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Effect of surrounding texture on the pursuit-pursuing illusion

Yuanyuan Bai¶

Department of Design, Kyushu University, 4–9–1, Shiobaru, Minami-ku, Fukuoka-shi 815–8540, Japan; e-mail: <u>hakuenen@gmail.com</u>

Hiroyuki Ito

Faculty of Design, Kyushu University, 4–9–1, Shiobaru, Minami-ku, Fukuoka-shi 815–8540, Japan; Research Center for Applied Perceptual Science, Kyushu University, 4–9–1, Shiobaru, Minami-ku, Fukuoka-shi 815–8540, Japan; e-mail: <u>ito@design.kyushu-u.ac.jp</u>

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Abstract. The pursuit-pursuing illusion is a visual illusion where a circular object placed in the centre of a radial pattern consisting of thin sectors is seen to move in the pursuit eye movement direction. The present study investigates the role of the surrounding texture, replacing the sectors with random dots or stripes in an orientation that was orthogonal, parallel or oblique to the pursuit direction. The experiments demonstrate that the acquired illusory effect was large for the orthogonal stripes. However, each surrounding texture produces a relatively smaller effect than the radial sectors. These results suggest that a hypothesis based on the property of a centre-surround relative-motion detector cannot fully explain the illusion and that the radial stimulus structure itself plays an important role in this illusion.

Keywords: motion illusion, smooth pursuit, eye movement, relative motion.

1 Introduction

Motion illusions have for long attracted vision researchers. Kitaoka and Ashida (2007) reviewed the illusions and classified them in two categories; some of them are classified as "illusory motion in a direction different from the retinal-image motion," i.e. producing perception of motion components at a right-angle direction to the retinal-motion direction (Gori & Hamburger, 2006; Ito, Anstis, & Cavanagh, 2009; Pinna & Brelstaff, 2000). The other illusions category is "illusory motion in the direction parallel to the retinal-image motion." For example, the swinging-motion illusion (Khang & Essock, 2000) produces illusory motion arising in an opposite direction to eye movement direction. The Filehne illusion (Filehne, 1922) also produces illusory motion in the direction opposite to the pursuit direction. An illusion of floating motion (Figure 1 [bottom] in Pinna & Spillmann, 2002) and a kind of sliding-motion illusion (Figure 5 in Pinna & Spillmann, 2005) are rare examples of illusory motion produced in the same direction as the eye movement direction. The pursuit-pursuing illusion (Ito, 2012) should be classified in the latter category, i.e. illusory motion in the direction parallel to the retinal-image motion as the pursuit eye movement (Ito, 2012; see reviews in Kitaoka & Ashida, 2007).

The pursuit-pursuing illusion (Ito, 2012) is a visual illusion where a circular object placed in the centre of a radial pattern consisting of thin sectors is seen to move in the pursuit eye movement direction. Figure 1a presents an example of the typical stimulus that produces this illusion. A yellow disc is placed on a radial pattern consisting of 30 thin dark-grey "sectors" (although, strictly speaking, the sectors were not true sectors on the screen because they were partially occluded by a disc) on a light-grey field. When one pursues a moving target with one's eyes observing the stimulus figure in peripheral vision, the yellow disc is seen to move in the same direction as the pursuit direction as shown in Figure 1a (a PowerPoint file to demonstrate the illusion can be downloaded from http://www.design.kyushu-u.ac.jp/~ito/IOM.ppt). During the pursuit of a moving target, extraretinal signals indicating eye movement contribute to perceiving the stability of the sector pattern in the visual field, cancelling the retinal motion signals. At the same time, the extraretinal signals seem to contribute

[¶] Current affiliation: Hitachi, Ltd. Information & Telecommunication Systems Company, Marunouchi Center Building, 6-1, Marunouchi 1-chome, Chiyoda-ku, Tokyo, 100-8220, Japan.



Figure 1. Schematic illustration of the pursuit-pursuing illusion. (a) indicates illusory motion and its direction (broken arrow) during smooth pursuit eye movement tracking a horizontally moving target. (b) indicates illusory stability/illusory motion in a direction opposite to physical motion during the fixation of a stationary target. In each case, an illusion arises in a direction that is opposite to the retinal-motion direction.

to perceiving the motion of the disc in the same direction as the pursuit direction (see Wertheim, <u>1994</u>, for a review on illusions caused by interactions between retinal and extraretinal signals). However, this illusion can also appear as an illusion of perceived stillness against physical motion (Figure 1b). When one fixates on a point and the radial pattern with a disc slowly moves in a particular direction, the disc is perceived as stationary in the visual field or as moving in a direction opposite to the physical motion (see also Ito, <u>2012</u>). In this case, the extraretinal signals do not play a role. Thus, although the existence/nonexistence of the extraretinal signals changes the illusion's appearance, the essence of this illusion may be an illusory motion in a direction that is opposite to its physical motion on the retina. This point is again discussed in the General Discussion. One way to quantitatively measure the effect is to move the stimulus figure instead of moving the eyes. However, the fine radial sectors were not seen to move smoothly on a PC display; the artefact in wrong apparent motion caused by the monitor refresh and/or image persistence on the display reduced the quality of the illusion. More importantly, subjective stillness was more difficult to quantitatively measure than subjective motion. Therefore, we measured the illusory motion while moving the eyes using a stationary figure displayed with little flicker on an LCD screen.

Ito (2012) described the features of the pursuit-pursuing illusion; that is, (1) the illusory motion occurs in an opposite direction to the retinal-motion direction (i.e. the same direction as the pursuit eye movement), (2) the centre disc does not move when the sheet on which the radial patterns are printed is rotated (illusory stillness against physical motion, see also Figure 2 in Ito, 2012), (3) the effect does not change with pursuit direction (no anisotropy in the effect) because the radial pattern has virtually no orientation and (4) despite the radial stimulus configuration, this illusion needs one-dimensional retinal motion, not expansion/contraction of the stimulus pattern (e.g. "Pinna and Brelstaff illusion," Pinna & Brelstaff, 2000; "the Rotating-Tilted-Line illusion," Gori & Hamburger, 2006; "the Breathing Light Illusion," Gori & Stubbs, 2006; "the accordion grating illusion," Gori,



Figure 2. A radial pattern that produces the pursuit-pursuing illusion and assumed receptive fields of the relativemotion detectors: (a) typical radial stimulus; (b) model of a relative-motion detector with a central excitatory field accompanying a circularly inhibitory surround; (c) model application to the illusory figure (note that the left and right surround areas slightly signal motion when the retinal motion is horizontal); (d) assumed receptive field of a modified relative-motion detector tested in Experiment 3 and (e) another type of receptive field with bilateral inhibitory regions along the motion direction.

