We almost never experience visual instability, despite retinal image instability induced by eye movements. How the stability of visual perception is maintained through spatiotopic representation remains a matter of debate. The discrepancies observed in the findings of existing neuroscience studies regarding spatiotopic representation partly originate from differences in regard to how attention is deployed to stimuli. In this study, we psychophysically examined whether spatial attention is needed to perceive spatiotopic visual motion. For this purpose, we used visual motion priming, which is a phenomenon in which a preceding priming stimulus modulates the perceived moving direction of an ambiguous test stimulus, such as a drifting grating that phase shifts by 180°. To examine the priming effect in different coordinates, participants performed a saccade soon after the offset of a primer. The participants were tasked with judging the direction of a subsequently presented test stimulus. To control the effect of spatial attention, the participants were asked to conduct a concurrent dot contrast-change detection task after the saccade. Positive priming was prominent in spatiotopic conditions, whereas negative priming was dominant in retinotopic conditions. At least a 600-ms interval between the priming and test stimuli was needed to observe positive priming in spatiotopic coordinates. When spatial attention was directed away from the location of the test stimulus, spatiotopic positive motion priming completely disappeared; meanwhile, the spatiotopic positive motion priming at shorter interstimulus intervals was enhanced when spatial attention was directed to the location of the test stimulus. These results provide evidence that an attentional resource is requisite for developing spatiotopic representation more quickly.

Introduction

The human visual system contains specialized mechanisms for analyzing the velocity of moving objects (Adelson & Bergen, 1985; Anstis, 1980; Braddick, 1980; van Santen & Sperling, 1984; Watson & Ahumada, 1985). Lower visual areas, such as the primary visual cortex (V1), encode input information retinotopically (e.g., Wandell, Brewer, & Dougherty, 2005). Retinal images change in a complex manner because of eye, head, or body movements. Because we perceive the visual world as stable and detect object motion veridically from complex retinal images, there must be a mechanism that constructs nonretinotopic representation in the visual pathway. How the stability of visual perception is maintained has a long history of study and remains a matter of debate (Burr & Morrone, 2012; Cavanagh, Hunt, Afraz, & Rolfs, 2010; Marino & Mazer, 2016; Melcher & Morrone, 2015; Wurtz, 2008). A promising mechanism of visual stability was proposed by Helmholtz (1867), which was based on a copy of saccade motor command, termed efference copy, or corollary discharge (e.g., Duhamel, Colby, & Goldberg, 1992; Sommer & Wurtz, 2002; Wurtz, 2008). An efference copy, also called a corollary discharge, is a copy of a motor command sent to brain areas for interpreting sensory inflow. Theoretically, an efference copy signal could update the incoming visual signal to create a gaze-invariant spatiotopic representation from the retinotopic visual input; however, whether spatiotopic representation is actually a key factor in solving the problem of visual stability is also a matter of debate (Burr & Morrone, 2012; Zimmermann, Morrone, & Burr, 2014). In line with this discussion, the question of which reference frame, such as a retinotopic reference frame or a spatiotopic (or world-centered) reference frame, visual motion perception depends on is fundamental in the field of research of visual stability regarding visual motion perception (e.g., d’Avossa et al., 2007; Knapen, Rolfs, & Cavanagh, 2009; Turi & Burr, 2012; Wenderoth & Wiese, 2008).
To examine whether spatiotopic information is explicitly represented or encoded in the visual motion system, d’Avossa et al. (2007) measured functional magnetic resonance imaging (fMRI) responses while presenting visual motion stimuli and manipulating gaze direction. They consequently found spatiotopic responses in the human middle temporal (MT) area, which indicated spatial selectivity based on screen coordinate rather than retinotopic coordinate for visual motion perception. On the other hand, Gardner, Merriam, Movshon, and Heeger (2008), using a similar motion task, found no evidence of spatiotopic fMRI responses in the visual cortex and concluded that all representations in the visual cortex are retinotopic. Crespi et al. (2011) examined the discrepancy between these two studies by manipulating spatial attention, because the participants in d’Avossa et al. (2007) paid attention to peripherally presented motion stimuli, whereas those in Gardner et al. (2008) attended to the center of the display while motion stimuli were presented at the periphery. By conducting a peripherally presented motion discrimination task, Crespi et al. (2011) found spatiotopic responses in area MT or middle superior temporal (MST) in the free-viewing conditions, in which attention was not controlled. However, when the participants performed a dual task, in which their attention was confined to the fovea, only retinotopic responses were observed in the visual cortex. These findings of Crespi et al. (2011) indicate the necessity, for the spatiotopic fMRI response, of attending to motion stimuli or the location where the motion stimuli will appear. As highlighted by Melcher and Morrone (2015, p. 7), however, it is not certain whether the participants actually directed their attention to the peripherally presented motion stimuli in the free-viewing conditions of Crespi et al. (2011).

