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Running head: ILLUSORY MOTION

Illusory motion produced by dichoptic stimuli during saccades Hiroyuki Mitsudo^{a,*} and Sachio Nakamizo^b

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*Corresponding author Department of Human Sciences, Faculty of Human-Environment Studies, Kyushu University 6-19-1 Hakozaki, Higashi-ku, Fukuoka 812-8581, Japan E-mail: hmitsudo@lit.kyushu-u.ac.jp Tel & Fax: + 81926427413 This study reports a new motion illusion in which saccadic eye movements can produce a perceived jump of a static stimulus presented dichoptically. In three experiments, observers made saccades while viewing a stationary stimulus consisting of a disk and random dots presented separately to the two eyes. In Experiments 1 and 2, by measuring the strength of the perceived motion and the velocity of binocular eye movements, we found that (a) motion ratings were high for the stimulus that contained a large interocular difference in luminance, and (b) the saccadic strategy of the observer was virtually identical across different stimulus conditions. In Experiment 3, by measuring the detectability of a short temporal gap introduced into the stimulus around saccades, we found that saccadic suppression was normal in the dichoptic presentation. We discussed possible mechanisms underlying the illusory motion.

Introduction

When the eye changes its position, the image of the scene moves across the retina. Despite such an obvious image-displacement, the visual world appears stable in daily life. In the case of saccadic eye movements, the visual system is thought to use extraretinal signals accompanying saccades to maintain perceptual stability (Morrone and Burr 2009; Wurtz 2008). The importance of extraretinal signals has been suggested by studies that have measured saccadic suppression, a transient reduction in visual sensitivity, particularly to motion, at the time of saccades (Bridgeman et al 1975; Burr et al 1982; Burr et al 1999; Volkmann et al 1968; Matin 1974; McConkie and Currie 1996; Shioiri and Cavanagh 1989; Thiele et al 2002; Watson and Krekelberg 2009).

Extraretinal signals are also likely to be used to update the spatial representation of visual stimuli presented around a saccade by counteracting the image displacement produced by the saccade (Duhamel et al 1992; Merriam et al 2003). Evidence for this idea is based on psychophysical experiments using briefly presented stimuli (e.g., Honda 1990; Melcher 2007; Wittenberg et al 2008). For example, Honda (1990) and Dassonville et al (1992) reported that a flashed stimulus was perceived at an incorrect position when presented around a saccade. Mateeff (1978) argued that the time-course of mislocalization can be accounted for by assuming that the extraretinal signals for eye position available to the visual system change more slowly than visual signals (see also Honda 1990; Dassonville et al 1992).

Under conditions where visual stimuli stationary relative to the head are presented continuously across a saccade, the contribution of extraretinal signals to spatial updating is unclear. This is because continuous visual stimuli themselves are thought to contribute directly to perceptual stability in several ways (Campbell and Wurtz 1978; Deubel et al 1996; Macknik et al 1991; Castet et al 2002; Honda 2006; Matin and Pearce 1965). For instance, Castet et al (2002) argued that, based on the results of their motion-judgment experiments, continuous stimuli presented immediately after the saccade may contribute to visual stability by masking the saccade-produced image displacement. In addition, Deubel et al (1998) pointed out that continuously presented stimuli act as a visual reference for stability judgments.

The purpose of the present study is to report a new motion illusion that provides insights into the issue of whether or not extraretinal signals are used for spatial updating of continuously presented stimuli. Consider a situation where the two eyes make saccades while viewing static images that are binocularly different (i.e., dichoptic stimuli). In humans, the movements of the two eyes are known to be similar in size and timing at the time of saccades, irrespective of stimulus conditions (i.e., binocular and monocular: Collewijn et al 1988; but see Liversedge et al 2006). For example, Collewijn et al (1988) reported that binocular saccades with an amplitude of less than 40° produced a mean binocular misalignment of less than 0.5° for horizontal saccades. When static visual images are presented continuously, binocular misalignment produces an equivalent amount of image displacement between the two eyes. In this manuscript, we refer to such a misalignment-produced image displacement as *relative* image displacement, and distinguish it from *common* image displacement between the two eyes. If the movements of the two eyes are identical to each other, there would only be common image displacement on the retina. To update the spatial representation of visual stimuli correctly, the visual system must counteract both types of image displacement appropriately. If the continuous retinal stimuli presented to each eve are sufficient for visual stability, and extraretinal signals are unnecessary, the observer would not perceive any motion even when viewing dichoptic stimuli. The basic phenomenon we report here, however, is that normal saccades can produce an illusory motion in certain conditionswhere dichoptic stimuli contain a large interocular difference in luminance.

