 (5.8)	212.9 (31.5)
	Expt. 4, 20 ms	184	7.13 (1.09)	40.6 (6.1)	221.1 (33.5)
	Expt. 4, 50 ms	171	7.21 (1.19)	40.5 (5.7)	222.2 (32.9)
	Expt. 4, 100 ms	169	7.24 (1.26)	40.7 (5.9)	224.8 (31.0)
	Expt. 4, 200 ms	160	7.11 (1.27)	40.3 (5.7)	222.9 (30.5)
Y.A.	Expt. 1	206	6.92 (1.05)	39.0 (4.9)	213.5 (48.6)
	Expt. 2	214	7.62 (1.38)	42.6 (5.9)	212.7 (40.5)
	Expt. 3	171	7.54 (1.02)	41.6 (5.5)	208.8 (33.9)
	Expt. 4, 20 ms	201	6.92 (1.12)	40.0 (5.3)	212.6 (32.0)
	Expt. 4, 50 ms	181	6.96 (1.05)	40.3 (5.0)	206.0 (35.9)
	Expt. 4, 100 ms	182	6.95 (1.10)	40.0 (5.0)	219.6 (50.6)
	Expt. 4, 200 ms	183	6.95 (1.08)	39.5 (5.0)	222.5 (50.7)
K.F.	Expt. 1	181	7.17 (1.26)	38.0 (6.2)	258.4 (45.2)
	Expt. 1 (1.6 cd/m^3)	166	7.20 (1.35)	36.9 (5.8)	248.9 (41.8)
	Expt. 2	176	7.60 (2.17)	41.0 (9.2)	222.4 (35.3)
	Expt. 2 (cont.)	153	7.00 (1.65)	35.4 (9.1)	218.4 (20.2)
	Expt. 3	167	7.29 (1.47)	41.9 (8.3)	244.3 (48.9)
	Expt. 3 (cont.)	176	7.30 (1.86)	35.5 (6.0)	230.8 (32.8)
	Expt. 4, 20 ms	189	6.98 (1.16)	38.5 (5.4)	228.7 (42.8)
	Expt. 4, 50 ms	184	6.97 (1.16)	38.9 (5.4)	223.0 (40.9)
	Expt. 4, 100 ms	168	6.87 (1.18)	38.3 (5.4)	227.5 (42.0)
	Expt. 4, 200 ms	169	7.06 (1.22)	39.1 (6.0)	223.8 (39.5)

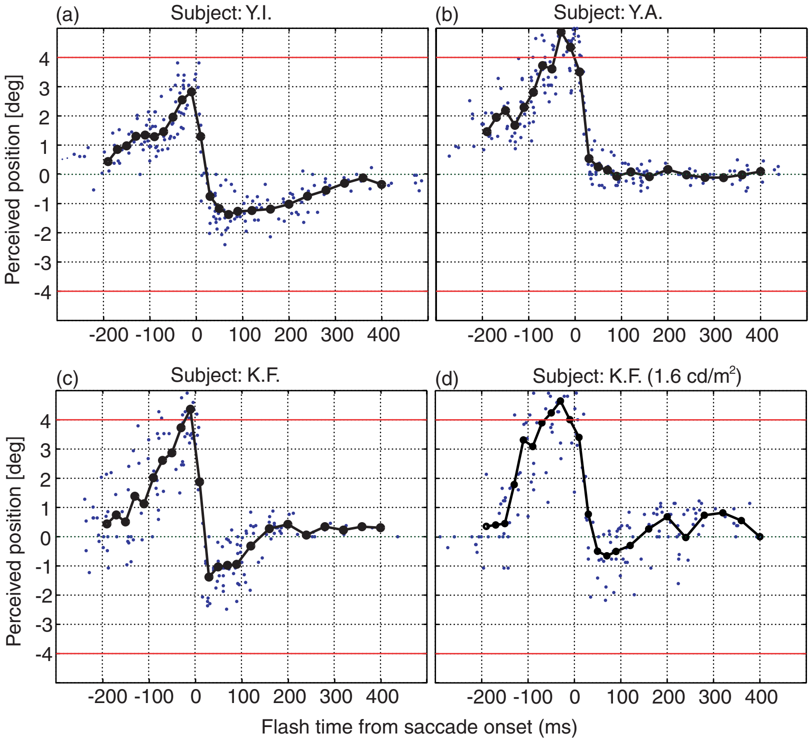


Fig. 2. Perceived positions for a briefly flashed stimulus. The abscissa (horizontal axis) represents the temporal difference between the flash time and the saccade onset (ms). A negative value indicates that the stimulus flashes before the saccade onset. The ordinate (vertical axis) represents perceived position (deg). Saccades were made from −4 deg to +4 deg. Lined-dots represent averages of perceived positions, which was computed for every 20 ms interval from −200 to +100 ms and for every 40 ms interval from +100 to +420 ms. In the following figures, the averages were computed in the same way.

the present results are coincident with the previous studies (Bockisch & Miller, 1999; Boucher et al., 2001; Dassonville et al., 1995; Honda, 1990). If each flash in a flicker is localized independently in the same way as a single flash, the apparent position and length of the flicker should be predicted from these time courses.

3. Experiments 2 and 3: Localization of a continuous flicker from long before, until long after a saccade

The following experiments investigated the time course of localization for continuous stimuli. In the second and third experiments, a flickering stimulus was presented from long before or until long after a saccade, respectively. The duration of the flicker was varied. We compared the time courses obtained in Expts. 2 and 3 with that of Expt. 1.

3.1. Procedure

In Expt. 2, the same procedure was used as Expt. 1 except for the flash timing of the S. As depicted in Fig. 1b, the S started to flicker at 500 Hz (0.5 ms on, 1.5 ms off) as the FP turned on. The duration of the S was varied in such a way that the S terminated during the interval from 10 ms to 600 ms after the offset of the TP (i.e., from about 200 ms before to about 400 ms after the onset of a saccade). According to the flicker offset time, the subject perceived either a dot or a dot array. When the subject perceived a dot, he localized it using one laser pointer, and when a dot array was perceived, he localized the left and right ends at the same time using two laser pointers.

In Expt. 3, the S started to flicker during the interval from 10 ms to 600 ms after the offset of the TP (i.e., from about 200 ms before to 400 ms after the onset of a saccade). The flicker offset time of the S was fixed at 500 ms after the onset of the saccade. According to the flicker onset time, the subject perceived either a dot or a dot array. The subjects localized it with one or two laser pointer(s). One subject, K.F. was also tested with continuous light, which was presented at the same onset and offset timing as in Expts. 2 and 3, respectively. In this case, the subject perceived a dot or a continuous line.

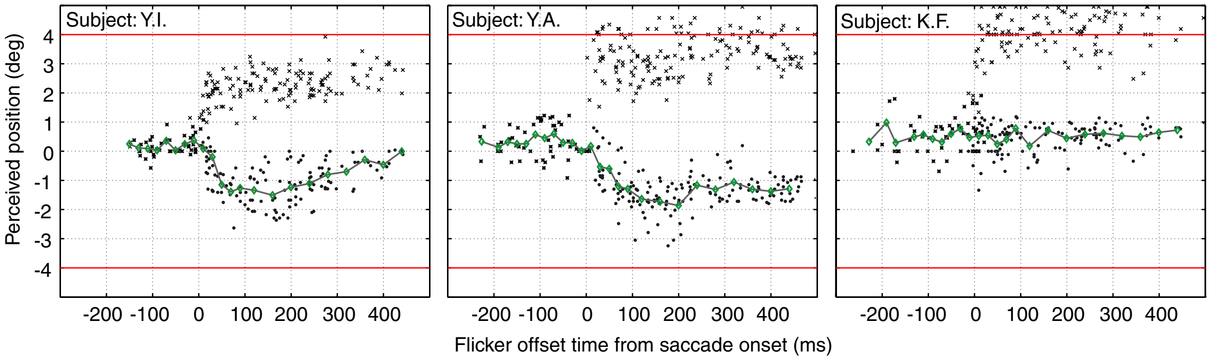
The luminance of the S was 1.6 cd/m^2 (which was 10 cd/m^2 in Expt. 1). A darker luminance was used in Expts. 2 and 3, because the S was presented for a longer time than the 2 ms in Expt. 1. If a stimulus with the same luminance was used, the subjects perceived it as brighter. Note also that reducing the luminance of the S to 1.6 cd/m^2 had only a minor effect for K.F. in Expt. 1.

