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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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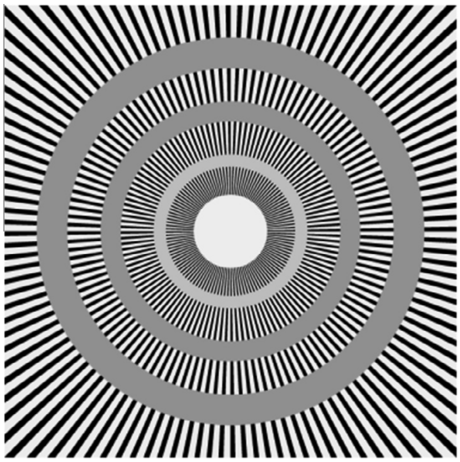

Fig. 1. An Enigma pattern composed of simplified elements of the original *Enigma* (Leviant, 1982, 1996). Rapid rotation of an illusory white stream is perceived within the gray rings superimposed on black spokes. The direction of rotation reverses spontaneously.

(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 $9^\circ \times 9^\circ$. 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