To perceive the illusory motion, try the following four steps: (a) Prepare a cardboard tube such as that from a kitchen roll (approximate length, 30 cm; diameter, 3 cm; thickness, 2 mm) and a white paper on which text is printed. (b) Hold the tube in the left hand and look through it from one end of the tube with the left eye, and then firmly cover the other end of the tube with the right half of the right hand palm. At this time, one will see a dim ring on a totally dark background, just like a total eclipse of the sun, with the left eve and the text with the right eye. (c) Look at the text under daylight or room-light conditions. Consequently, one can perceive an overlap (rather than binocular rivalry) between the ring and the text, just as shown in Figure 1. Note that the background of the ring exceedingly differs from that of the text in luminance¹. (d) When reading the text repeatedly, one will notice the ring apparently jumping in the opposite direction to that of the saccades. Whereas the ring appears unstable, the text remains perceptually stable. The size of the perceived jump may be small relative to the size of the saccades. By following this procedure, many observers reported the apparent jump only when moving their eyes. Because no motion is perceived during fixation, this illusion seems to be involved in relatively large eye movements, rather than fixational eye movements.

To examine this illusion formally, we conducted three psychophysical experiments. Instead of the demonstration with a cardboard tube, we used static dichoptic stimuli presented continuously on a computer screen. We measured (a) the strength of the perceived motion (in Experiments 1 and 2) and (b) the detectability of a temporal gap introduced into the stimulus (in Experiment 3) while recording binocular eye movements. In Experiments 1 and 2, we intended to show (a) that the illusory jump requires a large interocular difference in luminance, and (b) that the jump is not due to particular saccadic strategies. In Experiment 3, we examined whether or not saccadic suppression, generally assumed to contribute to visual stability during saccades, is affected by the dichoptic stimulus.

Experiment 1

-----Insert Figure 1 about here-----

The basic test stimulus we used consisted of a gray disk presented on a dark background to one eye and gray random dots presented on a bright background to the other eye (Figure 2). In each trial, observers were asked to make voluntary saccades while viewing the test stimulus. According to the demonstration described above, the physically static disk was expected to appear to jump only when the luminance of the disk was low. To examine the phenomenon quantitatively, we asked the observers to rate the strength of the perceived jump of the disk. In particular, the observers were instructed to concentrate on judging the perceived motion of the disk relative to the random-dot background by taking into account both its size and frequency. (No observer reported the motion of the background in preliminary observations or practice trials.) We varied the luminance of the disk across trials; when the luminance of the disk was low, there was a large interocular difference in luminance. Based on our preliminary observations, motion ratings were expected to be high only when the luminance of the disk was low.

We also measured and analyzed the observers' binocular eye movements made during the test period. The purpose of this analysis was to examine whether or not the perceived motion was directly caused by the specific or unnatural saccadic strategies of the observers. For each trial, we computed (a) the number of the saccades, (b) the mean length of the saccades, and (c) the cumulative binocular positional misalignment produced by the saccades.

¹A tube made with thin cardboard may be inadequate for this demonstration because it does not sufficiently block the light from the environment. In addition, if one does not firmly cover the end of the tube, the resulting "bright" ring will appear to be stationary.

Figure 1 (Mitsudo & Nakamizo)

To perceive the illusory motion, try the following four steps: (a) Prepare a cardboard tube such as that from a kitchen roll (approximate length, 30 cm; diameter, 3 cm; thickness, 2 mm) and a white paper on which text is printed. (b) Hold the tube in the left hand and look through it from one end of the tube with the left eye, and then firmly cover the other end of the tube with the right half of the right hand palm. At this time, one will see a dim ring on a totally dark background, just like a total eclipse of the sun, with the left eye and the text with the right eye. (c) Look at the text under daylight or room-light conditions. Consequently, one can perceive an overlap (rather than binocular rivalry) between the ring and the text, just as shown in Figure 1. Note that the background of the ring exceedingly differs from that of the text in luminance. (d) When reading the text repeatedly, one will notice the ring apparently jumping in the opposite direction to that of the saccades. Whereas the ring appears unstable, the text remains perceptually stable. The size of the perceived jump may be small relative to the size of the saccades. By following this procedure, many ob-

Figure. 1. A schematic illustration of the percept produced with a cardboard tube. See the text for details.

Figure 2 (Mitsudo & Nakamizo)

6



Figure 2. A schematic illustration of the trial sequence in Experiments 1 and 2. The gray-scale values of the elements and the background are not the actual value. To experience the illusion, see the main text. The three open squares in the saccade-cue display were colored in red, green, and blue in the experiments.

