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Directional bias of illusory stream caused by relative motion adaptation

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ABSTRACT

Enigma is an op-art painting that elicits an illusion of rotational streaming motion. In the present study, we tested whether adaptation to various motion configurations that included relative motion components could be reflected in the directional bias of the illusory stream. First, participants viewed the center of a rotating Enigma stimulus for adaptation. There was no physical motion on the ring area. During the adaptation period, the illusory stream on the ring was mainly seen in the direction opposite to that of the physical rotation. After the physical rotation stopped, the illusory stream on the ring was mainly seen in the same direction as that of the preceding physical rotation. Moreover, adapting to strong relative motion induced a strong bias in the illusory motion direction in the subsequently presented static Enigma stimulus. The results suggest that relative motion detectors corresponding to the ring area may produce the illusory stream of Enigma.

1. Introduction

There are phenomena where illusory motions are perceived in physically static images. For example, when one's head moves toward a static image in which tilted line components are circularly aligned, the components seem to rotate [e.g., illusions called the Pinna–Brelstaff illusion (Pinna & Brelstaff, 2000) and the rotating tilted lines illusion (Gori & Hamburger, 2006)]. Similarly, when one moves one's eyes smoothly across static images in which doted black and white lines or yellow circles on radial patterns are aligned, the components seem to move [e.g., the examples reported by Ito, Anstis, and Cavanagh (2009) and the pursuit–pursuing illusion (Bai & Ito, 2014; Ito, 2012)]. In these illusions, the dominantly detected motion direction is considered to differ from the retinal motion direction when voluntary head or eye movements produce retinal motion. Meanwhile, illusory motions are still observed even when explicit voluntary eye movements or head movements are absent. For example, a black-and-white checkered circle on an orthogonally oriented checkerboard seems to drift [i.e., the Ouchi–Spillmann illusion (Spillmann, 2013; Spillmann, Heitger, & Schuller, 1986)]. An arrangement of radial patterns [i.e., MacKay rays (Mackay, 1957)] or repeatedly arranged sectors that change shade gradually from black to white or in asymmetric four step luminances [i.e., the Fraser–Wilcox/rotating-snakes illusion (Fraser & Wilcox, 1979; Kitaoka & Ashida, 2003)] also produce illusory motion (see also a review by Gori and Stubbs (2013)). The origin of these motion illusions has been discussed relating to fixational eye movements (e.g. Beer, Heckel, and Greenlee (2008), Murakami, Kitaoka, and Ashida (2006)) or the cortical contribution (e.g. Kuriki, Ashida, Murakami, and Kitaoka (2008), Zeki, Watson, and Frackowiak (1993)). More recent research revealed that the illusory motion of the Fraser–Wilcox/rotating-snakes illusion is perceived not only by humans but also by monkeys (Agrillo, Gori, & Beran, 2015) and even fish that do not have a developed cortex (Gori, Agrillo, Dadda, & Bisazza, 2014).

The Enigma illusion (Leviant, 1982, 1996), which is investigated in the present research, is categorized into the latter group; that is, the Enigma illusion occurs without explicit voluntary eye or head movements. *Enigma* (Leviant, 1982, 1996), which is composed of concentric rings on radial spokes, is an artwork that elicits "illusory streams"; specifically, these are whitish streams that rapidly rotate within the ring areas, when one views the center of the image (Fig. 1). The appearance of the illusory stream gradually develops within several seconds (Tomimatsu, Ito, Sunaga, & Remijn, 2011). The illusory stream appears to travel in either a clockwise (CW) or counter-clockwise (CCW) direction, with the direction reversing spontaneously. Gori, Hamburger, and Spillmann (2006) demonstrated that the mean duration of a stable perceived direction of the illusory stream, either CW or CCW, is 4.7 s. Previous studies have proposed several causes of the illusion: fluctuation of accommodation or small eye movements (Gregory, 1993), fixational eye movements (Mon-Williams & Wann, 1996), microsaccades

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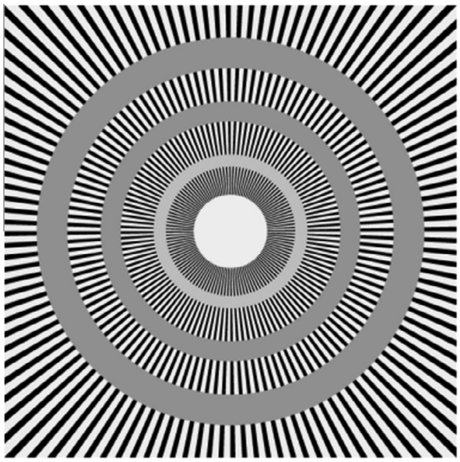

Fig. 1. An Enigma pattern composed of simplified elements of the original *Enigma* (Leviant, 1982, 1996). Rapid rotation of an illusory white stream is perceived within the gray rings superimposed on black spokes. The direction of rotation reverses spontaneously.

(Troncoso, Macknik, Otero-Millan, & Martinez-Conde, 2008), cortical mechanisms (Kumar & Glaser, 2006), a neural mechanism (Hamburger, 2007), direction-sensitive neurons in MST/MSTd (Hamburger, 2007, 2012) and motion processing in V5/MT (Zeki et al., 1993). Experiments employing positron emission tomography (Zeki et al., 1993) or repetitive transcranial magnetic stimulation (Ruzzoli et al., 2011) indicate that the activation of V5/MT, rather than V1, correlates with the perception of the illusion. However, the mechanism in V5/MT that produces the illusory motion effect is unclear. A motion illusion might be caused by a representational position shift due to nearby motion in MT+, as Maus, Fischer, and Whitney (2013) demonstrated. However, the results of Maus et al. (2013) might not indicate a direct cause of the illusory Enigma stream because they investigated the flash-drag effect, in which an illusory position shift appears in the same direction as nearby motion and the direction is opposite to that of the Enigma stream we demonstrate below. As for small eye movements, although microsaccades are synchronized with the perceptual change of the illusory motion (Troncoso et al., 2008), they might simply provide a trigger for the change (Hamburger, 2007; Troncoso et al., 2008). There may not be a unique mechanism behind the perceptual effect, and the illusory motion likely reflects a combination of peripheral and central factors (Fermüller, Pless, & Aloimonos, 1997). Billino, Hamburger, and Gegenfurtner (2009) found that percentages of occurrence of the Enigma illusion in young children (3–6 years) were lower than those in young adults (18–39 years). This might indicate that the ability to process some motion components related to the Enigma illusion further develops after ages of 3–6 years.