3.2. Results

Expts. 2 and 3 are referred to respectively as “flicker offset-variable condition” and “flicker onset-variable condition” in Fig. 3. The results of Expt. 2 are shown in Fig. 3a. Since the flicker onset time was fixed, the apparent location of the first flash (right end) and the last flash (left end) are both plotted to the flicker *offset* time (as discussed at the end of this section, we assumed that the dot, which appeared first, was located at the right end of the perceived line and the dot, which appeared last, was located at the left end). For example, when a stimulus continued to flicker until 100 ms after the onset of the saccade, the subject Y.I. perceived a dot array and pointed to the right and left ends at the position of about +2.0 deg and −1.5 deg, respectively. In Fig. 3a, the indicated positions both are plotted at 100 ms in the abscissa and at each perceived position in the ordinate. The results of Expt. 3 are shown in Fig. 3b. Since the last flash (left end) was presented long after the saccade, the two ends are both plotted to the flicker *onset* time (right end). In Fig. 3a and b, all filled circles are plotted corresponding to the time when the flash was presented, and the crosses are not. Fig. 3c shows the apparent line length of the dot array obtained in Expts. 2 and 3 relative to the saccade amplitude. When a dot is perceived, the value is zero.

In Expt. 2 (flicker offset-variable condition, Fig. 3a and c), all subjects perceived just a dot near the veridical position (0 deg) before the saccade. After the saccade onset, a dot array began to spread, then the length of the dot array saturated at the time of the saccade offset. This indicates that the dot spread only during the saccade. Although there were some individual differences, the length of the dot array was about half the saccade amplitude, as reported by Hershberger (1987). The perceived length was always smaller than the length painted on the retina. As to the perceived positions of the right

(a) Perceived positions in flicker offset-variable condition



(b) Perceived positions in flicker onset-variable condition

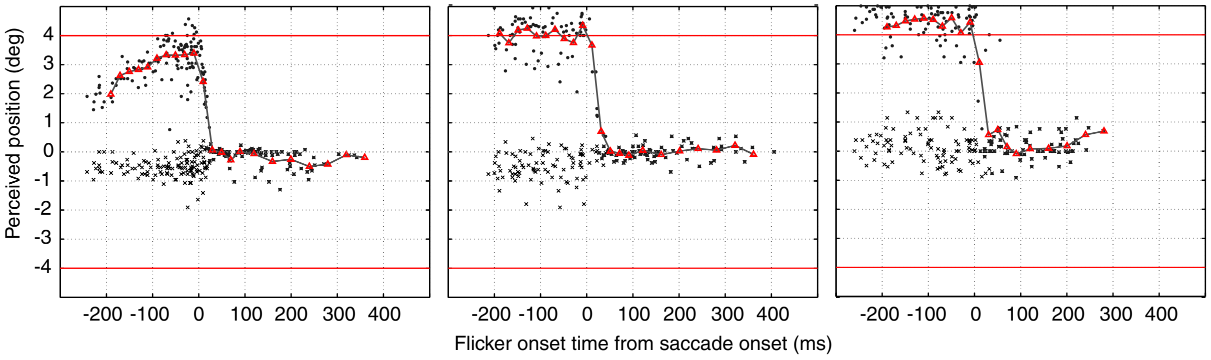
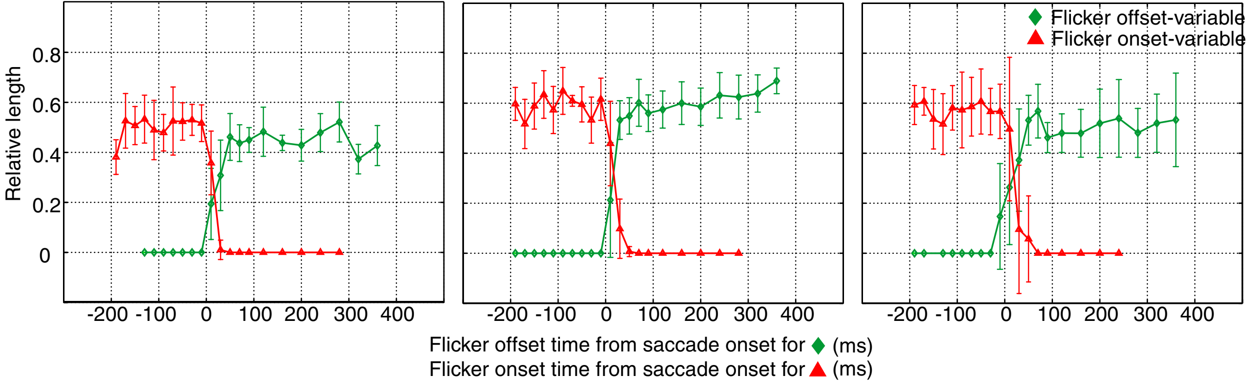


Fig. 3. The perceived positions of right and left ends in Expt. 2 (a) and Expt. 3 (b). The abscissas represent the temporal difference of the flicker offset or flicker onset time to the saccade onset (ms). The ordinates represent the perceived position of either the dot or dot array (deg). In (a), the crosses represent the right ends of the perceived dot arrays, and the filled circles represent the left ends. The diamonds represent averages of the left ends. The two ends are both plotted to the flicker offset time (the presentation time of the last flash). In (b), the crosses represent the left ends of the perceived dot arrays, and the filled circles represent the right ends. The triangles represent averages of the right ends. The two ends are both plotted to the flicker onset time (the presentation time of the first flash). (c) The apparent line length of the dot array obtained in Expts. 2 and 3 relative to the saccade amplitude. The abscissa represents the same value as in (a) and (b). The ordinate represents the relative length of perceived dot array to the saccade amplitude. When a dot is perceived, the value is zero. The diamonds and triangles are means of the data from Expts. 2 and 3. (d) Averages of perceived positions in Expts. 1 (dots), 2 (diamonds) and 3 (triangles). The abscissa represents the temporal difference of the flash presentation time to the saccade onset (ms). Ordinates represent perceived position (deg).