If particular saccadic strategies play a critical role in producing the perceived motion, disk luminance would affect some of these saccade-related variables, as in the case of motion rating. On the other hand, if normal saccades cause the illusory motion, disk luminance was not expected to influence any of these variables.

-----Insert Figure 2 about here-----

Methods

Observers. Six observers (five naive and the first author) participated in Experiment 1. All had corrected-to-normal visual acuity. Written consent was obtained from all observers. The data obtained from one observer were excluded from analysis because there was a technical difficulty in calculating her eye position from the video images.

Apparatus. Stimuli were presented on a 21-inch CRT monitor (Eizo FlexScan T961) viewed with a mirror stereoscope at a frame rate of 75 Hz. Stimulus presentation was controlled by an Apple iBook G4. The viewing distance was 67.5 cm. The observer's head movement was minimized with a chin-and-forehead rest. The experiment was conducted in a darkened room; the region outside the stimulus area was masked by pieces of black cardboard.

Stimuli. Test stimuli were dichoptic patterns presented within a square region subtending $12 \times 12^{\circ}$ in visual angle for each eye. The test stimulus (Figure 2) consisted of a disk (diameter, 1.83°) presented on a dark background (0.06 cd/m^2) to the left eye and approximately 500 random dots (each subtending $0.12 \times 0.12^{\circ}$; 0.44 cd/m^2) presented on a bright background (50.46 cd/m^2) to the right eye. The luminance of the disk varied across trials ($0.09, 0.11, 0.15, 0.27, 0.52, 1.02, 2.12, 4.13, 7.87, 14.31 \text{ cd/m}^2$). During the test period, the disk and the random dots appeared to be fused and overlapped with each other; no binocular rivalry was observed.

When the test stimulus was not presented, a binocularly fusible fixation (0.79°) was presented in the center of the screen (Figure 2). The pattern was binary-textured (i.e., drawn in black and white) to hold the gaze of both eyes on the fixation. Throughout the experiment, two zero-disparity binary-textured rectangles (width, 12° ; height, 0.31°) were presented at the upper and lower positions of the screen. Because the dots contained by the horizontally oriented rectangles were big and sparsely distributed, they were expected to keep the two eyes relatively aligned even when viewed in the perifovea. Similar patterns were used in Maruya and Blake (2009).

Procedure. At the beginning of each trial, the fixation pattern was presented for 1.0 s. Subsequently, eight small squares $(0.31 \times 0.31^{\circ})$ were presented for 1.0 s to the right eve (Figure 2). Each square was placed on the four corners and on the horizontal and vertical meridians of an imaginary square frame subtending 6 x 6° at the center of the screen. Three of them were adjacent to each other and colored in red, green, and blue in a clockwise or counter-clockwise direction. The three colored squares served as a positional cue for the eve movements required during a subsequent test period. In the test period, the dichoptic test stimulus, consisting of the disk and the random dots, was presented for 3.0 s. During the test period, observers were instructed to move their eyes to the remembered positions of the red, green, and blue dots in that order. Neither fixation nor cue was presented during the test period. After the test period, a rating scale was presented. The observer's task was to rate the strength of the perceived motion of the disk relative to the background by using a continuous scale (0, no motion; 4, a strong impression of motion). The disk was positioned almost at the center of the display-far from the borders of the random-dot region-in order to avoid position-based displacement judgments, rather than motion judgments. The indicator on the scale was adjustable using the computer mouse. In each block, the ten values of disk luminance were tested in randomized order. Each observer completed at least four blocks.

Eye-movement recording and data analysis. During the experimental trials, the observer's binocular eye movements were recorded by a video-based infrared eye-tracker at

29.97 Hz. The images of the two eyes were recorded with two cameras. The two frames sampled at the same time were integrated into one frame by using a color quad processor. Before the experimental blocks, a nine-point linear calibration was conducted. The horizontal and vertical position of each eye was estimated by calculating the gravity center of the pupil relative to a reference position for each video frame in an offline manner. The measurement accuracy and precision of the eve tracker were 0.22° and 0.05°, respectively. We calculated the two-dimensional velocity of each eye's movements as a function of time for every trial. Saccades were automatically detected with the algorithm proposed by Engbert and Kliegl (2003). In their original algorithm, velocity data were averaged over three successive samples to reduce noise. We skipped this averaging procedure because (a) the sampling rate of our eye-tracking system was not so high, and (b) noise in our measurements was low. We then computed the number of saccades and the mean saccade length for each trial; the two eyes' data were averaged. We also computed the binocular positional misalignment produced by the saccades. In particular, we calculated the binocular positional difference produced by a saccade, defined by $\sqrt{(v_{1x} - v_{rx})^2 + (v_{1y} - v_{ry})^2}$, where (v_{1x}, v_{1y}) is the 2D saccade vector for the left eye and (v_{rx}, v_{ry}) is that for the right eye. By accumulating the binocular positional difference produced by the saccades over every test period, we obtained cumulative saccadeproduced binocular misalignment.