Giora, Yazdanbakhsh, & Mingolla, 2011). This is also different from those that do not need explicit physical motion of the stimulus image (e.g. "Enigma," Leviant, <u>1982</u>, <u>1996</u>; "MacKay Rays," MacKay, <u>1957</u>; "Ouchi illusion," Ouchi, <u>1977</u>, Spillmann, <u>2013</u>; "the Rotating Snakes," Kitaoka, <u>2003</u>). The strength of the pursuit-pursuing illusion is determined by several factors (Ito, <u>2012</u>). The best illusion occurs when (1) the centre yellow disc is equiluminant with the average luminance of the surround, (2) the luminance contrast between the dark sectors and the light background is high, (3) the diameter of the radial pattern is more than twice as large as the disc diameter and (4) the number of the sectors is around 30.

One of the proposed hypotheses for the illusion (Ito, 2012) is that a centre-surround relativemotion (or motion-contrast) detector (Figure 2b) produces an illusory motion component of the centre disc. The centre-surround antagonism for motion in V5/MT cells has been investigated physiologically and psychophysically (Allman, Miezin, & McGuinness, 1957; Born & Tootell, 1992; Born, Groh, Zhao, & Lukasewycz, 2000; Murakami & Shimojo, 1996; Shioiri, Ono, & Sato, 2002; Tadin, Lappin, Gilroy, & Blake, 2003; Tadin, Silvanto, Pascual-Leone, & Battelli, 2011; Takemura, Ashida, Amano, Kitaoka, & Murakami, 2012; van der Smagt, Verstraten, & Paffen, 2010). The typical receptive field of the detector consists of a classical receptive field for motion and the surround inhibitory area as shown in Figure 2b. The radially arranged sectors always include sectors in an orientation orthogonal to the retinal-motion direction irrespective of the eye movement direction. This results in strong motion detection in the surround area. In contrast, motion of the centre disc is weakly detected because the disc is equiluminant with the surround. Thus, the combination of the strong motion signals in the surround and the weak motion signals in the centre may activate the centre-surround relativemotion detector (Figure 2c). This may produce the illusory motion of the centre disc in the same direction as the pursuit eye movement direction. In this study, we examined this hypothesis manipulating the characteristics of the surrounding texture.

Experiments 1 and 2 tested the illusory effect when the radial surround was replaced by stripes or random dots. The radially arranged surround always included not only sectors in an orientation orthogonal to the retinal motion but also sectors in an orientation nearly parallel to the retinal motion. When the entire surround area was filled with orthogonal stripes or random dots, the detected motion signal would be much stronger than that when the surround area was filled with radially arranged sectors. In contrast, when the orientation of the surround area would be markedly weaker. According to the centresurround relative-motion detector hypothesis, we could expect that in the former orthogonal-stripe or random-dot condition the illusion would be stronger than that in the radially surround condition and that in the latter parallel-stripe condition the illusion, if any, would be weaker.

Through the experiments here, we examined the centre-surround relative-motion detector hypothesis and its variant for the pursuit-pursuing illusion. If motion detection in the surround areas is critical for the illusion, a radial pattern may not be the best surrounding texture for the illusion.

2 Experiment 1

2.1 Method

2.1.1 Participants

Eight graduate or undergraduate students (aged 22–27, six males and two females) participated in Experiment 1. Before formal data collection, an experimenter confirmed that each participant perceived the illusory motion in a typical stimulus that was considered to robustly produce the effect. All participants had normal or corrected-to-normal visual acuity and gave informed consent before taking part in the experiments. None of them knew the purpose of the experiment.

2.1.2 Apparatus and stimuli

The stimuli were produced by a computer (Dell Inspiron 580s) and displayed on a 24-inch LCD monitor (Eizo, FlexScan SX2462w). The screen area used was 32.5 cm (horizontal) \times 32.5 cm (vertical), treated as a 1,200 \times 1,200 pixel matrix. The screen subtended 49.8 (H) \times 49.8 (V) deg in visual angle at a viewing distance of 35 cm. As shown in Figure 3, at the top of the screen, we presented three standard-stimulus figures with radially arranged sectors. In each figure, a yellow disc was placed in the centre of 30 radial sectors on a light-grey background. The thickness of the sectors

decreased towards the centre, maintaining the duty ratio at 50% along centric paths (see Figure 2a). The diameters of the disc and the radial pattern were 5.9 deg and 16.6 deg in visual angle. The disc luminance was 103.5 cd/m^2 . The sector and background luminances were 69.7 and 137 cd/m^2 , respectively. At the bottom of the screen, we presented three test stimulus figures with varied surround stripes or plain backgrounds.

In the stripe conditions, the orientation of the surround stripes was horizontal or vertical. The width of the dark/light area in the stripe was varied in five, i.e. from 0.31 to 0.87/deg in a 50% duty ratio, corresponding to the narrowest or the widest part of the dark sector of the standard stimulus.

In addition, three plain surround conditions were tested. Luminances of the three surrounds were 137, 69.7 and 103.5 cd/m², which corresponded to the luminances of the stripe conditions' light background, the dark sectors and the average of the two, respectively. A control stimulus that was the same as the standard stimulus was also tested with the same procedure as used in the other conditions.

In <u>Figure 3</u>, the centre dot that subjects tracked moved horizontally between the standard (upper) and test (lower) stimuli. Under the vertical eye-movement conditions, the entire stimulus set was rotated at 90 deg.

2.1.3 Procedure

At the top of the screen, the standard stimuli (radial condition) were presented and at the bottom of the screen, the test stimuli were presented. A fixation dot (1.3 deg in diameter) was presented in the centre of the screen. As shown in Figure 3, one second later, the fixation dot moved along a horizontal or vertical path (21.8 deg in length) at a speed of 10.9 deg/s. Subjects tracked the dot with their eyes keeping their head fixed by a chin rest. After 16 seconds (four sets of round trips), the dot stopped and participants evaluated the strength of the illusory motion that appeared in the test stimulus. The illusion rating of 100 was defined as the score when the illusion strength in the test stimulus was the same as that in the standard stimulus, whereas 0 was defined as the score when no illusory motion



Figure 3. Schematic illustration of the experimental condition in Experiment 1. The centre dot indicates the tracked target moving horizontally. The upper radial patterns indicate standard stimuli. The lower patterns indicate a test condition.

perception occurred. Over a 100- or under a 0-score (i.e. the illusory motion in the opposite direction) was permitted for the rating.

There were 20 stripe conditions (5 grating widths \times 2 grating orientations \times 2 eye movement directions), six plain surround conditions (3 luminance levels \times 2 eye movement directions) and one control condition (the same figure as the standard stimulus). These were presented in a random order once per session. Four sessions were conducted for each participant.

2.2 Results and discussion

Figure 4 presents the results of Experiment 1. As the figure clearly shows, in the vertical eye-movement conditions, the illusion strength was higher in the horizontal-stripe condition than in the vertical-stripe condition. Inversely, in the horizontal eye-movement conditions, the illusion strength was higher in the vertical-stripe condition than in the horizontal-stripe condition. Thus, when the stripe orientation and the eye movement direction were orthogonal, the illusion was strong. Conversely, when they were parallel, the illusion barely appeared (the scores were around 0).

The thinner stripe width had a higher rated illusion strength within the range tested. This was true for both the vertical eye-movement horizontal-stripe condition and the horizontal eye-movement vertical-stripe conditions. However, in the thinnest condition, the effect seems to reach the ceiling.