(c) Relative length to saccade amplitude in flicker offset- and onset- variable conditions



(d) Averages of perceived positions in flash, flicker offset- and onset- variable conditions

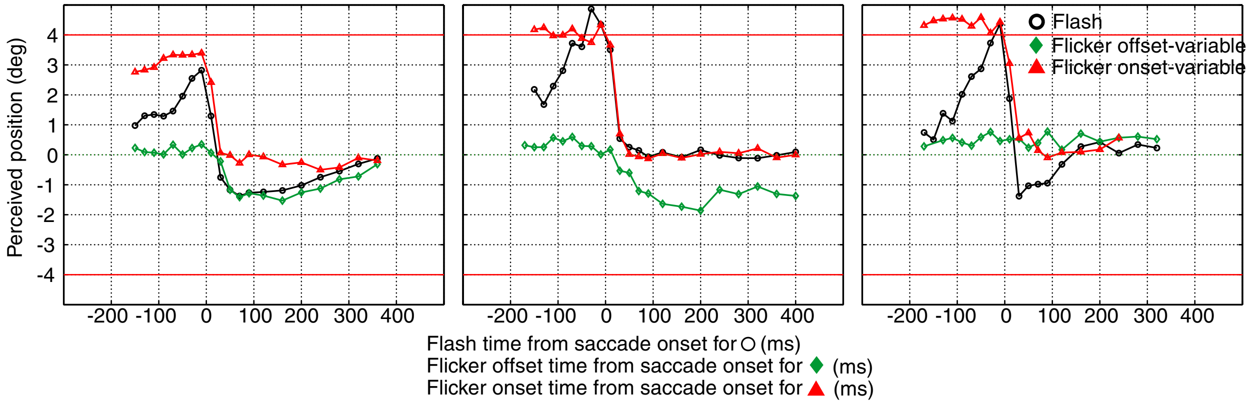


Fig. 3 (*continued*)

and left ends after the saccade onset, there were differences among individuals. Y.I. perceived the left end displaced in the opposite direction of the saccade. As the flicker offset time extended after the saccade, the perceived position of the left end gradually approached the veridical position (i.e., 0 deg). In the data of Y.A., the displacement in the opposite direction continued until more than 400 ms after the saccade onset. K.F. always perceived the left end nearly at the veridical position.

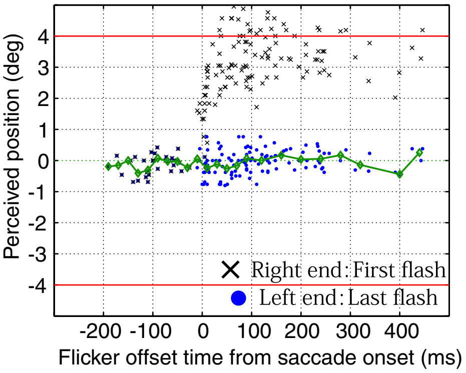
In Expt. 3 (flicker onset-variable condition, Fig. 3b and c), all subjects perceived a dot array when the S started to flicker before the saccade offset. The maximum length of the dot array was also about half the saccade amplitude. At the saccade onset, the length started to diminish, and became zero at the saccade offset. When the S started to flicker after the saccade offset, the subjects perceived a single dot at the veridical position (0 deg). In spite of the variation of the flicker onset time, the left end of the dot array (or the single dot) was localized roughly at the veridical position. For subjects Y.A. and K.F., the right end was perceived at 4 deg before the saccade, and suddenly shifted to zero after the saccade onset. For subject Y.I., the magnitude of mislocalization of the right end gradually increased during the pre-saccadic period, while the relative length of the dot array was nearly constant. This is because this subject had a tendency to make small saccades when the S was presented long before the saccade.

Fig. 4 shows the results obtained with using a continuous light for subject K.F. Overall, the results were nearly the same as those obtained with a 500 Hz flicker. The similarity between the two stimulus conditions can be regarded as justification of our choice of using a 500 Hz flicker as a probe for investigating space constancy in continuous environments.

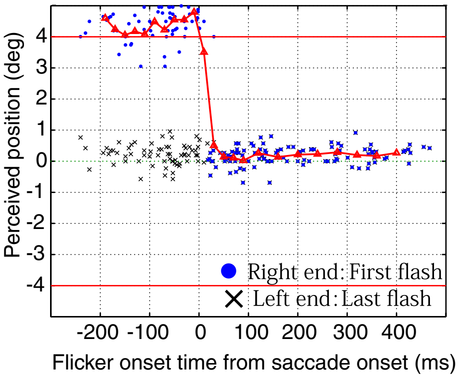
In the above analyses, we assumed that the first dot of the flicker should be seen at the right end of the perceived dot array and the last dot should be seen at the left end. Indeed, as Hershberger and Jordan (1992) reported, all subjects in our experiments perceived either a displacement in the opposite direction to the saccade or no movement. Additionally, a pilot experiment was conducted to clarify the relationship between the perceived location and the physical temporal order of each flash in the dot array. A flickering stimulus, whose first or last dot had a different color (the first or last dot was red, others were green), was presented around the time of a saccade. The subjects perceived a dot array only during the saccade, and when rightward saccades were made, all subjects always perceived the first red flash

Subject: K.F. (Continuous light)

(a) Perceived positions
in flicker offset-variable condition



(b) Perceived positions
in flicker onset-variable condition



(c) Relative length to saccade amplitude
in flicker offset- and onset- variable conditions

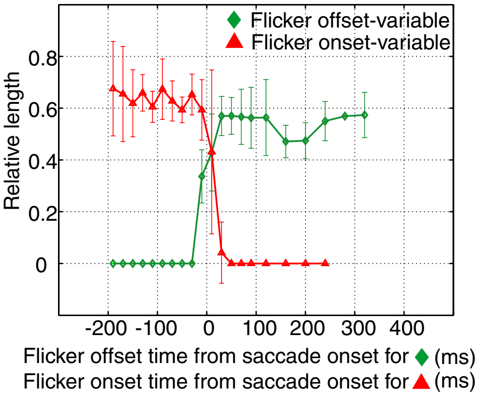


Fig. 4. The results obtained with a continuous light, for subject K.F. The perceived positions of right and left ends obtained in Expt. 2 (a) and Expt. 3 (b), and the apparent line length (c).

at the right end and the last red flash at the left end of the perceived dot array, respectively. When leftward saccades were made, vice versa. These observations demonstrate that each dot in the dot array physically spread in the opposite direction of the saccade.

3.3. Discussion

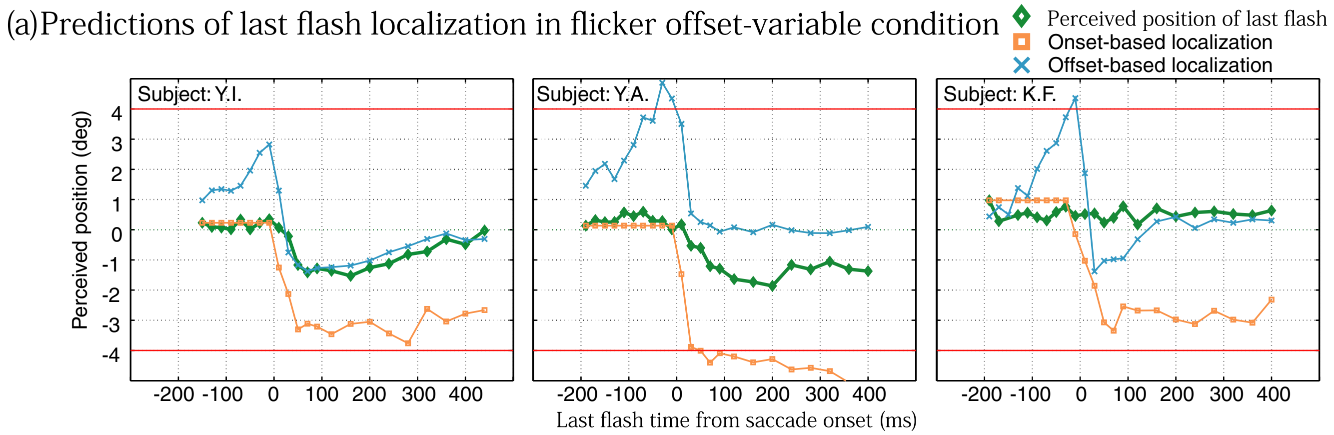
Can the perisaccadic localization of flickers, obtained in Expts. 2 and 3, be explained by the time course of localization of single flashes, obtained in Expt. 1? In Fig. 3d, the apparent position of the last flash in Expt. 2 (filled circles of Fig. 3a) and the apparent position of the first flash in Expt. 3 (filled circles of Fig. 3b) are plotted together with the averaged position of single flashes in Expt. 1 (Fig. 2). Since all these data are correctly plotted to the horizontal time axis, the three time courses should overlap if each flash of a flicker was localized individually along with the time courses of localization for a single flash. It is obvious that Fig. 3d does not support this prediction. Consequently, as to the perceived position, the prediction of individual localization of each flash does not coincide with our results.