In this study, therefore, we directly manipulated spatial attention to psychophysically examine whether spatial attention is needed for spatiotopic visual motion perception. A standard way of examining the spatiotopic effect is to present an observer with two stimuli over time in the same spatial (screen-based) position, separated by a saccade that causes the two stimuli to fall in different retinal locations (Melcher, 2005; Melcher & Colby, 2008; Melcher & Morrone, 2015). Preparing two moving stimuli and examining whether these moving stimuli interact through adaptation or priming would help us to understand the characteristics of spatiotopic effects on visual motion perception (Biber & Ilg, 2011; Burr, Cicchini, Arrighi, & Morrone, 2011; Burr, Tozzi, & Morrone, 2007; Ezzati, Golzar, & Afraz, 2008; Fracasso, Caramazza, & Melcher, 2010; Knapen et al., 2009; Melcher & Fracasso, 2012; Melcher & Morrone, 2003; Ong, Hooshvar, Zhang, & Bisley, 2009; Seidel Malkinson, Mckyton, & Zohary, 2012; Turi & Burr, 2012; Wenderoth & Wiese, 2008; Yoshimoto, Uchida-Ota, & Takeuchi, 2014a; Yoshimoto, Uchida-Ota, & Takeuchi, 2014b; see summary by Marino & Mazer, 2016, table 3). In this study, consequently, we used the visual motion priming paradigm (Ong et al., 2009; Yoshimoto et al., 2014a; Yoshimoto et al., 2014b) in addition to concurrently conducting a dot contrast-change detection task (Crespi et al., 2011) to control the spatial attention of spatiotopic motion perception.

Visual motion priming is a phenomenon in which the preceding moving stimulus (primer) modulates the perceived direction of a directionally ambiguous test stimulus (Anstis & Ramachandran, 1987; Campana, Pavan, & Casco, 2008; Heller & Davidenko, 2018; Jiang, Luo, & Parasuraman, 2002; Jiang, Pantle, & Mark, 1998; Kanai & Verstraten, 2005; Pantle, Gallogly, & Piehler, 2000; Pavan, Campana, Guerre-schi, Manassi, & Casco, 2009; Piehler & Pantle, 2001; Pinkus & Pantle, 1997; Ramachandran & Anstis, 1983; Raymond, O’Donnell, & Tipper, 1998; Takeuchi, Tuladhar & Yoshimoto, 2011; Yoshimoto & Takeuchi, 2013). In negative motion priming, the test stimulus is perceived to move in the opposite direction to the priming stimulus. Meanwhile, in positive motion, priming the test stimulus is perceived to move in the same direction as that of the priming stimulus. As described in the Methods section of Experiment 1, whether positive or negative priming occurs depends on a range of factors, such as the presentation duration, luminance contrast, and velocity of the priming stimulus used (Pinkus & Pantle, 1997; Kanai & Verstraten, 2005; Takeuchi et al., 2011; Yoshimoto & Takeuchi, 2013).