The effects under the plain background conditions changed depending on the luminance in the surround area. When the surround was dark grey, i.e. in the same luminance as that of the dark stripes, no illusion occurred. When the surround was in the average luminance of the dark stripes and the light background in the stripe conditions, the strength of the illusion was slightly evident (this equiluminant



Figure 4. Results from Experiment 1. Error bars indicate standard errors of the mean (SEs). Stripes in an orientation that was orthogonal to the eye movement direction, especially in thin stripe conditions, produced strong motion illusions while stripes in an orientation that was parallel to the eye movement direction did not produce the illusion irrespective of the thickness. Homogeneous background conditions did not clearly produce the illusion or even produced the opposite illusion. In no condition was the strength of the pursuit-pursuing illusion as strong as in the control condition.

plain background condition was tested again in Experiment 4). When the surround was white, i.e. in the luminance of the background in the stripe conditions, the illusion occurs in the opposite direction. This may be a type of Filehne illusion (Filehne, <u>1922</u>).

A three-way ANOVA was conducted for the results in the stripe conditions to analyse the effects of the direction of eye movement (horizontal or vertical), the orientation of the stripes (parallel or orthogonal to eye movement direction) and the width of the stripes. The main effect of the stripe orientation was significant (F(1, 7) = 138.668, p < 0.0001). Although the main effect of the eye movement direction was not significant (F(1, 7) = 4.048, p > 0.05), the interaction between the effect of the stripe orientation and the effect of the eye movement direction was significant (F(1, 7) = 7.227,p < 0.05). A simple main effect of the eye movement direction in the orthogonal-stripe condition was significant (F(1, 14) = 11.240, p < 0.01), while that in the parallel-stripe condition was not significant (F(1, 14) = 0.558, p > 0.05). This may occur because no illusion occurred under the parallelstripe conditions. The difference in the rated illusion strength between the vertical- and horizontal eye-movement direction conditions may be due to the smoother pursuit or the larger amplitude in the eye tracking path in the horizontal eye-movement conditions. In both conditions, there was a standard stimulus with radially arranged sectors. However, the illusion strength rating may be partly affected by the overall experimental sequence, resulting in the lower ratings in the vertical eye-movement conditions. The effect of stripe width was significant (F(4, 28) = 23.592, p < 0.0001). The interaction between the effects of stripe width and orientation was significant (F(4, 28) = 17.427, p < 0.0001). This is clearly seen in Figure 4, i.e. the strength of the illusory effect changed according to the stripe width in the orthogonal orientation conditions while there was little illusion irrespective of the stripe width in the parallel orientation conditions. Multiple comparison tests (Ryan's method) revealed that there were significant differences (p < 0.05) between all the pairs of width conditions with orthogonal stripes except the pair of the thinnest and the second thinnest stripe conditions. The effect seems to reach the maximum possibly when the stripe is thinner than 0.47 deg, whereas the illusion was weaker when the stripes are thicker than that. The illusion ratings from the 0.31 deg stripe conditions were compared with the rating of the control stimulus conditions. The difference between them was significant (t(7) = -5.478, p < 0.0001, for vertical eye movement; t(7) = -4.474, p < 0.01, for horizontal eye movement). Even when the stripes that were orthogonal to the motion direction filled the entire surround area, the illusion was still weaker than that with the radial sector surround.

Two contradicting results were acquired in Experiment 1. First, motion detection in the surround is important for the illusion because only surround stripes in an orientation orthogonal to the motion direction cause the illusion. Ito (2012) demonstrated that the increasing luminance contrast between the sectors and the background positively affected the strength of the illusion and that increasing the length of the sectors also affected it positively. These results suggest that increasing motion signals in the surround increases the illusion strength, which fits the centre-surround relative-motion detector hypothesis. A similar tendency of peripheral-stripe-orientation dependency, as seen in Experiment 1, was found in the strength of the Enigma illusion (Gori, Hamburger, & Spillmann, 2006). Gori and colleagues showed that the illusory stream motion was strongest when the stripe orientation was orthogonal to a band in which the illusory stream was perceived. Hamburger (2007) also showed the importance of orthogonal stripes in inducing the Enigma illusion. In our stimulus, both horizontal and vertical stripes were partly orthogonal to the edge of the centre disc; only vertical stripes were orthogonal to the motion direction when eye movement direction was horizontal. We are interested in the similarity between the pursuit-pursuing illusion and the Enigma illusion (Ito, Tomimatsu, & Bai, 2012) and, inversely, we think we can propose an explanation of the Enigma illusion from the point of the relative-motion detector (Tomimatsu & Ito, 2012).

Second, only the amount of motion signals in the surround area does not determine the illusion strength because the illusion with the orthogonally striped surround never exceeds the effect produced by the radial surround, which the hypothesis cannot explain. However, the present experiment demonstrated that although stronger motion signals by the surround filled with orthogonal stripes actually enhanced the illusion, compared to the parallel stripe surround, the motion signals from the radial sector pattern were more effective than those from the orthogonal striped patterns. The difference may be critical for the illusion.

As for the stripe width, the thinner stripes produced stronger effects. Comparing the disc and the stripe, the two had different spatial frequency components, i.e. the stripe had higher frequency components than the disc. This difference might give the impression of having different velocities,

i.e. the disc being slower, which could produce effective relative motion between them. Accordingly, the higher spatial frequencies of the surround may have enhanced the relative motion. However, this hypothesis cannot explain the strongest effect of the radially arranged sectors.

Interestingly, the stimulus proportion for the best illusion using stripes is similar to that for the Ouchi illusion (Ashida, 2002). When the sizes of our stimulus were calculated for a left or right (i.e. peripheral) stimulus patch where the illusion was stronger than the centre patch, they were 16.0 deg for the stripe pattern and 5.7 deg for the centre disc. In that case, the thinnest stripe had a spatial frequency of 3.3 c/deg. In Ashida (2002), when the outer disc size was 16 deg and the inner disc size was 6 deg for a stripe version of the Ouchi illusion stimulus, the optimal spatial frequency was 3.4 c/deg. Although our stimulus was generally considered to be observed in more peripheral vision (typically 23.6 deg in eccentricity) than Ashida (2002), it is surprising that the best proportions of the striped figures were similar. This may suggest that the surface segmentation process suggested by Ashida (2002) is common between the two illusions when both illusion stimuli are produced by striped patterns. As seen in the Ouchi illusion, the centre disc in the present illusion is perceived as floating when the illusion is strong.

3 Experiment 2

In Experiment 2, we tested the relative-motion detector hypothesis again with a different surrounding texture, i.e. random dots. Motion could be detected in every local part of the surround, the same as for the surround filled with vertical stripes in horizontal motion.

3.1 Method

3.1.1 Participants

Eight students (aged 22–24, four males and four females) participated in Experiment 2. Seven of them participated also in Experiment 1. All participants had normal or corrected-to-normal visual acuity, and gave informed consent before volunteering in the experiments. None of them knew the purpose of the experiment.