Results and discussion

Figure 3A shows the mean motion ratings as a function of disk luminance, averaged over the five observers. A one-way repeated-measures analysis of variance (ANOVA) was conducted on the motion ratings, with the factor of disk luminance. The main effect of disk luminance was significant, F(9, 36) = 7.36, p < 0.0001. To reveal the overall effect of disk luminance on perceived motion further, we performed a linear regression analysis on the motion ratings, with the independent variable of the logarithm value of disk luminance. We found a significant negative correlation between luminance and motion ratings for all observers (mean, -0.57; s.d., 0.27; ps < 0.05).

-----Insert Figure 3 about here-----

To examine whether or not the perceived motion is related to particular saccadic strategies, we conducted three one-way repeated-measures ANOVAs independently on the number of saccades, the mean saccade length, and the cumulative saccade-produced binocular misalignment, with the factor of disk luminance. If the perceived motion entirely depends on saccadic strategies, disk luminance would affect some of the saccade-related variables. For example, it is possible that the observers made saccades more frequently in the low-luminance conditions than in the high-luminance conditions, resulting in high motion ratings in the low-luminance conditions. The main effect of disk luminance, however, was not significant for any of the three variables [the number of saccades, F(9, 36) = 1.14, p = 0.36; mean saccade length, F(9, 36) = 1.40, p = 0.23; binocular misalignment, F(9, 36) = 1.11, p = 0.38]. Figures 3B-D show the mean number of saccades, the mean saccade length, and the mean cumulative saccade-produced binocular misalignment, averaged over the five observers. Whereas there was a large overall difference in saccade length across the observers, the saccade length averaged over the conditions and the five observers (2.71°) was approximately consistent with, but slightly shorter than the expected value (3.0°).

Figure 3 (Mitsudo & Nakamizo)



Figure 3. Results for Experiment 1. (A) Mean motion ratings as a function of disk luminance (n = 5). (B-D) The mean number of saccades (B), mean saccade length (C), and mean cumulative binocular misalignment (D) as a function of disk luminance (n = 5). Error bars represent standard deviation.

To strengthen the claim that saccadic strategies are not related to the perceived motion, we analyzed trial-by-trial changes in motion rating and saccade-related variables. In particular, we conducted a multiple regression analysis for each observer's data. The independent variables used were log-transformed disk luminance (varying across the conditions) and the three saccade-related statistics calculated for each trial (varying within, in addition to across, the conditions); the dependent variable was motion rating. As expected from the repeated-measures ANOVAs, the partial coefficient for disk luminance was significantly different from zero, except for Observer S5 (Table 1). On the other hand, none of the partial coefficients for the three saccade-related variables was significantly different from zero, except for Observer S5. These results strengthen our claim that saccadic strategies are not related to the illusory motion.

Observer	Partial coef	Intercept			
	Disk	Saccade	Saccade	Binocular	
	Tummance	number	length	misangiment	
S 1	-1.07*	0.146	0.684	0.462	-2.45
S2	-1.04**	0.276	0.203	0.264	-2.35*
S3	-3.02***	0.0379	1.20	-0.0141	-2.27
S4	-2.71***	0.115	0.276	0.202	-2.45
S5	-0.511	-0.143	0.248	0.308*	-0.45

Table 1. Summary of the multiple regression analysis for Experiment 1.

*p < 0.05, **p < 0.01, ***p < 0.001.

The main results are that (a) motion was perceived for the low-luminance targets but not for the high-luminance targets, and (b) saccades produced common and relative image displacements between the two eyes equally across the different luminance conditions. These results imply that (a) both common and relative image displacements are correctly counteracted in the high-luminance conditions, and (b) both common and relative image displacement are not correctly counteracted in the low-luminance conditions. To explain these results, we assume that low-luminance signals have longer latency than high-luminance signals in visual processing (Kitaoka and Ashida 2007) in dichoptic presentation, whereas extraretinal signals are generated and used at the same timing across different stimulus conditions. As a consequence, low-luminance dichoptic signals are not appropriately combined with extraretinal signals, resulting in the illusory motion. This idea can explain the result that no relationship was found between saccadic strategies and the strength of the illusion by assuming saccadic parameters would not be directly related to the latency between the retinal signals and extraretinal saccade-related signals. The present results are, however, not sufficient to resolve the issue of whether common or relative image displacement is particularly related to the illusory motion because the eye-tracking system used in Experiments 1 and 2 had low temporal resolution. Specifically, to examine whether or not binocular differences in saccadic latency are related to the illusory motion, measurements of eye movements at high temporal resolution will be necessary.