Gori et al. (2006) showed their participants rotating radial sectors as an adaptation stimulus. This produced a directional bias for the illusory stream in Enigma as a test stimulus toward rotation in a direction that was opposite to the preceding physical motion direction. That is, the motion aftereffect could determine the direction of the illusory stream in the ring. In our preliminary observation, however, we observed somewhat different phenomena when an Enigma stimulus is used as both adaptation and test stimuli. The illusory stream in the ring area seems to rotate in a direction opposite to the physical rotation of the adaptation stimulus during the adaptation period and to rotate in the same direction as that of the preceding physical rotation of the adaptation stimulus during the test period, despite the ring area remaining stationary during the trial. This phenomenon is similar to that found by Anstis & Reinhardt-Rutland, 1976, who showed that background rotational motion caused the induced movement and motion aftereffect of a stationary textured ring overlaid on the background. They concluded that visual neurons that were sensitive to relative motion caused the induced motion and motion aftereffect of the ring. From analogical reasoning, we hypothesized that the appearance of an illusory stream in the rotating Enigma stimulus could reflect a visual process for relative motion.

In the present study, we investigated the effect of adaptation to various motion configurations that included relative motion components on the illusory stream in a static Enigma stimulus presented subsequently. In Experiment 1, we investigated the directional bias of an illusory stream in a static Enigma stimulus presented after adaptation to a rotating Enigma stimulus and compared it with that during the adaptation period to confirm our preliminary observation mentioned above. In Experiment 2, we investigated the directional bias of an illusory stream in the test stimulus (i.e., a static Enigma stimulus) presented after adaptation to varied combinations of the spoke motion and textured ring motion where relative motions were considered to differ in strength.

2. Experiment 1

In Experiment 1, we exposed participants to a rotating Enigma stimulus as an adaptation stimulus. After viewing the adaptation stimulus, a static Enigma stimulus was presented as a test stimulus. The aim of Experiment 1 was to measure the effect of the stimulus rotation on the directional bias of the illusory stream during the adaptation and test periods.

2.1. Method

2.1.1. Participants

Ten individuals participated in Experiment 1. One of them was the first author, and the others were graduate or undergraduate students who were naïve as to the purpose of this study. All of the participants had normal or corrected-to-normal vision. This experiment was approved by the local ethics committee at Kyushu University. The experiment was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki) and informed written consent was obtained from the participants.

2.1.2. Apparatus

The stimulus displays were produced by a computer (Dell, Latitude D520) and presented on a cathode-ray-tube monitor (EIZO, FlexScan T561). The participants observed the stimuli from a distance of 140 cm in a darkened room. Their heads were stabilized with a chinrest.

2.1.3. Stimuli

In Experiment 1, the adaptation and test stimuli were a further simplified version of *Enigma*, as shown in Fig. 2. The Enigma stimulus subtended a visual angle of $9° \times 9°$. The diameters of the inner and outer edges of the ring were 4.9° and 6.4°, respectively. The number of black spokes was 100. The luminances of the black spokes, uniform gray ring, and background were 0.3, 10, and 27 cd m^{-2}, respectively. A fixation point was superimposed on the center of the Enigma image, which was also the center of rotation. The angular speed of the rotation was 15.8° s^{-1}.

2.1.4. Procedure

As shown in Fig. 2, our first experiment included six adaptation conditions, which were combinations of two adaptation durations

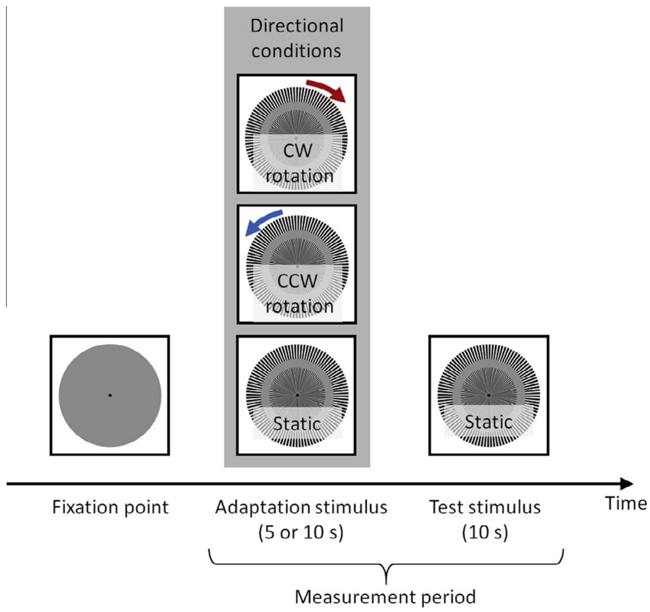

Fig. 2. Schematic illustration of the experimental paradigm in Experiment 1. A fixation point was presented on a plain gray disk. Afterward, one of three rotational conditions—CW rotation, CCW rotation or static (control) condition—was presented as an adaptation stimulus for 5 or 10 s. At the end of a trial, a static Enigma stimulus, which was the same as the static stimulus under the adaptation condition, was presented as a test stimulus for 10 s.

(5 and 10 s) and three directions of rotation of the Enigma stimulus [CW, CCW and static (control)]. Under the CW rotation condition, a gray ring was superimposed on spokes rotating in a CW direction. Under the CCW rotation condition, the spokes rotated in a CCW direction. Under the static condition, there was no physical motion in the stimulus. After participants viewed the adaptation stimulus, the static Enigma stimulus as the test stimulus was presented for 10 s. There was no physical motion in the ring area during the trials under the three directional conditions. Under the static condition, there was no physical change during the trial; i.e. the classical viewing condition of the Enigma illusion for 15 or 20 s.

There were two observation-area sessions: an illusory-stream observation session and spoke observation session. In the illusory-stream observation session, participants reported the perceived motion direction of the illusory stream in the gray ring in the adaptation and test periods, by pressing and holding one of two buttons corresponding to CW and CCW motion perception, while perceiving the illusory motion. If they could not determine the perceived motion direction or just perceived flickering, they did not press either button. Button-press data were sampled 10 times per second throughout the adaptation and test periods. In the spoke observation session, participants reported the perceived motion direction of the spokes in the CW and CCW conditions – that is, real motion during the adaptation period and motion aftereffect during the test period, using the same procedure used in the illusory-stream observation session.