How about the perception of the dot spread? If each flash in the flicker is localized individually in the same way as a single flash, the apparent length of the stimulus may be predicted from the results of Expt. 1: for instance, in Expt. 2, the dot may start to spread about 200 ms before the saccade and, in Expt. 3, a dot spread may be perceived until about 200 ms after the saccade. However, our results did not support these predictions. Fig. 3c indicates that the dot spread during the saccade, but not before and after the saccade. Thus, predictions based on the individual localization of each flash cannot explain both the perceived position and length of perisaccadic flickers.

Our results are compatible with the study by Schlag and Schlag-Rey (1995), which reported that the apparent elongation of a continuously flashing stimulus did not occur before a saccade, as well as with the study by Sogo and Osaka (2001), which made a similar observation with a flicker (frequency 200 Hz, duration 80 ms) presented before a saccade.

We observed that as long as the eyes are stationary before and after the saccade, a continuous flicker was perceived as a single dot, and that when the flicker is presented during the saccade, it was perceived as a dot array. This dot array is likely originated from a retinal image physically drawn by the flicker. Notice also in Fig. 3c that the apparent length of a fully-developed dot array, expressed in terms of the ratio to the saccade amplitude, was quite stable within each subject, regardless of a large change in temporal conditions of flicker presentation. These findings led us to a hypothesis that the representation of local geometrical configuration between stimulus elements (e.g., a dot or a dot array) is first established based mainly on retinal information, and then the local geometrical configuration is localized as a whole in the egocentric or exocentric coordinates. Although the observed shrinkage of a dot array to a half length of the retinal image may indicate some effects of non-retinal information on shape perception (see Section 5.2 for further discussion), they could be considered separately from the effects on the following localization process. According to our hypothesis, the time course of mislocalization for single flashes is dependent mainly on the characteristics of the localization process only, but the time course of mislocalization for continuous stimuli is influenced by the configuration process as well. This difference might produce dissociations we found in the above experiments.

Consider next the localization process for continuous flicker in more detail. We agree with the suggestion by Schlag and Schlag-Rey (1995) that the perceived location of each shape is not continuously updated with a change in non-retinal information. Localization is likely to be determined by the localization cues sampled at a given point in time, or those averaged over a given period. However, given the eye position signal changes overtime, which eye position signal is used for localization? If the eye position signal for a single flash is sampled at the time of flash presentation, it is possible that the eye position signal for a continuous flicker is also sampled at a transient event such as flicker onset or flicker offset. To test this hypothesis, we calculated the expected position of the first and last flash in a flicker, when the eye position signal is sampled at the time of the flicker onset (onset-based localization) or flicker


(a) Predictions of last flash localization in flicker offset-variable condition

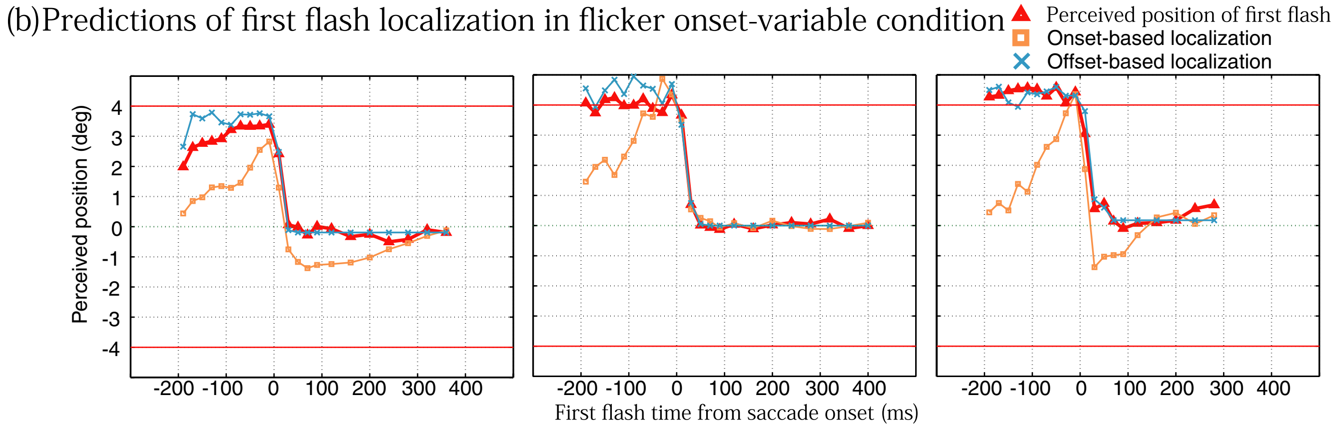

(b) Predictions of first flash localization in flicker onset-variable condition

Fig. 5. Comparison of the results of Expts. 2 (diamonds) and 3 (triangles) with the positions predicted from localization based on flicker onset (squares), and flicker offset (crosses). In (a), the perceived position of the last flash in Expt. 2 is compared. In (b), the perceived position of first flash in Expt. 3 is compared. The abscissa represents the temporal difference of the flash presentation time to the saccade onset (ms). Ordinates represent perceived or predicted position (deg).

offset (offset-based localization). The following are the equations for our proposed model.

Onset-based localization

$$X_{\text{first}}(t_1, t_2) = F(t_1)$$
$$X_{\text{last}}(t_1, t_2) = F(t_1) - L(t_1, t_2)$$

Offset-based localization

$$X_{\text{first}}(t_1, t_2) = F(t_2) + L(t_1, t_2)$$
$$X_{\text{last}}(t_1, t_2) = F(t_2)$$

Assume that the S flickers from time t_1 to t_2 (time to the saccade onset), $F(t)$ as the time course of localization for a single flash, $L(t_1, t_2)$ as the perceived length, X_{first} as the predicted position of the first flash (right end), and X_{last} as the predicted position of last flash (left end). In either case, the position of first and last flash can be easily predicted by the perceived position of a single flash and perceived length of the flicker. If the localization is based on the stimulus onset, as Schlag and Schlag-Rey (1995) suggested, the predicted position of the first flash in a flicker coincides with the perceived position of a single flash at time t_1, and the predicted position of last flash is determined by both the perceived position of a single flash at time t_1 and the perceived length. On the other hand, if the localization is based on the stimulus offset, the predicted position of the last flash coincides with the perceived position of a single flash at time t_2, and the first flash is determined by both the perceived position of a single flash at time t_2 and the perceived length.

In Fig. 5a, the perceived positions of the last flash in Expt. 2 were compared with the predicted time courses of the onset- and offset-based localization. For the flickering stimulus ending before the saccade, the perceived positions overlap with the predicted time course of the onset-based localization. For the flickering stimulus continuing until after the saccade, on the other hand, the perceived positions were closer to, or nearly coincide with, the time course of the offset-based localization.

In Fig. 5b, the perceived positions of the first flash in Expt. 3 were compared with the predicted time courses of the onset- and offset-based localization. For all timings, the perceived positions overlap with the predicted time course of the offset-based localization.

These results suggest that when a flicker ends before the saccade, the localization is based on the flicker onset, but when the flicker continues until after the saccade, the localization is based rather on the flicker offset. In either case, the eye position signal is sampled at a time temporally distant from the saccade. To test the generality of these tendencies, both the onset and offset of the flicker were systematically changed in the next experiment.