Experiment 2

In Experiment 2, we added three stimulus conditions different from the dichoptic stimulus used in Experiment 1 (see Figure 4A) to examine the role of dichoptic presentation in the illusory motion. The three conditions were: (a) the monoptic condition, in which both the random dots and the disk were presented to the same eye (on the dark background), (b)

the no-dot condition, in which the random dots were removed, whereas the disk was the same as that used in Experiment 1, and (c) the interchanged condition, in which the spatial structure (not the value of luminance) of the stimulus was interchanged between the two eyes. As a baseline for the illusory motion, we also used the dichoptic condition identical to that used in Experiment 1 (a disk condition). The luminance of the disk was low as 0.44 cd/m^2 in all the conditions.

It is possible that the illusory motion observed in Experiment 1 is entirely due to long latency for processing low-luminance stimuli (Kitaoka and Ashida 2007). In other words, the visual system could not cancel out the transsaccadic retinal motion of a low-luminance element because stimuli presented in low luminance would require more processing time than those presented in high luminance. If the long visual latency for the low-luminance element (i.e., the disk) determines the perceived motion, motion ratings would be high even in the monoptic and no-dot conditions because the luminance of the disk was kept low. On the other hand, if dichoptic presentation plays a critical role in producing the illusory motion, motion ratings were expected to be low in the monoptic and no-dot conditions because there was no dichoptic element in these two conditions (i.e., no spatial overlap between patterns presented to the two eyes) and to be high in the two dichoptic conditions (i.e., the disk and interchanged conditions). As in Experiment 1, we also recorded and analyzed the observers' binocular eye movements made during the test period. *Methods*

Observers. Four observers (three naive and the first author) participated in Experiment 2. All had corrected-to-normal visual acuity. Written consent was obtained from all observers.

Apparatus, stimuli, and procedure. The apparatus, stimuli, and procedure were identical to those used in Experiment 1, except for the following. Four stimulus configurations were tested: disk, monoptic, no-dot, and interchanged conditions. In the disk condition, the stimulus was identical to that of Experiment 1 (Figure 4A). In the monoptic condition, both the dark disk and random-dots (14.31 cd/m^2) were presented to the left eye. In the no-dot condition, the stimulus was the same as that used in the disk condition except that the random dots were not presented. In the interchanged condition, the disk was presented on the bright background to the right eye, and the random dots were presented on the dark background to the left eye. An example of these conditions is shown in Figure 4A.

In each block, the four conditions were tested three times in randomized order. After a practice block, each observer completed at least three experimental blocks.

-----Insert Figure 4 about here-----

Eye-movement recording and data analysis. The eye-movement recoding and data analysis were identical to those used in Experiment 1.

Results and discussion

Figure 4B shows the mean motion ratings in the four conditions, averaged over the four observers. We conducted a one-way repeated-measures ANOVA on the motion ratings, with the factor of stimulus configuration. The main effect was significant, F(3, 9) = 13.24, p < 0.005. Motion ratings were much lower in both the monoptic and no-dot conditions than in the baseline, dichoptic disk condition. In addition, motion ratings in the interchanged condition were comparable to that of the disk condition². These results indicate that dichoptic presentation plays an important role in producing the illusory motion. The absence of

²Based on our informal observations, the direction of the perceived jump in the interchanged condition was varied from saccade to saccade. This is different from that of the disk condition because most observers reported that the direction of the jump perceived in the disk condition was opposite to that of the saccade. We currently have no clear explanation for this difference.