In our previous studies (Yoshimoto et al., 2014a; Yoshimoto et al., 2014b), participants performed saccades after the offset of a drifting sine-wave priming stimulus and judged the direction of a directionally ambiguous test stimulus that was displayed in retinotopic or spatiotopic coordinates. Through these examinations, we found that positive motion priming is spatiotopic whereas negative priming is predominantly retinotopic. Thus, positive priming was never perceived when the spatial locations of the priming and test stimuli were retinotopically coincident before and after the saccade; on the other hand, negative motion priming did not occur when the spatial locations of the priming and test stimuli were coincident.

By using these characteristics of visual motion priming, such that spatiotopic positive motion priming and retinotopic negative motion priming can be exclusively observed, we examined whether manipulation of spatial attention affects spatiotopic and/or retinotopic motion perception. If spatial attention is requisite for inducing spatiotopic motion perception, as predicted from the aforementioned fMRI studies (Crespi et al., 2011; d’Avossa et al., 2007; Gardner et
al., 2008), it is expected that positive motion priming is not perceived if participants’ attention is directed away from the future location of the test stimulus. To control spatial attention, we conducted a dot contrast-change detection task similar to that used in Crespi et al. (2011) as a secondary task.

**Experiment 1**

**Methods**

**Participants**

Twenty-six individuals (11 men and 15 women; average age = 21.6 years, range 19–27 years) with normal or corrected vision participated in Experiment 1; all were undergraduate and graduate students from Hiroshima University who volunteered to participate in this study and were naïve to the purpose of the experiment. The study followed protocols approved by the Institutional Research Boards of Hiroshima University and was conducted in accordance with the Declaration of Helsinki. All participants provided written informed consent before engaging in the study. Two participants were excluded because their performance in the attentional task was too low, as described below; thus, the reported results were derived from 24 participants (10 men and 14 women; average age = 21.7 years, range 19–27 years).

**Apparatus**

The stimuli were generated using MATLAB R2017b (MathWorks, Natick, MA) and the Psychophysics Toolbox Version 3 (PTB-3; Brainard, 1997; Pelli, 1997) on a PC (Applied WST-E52609V4S3Q1TT workstation, Applied Co., Ltd., Fukuoka, Japan). These were then displayed on a 27-in. flat screen liquid crystal display (LCD) monitor (EIZO FORIS FS2735, EIZO Co., Ishikawa, Japan). This high-end gaming monitor is a successor model to the EIZO FG2421, which was used in our previous studies (Yoshimoto et al., 2014a; Yoshimoto et al., 2014b) in order to allow comparison with the present results. An achromatic vertical sine-wave grating (spatial frequency = 0.5 cycles per degree in visual angle [c/°]) was displayed in a rectangular window (10.0° w × 3.3° h). The edges of the stimulus were tapered using a Gaussian function (σ = 1.0°). The stimuli were presented on a uniform gray-colored background with a luminance identical to the space-averaged luminance of the stimuli.

Various stimulus parameters have been shown to influence the perception of visual motion priming (Kanai & Verstraten, 2005; Pantle et al., 2000; Pavan & Skujevskis, 2013; Pinkus & Pantle, 1997; Takeuchi et al., 2011; Yoshimoto & Takeuchi, 2013). Yoshimoto and Takeuchi (2013) found that the velocity and duration of the primer determined motion priming effects when the stimuli presented in the parafovea had a high luminance contrast (higher than 10 times the direction discrimination threshold). At a velocity of 3 Hz, positive priming was observed when the primer duration was shorter than 300 ms; in contrast, when the primer duration was longer, negative motion priming was observed. However, at velocities lower than 3 Hz, positive priming was prominent even when the primer duration was as high as 2,000 ms. At velocities higher than 3 Hz, negative priming was observed regardless of primer duration. These results indicate that the specific priming effect (negative or positive) is robustly induced by properly manipulating the velocity and duration of the priming stimulus.

In this study, we examined the effect of certain combinations of primer duration and velocity in terms of inducing positive or negative priming. The duration of the primer was set to 167 or 1,000 ms and its velocity was set to 2, 3, or 4 Hz. To equate the velocity of the test stimulus to that of the primer, the duration of one frame of the test stimulus was set to be equal to the duration required for the primer to shift 180°. The test stimulus had a total of four frames. The luminance contrast determined by the Michaelson relationship of the priming and test stimuli was 50%.