4. Experiment 4: Localization of a continuous flicker with varying onset, offset and duration

4.1. Procedure

In Expt. 4, we changed the presentation timing and duration of the flicker. The same procedure as Expt. 1 was employed except for the flash timing of the S. The duration of the flicker was selected from among 20, 50, 100 and 200 ms. As depicted in Fig. 1b, the S was presented within the time interval from 10 ms to 600 ms after the offset of the TP (i.e., from about 200 ms before and to 400 ms after the onset of the saccade). For instance, a 200 ms flicker started at a random time from 10 ms to 400 ms after the offset of the TP. The subjects were asked to point to the perceived dot, or ends of the dot array with one or two laser pointer(s). The luminance of the S was 1.6 cd/m^2, which was the same as the luminance in Expts. 2 and 3. Although the apparent intensity of the stimulus might change as the flickering duration varied, for the perception of the stimulus near the time of the saccade, the subjects could not distinguish the four conditions of duration. When the flicker of the S ended before the saccade or started after the saccade, subjects perceived a single dot that was apparently quite similar to a single flash of 10 cd/m^2 as used in Expt. 1. In this experiment, the four conditions (20, 50, 100, 200 ms) were randomized in a block.

4.2. Results

The results are shown in Fig. 6. The apparent positions of the right and left ends, each corresponding to the position of the first and the last flash, are plotted as functions of presentation timing. For instance, if a 100 ms flicker was presented from −100 ms to 0 ms, the positions of the right and left ends are plotted at −100 ms and 0 ms in the abscissa, respectively. When the subject reported a single dot, the two data are plotted on the same position in the ordinate. The average positions of the right and left ends, together with the single-flash positions of Expt. 1, are plotted separately for four different durations in Fig. 6a–d.

When the stimulus duration was 20 ms (Fig. 6a), the time courses of localization for the first and last flashes were similar. For longer durations (Fig. 6b–d), however, the two time courses significantly deviate from each other. In the pre-saccadic range, the mislocalizations of the first flashes were larger, while in the post-saccadic range those of the last flashes were larger. In addition, neither of them exactly matches the time course for a single flash.

A notable deviation, observed for all the stimulus durations, was that there was no post-saccadic displacement in the opposite direction of the saccade when the flicker started after a saccade ($t > 40$ for first flashes

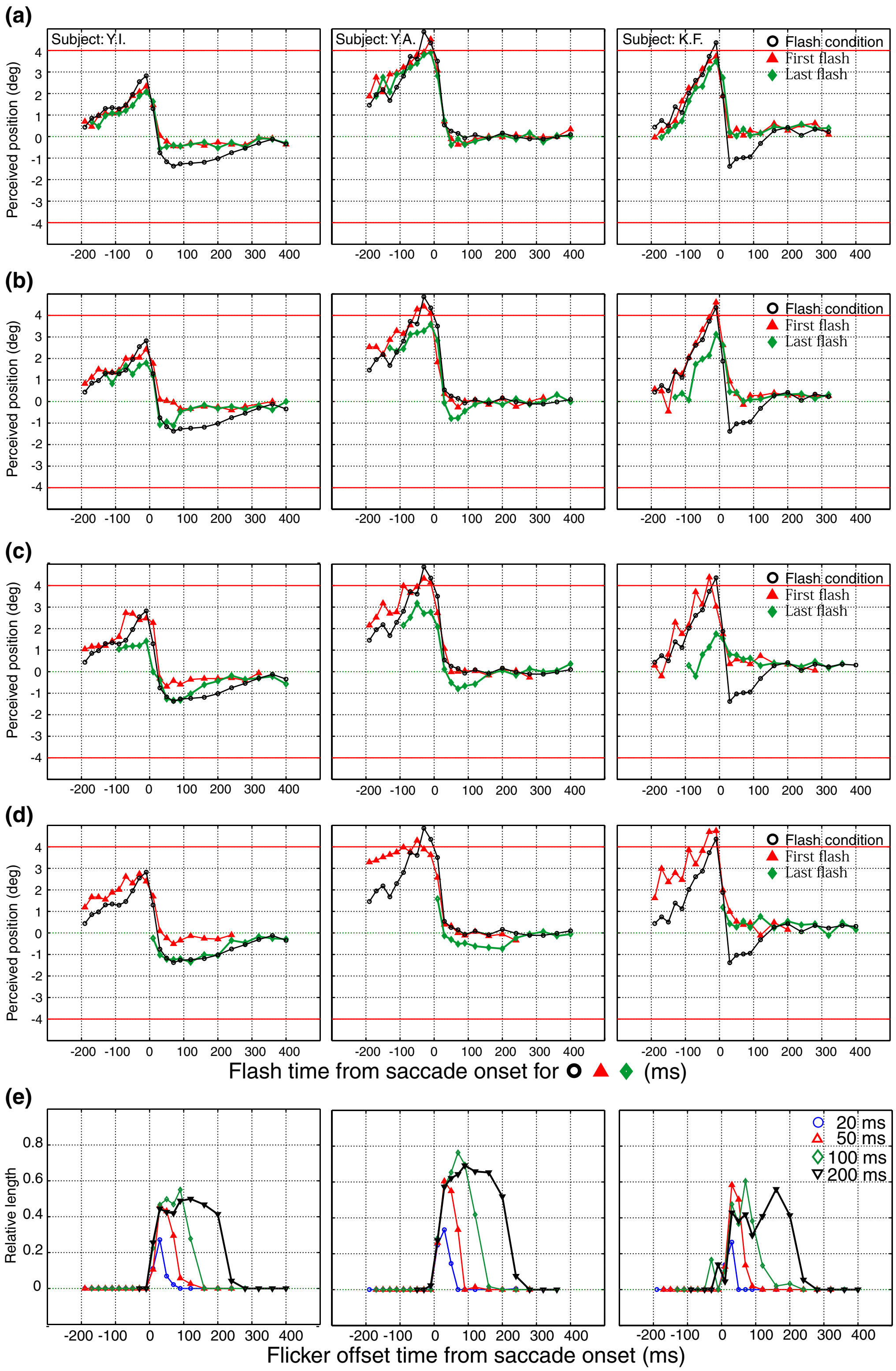


Fig. 6. The results of Expt. 4. (a–d) The average perceived position of the right end (first flash of a flicker) and the left end (last flash of a flicker) when the duration was 20, 50, 100 or 200 ms. The abscissa represents the temporal difference of the flash time to the saccade onset (ms), and the ordinate represents perceived position (deg). The triangles and diamonds represent the right ends and left ends of the flicker. The circles are averages of perceived position in Expt. 1. (e) The apparent line length of the dot array relative to the saccade amplitude. The abscissa represents the temporal difference of termination time of the S to the saccade onset. The ordinate represents the relative length to the amplitude of the saccade. The circles, up-triangles, diamonds and down-triangles represent the results obtained for 20, 50, 100 and 200 ms conditions, respectively.

and $t > 40 + d$ for the last flashes, where t is time on the abscissa and d is duration of the flicker). In the data of Y.A., the time courses of the first and last flashes were quite similar to that of a single flash, because this subject did not show post-saccadic displacement even with single flashes.

In Fig. 6e, the apparent line length of the dot array relative to the saccade amplitude is plotted as a function of the temporal difference from the flicker *offset* time of the S to the saccade onset. The results indicate that the dot array was observed only when the S flickered during a saccade. For example, for the 200 ms condition, the apparent length was greater than zero from 0 ms (when the flicker ended just before the saccade) to 240 ms (when the flicker started at the end of the saccade). Note that the duration of the saccade was about 40 ms. For the 20 ms condition, the maximum length was smaller than those of the other conditions. This could be ascribed to the stimulus duration being shorter than the duration of a saccade. For the 50, 100 and 200 ms conditions, the maximum length was almost constant within each subject (0.5–0.7).