All participants participated in both observation-area sessions. The order of the two sessions was balanced. In the illusory-stream observation session, the six conditions (three directions including the static condition × two durations) were tested in random sequences. In the spoke observation session, the four conditions (two directions excluding the static condition × two durations) were also tested in random sequences. Each participant was presented with 10 repetitions of all conditions: six conditions × 10 trials for the illusory-stream observation session and four conditions × 10 trials for the spoke observation session.

2.1.5. Quantification

Button presses for CCW perception were scored as “1” and those for CW perception were scored as “−1”. When the participant did not press either button, a score of “0” was recorded. The button-press data were sampled every 0.1 s. At each sampled point, we accumulated the scores acquired from 100 trials (10 trials × 10 participants for each condition). The accumulated score indicates the subtraction of the number of button presses for CW from that for CCW. For example, “100” means that all participants saw the CCW motion in all trials and did not see the CW motion at the sampled point. Thus, the accumulated score indicates the difference in occurrence frequency between the CCW and CW perceptions (i.e., the bias in the perceived motion directions). In contrast, “0” indicates that there was no directional bias observed throughout the 100 trials. Because no motion observed also results in “0”, we also calculated the percentage of trials in which the motion was perceived in either one of the two directions out of the 100 trials at each sampled point (i.e., the percentage of motion perception) to confirm the presence of motion perception itself during stimulus presentation. If the participants answered CCW in half of all trials and CW in the remaining half, for example, the percentage of motion perception is 100% although there is no bias in the perceived motion direction.

2.2. Results and discussion

Fig. 3 shows the results of the bias in the perceived motion directions in illusory-stream observation and spoke observation sessions. During the adaptation period, participants saw the illusory stream on the ring move in the direction opposite to that of the physical spoke motion. During the test period, the perceived direction of the illusory stream reversed, such that the illusory stream appeared to be moving in the direction of the previous physical spoke motion (see Supplementary Video 1). For example, an illusory CCW stream was generally perceived while viewing CW rotation of the spokes in the adaptation period (Fig. 3a, red lines). After the spoke motion stopped, the illusory stream reversed. A CW stream was dominantly perceived from the test stimulus for several seconds during the test period. The illusory stream during the adaption and test periods seemed to be the same as that in the original *Enigma* in terms of quality, where a whitish stream rapidly rotates, according to the participants' introspection report. However, less of a flickering impression was acquired during the adaptation period (i.e., during physical rotation).

We used 19 data points, taken every 0.5 s from 1 to 10 s after the test stimulus onset, to evaluate changes in the bias in the perceived stream direction over time. Because the crossing points indicating the reversals in the dominant perceived-motion direction around 0.7 s probably indicate the lag of the reaction time, data processing was started 1 s after the test stimulus onset. A three-way analysis of variance (ANOVA) [adaptation duration (2)/spoke-motion condition (3)/and time passage in the test period (19)] demonstrated a significant main effect of the spoke-motion condition [$F(2, 18) = 53.95$, $p < 0.001$]. The interaction between the adaptation duration and spoke-motion condition was also significant [$F(2, 18) = 7.55$, $p < 0.005$]. Post-hoc analysis revealed that the bias in the illusory-stream direction during the test period was significantly larger when the duration of the adaptation period was 10 s than when the period was 5 s, under both the CW and CCW spoke-motion conditions ($p < 0.05$). The interaction between the spoke-motion condition and time passage was also significant [$F(36, 324) = 8.89$, $p < 0.001$]. Post-hoc analysis revealed that the differences between all combinations of the three spoke-motion conditions (i.e., CW–CCW, CW–control and CCW–control) were significant during the 5.5-s period starting 1.5 s after the test stimulus onset ($p < 0.05$). Under the control condition, where we used a

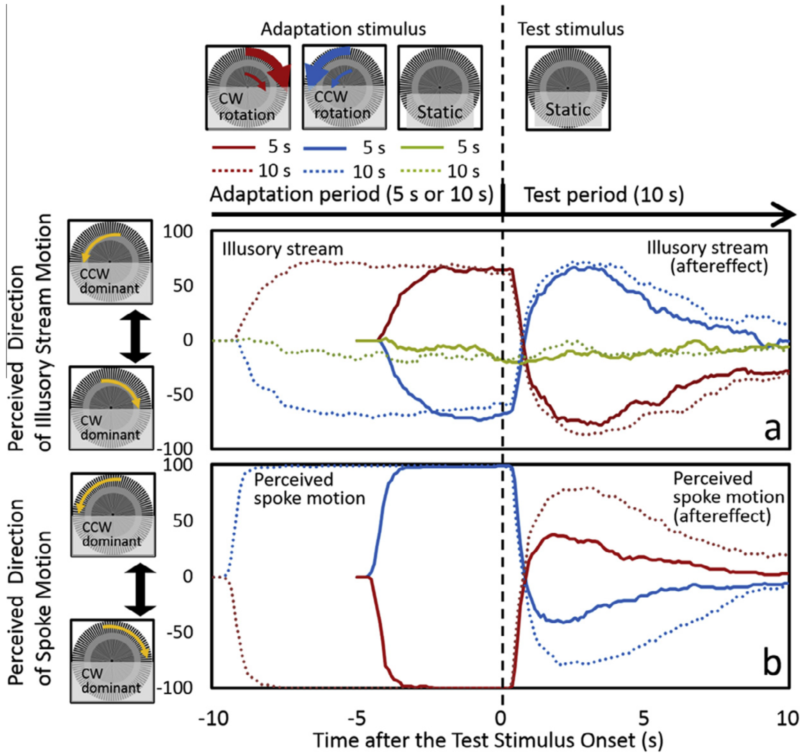

Fig. 3. Results of the directional biases in Experiment 1. The vertical axis indicates the difference in occurrence frequency between the CCW and CW perceptions (i.e., the bias in the perceived motion directions). Positive values indicate that CCW rotation was dominantly perceived; negative values indicate that CW rotation was dominantly perceived. The horizontal axis indicates the time course of the trial. The time point at "0" indicates the onset of the test stimulus. The left section of the graph shows data for the adaptation period in which the adaptation stimulus was CW rotation, CCW rotation, or static. The right section shows the test period in which the static stimulus was presented. Red, blue, and green traces correspond to CW-rotation, CCW-rotation, and static conditions of the adaptation stimulus, respectively. Dotted and continuous lines represent data obtained when the adaptation stimuli were presented for 10 and 5 s, respectively. (a) Illusory stream data for the illusory-stream observation session and (b) perceived spoke motion data for the spoke observation session. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

static stimulus as an adaptation stimulus, the participants observed no such bias in perceived stream direction throughout the trials, although the stream itself was observed sufficiently as shown in Fig. 4. The average durations of illusory motion perceived in either direction under the control conditions were 5.74 s for 15-s presentation and 7.88 s for 20-s presentation. The values were significantly larger than zero [$t(9) = 3.80$, $p < 0.005$ for 15-s presentation; $t(9) = 7.88$, $p < 0.005$ for 20-s presentation]. These results indicate that participants surely perceived the illusory motion without any motion aftereffect.