Figure 5. Results from Experiment 2. Error bars indicate SEs. Generally, the illusion ratings for random-dot conditions were very low compared with the ratings for the control condition. The ratings in the random-dot conditions were highest for the smallest dot-size condition. However, even this condition produced a weaker effect than the vertical-stripe conditions in Experiment 1.

3.1.2 Apparatus and stimuli

The apparatus was the same as in Experiment 1. Stimuli were a yellow disc on random dots. The horizontal and vertical dot size was varied corresponding to the stripe widths used in Experiment 1 as shown in Figure 5. Half of the dots were dark grey and the other half white. Their luminances were the same as those of the stripes and the background in Experiment 1. The two standard stimuli (the left and right radial figures in the top row in Figure 3) were placed at the top of the screen while two tested stimuli were presented at the bottom (i.e. at the positions of the left and right radial figures in the bottom row in Figure 3). The other methods were the same as those in Experiment 1.

3.1.3 Procedure

There were six stimulus conditions, i.e. five dot-size conditions and a control condition. The six conditions were tested once per session in a random order. Four sessions were conducted for each participant. After the data collection, a further small dot-size condition (the 0.16 deg condition) was additionally tested.

3.2 Results and discussion

The results are shown in Figure 5. As a whole, the ratings of the illusion strength were very low compared with the control condition. These results again do not fit the centre-surround relative-motion detector hypothesis. The differences among the ratings under the seven conditions were analysed by a one-way ANOVA. The main effect was significant (F(6, 42) = 97.675, p < 0.0001). Multiple comparisons (Ryan's method) revealed that the ratings under the smallest dot-size condition were higher than those under the other dot-size conditions (p < 0.05) and that the ratings under the control condition were higher than those under the all dot-size conditions (p < 0.05).

Within the tested dot sizes, the illusion favoured a smaller size. The smallest dot size here was smaller than the width of the thinnest stripes in Experiment 1 and thinner than the thinnest part of the sector used in the standard stimulus. With further smaller dots, the surround texture may become perceptually grey and not produce strong motion signals (approaching the equiluminant grey condition in Experiment 4). However, the larger dots seem to weaken the illusory effect. We believe that random dots in a larger dot size broke local equiluminance around the disc edge, which inhibited the illusion from occurring. Another explanation is that the larger random dots were perceived as groups of subparts of textured areas. Giora and Gori (2010) reported that a smaller dot size or a random dot pattern as a filled texture reduced the filled area illusion, compared with a larger dot size or a regular checker pattern. In the filled area illusion, the perceptual area enlargement was reduced with a weaker subparts' articulation while the present illusion was reduced with a background perceptually divided into groups of subparts. It is possible that a background consisting of groups of subparts interferes with the perception of the figure-ground relationship between the disc and the background random dots because some subparts of the random dot texture could be a figure. In the case of the background of radially arranged sectors, the sectors are clearly distinguishable and enhance the illusion when the contrast is high (Ito, 2012). However, even in that case, the sectors are indistinguishable just around the sectors, producing the impression of figure-ground relationship between the disc and the sectored background. As in Experiment 1, a difference in spatial frequency between the disc and the dots could explain why the smaller dots produced a stronger effect. However, this factor cannot explain why dots cannot produce the illusory effect as strongly as a stripe or radially arranged sectors.

The weakness of the illusion in the random-dot condition, compared with the striped background condition, is also seen in the Enigma illusion (Hamburger, 2007). One of the reasons for the random dots not producing a strong illusory effect may be that the centre disc was seen as being attached to the surround, possibly because there was no T-junction or end-stop of the surrounding texture at the disc contour. This explanation may be common to Hamburger (2007) or Gori et al (2006). In contrast, the stripes created T-junctions at the disc edge, which may have produced the impression of the disc being in front of the stripes. In addition, the radially arranged sectors created more T-junctions that touched the disc contour orthogonally. The difference in their appearance, i.e. attached or floating, was common with that caused by the difference in sector length (Ito, 2012), where short radial sectors appeared as attached to the centre disc that seemed to be floating in front of it and caused a strong illusion. It is possible that, in addition to motion detection in the surround areas, the perceived figure–ground relationship produced by the end-stops of stripes or radially arranged thin sectors affects the illusion.

The figure–ground relationship and perceived depth separation as a determinant of an illusory motion effect is also reported by Pinna and Spillmann (2002).

4 Experiment 3

The stripes in an orientation orthogonal to the motion direction produced an illusory effect while the stripes in an orientation parallel to the motion direction did not contribute to the illusion in Experiment 1. However, a radially arranged sector pattern including sectors in both orientations produced the strongest illusion. Accordingly, we propose a modified hypothesis that the combination of the surround stripes in both orientations could produce a stronger illusion than do the whole-field orthogonal stripes, as seen in the radial sector stimulus. Particularly, when the eye movement was horizontal, the combination of the vertical stripe in the top and bottom areas of the test stimulus and the horizontal stripes in the left and right areas could produce the illusion as strongly as seen in the radial sector stimulus. We hypothesize that the radial sectors could be replaced by the two components in orientations both orthogonal and parallel to the motion direction. This stimulus configuration may fit a receptive field of a modified relative-motion detector shown in Figure 1d. In this model, horizontal motion is strongly detected in the top and bottom areas because the stripes are vertical, whereas motion is weakly detected in the middle area (between the top and bottom areas) because the sectors in the middle area to the disc is equiluminant with the surround. Experiment 3 is aimed to test the modified relative-motion detector hypothesis.

4.1 Method

4.1.1 Participants

Seven graduate or undergraduate students (aged 22–25, four males and three females) participated in Experiment 3. Five also participated in Experiment 1 while the others did not. All participants had normal or corrected-to-normal visual acuity, and gave informed consent before volunteering in the experiments. None of the participants knew the purpose of Experiment 3.

4.1.2 Apparatus and stimuli

The apparatus was the same as that in Experiment 1. We divided the surround into four equal sector areas as shown in Figure 6a. The top and bottom areas were paired, the left and right areas were paired, and each paired area was filled with averaged luminance grey, horizontal stripes, vertical stripes or radial sectors; thereby, producing 16 combined surrounds. The horizontal or vertical stripe was the same as the thinnest one used in Experiment 1, which produced the strongest illusion among the orthogonal-stripe conditions. The radial sectors were the same as the control stimulus used in Experiment 1.

4.1.3 Procedure

The eye movement direction was horizontal in all trials. The black dot to be tracked moved leftward for 2 seconds and then reversed direction. The round trip was repeated three times, i.e. the participants observed the stimulus for 12 seconds. Then, participants judged the illusion strength as in Experiment 1.

One session included 16 trials (4 surround patterns in the top-bottom area \times 4 surround patterns in the left-right areas). Four sessions were conducted for each participant. The order of the trials was randomized within each session. The remaining procedure was the same as in Experiment 1.

4.2 Results and discussion

Figure 6 presents the results of Experiment 3. The graph clearly shows that grey or horizontal stripes slightly contributed to producing the illusion, that vertical stripes modestly contributed and that radial sectors greatly contributed. These effects did not depend on the presented area, i.e. the top-bottom or left-right areas. The illusion produced by the radial surround was stronger than that produced by any other combination of the textures tested here.