4.3. Discussion

In Fig. 6, the results of Expt. 4 again demonstrate clear dissociations in the time courses of localization among the first and last flashes of flickers and single flashes. They are localized at different positions, even when they are presented at the same timing to the saccade, namely at the same position on the retina. Fig. 6e also shows that all subjects perceived a dot array during the saccade, but not before and after the saccade. These results, together with those of Expts. 2 and 3, indicate that the individual localization of each flash in a flicker cannot explain the localization of flickers, and that the perceived geometrical configuration is mainly generated by the retina-originated information.

The results of Expts. 2 and 3 (Fig. 5) suggest that when a flicker ends before the saccade, the localization is based on the flicker onset, but when the flicker continues until after the saccade, the localization is based rather on the flicker offset. To test whether the same rule accounts for the results of Expt. 4, we compared the obtained data with the predicted time courses of onset- and offset-based localizations in Fig. 7a–h.

When a flicker started and ended before the saccade ($t_1 < -d$, or $t_2 < 0$; left no-colored range, given S flickers from time t_1 to t_2 for $d = t_2 - t_1$), only a single dot was perceived. The time course of the perceived position in this range roughly overlaps the predicted time course of the onset-based localization, but not the offset-based localization. On the other hand, when a flicker started after the saccade ($t_1 > 40$ or $t_2 > 40 + d$; right no-colored range), only a dot was perceived again, but the time course of the perceived position is closer to the predicted time course of the offset-based localization. Between these two ranges ($-d < t_1 < 40$ or $0 < t_2 < d + 40$) colored in Fig. 7, the subject made a saccade while a flicker was presented, and perceived a dot array. In this time range, whether the localization is based on the onset or offset is not clearly discernible.

To quantitatively evaluate how well the perceived positions in each time range can be predicted by onset- and offset-based localizations, we calculated the following values:

$$D_{\text{onset}} = \sqrt{M[(d_{\text{onset}}^2)]} = \sqrt{M[(P_{\text{onset}} - P)^2]}$$

$$D_{\text{offset}} = \sqrt{M[(d_{\text{offset}}^2)]} = \sqrt{M[(P_{\text{offset}} - P)^2]}$$

$$\partial = M[(d_{\text{offset}}^2 - d_{\text{onset}}^2)/(d_{\text{offset}}^2 + d_{\text{onset}}^2)]$$

Here, $M[\ldots]$ denotes taking the mean. P represents the perceived position, and P_{onset} and P_{offset} are the predicted position based on the flicker onset and offset, respectively. D_{onset} and D_{offset} (deg) represent the prediction error of onset- and offset-based localization. When the value of D_{onset} or D_{offset} is small, the onset- or offset-based localization is close to the perceived position. When localization index ∂ is positive (i.e., d_{onset}^2 is smaller than d_{offset}^2), the onset-based localization is closer, and when the value is negative (i.e., d_{offset}^2 is smaller than d_{onset}^2), the offset-based localization is closer. Fig. 8 shows D_{onset} and D_{offset}, and the localization indexes ∂ in three time sections for the averaged data of all subjects. The first time section denoted as "Before" in Fig. 8 includes the cases where the flicker started and ended before or during the saccade (the left no-colored and left blue-colored ranges in Fig. 7: these two subranges showed similar tendencies). In this time section, ∂ is positive for all durations. Thus, when the flicker started before the saccade but did not last until the end of the saccade, the localization was performed based rather on the onset of the stimulus. The second time section denoted as "Before/After" in Fig. 8 is the case where the flicker started before and ended after the saccade (yellow-colored range in Fig. 7). In this time section, while ∂ is slightly positive for 100 ms, it was negative for 200 ms. That is, when a saccade was made during the presentation of a 200 ms flicker, the localization was based on the stimulus offset. The third time section denoted as "After" in Fig. 8 includes the cases where the flicker started during or after the saccade and ended after the saccade (the right blue-colored and the right no-colored ranges in Fig. 7: these two sub-ranges showed similar tendencies). For all durations, ∂ is negative, indicating offset-based localization in this time section.

The finding that the localization was based on the flicker onset in the "Before" section, while on the flicker

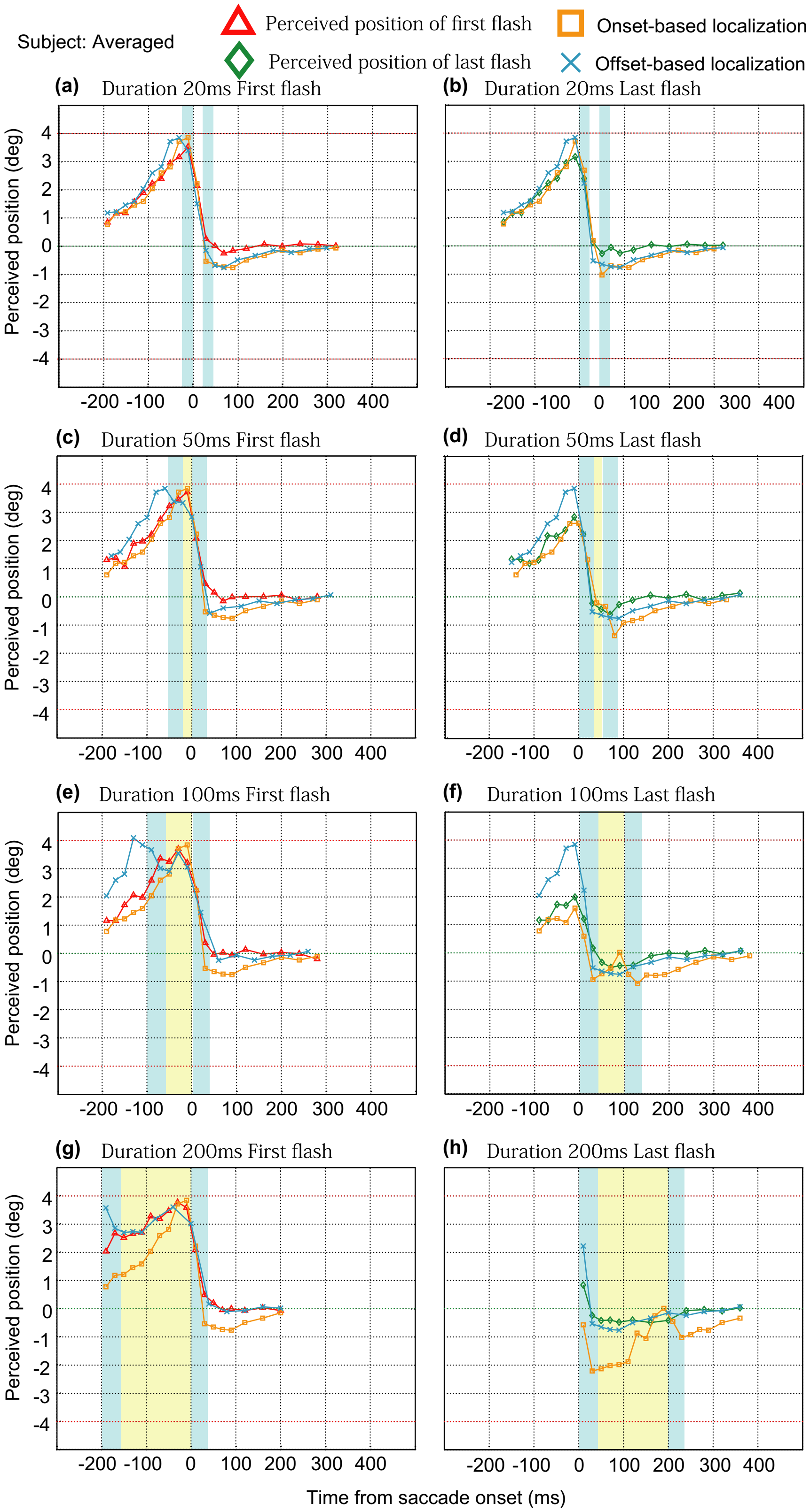


Fig. 7. Comparison of the results of Expt. 4 (triangles and diamonds for the first and last flash in a flicker) with the positions predicted from localization based on the flicker onset (squares), and the flicker offset (crosses), each being referred to as onset- and offset-based localization. The averaged data of three subjects are shown. The abscissa represents the temporal difference of the flash time to the saccade onset (ms). The ordinate represents perceived or predicted position (deg). The left white area represents the time range when the flicker started and ended before the saccade. The left blue-colored area represents the time range when the flicker started before and ended during the saccade. The yellow-colored area represents the time range when the flicker started before and ended after the saccade. The right blue-colored area represents the time range when the flicker started during and ended after the saccade. The right white area represents the time range when the flicker started and ended after the saccade.