Additionally, we calculated the percentages of the CW and CCW rotations in the firstly perceived illusory motion in each control (static) trial to investigate the existence of a natural CW or CCW directional bias. The data for the 15- and 20-s conditions were combined. The data obtained for one participant who did not see any motion in the static condition were omitted from the calculation. The percentages of CW and CCW rotation were 61.4% and 38.6%, respectively. These percentages are similar to the directional bias found by Gori et al. (2006); i.e., 64.8% for CW and 35.2% for CCW. However, the directional bias under the static condition seems small compared with that under the CW and CCW conditions when we look at the whole range of presentation duration.

Fig. 4 shows the results of the percentage of motion perception of the illusory stream in either the CW or CCW direction in the illusory-stream observation session. In the adaptation and test periods, the percentage of motion perception under the CW or CCW condition was higher than that under the static condition, and decreased with time to about 45%. However, the percentage of motion perception under the static condition was fairly constant. At the end of the test period, there was no difference among the three conditions although the illusory motion was sufficiently perceived (i.e., the percentage of motion perception remained about 45%). A three-way ANOVA [adaptation duration (2)/spoke-motion condition (3)/and time passage in the test period (19)] demonstrated significant main effects of the spoke-motion condition [$F(2, 18) = 8.13$, $p < 0.005$] and time passage [$F(18, 162) = 6.64$, $p < 0.001$]. The interaction between the spoke-motion condition and time passage was also significant [$F(36, 324) = 3.55$, $p < 0.001$]. Post-hoc analysis revealed that the differences between the each spoke motion and control condition (i.e., CW–control and CCW–control) were significant during the 4.5-s period starting 1 s after the test stimulus onset ($p < 0.05$).

These results indicate that participants adequately perceived the illusory motion under the static condition, and the tendency of the value in Fig. 3a under the static condition to be around zero was thus not due to no motion being observed but due to there being no directional bias under the traditional viewing condition (i.e., static condition) of the Enigma illusion. Moreover, the participants saw illusory motion more frequently under the CW and CCW conditions than under the static condition in the first half of the test period. In the second half of the test period, the effect of adaptation to directional motion under the CW or CCW condition was diminished. However, the illusory motion itself was perceived as much as it was under the control condition. Thus, the value in Fig. 3a under the CW or CCW condition tended to approach zero at the end of the test period not because the illusory-stream perception itself disappeared but because directional bias in the illusory-stream perception weakened.

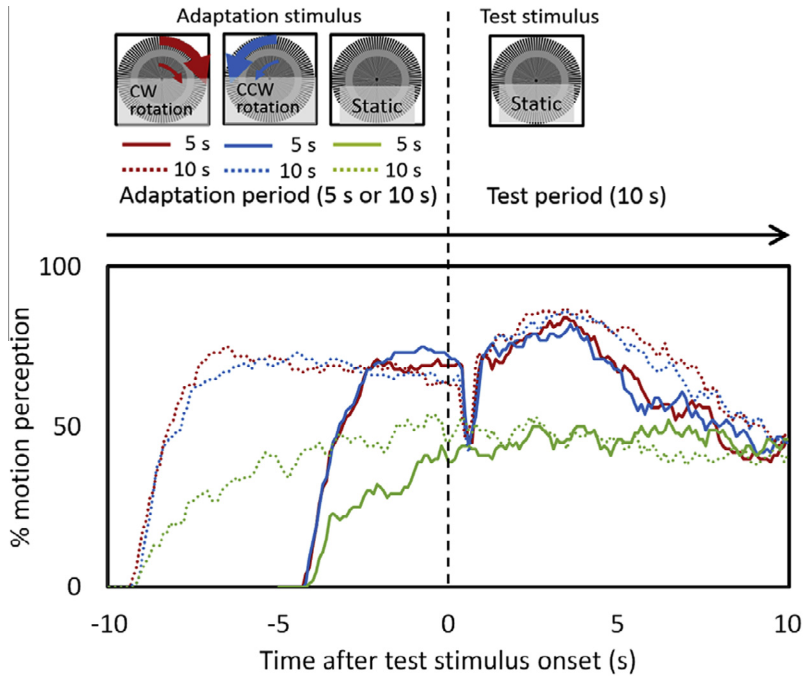

Fig. 4. Results of percentage of illusory-stream perception in Experiment 1. The vertical axis indicates the percentage of either CW or CCW illusory stream perception reported in 100 trials (10 participants × 10 trials per condition). The horizontal axis indicates the time course of the trial, as in Fig. 3. Red, blue, and green traces correspond to CW-rotation, CCW-rotation, and static conditions of the adaptation stimulus, respectively. Dotted and continuous lines represent data obtained when the adaptation stimuli were presented for 10 and 5 s, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

In the spoke observation sessions, we measured the perception of motion in the spoke area employing the same method used in the illusory-stream observation sessions and calculated the directional bias of the motion perception (see Fig. 3b). Participants responded to the physical rotation during the adaptation period. During the test period, the participants reported a normal motion aftereffect in the direction opposite to that of the motion of the adapted stimulus. Thus, after viewing the rotating stimulus, the direction of the illusory stream was opposite to that of the perceived spoke motion induced by motion aftereffect (see Fig. 3a and b).

Throughout the trial sequence, the illusory stream and the spokes always appeared to move in opposite directions. Therefore, our results show that relative-motion detection plays a key role in the Enigma illusion. Following Anstis and Reinhardt-Rutland (1976), we interpreted the present results as (1) the rotating stimulus induced motion of the illusory stream against the spoke motion during the adaptation period; (2) adaptation to the rotating stimulus reduced the sensitivity of the relative-motion detectors (e.g. Murakami and Shimojo (1996), Tynan and Sekuler (1975)) tuned to the direction; (3) the reduced relative-motion detection induced an imbalance between the relative-motion signals in the CW and CCW directions acquired by involuntary eye movement or spontaneous activities of relative motion detectors; (4) the illusory stream in a direction that was opposite to that during the adaptation period was dominantly seen during the test period (relative motion aftereffect); and (5) at the end of the test period, the gain of the adapted relative motion detection recovered, removing the directional bias of the illusory stream.