A two-way ANOVA was conducted to analyse the effects of the surround. The main effect of the four types of surround in the top-bottom area was significant (F(3, 21) = 85.943, p < 0.0001). Multiple comparisons (Ryan's method) revealed that the difference between every pair of the four types of surrounds was significant (p < 0.05) except the pair of grey and horizontal surrounds (p > 0.05). The main effect of the four types of surround in the left-right area was significant (F(3, 21) = 47.111,



Figure 6. Tested stimuli and the produced illusion strength. The stimulus matrix in the left panel corresponds to the condition matrix in the graph in the right panel. Thin black lines above the bars indicate SEs.

p < 0.0001). Multiple comparisons (Ryan's method) revealed that the difference between every pair of the four types of the surrounds was significant (p < 0.05) except the pair of grey and horizontal surrounds (p > 0.05). Moreover, the interaction of the two main effects was significant (F(9, 63) = 6.685, p < 0.0001), revealing that the combination of radial sectors in both areas prominently enhanced the illusion.

To further analyse the position effect, we compared the following stimuli: horizontal stripes, vertical stripes or radial sectors in the left-right areas combined with the grey field in the top-bottom areas versus horizontal stripes, vertical stripes or radial sectors in the top-bottom areas combined with the grey field in the left-right areas. A two-way ANOVA revealed that although the effect of the surround types (the horizontal stripe, vertical stripe or radial sectors) was significant (F(2, 14) = 24.026, p < 0.0001), the effect of the presented position (the left-right areas or the top-bottom areas) was not significant (F(1, 7) = 1.445, p > 0.05). The interaction of the two main effects was not significant (F(2, 14) = 2.008, p > 0.05). These statistics suggest that the surround pattern equally contributes to the illusion irrespective of the presented area. It is noteworthy that although the orientations of the radial sectors in the left-right areas were near to the horizontal, i.e. the parallel orientation to the motion direction, the effect was stronger than that of the vertical stripes.

We could make a simple model to predict the strength of the illusion appearing in a combined surround condition by adding the two illusory effects from each area. For example, the illusion strength in a combined surround consisting of vertical stripes at the top and bottom areas and horizontal stripes at the left and right areas might be predicted by the addition of illusion strength produced by vertical stripes at the top and bottom areas at the top and bottom areas with plain grey areas at the left and right and illusion strength produced by horizontal stripes at the left and right areas with plain grey areas at the top and bottom. Figure 7 presents a correlation between the rated illusion strength under the combined surround conditions and the sum of rated illusion strength under each half-surround condition. The coefficient of determination was 0.92, indicating that 92% of variation in the illusion strength ratings in the combined surround condition. This indicates that there is little interaction between the two combined surround condition. This indicates that there is produces no new effect.



Addition of Ratings for Each Component

Figure 7. Correlation between illusion ratings from combined-texture surround conditions and addition of ratings from each texture surround condition. The illusion strength under the combined-texture conditions can be predicted by simple addition of the effect of each texture component. See details in the text.

In Experiment 3, we proposed the modified hypothesis that the combination of the surround components in two orientations orthogonal or parallel to the motion direction could replace the radial pattern. The assumed underlying mechanism was a modified version of the relative-motion detector shown in Figure 2d. Despite the results of Experiment 3 having rejected that hypothesis, they did demonstrate that even the radial sector pattern in the left and right areas contributed to producing the illusion although the sector orientations in the areas were nearly parallel to the motion direction when eyes move horizontally.

5 Experiment 4

Experiment 4 quantitatively measured the strength of the illusory effect. The experiments noted above used a magnitude estimation method to test the illusion. Therefore, strictly, the illusory strength measured so far was limited to indicating the relative effectiveness among the tested stimulus conditions. Here, the illusion strength with various kinds of backgrounds was measured by comparing real and illusory motions to quantitatively show the amount of the illusion. In this experiment, the point of each participant's individual equiluminance between yellow and mid-grey was measured and used to set the luminance condition for each participant to see the best illusion.

Another purpose of Experiment 4 was to assess the contribution of equiluminance to the pursuitpursuing illusion. Ito (2012) showed that the pursuit-pursuing illusion was best observed when the luminance of the yellow disc was equal to the average of the sector and background luminances while the illusion robustly arose even if the yellow disc luminance was apart from the precise equiluminance. On the other hand, equiluminance itself could produce a similar motion illusion (Terao & Murakami, 2011). It is possible that an individual best equiluminance setting drastically increases the illusory effect in the plain surround condition because the illusion with an equiluminant plain surround would be quite sensitive to the difference between the disc and surround luminances. If the illusion strength was equal between the radially arranged sector and plain surround conditions in this luminance between the disc and its surround and that the only role of the surround texture is to increase the tolerance to the difference between the disc and the average surround luminances.

5.1 Method

5.1.1 Participants

Six graduate or undergraduate students (aged 22–25, three males and three females) including the first author participated in Experiment 4. Four participants also participated in at least one experiment noted above. Aside from the first author, no participants knew the purpose of the experiment.



Figure 8. Schematic illustration of the stimulus configuration. The horizontally moving dot was tracked by eyes. The matching disc moved horizontally in phase with the dot. The amplitude of the physical motion of the disc was varied.

All participants had normal or corrected-to-normal visual acuity, and gave informed consent before volunteering in the experiments.

5.1.2 Apparatus and stimuli

The apparatus was the same as that in Experiment 1. The luminances of the background and the sectors were 137 cd/m² and 69.7 cd/m². The participants sat on a chair with a chin rest and tracked a black dot with their eyes at a viewing distance of 35 cm.

Figure 8 shows the schematic illustration of the stimulus display. In the centre of the screen, a horizontally moving black dot was presented, which participants tracked with their eyes. The translation speed was 10.9 deg/s. The length of the horizontal path was 21.8 deg. In the left-lower part, a static stimulus figure was presented. There were five background texture conditions; radially arranged sectors, vertical stripes, horizontal stripes, random dots and the equiluminant plain background. The diameter of the whole radial shape was 16.6 deg and that of the central disc was 5.9 deg. The width of the stripes and dots was 0.31 deg. The distance between the centre of the stimulus disc and the centre of the horizontal path of the dot motion was 28.0 deg.

In the lower-right part, a horizontally moving yellow disc was presented. The phase was matched with that of the tracking target. The length of the horizontal path of the physical motion of the disc could be changed from 0 deg to 11.75 deg in 0.59 deg steps (from 0% to 200% of the disc diameter with 10% steps). The diameter and the luminance of the physically moving disc were identical to that in the illusory figure. The distance between the stimulus disc and the centre of the physical motion path of the compared disc was 30.4 deg.