The priming stimulus was displayed in the center of the screen. The spatial distance between the center of
Figure 1. Stimulus configuration of a trial in Experiment 1. A fixation dot (depicted in red here for the purpose of illustration, but it was actually dark gray in the experiment) was displayed to help participants to maintain fixation. Under the retinotopic (A) and spatiotopic (B) conditions, participants performed a saccade when the fixation dot jumped to a new location after the offset of the primer. After a variable ISI, the test stimulus was displayed above (A) or below (B) the new fixation dot. Under the full (C) and unmatched (D) conditions, the position of the fixation dot was not changed; thus, saccades were not required. After the ISI, the test stimulus was displayed above (C) or below (D) the fixation dot. Three conditions were examined to control spatial attention. In the
condition with no attentional task (“w/o task”), only the fixation dot was presented. In the “Identical” and “Different” conditions, another dark-gray dot was presented during a variable ISI, either in the same (“Identical”) or opposite (“Different”) side of the test stimulus. The dot contrast was increased or decreased at some points during the ISI after the saccade. In this figure, only the condition when the dot contrast increased is presented.

The gratings and the fixation dot was set to 3.3°. A dark-gray dot with a luminance of 57.9 cd/m² and a diameter of 0.5° was displayed to help participants maintain fixation during trials. Similar to our previous studies (Yoshimoto et al., 2014a; Yoshimoto et al., 2014b), we measured the priming effect at four frame of reference conditions (Figure 1). In the retinotopic condition, a dark-gray-colored fixation dot (depicted as a red pot in Figure 1) shifted to the upper region of the screen immediately after the termination of the primer, and the test stimulus was presented in the same retinotopic location as the primer relative to fixation after a variable interstimulus interval (ISI; Figure 1A). In the spatiotopic condition, the fixation dot was shifted as in the retinotopic condition, but the test stimulus was presented in the same screen location as the primer (Figure 1B). In the full condition, the test stimulus was presented in the same location as the primer after a variable ISI. Because the fixation dot was not shifted, this condition represented both retinotopic and spatiotopic coordinates (Figure 1C). In the unmatched condition, the test stimulus was presented after a variable ISI in a position that matched neither the spatiotopic nor retinotopic location of the primer, with no shift in the fixation dot (Figure 1D). The unmatched condition was used to examine the possibility that the effects of motion priming could result from motion integration over a large spatial region in the spatiotopic condition when the priming and test stimuli were separated retinotopically.

To confirm whether the priming effect is robust to the retinal location, four individuals who were not involved in Experiment 1 performed the motion priming task not only when the primer was presented in the upper peripheral retina (above the fixation dot) but also when the primer was presented in the lower peripheral retina (below the fixation dot), prior to the actual data acquisition. The spatial location of the test stimulus was determined based on the frame of reference condition (retinotopic, spatiotopic, full, or unmatched). Consequently, no systematic difference in the priming effect was found between upper and lower peripheral retina. Therefore, in the actual experiment, the primer was presented only in the upper peripheral retina (Figure 1). Participants made 6.7° upward saccades with the shift of the fixation dot under the retinotopic and spatiotopic conditions (Figures 1A and 1B) but not under the full and unmatched conditions (Figures 1C and 1D).

The combinations of the durations and velocities of the primer in Experiment 1 are shown in Table 1. We examined combinations of the duration and velocity of the primer because manipulating a single parameter is not sufficient to determine the priming effect. Predictions regarding the perceived direction of the test stimulus were also included; they were based on a previous study that demonstrated the effects of the durations and velocities of priming stimuli in various coordinate frames (Yoshimoto et al., 2014b). No effect of spatial attention has been taken into account in the actual data acquisition. The spatial location of the test stimulus was determined based on the frame of reference condition (retinotopic, spatiotopic, full, or unmatched). Consequently, no systematic difference in the priming effect was found between upper and lower peripheral retina. Therefore, in the actual experiment, the primer was presented only in the upper peripheral retina (Figure 1). Participants made 6.7° upward saccades with the shift of the fixation dot under the retinotopic and spatiotopic conditions (Figures 1A and 1B) but not under the full and unmatched conditions (Figures 1C and 1D).