It is possible to argue that the apparently moving spokes due to the normal motion aftereffect induced relative motion in the illusory stream during the test period. However, during the test period, the directional bias in perceived spoke motion (i.e., normal motion aftereffect) after the 5-s adaptation was rather small compared with the bias in the illusory stream after the 5-s adaptation (see continuous lines in Fig. 3a and b). This result suggests that the illusory stream in the test period was seen frequently without the normal motion aftereffect in spoke motion, and was thus directly affected by the relative-motion adaptation. In the next experiment, we investigated the effect of enhancing or canceling relative motion during the adaptation period on the directional bias in the illusory stream during the test period to confirm whether the stream in the test period was the aftereffect of the relative-motion adaptation itself.

3. Experiment 2

In Experiment 2, we filled the ring area with random dots during the adaptation period. To investigate the effect of adaptation to relative motion in the Enigma illusion, we rotated the ring filled with random dots and the spokes independently in the adaptation period, in the same or opposing directions.

3.1. Method

3.1.1. Participants

Of the 10 participants, seven, including the first author, had participated in Experiment 1. The remaining three participants were graduate students who had not participated in Experiment 1. All the participants had normal or corrected-to-normal vision. This experiment was approved by the local ethics committee at Kyushu University. The experiment was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki) and informed written consent was obtained from the participants.

3.1.2. Apparatus

The apparatus was the same as that used in Experiment 1.

3.1.3. Stimuli

The stimuli were the same as those used in Experiment 1, except that the gray ring in the adaptation period was replaced with a ring filled with random dots (an array of black and white pixels that were randomly arranged), as shown in Fig. 5. In the test period, the ring was uniform gray as in Experiment 1.

3.1.4. Procedure

The random dots or the spokes rotated in a CW direction, rotated in a CCW direction, or remained stationary (no motion). Under the no-motion condition, the random dots were refreshed every 1 s to avoid the production of afterimages or perceptual fading. The adaptation period was followed by a test period, where an Enigma image with static spokes and a uniform gray ring was presented as a test stimulus, as in Experiment 1. In Experiment 2, both the adaptation and test stimuli were presented for 10 s. Participants reported the perceived motion in the test period by pressing one of two buttons corresponding to CW and CCW motion perception, as in Experiment 1. There were two observation-area sessions: an illusory-stream observation session and spoke observation session. All participants participated in both observation-area sessions. The order of the two sessions was balanced.

3.2. Results and discussion

Fig. 6 shows the results of the bias in the perceived motion directions in the test period. The perceived stream in the test stimulus was predominantly seen moving in the same direction as the spokes in the adaptation period. The stream in the gray ring seemed to be the same as that in the original *Enigma* in terms of quality, with a whitish stream rapidly rotating, according to the participants' introspection report, even though the random dots were previously presented in the ring area. The participants experienced a strong directional bias when viewing the illusory stream in the test period after the random dots and the spokes had moved in opposite directions in the adaptation period (Fig. 6a). The perceived direction of the illusory stream was also strongly biased in the test period when the spokes had moved in either a CW or CCW direction against static random dots during the adaptation period (Fig. 6b). When only the random dots rotated during the adaptation period, we detected a small amount of directional bias in the illusory stream during the test period (Fig. 6c).

When the random dots and the spokes moved in the same direction during the adaptation period (i.e., both in the CW or CCW direction), we detected only a minimal bias in the direction of the illusory stream during the test period (Fig. 6d). Under this condition, there was no relative motion adaptation between the movement of the spokes and the random dots during the adaptation period. Although local motion adaptation in the ring area should have occurred under this condition, the motion aftereffect from the random-dot motion was not reflected in the perception of the illusory stream during the test period. These results indicate that the directional bias of the illusory stream during the test period did not exhibit the characteristics of the normal motion aftereffect in the ring area, but rather the aftereffect of relative motion.

Fig. 7 shows the effect of spoke motion during the adaptation period on the direction of the illusory stream during the test period. For each panel (a, b or c), the random-dot motion was identical during the adaptation period; that is, panels a, b, and c present results when the condition of the random-dot motion was CCW, no motion, and CW, respectively. Thus, local adaptation to movement in the ring area, where the illusory stream would appear during the subsequent test period, was identical within each panel. However, the bias in the direction of the illusory stream during the test period was not determined by the direction of random-dot motion during the adaptation period, but strongly depended on the combination of the random-dot and spoke motion directions during the adaptation period.