5.1.3 Procedure

Before measuring the illusion, an individual equiluminance was set where the yellow disc luminance was effectively equated to the averaged luminances of the surrounding grey (103.5 cd/m², i.e. the average of the sector and background luminances) by heterochromatic flicker photometry. During the measurement of equiluminance, participants fixated a cross presented at the centre of the horizontal path of the dot motion to be tracked. The yellow and grey squares were alternated at 10 Hz in the screen position where the stimulus was presented. Keeping their fixation on the cross, the participants adjusted the yellow luminance by button pressing to minimize the perceived flicker. Four measurements were conducted for each participant. The average of the measured values was used to set the yellow disc luminance for each participant.

The amount of the illusion was measured with a method of limits. Participants judged which motion impression was stronger, the physical motion of the matching disc or the illusory horizontal motion, while tracking the physically translating dot with the eyes, as shown in Figure 8. Six meas-



Figure 9. Matched path length of physical motion to produce subjectively equal motion impressions to the illusory motion. Error bars indicate SEs.

urements including ascending and descending series within a range of 0 to 11.75 deg with a step of 0.59 deg were conducted under the five background texture conditions for each participant.

5.2 Results and discussion

As clearly seen from Figure 9, the results show that the radially arranged sector condition produced the strongest illusion, followed by the vertical-stripe condition. We can see the effect of equiluminance itself in the plain surround condition. While the individual equiluminance setting disclosed the effect, the illusion strength was not strong compared to that in the other conditions. A one-way ANOVA revealed that the effect of the surround textures was significant (F(4, 20) = 36.619, p < 10000.0001). Multiple comparisons (Ryan's method) revealed that all pairs, except for the pair of the horizontal-stripe and plain surround conditions and the pair of the random-dot and plain surround conditions, showed significant differences (p < 0.05). These results are consistent with the results acquired from Experiments 1 and 2. That is, the radially arranged sectors produced the best illusion, followed by the vertical-stripe condition, while the horizontal-stripe and plain-surround conditions produced slight effects (Experiment 1). The illusion strength in the random-dot condition was between the vertical-stripe and horizontal-stripe (or plain surround) conditions in their rated values (Experiment 2). The little effect of equiluminance in the previous experiments is explained by the differences in individual equiluminance point and by the contrast in illusion strength between the plain surround condition and the radially arranged sector condition (as a standard stimulus). The illusion arising under the horizontal-stripe condition in Experiment 4 may come from the equiluminance between the disc and the average surround luminances. However, the effects found in the radially arranged sector and vertical-stripe conditions were much larger than that in the plain surround condition and, therefore, cannot be explained only by the effect of equiluminance. On the other hand, the illusion found in the radially arranged sector and vertical-stripe conditions may be also enhanced by the individual equiluminance setting.

In short, the results of the subjective ratings were quantitatively confirmed here. The effect of equiluminance itself actually existed but was not so strong as to explain the pursuit-pursuing illusion. In other words, the effect of equiluminance is one component of the pursuit-pursuing illusion. A striped surround may add a factor of relative motion. The radially arranged sectors may add a further figural factor.

6 Experiment 5

We conducted two additional experiments, Experiments 5 and 6. Experiment 5 investigated the effect of oblique components. One possible difference between the radial pattern and the tested stripes in Experiments 1 and 3 is the existence of oblique components. In some illusory motion figures, motion components that are detected in an oblique orientation and the aperture problem for the oblique motion seem to be important to produce illusory motion that is orthogonal to the retinal motion. For example, the Pinna–Brelstaff illusion (Pinna & Brelstaff, 2000) is considered to be induced by detected oblique motion components owing to the implicit figural oblique components in the micropattern (Gurnsey, Sally, Potechin, & Mancini, 2002; Gurnsey & Pagé, 2006). In the Rotating-Tilted-Line illusion, lines that are oblique to motion directions explicitly exist (Gori & Hamburger, 2006; Gori & Yazdanbakhsh, 2008; Yazdanbakhsh & Gori, 2008). Ito et al. (2009) showed some illusions caused by motion detection in an oblique orientation. The recently discovered accordion grating illusion (Gori et al., 2011; Gori, Giora, Yazdanbakhsh, & Mingolla, 2013; Yazdanbakhsh & Gori, 2011) has been demonstrated to arise from the aperture problem for oblique retinal motion.

The radial sectors included figural components that are oblique to motion direction. These oblique figural components may induce motion detection in oblique directions that could be ambiguous in the interpreted motion direction owing to the aperture problem for motion. Experiment 5 investigated whether the radial sector pattern could be replaced by a combination of oblique stripes.

6.1 Method

Eight graduate or undergraduate students (aged 22–24, four males and four females) participated. Six also participated in at least one experiment described above while the others did not.

The surround area was divided in four, i.e. top-left, top-right, bottom-left and bottom-right areas. The stimuli were presented in Figure 10. In all conditions, the width of the oblique stripe was the same as the thinnest one used in Experiment 1. The seven stimuli were tested in two eye movement directions, i.e. left to right or right to left, because four of the seven stimulus figures were not horizontally symmetrical. The other methods were the same as those in Experiment 2.



Figure 10. Effects of oblique stripes on the illusion. Error bars indicate SEs. Combinations of oblique stripes cannot produce the illusion at an adequate strength.

6.2 Results and discussion

Results indicate that any of the stimulus figures with oblique stripes could not match the illusory effect of the control figure, i.e. the ratings never exceeded 40. Particularly, in the Diamond condition, little illusion was reported. The most important figural characteristic of the Diamond figure would be that the oblique stripes in it touched the disc almost in parallel to the disc contour. The centre disc was seen as being fused to the oblique lines in the Diamond figure, whereas the centre disc in the pseudo-radial figure was seen as being in front of the oblique stripes. Clear T-junctions and perceptual depth separation of the disc from the surround might be one of the factors that enhances the illusion as previously noted.

A two-way ANOVA shows that the main effect of the seven stimulus types was significant (F(6, 42) = 60.327, p < 0.001). Multiple comparisons (Ryan's method) revealed that there were significant differences between the control and the other conditions (p < 0.05) and between the pseudo-radial and the Diamond conditions (p < 0.05). The other pairs did not show any significant differences (p > 0.05). The main effect of eye-movement direction was not significant (F(1, 7) = 2.978, p > 0.05). The interaction between the two factors was not significant (F(6, 42) = 1.367, p > 0.05). These results suggest that the radial sector pattern cannot be replaced by a combination of oblique stripes in two orientations perpendicular to each other.

Experiment 3 demonstrated that the radially arranged sectors contribute to producing the illusion irrespective of the presented areas, and thus, the sector orientations. Even the sectors in an orientation nearly parallel to the pursuit direction contributed to the effect as well as did the sectors in an orthogonal orientation, although stripes in an orientation perfectly parallel to the pursuit direction made no contribution. Ito et al. (2012) showed that the illusion strength depended only on the percentage in the surround area where radially arranged sectors were presented irrespective of both the pursuit direction and the presented areas. This result corresponds well to the results in Experiment 3. These results suggest that the radial pattern is a special figure that cannot be replaced by combinations of stripes.

7 Experiment 6

We conducted another additional experiment to investigate the effect of the relative position shift of the yellow disc within the radial sectors on the production of the illusion. Even if the radial sectors exist as a globally structured background, the locally surrounding texture touching the disc changes with the changes in disc position on the radial pattern.