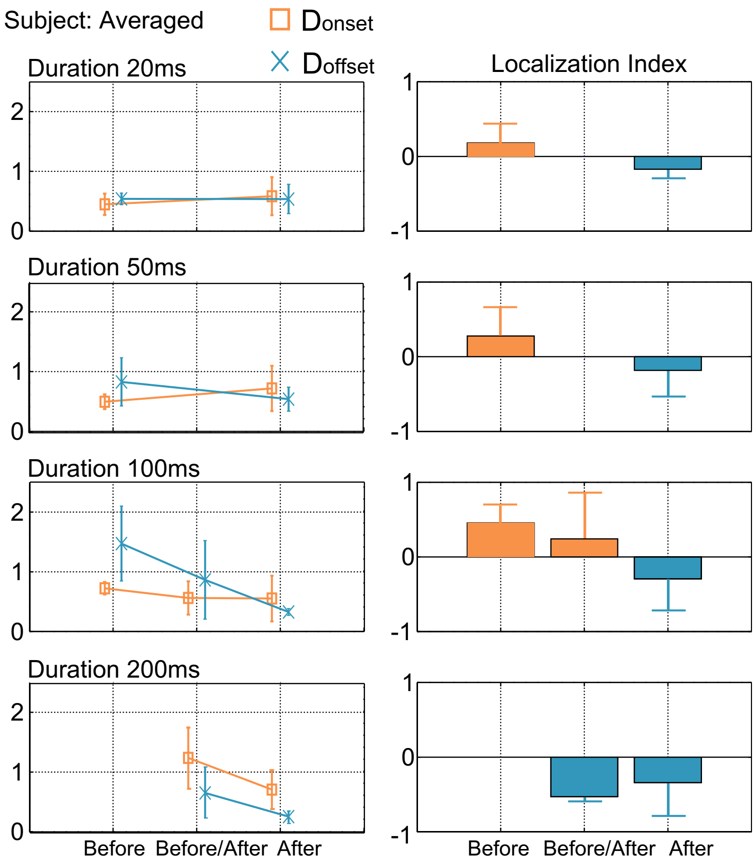


Fig. 8. Evaluation of similarity of the onset- and offset-based localization to the perceived position for the averaged data of three subjects. The time ranges are classified into three time sections, "Before" section when the flicker started before and did not continue until after the saccade ($40 - d > t_1$ or $40 > t_2$; flicker is presented from t_1 to t_2 and d is duration of the flicker), "Before/After" section when the flicker started before and ended after the saccade ($40 - d < t_1 < 0$ and $40 < t_2 < d$), and "After" section when the flicker started during or after the saccade ($0 < t_1$ or $d < t_2$). The data of the cases when the flicker started and ended during the saccade in the 20 ms condition, when the flicker started before and ended after the saccade in the 50 ms condition, and when the flicker started before and ended during the saccade in the 200 ms condition are excluded, because these time ranges are too short to calculate averages. D_{onset} (square) and D_{offset} (cross) for each time section are shown in the left column, and localization index ∂ are shown in the right column. In each condition, the data of the first and last flash are added together. The standard deviations among individuals are also presented.

offset in the "After" section, is consistent with a rule that a flash temporally distant from the saccade was used for localization. In the "Before/After" section, both the onset- and offset-based localization were equally possible, and different results were obtained for the 100 and 200 ms conditions.

The results of Expt. 4 also show another interesting trend: when the flicker starts after the saccade (right no-colored range in Fig. 7, also see Fig. 6), the perceived location was almost veridical, showing no post-saccadic displacement in the opposite direction of the saccade. Although this tendency can be in part predicted by the localization based on the last flash, the perceived location was more veridical than predicted, especially for the results of Y.I. in the short (i.e., 20, 50 ms) duration conditions. We interpret this finding as an indication that a flicker presented after the saccade is localized based on the eye position signal later than the physical stimulus termination. This is a reasonable strategy if it enabled subjects to use more reliable eye position signal for localization of remembered target. Even if that is the case, however, one may wonder how can the visual system tell very brief flickers from single flashes? We speculate that a flicker stimulating the same retinal position may generate a 'no-motion' signal that tells the visual system that the stimulus did not move on the retina. Then the visual system can localize the flicker based on the stable eye position signal sampled sufficiently after the saccade. On the other hand, a flash does not generate such a 'no-motion' signal. Since the visual system cannot tell how the flash moved, the system has to use an erroneous instantaneous eye position signal near the time of the saccade.

In summary, the results of Expt. 4 indicate a trend that the perisaccadic localization of a flicker is based on the eye position signal sampled at a time temporally distant from the saccade: when the flicker starts before and does not continue until after the saccade, the localization is based on the eye position signal sampled at the flicker onset, while when the flicker starts during or after the saccade and ends after the saccade, the localization is based on the eye position signal sampled at the flicker offset or later. This tendency is consistent with the results of Expts. 2 and 3.

5. General discussion

5.1. Two-stage localization of perisaccadic flickers

When a flash is presented around the time of a saccade, the apparent position is shifted (as shown in Fig. 2). This mislocalization has been explained by the cancellation theory, which postulates that it is generated by the integration of the retinal image and the dumped internal eye position signal (EPS) (Honda, 1989, 1990; Mateeff, 1978). Based on this theory, Hershberger (1987) interpreted the perception of a dot array for repetitively presented flashes (flicker) during a saccade as a result of position compensation for each individual flash. However, the present study shows that the perceived lengths and positions for perisaccadic flickers do not coincide with the prediction from the time course of localization for a perisaccadic single flash (Expts. 1–4). This finding clearly rejects a simple cancellation theory as an explanation of localization of perisaccadic continuous flickers.

Instead, we proposed a two-stage localization process. Namely, the representation of local geometrical relationships between stimulus elements is first established based primarily on retinal information, then the local geometrical relationship is localized as a whole in the egocentric or exocentric coordinates. This hypothesis is supported not only by the dissociation between flashes and flickers, but also by the finding that the perceived shape is mainly based on the retina-originated information (Expts. 2–4; see also Schlag & Schlag-Rey, 1995; Sogo & Osaka, 2001). As long as a flicker stimulates the same retinal area, a single dot is perceived. A dot array is perceived only when it is drawn on the retina by an eye movement. Although the length of the dot array does not correspond to the retinal size (Hershberger, 1987), it is quite stable within each subject in spite of large variations in perceived position (Expts. 2–4). It should be also noted that if all flashes of a flicker are localized individually, as Hershberger assumed, the retinal signal and eye position signal should be integrated n times when the flashes are presented n times. In contrast, our two-stage mechanism is much more economical, since it integrates the two signals only once per saccade.