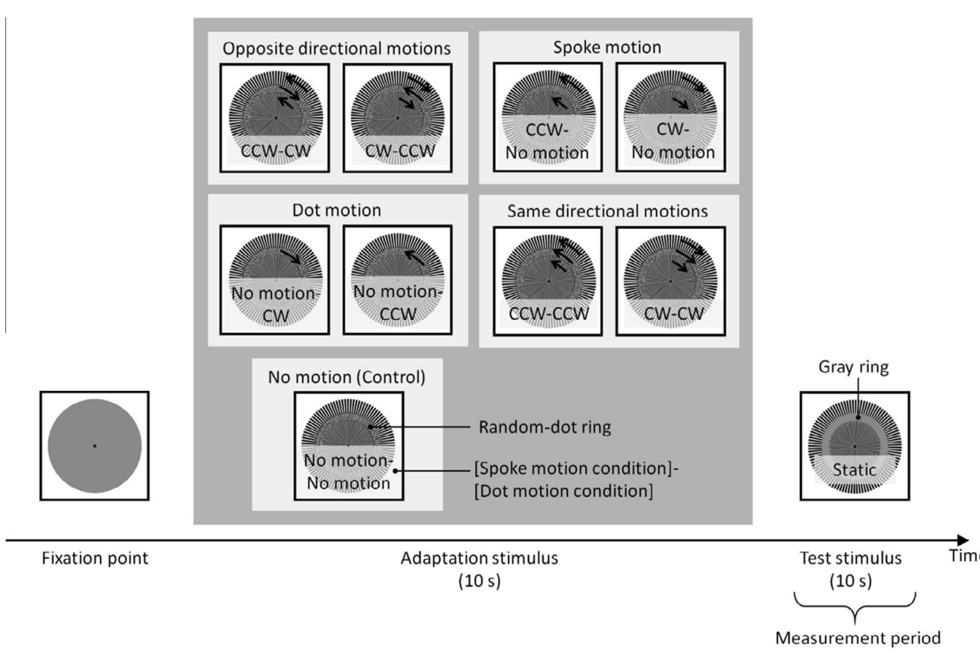

Fig. 5. Schematic illustration of the experimental paradigm in Experiment 2. A fixation point was presented on a gray disk. Afterward, one of nine directional conditions was presented, sorted into opposite-direction motions (i.e., CCW spoke with CW random dot motion condition and CW spoke with CCW random dot motion condition), spoke motion (i.e., CCW spokes with no random dot motion condition and CW spokes with no random dot motion condition), dot motion (i.e., no spoke with CW random dot motion condition and no spoke with CCW random dot motion condition), same-direction motions (i.e., CCW spoke with CCW random dot motion condition and CW spoke with CW random dot motion condition), and no motion (i.e., control) by strength of relative motion, as an adaptation stimulus for 10 s. At the end of a trial, an Enigma image with static spokes and a gray ring was presented as a test stimulus, as in Experiment 1.

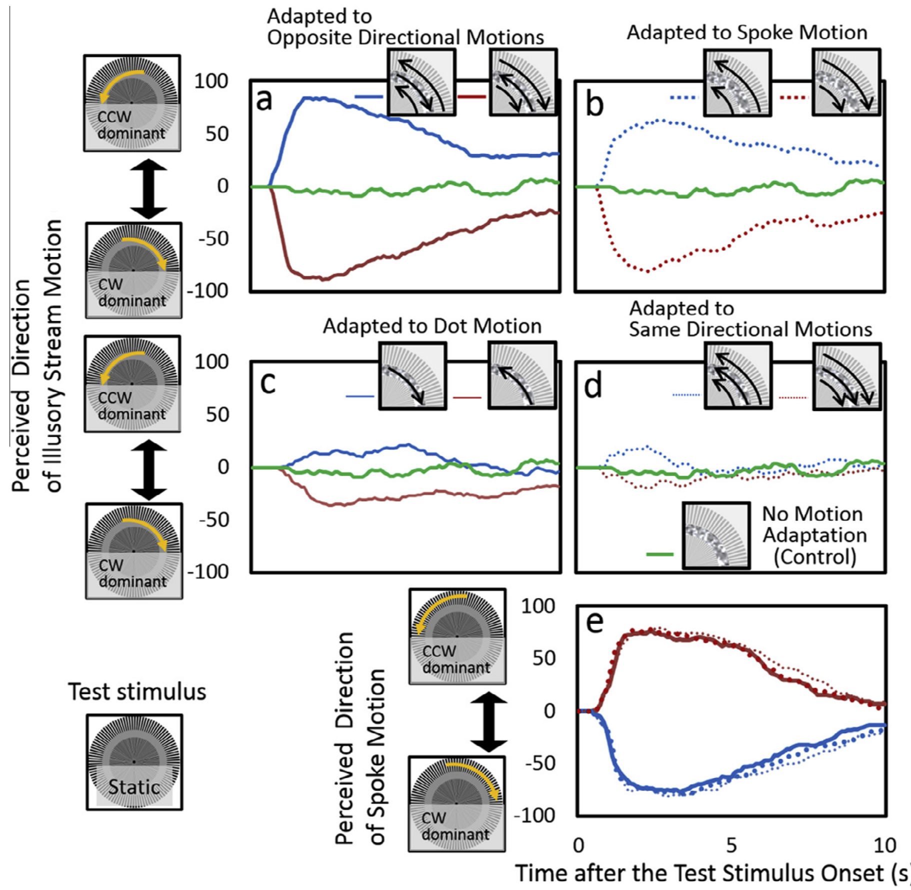

Fig. 6. Results of the directional biases in Experiment 2. The vertical axis indicates the difference in occurrence frequency between the CCW and CW perceptions (i.e., the bias in the perceived motion directions). Positive values indicate that CCW rotation was dominantly perceived; negative values indicate that CW rotation was dominantly perceived. The horizontal axis indicates the time course of the test period. (a) Results for the illusory stream when spokes and random dots moved in opposite directions. Heavy blue and red traces present the results for the CCW spoke with CW random dot motion condition and for the CW spoke with CCW random dot motion condition, respectively. (b) Results for the illusory stream when participants adapted to spoke motion only. Heavy dotted blue and red traces present the results for the CCW spoke with no random dot motion condition and for the CW spoke with no random dot motion condition, respectively. (c) Results for the illusory stream when participants adapted to random-dot motion only. Thin blue and red traces present the results for the no spoke with CW random dot motion condition and for the no spoke with CCW random dot motion condition, respectively. (d) Results for the illusory stream when spoke and random dots moved in the same direction. Thin dotted blue and red traces present the results for the CCW spoke with CCW random dot motion condition and for the CW spoke with CW random dot motion condition, respectively. (e) Perceived spoke motion data. Each trace corresponds to the trace in panel a, b, or d. Green lines in panels a, b, c, and d indicate the same data for the no motion (control) condition. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

A one-way ANOVA of the information in each panel (i.e., each random-dot condition) revealed the significance of spoke-motion conditions [for panel a, $F(2, 18) = 15.47$, $p < 0.001$; for panel b, $F(2, 18) = 25.16$, $p < 0.001$; for panel c, $F(2, 18) = 6.38$, $p < 0.01$]. Post-hoc analysis revealed that the differences among all three spoke-motion conditions (i.e., CW–CCW, CW–control and CCW–control) were significant ($p < 0.05$), except for the difference between CW and control conditions when the random dots were moving in a CW direction.

It is possible that the small directional bias acquired under the same-direction condition (i.e., near "0" in Fig. 6d, and also in Fig. 7a-left, and 7c-right) was owing to a low level of illusory stream perception in the test period. To exclude this possibility, we also calculated the total duration of the illusory motion perceived in either direction (see Fig. 8) and confirmed that participants reported a sufficient duration of illusory stream perception. The average durations were 5.78, 5.40, 3.34, 4.40, and 2.89 s, and were significantly larger than zero, for motion in an opposite direction (Fig. 6a), spoke motion only (Fig. 6b), random-dot motion only (Fig. 6c), the same direction of motion (Fig. 6d), and no-motion condition (green lines in Fig. 6), respectively [$t(9) = 7.73$, $p < 0.001$; $t(9) = 7.11$, $p < 0.001$; $t(9) = 3.73$, $p < 0.005$; $t(9) = 5.01$, $p < 0.001$; $t(9) = 3.30$, $p < 0.01$]. A one-way ANOVA revealed a main effect of the condition [$F(4, 36) = 19.65$, $p < 0.001$] and post hoc analyses showed that the duration of the illusory stream under the same-direction condition was longer than that under the random-dot-motion and no-motion conditions, and shorter than that under the opposite-direction-motion and spoke-motion conditions ($p < 0.05$). These results indicate that the small directional bias acquired under the same-direction condition was not based on a short duration of illusory stream perception in the test period. The duration of the illusory stream perception was sufficient to discuss the bias under the same-direction condition.