Figure 4 (Mitsudo & Nakamizo)



Figure 4. Stimuli and results for Experiment 2. (A) The four stimulus configurations used (the disk, monoptic, no-dot, and interchanged conditions). In each panel, the left half of the pattern was presented to the left eye, and the right half was presented to the right eye. (B-E) Mean motion ratings (B), the mean number of saccades (C), mean saccade length (D), and mean cumulative binocular misalignment (E) for the four stimulus configurations (n = 4). Error bars in (B-E) represent standard deviation.

perceived motion in the no-dot condition also indicates that the effect reported here differs clearly from the autokinetic motion, in which a small visual target presented on a dark background appears to move during fixation (Aubert 1887). If the illusory motion were similar to the autokinetic motion, motion ratings would be higher in the no-dot condition than in the disk condition because the autokinetic motion is known to be more frequent when the target is presented in isolation (Crone and Verduyn Lunel 1969). To check whether or not the saccadic strategy of the observers was virtually identical across the different stimulus conditions, we computed the number of saccades, the mean saccade length, and cumulative saccade-produced binocular misalignment as in Experiment 1 (Figures 4C-E). We then conducted three one-way repeated-measures ANOVAs independently on each of the three saccade-related variables, with the factor of stimulus configuration. The main effect of stimulus configuration was not significant for any of the number of saccades, the mean saccade length, and cumulative saccade-produced binocular misalignment [the number of saccades, F(3, 9) = 2.19, p = 0.16; mean saccade length, F(3, 9) = 1.27, p = 0.34; binocular misalignment, F(3, 9) = 2.12, p = 0.17], indicating that the observers' saccadic strategies did not vary among the four conditions.

To strengthen the claim that saccadic strategies are not related to the perceived motion, we analyzed the trial-by-trial variability of motion rating and saccade-related variables by conducting a multiple regression analysis as in Experiment 1. The independent variables were similar to those used in Experiment 1, except for the stimulus pattern. Because the stimulus pattern was categorical, we added three dummy variables for the monoptic, no-dot, and interchanged conditions. We found that the partial coefficients for the monoptic, no-dot, and interchanged conditions were significantly different from zero for all observers (Table 2). On the other hand, none of the partial coefficients for the three saccade-related variables (the number of saccades, mean saccade length, binocular misalignment) was significantly different from zero. These results confirm the idea that saccadic strategies are not related to the perceived motion.

Observer	Partial coefficients for independent variables						Intercept
	Monoptic	No dot	Interchanged	Number of saccades	Saccade length	Binocular misalignment	
S 1	-2.02***	-2.50***	-1.21***	-0.116	-0.0733	0.00682	3.65***
S2	-0.984***	-0.922***	-0.584*	-0.0344	-0.29	0.239	3.34**
S3	-2.68***	-2.64***	-1.62***	-0.0186	-0.606	0.183	3.14***
S4	-3.50***	-3.46***	-0.839***	0.0202	0.116	-0.0441	1.83*

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p* < 0.05, *p* < 0.01, ****p* < 0.001.

Taken together, these results revealed that the illusory motion is not solely due to the visual latency for a low-luminance element, and requires a dichoptic presentation. Therefore, (a) the presence of continuous visual stimuli is insufficient for perceptual stability, and (b) appropriate extraretinal signals must therefore be used for maintaining the perceived stability of continuous stimuli in normal conditions.

As noted in the Introduction, extraretinal signals accompanying saccades can be used in two ways: saccadic suppression and spatial updating. As a possible mechanism for the illusory motion, one might think that saccadic suppression is abnormal in Experiments 1 and 2. For example, it is possible that the dichoptic stimulus might reduce saccadic suppression for the low-luminance disk because the magnitude of saccadic suppression is known to depend on the luminance of stimuli (MacAskill et al 2003; Michels and Lappe 2004).

Furthermore, it is also possible that the dichoptic stimulus might cause a failure to synchronize saccadic suppression with the processing of the dark disk. Indeed, this explanation is similar to that proposed by Tatler and Troscianko (2002) to account for the phenomenon in which an observer's own saccades can be perceived when the eyes are viewed in a mirror through a dark filter. Therefore, in Experiment 3, we investigated whether or not the dichoptic stimulus alters saccadic suppression.

Experiment 3

In Experiment 3, we examined the timing and amount of saccadic suppression (Diamond et al 2000; MacAskill et al 2003) produced with dichoptic and non-dichoptic test stimuli similar to those used in Experiment 2. The observer's task was to make a saccade while viewing the test stimulus and then to determine whether a short temporal gap introduced into the test stimulus was present or not (Figure 5). To analyze the timing and amount of saccadic suppression, we calculated (a) the proportion of "present" responses for the gap according to the onset time of the gap relative to the saccade and (b) detectability d' of the gap.