Figure 11. Results showing the effect of disc position offsets. Error bars indicate SEs. Even if the shift of the disc does not reveal the radiation centre (38% condition), the illusion is greatly reduced.

7.1 Method

Eight graduate or undergraduate students (aged 22–28, three males and five females) participated. Seven also participated in at least one experiment described above while one did not. The amount of horizontal or vertical shift in disc position was varied, i.e. 0 (the centre, i.e. control), 38% or 78% of disc diameter in a left, right, above or below direction, as shown in Figure 11. The size of the radial pattern was 21.8 deg in diameter. The other methods were the same as those in Experiment 2.

7.2 Results and discussion

When the disc was at the centre of the radial pattern, the illusion was strong. However, when the disc position was shifted, the rated illusion strength was markedly weakened. The decrease in strength was more rapid in horizontal shift conditions. A 38% shift in disc position left the centre of the radial pattern still behind the disc. However, the occlusion of the radiation centre was not a critical factor in producing a strong illusion. As the horizontal shift increased, the directly surrounding texture became similar to horizontal stripes. In contrast, as the vertical shift increased, the directly surrounding texture became similar to vertical stripes. This may explain why the illusion remained relatively strong in the 38% vertical shifted condition, whereas the discs that were 78% shifted in any direction produced a very weak illusion.

A two-way ANOVA was conducted. The main effect of shift direction (up-, down-, left- or rightward) was significant (F(3, 21) = 6.180, p < 0.01). Multiple comparisons (Ryan's method) indicated that the differences were significant for all pairs of direction conditions except the pair of upward and downward conditions and the pair of leftward and rightward conditions (p > 0.05). The main effect of the amount of shift (38% or 78%) was significant (F(1, 7) = 18.648, p < 0.01). The interaction between the two factors was also significant (F(3, 21) = 4.321, p < 0.05). The simple main effect of shift direction was significant in the 38% condition (p < 0.001), but not significant in the 78% condition (p > 0.05) where little illusory effect was perceived as seen in Figure 11.

Consequently, this experiment demonstrated that the radial sector pattern must radiate from the disc centre creating a symmetrical surround texture to produce a strong illusion. Thus, the radial texture as an illusion producer here acts not only as a global background of the disc but also as a local stimulus structure around the disc.

8 General Discussion

8.1 Summary of the results

Through the four experiments, we investigated how the surrounding texture affected the strength of the illusory motion of the centre disc, i.e. the pursuit-pursuing illusion. First, we tested a hypothesis that the centre-surround relative-motion detector caused the illusion. In Experiment 1, the stripes in an orientation orthogonal to the motion direction produced the stronger illusion than those in a parallel orientation. Although this result is consistent with the centre-surround relative-motion detector hypothesis (Figure 2c), the maximum illusion strength caused by the stripes was less than that caused by a figure with the radial sector surround. Experiment 2 tested the hypothesis again but employing random dots. The results demonstrated that the surround consisting of smaller dots produced an illusory effect, although the effect was much weaker than that of a radial sector surround. In Experiment 3, we examined a modified hypothesis that a combination of stripes in orthogonal and parallel orientations strengthened the illusion, assuming a modified receptive field of a relative-motion detector (Figure 2d). We tested various combinations of stripes and radial sectors. The results demonstrated that there was no new effect by combining the stripes and that the radial sectors produced a stronger illusion than the stripes in an orientation orthogonal to the motion direction, irrespective of the presented areas. These results showed that the motion signals in the surround area are important in causing the illusion. However, an effect as large as that obtained from the radial sector surround cannot be obtained from the surround consisting of stripes orthogonal to the pursuit direction, a combination of stripes or random dots.

8.2 Physiological correspondence

It is well known that V5/MT cells show a centre-surround antagonism for motion detection (Allman et al., <u>1985</u>; Born & Tootell, <u>1992</u>) as we assumed in Experiment 1. However, as noted above, a simple centre-surround relative-motion detector model as shown in <u>Figure 2b</u> cannot completely explain our

results. In addition, the modified model as shown in Figure 2d could not predict the results. Furthermore, another model shown in Figure 2e had difficulty in producing the effect when the motion direction is horizontal because assimilation would occur between the centre disc and the top-bottom areas, resulting in no illusion. Motion signals from the left-right areas may be weak. Probably the overlapped receptive fields of several types of cells, including cells with an asymmetric-inhibitory field, contribute to producing the illusion. In MT cells, a receptive field with an asymmetric-inhibitory surround was observed more frequently than that with bilaterally symmetric-inhibitory surrounds or that with a circularly symmetric-inhibitory surround (Xiao, Raiguel, Marcar, Koenderink, Orban, <u>1995</u>; Xiao, Raiguel, Marcar, & Orban, <u>1997</u>).

One important property of a V5/MT cell is that, under a low contrast display condition, the function shifts the surround inhibition to the spatial summation of motion signals (Pack, Hunter, & Born, 2005; Tadin et al., 2003; van der Smagt et al., 2010). We observed that our typical stimulus could produce the illusion even under a low contrast condition. Although a low contrast between the sectors and the background actually reduces the illusory effect, a simple grey surround still produces some effect. Thus, it is possible to separate the two factors to induce the illusion, i.e. the surround effect by the radially arranged background and the equiluminance between the disc and the surround. This point should be further examined by collecting quantitative data. One possible approach would be to employ an rTMS technique. Tadin et al. (2011) succeeded in reducing the surround suppression at V5 by rTMS, revealing spatial summation of motion in a large visual field. Ruzzoli et al (2011) found that rTMS targeting V5 weakened the illusory stream perception of Enigma. Whether rTMS targeting V5 also erases the present illusion or not could be a direct test of the centre-surround relative-motion detector hypothesis.

From the point of stimulus size, another approach is possible. We typically used radially arranged sector patterns 16.0 deg and centre disc 5.7 deg in diameter at an eccentricity of 23.6 deg although the eccentricity of the stimulus changed according to eye movement. The size of the excitatory centre of macaque MT cells with an inhibitory surround was reported by Raiguel, Van Hulle, Xiao, Marcar, and Orban (1995). According to them, at the eccentricity of 23.6 deg, the size is estimated as 5.6 deg. This is very close to the size of the centre yellow disc used in this study. The inhibitory surround is supposed to extend to a very wide area. It is possible to apply a model of a V5/MT cell as a centre-surround relative-motion detector to this illusion in the point of receptive field size. We have informally observed that the stimulus size (and disc size) for the best illusory effect closely relates to eccentricity. The present stimulus is not seen to move when observed in foveal vision. In parafoveal vision, the stimulus should be much smaller to produce the illusion. Distribution of optimized stimulus sizes measured at various eccentricity might be a clue to brain sites to respond to the illusion even if the relative-motion detection hypothesis is not valid. At the same time, we should consider that brain sites other than V5/MT also show centre-surround antagonism for motion and that attention can modulate the size of a classical receptive field size of V5/MT cells (Anton-Erxleben, Stephan, & Treue, 2009).