The normal motion aftereffect seen in the spoke area was perceived in the direction opposite to that of the spoke motion in the adaptation period, without any difference between the conditions (Fig. 6e). This result may demonstrate that the illusory stream direction bias observed during the test period was not induced motion from the normal motion aftereffect of the spokes, but determined by the preceding adaptation conditions. However, one may argue the possibility that the normal motion aftereffect of spokes produced illusory motion in the test period as induced motion, and that, at the same time, the motion aftereffect caused by random dot motion reduced the effect of the spoke motion aftereffect under the same direction condition. However, it seems that the motion aftereffect of random dots (Fig. 6c) was not strong

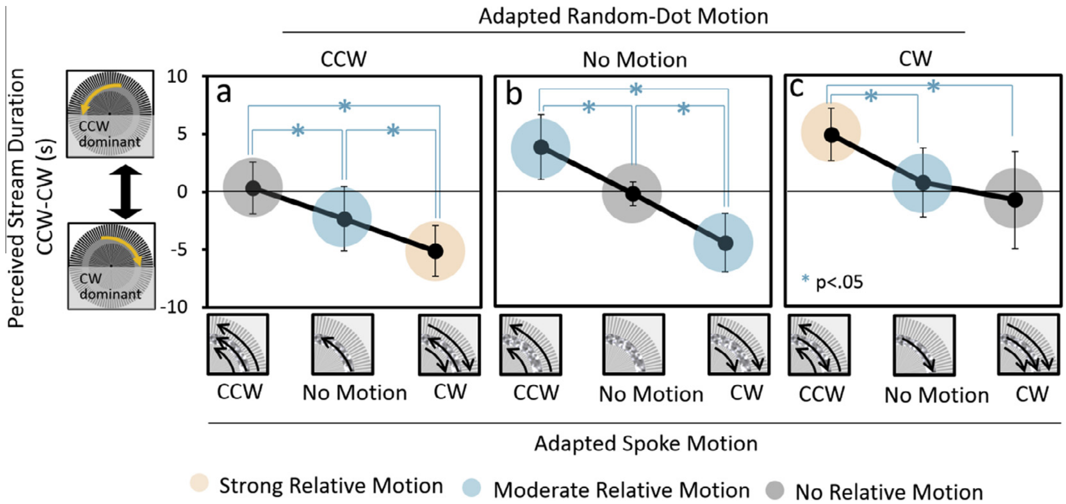

Fig. 7. Effect of spoke motion on the illusory stream aftereffect. The vertical axis indicates the duration of reported CCW motion perception minus the duration of reported CW motion perception. Positive values indicate that CCW rotation was dominantly perceived; negative values indicate that CW rotation was dominantly perceived. The horizontal axis in each panel indicates the spoke motion condition (i.e., the CCW, no motion, or CW spoke condition). Panels a, b, and c show results for CCW, no-motion, and CW random-dot conditions, respectively. Thus, each data point indicates one of the nine combinations of spoke and random dot motion conditions. Error bars indicate standard deviations.

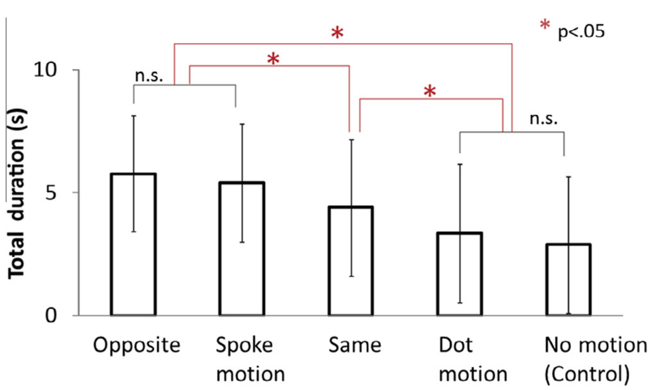

Fig. 8. Total durations of illusory motion in the 10-s test period for five sorted adaptation conditions. The vertical axis indicates the averaged total duration of either CW or CCW illusory stream perception (i.e., the sum of the duration of reported CW motion perception and the duration of reported CCW motion perception). The horizontal axis indicates five sorted conditions [i.e., opposite-direction motions, spoke motion, same-direction motions, dot motion and no motion (control)]. Error bars indicate standard deviations.

enough to cancel the strong spoke motion aftereffect (Fig. 6b) in the results obtained under the same direction condition in which the bias of the perceived direction was almost erased (Fig. 6d). Nevertheless, it is plausible that the relative motion plays a key role in the bias of the illusory stream that we found in the adaptation and test periods in the both cases; i.e., the illusory stream in the test period is induced by the spoke motion aftereffect or by relative motion adaptation (or by both).

In Experiment 2, we found that the individual preceding motion of the spoke or ring area was not the determinant of the perceived direction of the illusory stream in the ring area during the test period. The bias in the illusory stream direction during the test period was probably determined by the relative motion components between the spoke and ring areas.

4. General discussion

In the present study, we investigated the effect of adaptation to relative motion on the illusory motion in a static Enigma image. In Experiment 1, we presented a physically rotating Enigma stimulus as an adaptation stimulus. After the participant viewed the adaptation stimulus, a static Enigma stimulus was presented as a test stimulus. During the adaptation period, the illusory stream on the ring was mainly seen in the direction opposite to that of the physical rotation. After the physical rotation stopped, the illusory stream on the ring was mainly seen to be in the same direction as that of the preceding physical rotation. Throughout the trial sequence, the illusory stream and the spokes always appeared to move in opposite directions. In Experiment 2, we rotated the ring filled with random dots and the spokes independently in the adaptation period. The results showed that the determinant of the perceived direction of the illusory stream during the test period was probably not the individual preceding motion of the spoke or ring area, but the relative motion between them during the adaptation period.