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![Table 1. The stimulus parameters examined in Experiment 1 coupled with the predicted priming effects with saccade, which were based on the findings of Yoshimoto et al. (2014b). Notes: These predictions do not take the effect of spatial attention into account.](image)

<table>
<thead>
<tr>
<th>Primer duration (ms)</th>
<th>Velocity (Hz)</th>
<th>Predicted priming effects with no attentional task</th>
</tr>
</thead>
<tbody>
<tr>
<td>167</td>
<td>3</td>
<td>Positive under the spatiotopic and full conditions</td>
</tr>
<tr>
<td></td>
<td></td>
<td>No priming under the retinotopic and unmatched conditions</td>
</tr>
<tr>
<td>167</td>
<td>4</td>
<td>Negative under the retinotopic and full conditions</td>
</tr>
<tr>
<td></td>
<td></td>
<td>No priming under the spatiotopic and unmatched conditions</td>
</tr>
<tr>
<td>1,000</td>
<td>2</td>
<td>Positive under the spatiotopic and full conditions</td>
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<tr>
<td></td>
<td></td>
<td>No priming under the retinotopic and unmatched conditions</td>
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</tbody>
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Mathôt & Theeuwes, 2010; Morrone, Cicchini, & Burr, 2010; Zimmermann, Morrone, & Burr, 2014; Zimmermann, Morrone, Fink, & Burr, 2013). Yoshimoto et al. (2014a, 2014b) showed that positive priming in spatiotopic conditions was observed only when the interval between the priming and test stimuli was longer than 400 ms. Therefore, as in Yoshimoto et al. (2014b), the ISI between the offset of the primer and onset of the test stimulus was changed from 400 to 3,000 ms for this experiment. The ISI was also changed in the full and unmatched conditions in the same manner as for the retinotopic and spatiotopic conditions.

For each of the four conditions of the different reference frames shown in Figure 1, three task conditions for controlling spatial attention were examined. In the “w/o task” condition, no concurrent attentional task was conducted. Meanwhile, in the “Identical” and “Different” conditions shown in Figure 1, participants were required to perform dot contrast-change detection judgment (attentional task) in addition to motion direction judgment (priming task). In these two conditions, a dark-gray dot (red-colored dot in Figure 1) continued to appear 3.3° above or below the fixation dot during the ISI between the primer and test stimulus; the luminance and the diameter of this dot were the same as those of the fixation dot. In the “Identical” condition, the position of the dot was identical to that of the center of the test stimuli, whereas in the “Different” condition, the position of the dot was vertically opposite to the side of the test stimuli. The dot contrast was increased or decreased by 30% at a random time during the ISI, and the contrast change lasted 50 ms (depicted as a light-gray–colored dot in Figure 1). To avoid a saccadic inhibition in the retinotopic and spatiotopic conditions, the dot contrast was changed at least 300 ms after the fixation dot shifted. Therefore, as shown in Figures 1A and 1B, in both the “Identical” and “Different” conditions, the ISI was divided into the “saccade” period (continues for 300 ms) and the “attentional task” period (varying from 100 to 2,700 ms in duration, depending on the total length of the ISI). This procedure was also adopted in the full and unmatched conditions, in which no saccade was required. These parameters of dot presentation were adjusted to maintain the participants’ rate of correct answers at approximately 95%, which is the same criterion as that used by Crespi et al. (2011).