Concerning how the perceived shape is localized, our results indicate that the localization is based on the eye position signal sampled at a time temporally distant from the saccade. For a stimulus that ends by the time of the saccade onset, the localization is based on the eye position signal sampled at the stimulus onset, as Schlag and Schlag-Rey (1995) suggested. However, when the stimulus is visible even after the saccade, the localization is based on the eye position signal sampled at the stimulus offset or a time closer to the time of judgment. These findings are consistent with the notion that the visual system avoids using erroneous eye positional signals around the saccade to attain better space constancy across saccades.

Jordan and Hershberger (1994) presented a flicker stimulus during a saccade to have their subjects perceive a dot array. When they presented a flash at the same retinal position within 80 ms before the saccade, the subject perceived it as spatially coincident with the first flash of flicker, as opposed to the standard time course of localization of a pre-saccadic flash. Although this observation led Jordan and Hershberger to propose that the EPS changes discretely and not gradually (Discrete-EPS model), it can be explained by our hypothesis, given in the first stage, the flash and the flicker are temporally grouped together, and represented in the common retinal coordinates.

Sogo and Osaka (2002) examined perisaccadic localization of two flashes with systematic changing of the inter-stimulus interval. They found that when the intervals were longer than 120 ms, the perceived position of each flash followed the time course of single-flash localization, while when the intervals were shorter than 120 ms, the relative position of the two flashes was determined by retinotopic information. While Sogo and Osaka (2002) interpreted 120 ms as a critical point where subjects change the strategy of localization, we rather regard 120 ms as the length of the temporal window for temporal grouping. That is, the stimuli whose stimulus onset asynchronies are within 120 ms are grouped together, and localized as one image. If the interval is longer, the stimuli are analyzed separately, and localized individually.

The temporal window of grouping may vary depending on the stimulus condition. Using a bright display, Ross et al. (1997) and Morrone et al. (1997) found an apparent vernier offset of two collinear half-bars presented at the same position at different times with an inter-stimulus interval of 75 ms. Specifically, when the two bars were presented immediately before the saccade onset at the middle of the fixation and saccadic targets, the second bar appeared to be shifted towards the saccadic target (i.e., in the direction of saccade), as expected from mislocalization of single bars. That is, unlike a continuous flicker, the two bars separated in time only by 75 ms were independently localized. Similarly, in the completely dark room, Park, Schlag-Rey, and Schlag (2003) found an apparent verier offset of two physically aligned spots that were temporally separated by only 50 ms.

Cai et al. (1997) reported that when a flash was presented immediately before a saccade while a light was continuously presented until the flash termination time, subjects perceived misalignment of the flash relative to the continuous light. This observation can be explained also by our hypothesis, given the two stimuli were not temporally grouped together and localized separately based on each onset timing. The assumption that a flash and a continuous stimulus are processed separately, even when their presentation timings are physically overlapped, is further supported by their study on the flash-lag effect (Cai & Schlag, 2001).

According to our hypothesis, a sequence of stimuli on the retina is not egocentrically localized in real time, but after the determination of local geometric configuration via grouping of retinal information over time. Even when a flicker starts before the saccade, if it continues until long after the saccade as in Expt. 3, the localization is based on the post-saccadic spatial coordinates. This means that the interpretation of the past events is dependent on the information obtained afterwards up to the time when the judgment is made. Although this conclusion may sound paradoxical, it is a principle widely recognized in many perceptual phenomena, including time perception (Dennett & Kinsbourne, 1992; Libet, Wright, Feinstein, & Pearl, 1979; Nishida & Johnston, 2002), backward masking (Bachmann, 1994; Breitmeyer, 1984), temporal filling-in (Kamitani & Shimojo, 1999), and the flash-lag effect (Eagleman & Sejnowski, 2000a, 2000b, 2000c; Krekelberg & Lappe, 2000).

5.2. *Reduction of perceived length*

Given that perception of geometrical shapes is based on retinal information, why is the length of the dot array reduced relative to the retinal spread of the flicker?

One possibility is that the visual persistence is not long enough to sustain the whole flicker sequence, so that the first flash disappears before the last flash is presented. Indeed, Burr and Morrone (1996) reported a reduction in temporal impulse response during a saccade, and Bedell and Yang (2001) referred to the reduced visual persistence as a possible cause of reduced length of motion streak induced by a saccade. However, this account is rejected by the pilot experiment described in Section 3.2, which indicates that the subjects could see the first flicker on one end and the last flash on the other end of the dot array.

Several studies have shown that perisaccadic stimuli are localized toward the saccade target, as if the visual space is compressed (Awater & Lappe, 2004; Honda, 1993; Kaiser & Lappe, 2004; Matin & Pearce, 1965; Morrone et al., 1997; Ross et al., 1997). This phenomenon is most evident when the perisaccadic stimulus is localized relative to a post-saccadic visual reference (Lappe et al., 2000), but recent data (Awater & Lappe, 2003; Ma-Wyatt, Morrone, & Ross, 2002), suggesting that compression is present also in the dark. While the perisaccadic space compression strongly occurs for stimuli presented immediately before a saccade, it can also occur for those presented during a saccade. Thus, it is possible to ascribe the reduction in the apparent length of the dot array to the perisaccadic space compression.

It is also possible to regard the apparent shrinkage of the dot array as a result of partial cancellation of retinal slip induced by saccadic eye movement. If the cancellation were perfect, the observer would veridically perceive a single dot. The original cancellation theory states that the internal EPS compensates for the change in retinal position, but the compensation is not perfect since the change in EPS is slower than the actual eye movement. By assuming that a dot array is produced after cancellation of the retinal shift of each flash in the flicker by the sluggishly changing EPS sampled in real time, one can account not only for why the apparent length of dot array shrinks, but also for why the perceived length is roughly equal to the distance between the apparent positions of single flashes presented at the saccade onset and offset. However, as we have discussed, several lines of evidence support the notion that the EPS is integrated for localization only after a geometrical shape is determined. To resolve this apparent contradiction, we speculate that a computation similar to compensation by the EPS might be performed offline after generation of a geometrical shape from the retinal image. Castet, Jeanjean, and Masson (2002) reported that retinal motion induced by a saccade is perceptible. If the visual system has estimates for the speed of retinal motion (S_{retina}) and the speed of EPS change (S_{EPS}), the retinal slip can be compensated for by scaling the retinal image in the orientation of the saccade by a factor $(S_{\mathrm{retina}} - S_{\mathrm{EPS}})/S_{\mathrm{retina}}$. This hypothesis however remains highly speculative at the moment and merits future study.

Finally, Sogo and Osaka (2002) reported that when two flashes were presented within a short interval (e.g., 80 ms), the distance between the two dots coincides with the retinal distance, although we observed that when a flicker was presented for about the same duration, only half of the retinal length was perceived. Although we do not clearly know the reason behind this discrepancy, we propose a couple of possibilities. One is a potential difference of the stability of shape perception between two dots and a dot array (Matsumiya & Uchikawa, 2001). Another possibility is that successive flashes presented in the flicker condition stimulate motion sensors, and give an estimate of the retinal speed, much more effectively than the two dots do. If the shrinkage of the dot array is indeed based on the estimation of retinal speed, as we suggested above, the shrinkage may not occur for the two dots.

6. Conclusion

The perceived position and length of a flicker presented around the time of a saccade did not coincide with the prediction based on the individual localization along with the time course of localization for single flashes. Our results suggest a two-stage localization process, in which the representation of local geometrical configuration is first established based primarily on retinal information, and then the configuration is localized as a whole in the egocentric or exocentric coordinates. The localization is based on the eye position signal sampled at a time temporally distant from the saccade, which enables precise localization and space constancy for continuous stimuli.

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