Several factors contribute to the nature of the illusory stream in *Enigma*: (a) noisy flickers (e.g. Mackay (1957)) are perceived before/during observation of the illusory stream (mentioned in Hamburger, 2007), (b) the direction of the illusory stream spontaneously reverses after several seconds of observation (Gori et al., 2006), (c) the illusion is strongest when the spokes (i.e., radial lines) touch the ring at a right angle (Kumar & Glaser, 2006) or touch to make T-junctions (Gori et al., 2006), (d) there is a minimum spoke length at which robust illusory motion will appear (Kumar & Glaser, 2006), (e) high-contrast spokes strengthen the illusory stream (Kumar & Glaser, 2006), (f) high-contrast texture in the ring area weakens the illusory stream (Kumar & Glaser, 2006), (g) the spacing between the spokes and thickness of the spokes affect the strength of the illusion (Kumar & Glaser, 2006), and (h) changes in the speed of the illusory stream seem to be linked to microsaccades (Troncoso et al., 2008).

Among these characteristics, c, d, e, and g suggest that the strength of the illusory stream depends on motion detection in spokes in a specific direction along the ring. Additionally, characteristics a and b suggest the possibility that a conflict exists between two possible instances of motion in opposing directions (CW or CCW), just as two overlapping gratings moving in opposite directions exhibit a flicker motion aftereffect, which has been experimentally evaluated (Ashida & Osaka, 1995; Nishida & Sato, 1995). Characteristic f suggests that the illusion will be weakened by motion signals in the ring area because the texture in the ring travels in the same direction as the spokes when eyes move. These characteristics, together with the present results, suggest a contribution of relative-motion detection (Murakami & Shimojo, 1996; Shioiri, Ono, & Sato, 2002; Tadin, Lappin, Gilroy, & Blake, 2003; Tadin, Silvanto, Pascual-Leone, & Battelli, 2011; Takemura, Ashida, Amano, Kitaoka, & Murakami, 2012; Tynan & Sekuler, 1975; Van der Smagt, Verstraten, & Paffen, 2010) to the Enigma illusion.

Fig. 9 is a schematic illustration of our proposed mechanism. Hypothetical relative-motion detectors, placed along the ring, will be activated by spontaneous firing and/or responses to motion components in a direction along the ring, which are expected to arise from small eye movements, such as drifts and microsaccades. A conflict in motion signals from the directionally opposed relative-motion detectors may produce an illusory flicker. If the signal strength in one direction is dominated by spontaneous fluctuation or a trigger from retinal motion, the dominant motion signals may be organized and produce an illusory stream, creating a perception of CW or CCW rotation. The relative-motion detectors responsible for the Enigma illusion probably exist in V5/MT (Allman, Miezin, & McGuinness, 1985; Born, Groh, Zhao, & Lukasewycz, 2000; Born & Tootell, 1992; Tadin et al., 2011). This hypothesis would explain activation in V5/MT when viewing *Enigma* (Zeki et al., 1993). Meanwhile, one may relate the present effect to the motion-induced location shift that could indirectly bias perceived motion direction. For example, Kosovicheva et al. (2012) demonstrated that motion can affect even a lower-level orientation coding through a tilt aftereffect caused by adaptation to a "flash-dragged" grating. However, while the flash-drag effect occurs when an object is briefly flashed at moments of motion direction reversals, the perceived stream direction was continuously opposite to that of the spoke rotation for the Enigma stimulus. We assume that relative-motion detectors directly and continuously bias the direction of the illusory stream in a ring during their activation.

As for the stimulus shape that causes the Enigma illusion, the above hypothesis does not require a circular shape of the stimulus.

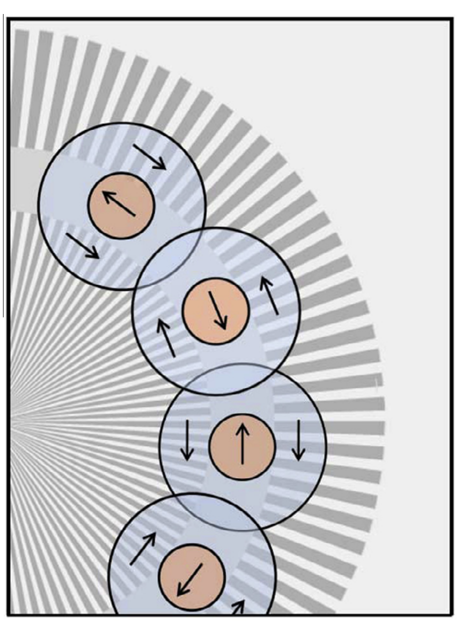

Fig. 9. Schematic illustration of relative-motion detection along the rings. Although no motion is detected in the center of the receptive field, the stimulus rotation might be caused by eye movements, and strong motion is detected in the periphery of the receptive field. As a result, detected relative motion suggests motion in the central field (ring) in a direction that is opposite to that of the peripheral field (spokes).

In fact, a circular shape is not necessary to produce the Enigma illusion (e.g. Kumar and Glaser (2006)). The circular shape of the Enigma figure may help the continuous integration of local motion signals and/or the generation of a continuous illusory stream because the ring has no ends, the same as for other motion illusions (e.g., the rotating-snakes illusion; Kitaoka & Ashida, 2003). Consequently, the circular shape may contribute to a vivid illusory stream that is stably perceived for a few seconds.

We note that one important aspect of the illusion remains unexplained, namely the origin of the whitish "matter" that appears to stream. Our interpretation noted above explains the behaviors of the illusory stream, but does not provide a clue to the solution of the problem. We plan to investigate the origin in future research.

5. Conclusion

In the present study, we revealed the possibility that relative motion adaptation affects the illusory motion in a subsequently presented Enigma image. The experiments described here illustrate a direct link between the illusory stream and relative-motion detection in the Enigma illusion. Activation of V5/MT while viewing Enigma (Ruzzoli et al., 2011; Zeki et al., 1993) indicates that the relative-motion detectors responsible for the Enigma illusion exist in these regions (Allman et al., 1985; Born & Tootell, 1992; Born et al., 2000; Tadin et al., 2011). Accommodation fluctuations or small eye movements (Gregory, 1993; Mon-Williams & Wann, 1996), including microsaccades (Troncoso, Macknik, Otero-Millan, & Martinez-Conde, 2008), act as triggers for reversing the directional dominance in the segregation of the opposing relative-motion signals. Our competitive-relative-motion-detector hypothesis explains known properties of the Enigma illusion and does not oppose current theories about this phenomenon.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.visres.2016.04.010.

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