8.3 The effect of stripe width

Experiment 1 showed the effect of stripe width. This could indicate a spatial frequency tuning of the illusion-inducing mechanism. Here, we used stripes in a square-wave luminance profile. To precisely investigate the spatial frequency tuning, stripes in a sine-wave luminance profile should be used. Varying the spatial frequency together with the presented retinal position and the size of the stimulus, a certain form of magnification factor will be found. As noted in Experiment 1, the best proportion between the outer disc size, the inner disc size, and the fundamental spatial frequency of the stripe for the present illusion is similar to that of the Ouchi illusion when both illusions are produced by gratings. It is worth testing whether the most appropriate proportion producing the present illusion is constant against the eccentricity changes.

However, for radially arranged sectors, the varied width of the stripes is included in the figure because the sector width was narrow around the centre disc and wide at the periphery. Thus, it is possible that the best width of stripes is almost always found in the radial sector figure, resulting in a robust motion illusion. Random dots in the surround, however, did not cause a strong illusion despite their inclusion of various spatial frequency components in various orientations. When the dot size was large, the evenness of the local luminance distribution was broken; thereby, breaking the equiluminance between the disc and the surrounding texture. In addition, large dot size makes the figure–ground relationship in the stimulus ambiguous. We plan to reproduce the random-dot stimulus

through various spatial frequency filters. These approaches may contribute to determining the spatial frequency tuning of the illusion-inducing mechanism.

8.4 Accuracy of detected motion direction

One may argue that the radial pattern includes many oriented figural components, resulting in accurate motion-direction detection. This condition may activate relative-motion detectors that could be highly tuned for the preferred orientation. In the orthogonal stripe pattern, orthogonal motion components are ambiguous because of the aperture problem for motion. Thus, the detected motion direction includes certain degree of ambiguity. However, in Experiment 2, we used random dots as a surrounding texture and demonstrated that the effect of random dots on producing the illusion is limited. The random dots may include many spatial frequency components in any orientation, which may result in accurate detection of the motion direction. Thus, we do not believe that accurate detection of the motion direction direction leads to a strong illusory effect in a radial sector pattern.

8.5 A radial pattern as an illusory figure

The appearance of the centre disc is another possible factor added by a radial pattern. It is possible that when the disc appears as floating in front of the surrounding texture, it tends to cause an illusory effect compared to the disc appearing as attached to the surround. For example, as Pinna, Spillmann, and Ehrenstein (2002) reported, the disc in the centre of a radial pattern appears to be floating and scintillating. Moreover, the disc in our typical figure (the control stimulus in all experiments) appears to be floating and scintillating (Takahashi, Fukuda, Watanabe, & Ueda, 2012). Pinna and Spillmann (2002) and Ashida (2002) suggested that the segregation of figure and ground contributes to inducing illusory motion. However, the disc on the random-dot texture or on the stripes forming a diamond does not appear to float on the background. It is plausible that a perceptually floating object is easier to move perceptually than is an object perceptually attached to or fused with the surrounding texture. We believe that the correlation between the scintillating lustre illusion and the pursuit-pursuing illusion should be investigated. It is possible that these illusions are two aspects of the same phenomenon sharing the same visual mechanism.

Recently, Sokoliuk and VanRullen (2013) found that the occipital alpha rhythm of the electroencephalogram (EEG) showed a correlation with the appearance of the illusory flicker of a static wheel stimulus with 32 spokes (the Flickering Wheel illusion). Our typical stimulus precisely corresponds to a centre disc placed on their typical stimulus. In fact, as noted above, we see some flicker or scintillation in our stimulus. We do not think that the alpha rhythm of EEG produces the present illusion. However, from a physiological point of view, it is possible that radially arranged sectors are a special pattern where physiological activity in the brain appears as a visual phenomenon.

8.6 Retinal and extraretinal signals for motion

Interactions between retinal and extraretinal motion signals could produce motion illusions. The Filehne illusion is considered to be induced by the underestimation of eye movement signals coming from an extraretinal origin, e.g. efference copy. However, when retinal signals for motion are weaker, the Filehne illusion can be reversed. Freeman and Banks (1998) showed that a test grating at a spatial frequency of 0.25 cycle/deg or lower was seen to move in the direction of pursuit eye movement. Terao and Murakami (2011) showed a similar effect using an equiluminant target. The present illusion is similar to their effects but can be only partly explained by them. In Experiment 4, the illusory motion in an equiluminant disc without surround texture is not as strong as with a background of orthogonal stripes or radially arranged sectors. Thus, although weak retinal motion signals certainly produce the reversed Fhilene illusion, the strength explains only a part of the present illusion.

Even without extraretinal signals, this illusion strongly arises although the appearance of the illusion is different as shown in <u>Figure 1</u>. We have demonstrated this illusion to many naïve people using a printed stimulus figure, with the method shown in <u>Figure 2</u> in Ito (2012), and found that all of them could see the illusion of stillness or illusory motion in the direction opposite to the physical motion direction. The fact that there is no need to track a moving target by eye movement may produce smoother retinal motion of the figure, resulting in a strong illusion experience, especially for people who are not good at smooth pursuit eye movement. We think that extraretinal signals change the appearance of the illusion but may not add another component that enhances the present illusion.

9 Conclusion

Here, we conclude that the centre-surround relative-motion detector hypothesis (as shown in Figure 2c) or its modified version (Figure 2d) alone cannot completely explain the illusion. Stripes and dots that carry many motion signals cannot substitute for the radial pattern that produces the strongest illusion. However, it is also clear that motion detection in the surround is important. Although equiluminance between the centre and surround areas enhances the illusion, the effect is not strong compared to that of the radial surround texture. It is worth trying to revise the relative-motion detection model for the illusion to directly or indirectly manage radial components.

Several motion illusions have been reported in a radial or circular stimulus configuration (Fraser & Wilcox, <u>1979</u>; Gori & Hamburger, <u>2006</u>; Kitaoka, <u>2003</u>; Kitaoka & Ashida, <u>2003</u>; Leviant, <u>1982</u>, <u>1996</u>; MacKay, <u>1957</u>; Pinna & Brelstaff, <u>2000</u>). Some of these illusions must be fixated on the centre or observed with back and forth head movement. However, they could also occur in their straight versions of the stimulus configurations. That is, the circular or radial stimulus configuration may not be necessary for the illusions to occur. However, to some degree, the effect in the pursuit-pursuing illusion depends on the radial stimulus configuration, although the illusion-producing motion is one-dimensional. This is an exclusive characteristic of this illusion.

At present, we think that the pursuit-pursuing illusion consists of three factors, i.e. weak motion detection of the central disc due to equiluminance or lower spatial frequency, relative motion detection between the disc and the surround, and some illusory effect originating in the radial configuration. The last factor may be partly common among the illusory figures in Ehrenstein (<u>1941</u>), MacKay (<u>1957</u>), Pinna et al (<u>2002</u>, 2004), Sokoliuk and VanRullen (<u>2013</u>) and the present illusion.

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