-----Insert Figure 5 about here-----

We compared the timing and amount of saccadic suppression for the element that appeared to move with those for the element that appeared to be stationary. Because the element that appeared to move was a low-luminance disk presented in the disk condition of Experiment 2, we introduced a temporal gap into the disk in Experiment 3 (a disk condition). To measure saccadic suppression for the element that appeared to be stationary, we introduced a temporal gap into the disk presented in the monoptic and no-dot conditions of Experiment 2. We also introduced a temporal gap into the random dots in the disk condition of Experiment 2 (a background condition). If saccadic suppression is irrelevant to the illusory motion, the timing and amount of saccadic suppression in the disk condition were expected to be virtually identical to those in the other three saccadic conditions. *Methods*

Observers. Three observers (two naive and the first author) participated in Experiment 3. All had corrected-to-normal visual acuity. Written consent was obtained from all observers.

Apparatus, stimuli, and procedure. The apparatus, stimuli, and procedure were identical to those used in Experiments 1 and 2, except for the following. The vertical refresh rate of the monitor was set to 120 Hz. Four stimulus conditions similar to those used in Experiment 2 were tested: disk, monoptic, no-dot, and background conditions. In the first three conditions the disk had a short temporal gap of 34 ms in three quarters of the trials. The background condition was identical to the disk condition except that the random dots had a temporal gap of 17 ms in three quarters of the trials.

At the beginning of each trial, the fixation pattern was presented for 1.0 s. Subsequently, a red dot was presented 3.1° right or left for 0.5 s. The observer was required to make saccades twice, as accurately as possible. First, the observer was instructed to make a saccade toward the red dot. One second later, he or she was instructed to make another saccade toward the center of the display. To assist in making the saccades, the timing of the saccades was specified by click sounds separated by 1-s intervals. When the second saccade was made, the test stimulus was presented for 1.0 s. The observer's task was to report whether or not the temporal gap of the stimulus element was present (a yes-no task). The onset time of the temporal gap varied within a range of 200 ms.

Figure 5 (Mitsudo & Nakamizo)



Figure 5. A schematic illustration of the trial sequence in Experiment 3. The actual display was dichoptic.

The element into which the temporal gap could be introduced (i.e., the disk or the random dots) was specified before every experimental block and was constant within a block. The ratio of gap-present trials to gap-absent trials was 3:1. The order of the trials was randomized. No feedback on incorrect responses was provided in the experimental trials. There were two additional control conditions, in which the disk and background conditions were tested without a saccade. The order of the six conditions was counterbalanced among blocks. Each block comprised 28 trials. Each observer received several practice blocks and completed at least 14 experimental blocks.

Eve-movement recording and data analysis. During the experimental trials, the binocular eye movements of the observer were recorded at 59.94 Hz. In Experiment 3, saccades were analyzed according to the following procedure. Each eye's saccade was primarily detected with a velocity criterion (above 50.0° /s). For gap-present trials, the proportion of "gap present" responses (the hit rate p_{hit}) was categorized according to the time relative to saccade onset. If two or more saccades were detected in gap-present trials, the one that was temporally closest to the gap of the stimulus was used for the analysis. The hit rate was calculated as a function of the time relative to saccade onset for each of the four saccadic conditions. To calculate the timing of saccadic suppression, the hit rate $p_{\rm hit}$ was fitted with a variation of the Gaussian function,

$$p_{\rm hit} = [1 + a/(2\pi c)^{1/2} \exp(-(t-b)^2/(2c^2))]^{-1},$$
(1)

where a is the depth of the function, b is the peak time of the function, c is the width of the function, and t is the time of the gap onset relative to saccade onset. The three free parameters, a, b, and c, were determined by the maximum-likelihood method. We regarded the peak-time parameter as the timing of saccadic suppression by assuming that this parameter was not affected by the amount of a (positive or negative) overall bias for responding "gap present". On the other hand, the depth parameter a and the width parameter c were considered to include an overall bias for responding "gap present" (depending on the conditions and observers). Therefore, to assess the amount of saccadic suppression, we computed a bias-free measure, detectability d', by combining the hit rate with the false-alarm rate (the proportion of "gap present" responses in gap-absent trials). Specifically, d' was calculated by $z(p_{\text{hit}})$ – $z(p_{\rm FA})$, where $p_{\rm FA}$ is the false-alarm rate, and z(p) is the inverse function of the cumulative standard normal distribution for probability p. If the value of p_{hit} or p_{FA} was 1 or 0, it was replaced by 1 - 1/2n or 1/2n, respectively (*n* is the sample size). The values of d' were computed for the six conditions.