Procedure

Each trial began with the presentation of a fixation dot for 1.5 s. The primer subsequently appeared while the fixation dot was continuously presented on the screen. In the retinotopic and spatiotopic conditions, the fixation dot immediately shifted to the upper region of the screen after the offset of the primer. Participants were required to make a saccade to the new location of the fixation dot and were instructed to maintain their gaze on the fixation dot throughout the trial. The task was to report the perceived direction (rightward or leftward) of the test stimulus. Participants pressed the corresponding arrow key on the computer keyboard to report their judgment. In the “Identical” and “Different” attentional conditions, another dot was presented either above or below the fixation dot during an ISI period. The contrast of this dot was changed at some point during the ISI. In the condition with no attentional task (the “w/o task”), only the fixation dot was presented during the ISI. After the ISI, a test stimulus was presented. In the two attentional conditions (“Identical” and “Different”), after the direction judgment, the participants also reported whether they perceived the dot contrast to have increased or decreased compared with the original contrast by pressing the 1 key (increased) or 2 key (decreased) on the keyboard. After they made a selection, a 1-s intertrial interval (in which a uniform field with space-averaged luminance was displayed) was inserted to reduce the effect of the former trial. Each session consisted of 64 trials: four trials for each of the eight ISIs between the primer and test stimulus (400, 600, 800, 1,000, 1,200, 1,600, 2,000, and 3,000 ms), and for the two directions of the primer (leftward or rightward), which were presented in a random order. In each session, the duration of the priming stimulus, the velocity, and the coordinate conditions were fixed. The four parameter combinations show in Table 1 were examined at each of the four coordinate conditions. When the participants performed the motion direction judgment as well as the dot contrast judgment, the dot position (“Identical” or “Different”) condition was also fixed in each session. Each participant completed four sessions for each of the four parameter combinations at each of the four reference frame conditions and at each of the three attentional task conditions in random order. Each session took approximately 10 min to complete. Each participant completed a total of 192 sessions in 3 months. Participants underwent at least 20 practice trials under each condition prior to data acquisition.

During the experiment, eye movement was monitored using the infrared video–based eye-tracking system described above. All eye movement analysis was conducted offline. Prior to the saccade detection, eye blinks were removed by the ViewPoint software (Arrington Research, Inc.) from the eye recording data. Saccade onset and offset were detected by applying a set of velocity and acceleration criteria, using 40°/s (velocity and 800°/s² acceleration thresholds (Krauzlis & Miles, 1996), by the combination of ViewPoint software and in-house software implemented by MATLAB.
Results

Fixation and saccades

We checked whether participants executed saccades in accordance with the shifts of the fixation dot (the red dot in Figure 1). For all trials in the retinotopic and spatiotopic conditions, the duration between the termination of the primer and end of the saccade ranged from 132 to 283 ms. Therefore, it can be concluded that the ISI of 400 ms was sufficiently long to perform a 6.7° saccade. In 6.9% of the trials, participants looked more than 1.5° away from the fixation dot in a single trial at both pre- and postsaccade. We did not conduct subsequent analyses for those trials.

Dot contrast-change detection judgment

For the “Identical” and “Different” attentional conditions, in most of the trials, the participants correctly judged whether the dot contrast had decreased or increased relative to that of the original dot (average of 94.3% correct responses). However, two participants scored well below 90% in regard to correct responses (62% and 55%), so we excluded their data from subsequent analyses.

Motion direction judgment

Conditions in which positive priming was predicted: Figure 2 shows the group-averaged results for each condition. In Figure 2A, the primer duration is 167 ms and the velocity is 3 Hz; in Figure 2B, these values are 1,000 ms and 2 Hz, respectively. As shown in Table 1, positive priming was expected to appear in these conditions. The percentage response to positive priming was plotted as a function of the ISI between the primer and test stimulus. In most of the trials, the participants reported that the perceived direction of the test stimulus was the same as that of the primer when the percentage response was higher than 50%. On the other hand, when the percentage response was lower than 50%, the participants reported in most of the trials that the perceived direction of the test stimulus was in
the direction opposite to that of the primer (negative priming).