Results and discussion

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First, we examined the timing of saccadic suppression. We analyzed a total of 1,524 trials in which the saccade was successful (98% of all trials). The mean length of the saccade was 4.1° across the three observers (the mean of the standard deviation was 1.3°). Figure 6A shows the proportion of "present" responses for the gap in gap-present trials (i.e., the hit rate) as a function of the time relative to saccade onset. Each symbol in Figure 6A represents the proportion calculated for each 40-ms interval. The hit-rate data were found to have a "dip" around saccade onset in all the four saccadic conditions. We fitted a variation of the Gaussian function to the hit-rate data for each condition (Equation 1). Fitting parameters were the peak time, width, and depth of the function. To examine whether the timing of saccadic suppression for the disk condition was different from that of the other three conditions, we conducted nested F tests (Dosher et al 2004; Wonnacott and Wonnacott 1981) on the peaktime parameter. All the nested F tests performed here were conducted across the observers. We compared a two-variable model (one variable for the disk condition and the other for the other three saccadic conditions) with a one-variable model (a single variable for all the four

Figure 6 (Mitsudo & Nakamizo)



Figure 6. Results for Experiment 3. (A) The proportion of "present" responses for the temporal gap (introduced into the disk or the random dots) in gap-present trials as a function of the time relative to saccade onset for each observer. Differently shaped symbols and colored lines represent data and fitting lines for the four saccadic conditions. (B) Mean detectability (d') of the temporal gap in the four saccadic and two non-saccadic conditions (n = 3). Different symbols represent data obtained from individual observers.

saccadic conditions). We found that the peak time for the disk condition was not significantly different from that of the other three conditions, F(1, 10) = 0.392, p = 0.55. In addition, this was true for the other two parameters [width: F(1, 10) = 0.900, p = 0.37; depth: F(1, 10) = 1.44, p = 0.26]. These results indicate that the timing of saccadic suppression was normal, even under the stimulus condition where the illusory motion was perceived.

-----Insert Figure 6 about here-----

Second, we analyzed the amount of saccadic suppression. Detectability d' was calculated for each of the six conditions (Figure 6B). The hit rates for the four saccadic conditions were based on the data where the time relative to saccade onset was from 0 to +100 ms. The results showed a typical pattern of saccadic suppression: a nested F test revealed that the value of d' was high in the two non-saccadic, control conditions and low in the four saccadic conditions [a two-variable model ($d'_{\text{disk, monoptic, no-dot, background}} \neq d'_{\text{disk without}}$ saccade, background without saccade) compared to a one-variable model (a single d' variable for all conditions): F(1, 16) = 179.6, p < 0.00001]. Detectability was consistently lower for the disk, monoptic, no-dot, and background conditions than for the disk-without-saccade and background-without-saccade conditions. Furthermore, to examine whether the value of d' for the disk condition was different from that of the monoptic, no-dot, and background conditions, we conducted an additional nested F test for a three-variable model ($d'_{disk} \neq$ $d'_{\text{monoptic, no-dot, background}} \neq d'_{\text{disk without saccade, background without saccade}}$). We found that the additional variable for the disk condition was not significant [the three-variable model compared to the two-variable model: F(1, 15) = 0.744, p = 0.40]. These results suggest that the amount as well as the timing of saccadic suppression produced with the dichoptic stimulus is normal, suggesting that the illusory motion is unlikely to be related to saccadic suppression.

General discussion

The present findings are summarized as follows: (a) saccades can cause perceived motion when the stimulus is dichoptic and has a large interocular difference in luminance, and (b) saccadic suppression produced with the dichoptic stimulus is normal. Because visible stimuli were continuously presented during and around saccades, the presence of visual signals is unlikely to be sufficient for appropriate spatial updating. These results therefore support the idea that the illusory motion produced with dichoptic stimuli is a consequence of saccade-produced image displacements inappropriately combined with extraretinal signals. The present data are, however, insufficient to address what type of image displacement— common or relative image displacement between the two eyes—is not correctly compensated for in the illusion, because the eye tracker used here had low temporal resolution (i.e., below 60 Hz). Nevertheless, our data are generally consistent with the notion that extraretinal eyeposition signals interact with visual signals (Krekelberg et al 2003; Park et al 2001).

Several researchers have hypothesized that the visual system usually assumes the scene to be stationary (Currie et al 2000; Deubel et al 1996; Deubel et al 1998). For example, Deubel et al (1996) proposed that the perceived stability of the visual scene is largely explained by the assumption that a continuously presented stimulus acts as a stationary reference. The stationary assumption, however, cannot explain the present results because instability was perceived even in the presence of continuous visual stimuli as found in Experiments 1 and 2. We can therefore state that dichoptic stimuli can override the stationary assumption.

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