Positive priming was prominent in the spatiotopic condition; meanwhile, no priming effect was observed in the retinotopic condition when attentional task was not required (“w/o task”). These results fitted our predictions described in the “167 ms/3 Hz” and “1,000 ms/2 Hz” conditions in Table 1, which are based on our previous studies (Yoshimoto et al., 2014a; Yoshimoto et al., 2014b). The arch-shaped curve in the spatiotopic “w/o task” condition represents that positive priming became prominent in the middle range of the ISI (approximately 800–1,600 ms), thus replicating the results in our previous studies (Yoshimoto et al., 2014a; Yoshimoto et al., 2014b). However, in the attentional condition in the spatiotopic condition, where the dot target appeared in the same position as the test stimuli (“Identical” condition), positive priming was observed in more than 80% of the trials, even with ISIs as short as 400–600 ms. Meanwhile, no motion priming was observed for any ISIs when the dot target appeared in a different location to that of the test stimuli (“Different” condition), regardless of the primer duration and velocity used.

To test whether the attentional task altered the positive priming in the spatiotopic condition, which was our main interest in Experiment 1, a two-way analysis of variance (ANOVA) for repeated measures with Tukey’s post hoc test was conducted. Angular transformation was applied for the percentage values to normalize the binomial distribution (Fernandez, 1992); thereafter, the homogeneity of variance for the transformed binomial distribution (Fernandez, 1992); then replicating the results in our previous studies (Yoshimoto et al., 2014a; Yoshimoto et al., 2014b). The arch-shaped curve in the spatiotopic “w/o task” condition represents that positive priming became prominent in the middle range of the ISI (approximately 800–1,600 ms), thus replicating the results in our previous studies (Yoshimoto et al., 2014a; Yoshimoto et al., 2014b). However, in the attentional condition in the spatiotopic condition, where the dot target appeared in the same position as the test stimuli (“Identical” condition), positive priming was observed in more than 80% of the trials, even with ISIs as short as 400–600 ms. Meanwhile, no motion priming was observed for any ISIs when the dot target appeared in a different location to that of the test stimuli (“Different” condition), regardless of the primer duration and velocity used.

To test whether the attentional task altered the positive priming in the spatiotopic condition, which was our main interest in Experiment 1, a two-way analysis of variance (ANOVA) for repeated measures with Tukey’s post hoc test was conducted. Angular transformation was applied for the percentage values to normalize the binomial distribution (Fernandez, 1992); thereafter, the homogeneity of variance for the transformed data sets was confirmed by Bartlett’s test before using the ANOVA. Effect sizes were reported as generalized eta-squared (η²G), as recommended for repeated-measures designs (Bakeman, 2005; Olejnik & Algina, 2003): 0.02 for a small effect, 0.13 for a medium effect, and 0.26 for a large effect according to Cohen’s recommendation (Cohen, 1988). At a primer duration of 167 ms and velocity of 3 Hz in the spatiotopic condition (Figure 2A), the main effects of the attentional task and ISI were significant, \( F(2, 46) = 384.0, p < 0.0001, \eta^2_G = 0.71 \), for the attentional task and \( F(7, 161) = 35.02, p < 0.0001, \eta^2_G = 0.31 \) for the ISI; the interaction between the attentional task and ISI was also significant, \( F(14, 322) = 21.51, p < 0.0001, \eta^2_G = 0.26 \). The Tukey’s test revealed significant differences in the positive priming between “w/o task” and “Identical” conditions at four ISIs (400, 600, 800, and 1,000 ms; \( q \geq 4.00, ps < 0.05 \)), marked by asterisks in Figure 2A. At a primer duration of 1,000 ms and a velocity of 2 Hz in the spatiotopic condition (Figure 2B), the main effects of the attentional task and ISI were significant, \( F(2, 46) = 390.0, p < 0.0001, \eta^2_G = 0.76 \), for the attentional task and \( F(7, 161) = 59.75, p < 0.0001, \eta^2_G = 0.41 \), for the ISI; the interaction between the attentional task and ISI was also significant (\( F(14, 322) = 31.69, p < 0.0001, \eta^2_G = 0.36 \)). Further, the Tukey’s test revealed significant differences in the positive priming between “w/o task” and “Identical” conditions at four ISIs (400, 600, 800 and 1,000 ms; \( q \geq 5.68, ps < 0.001 \), marked by asterisks in Figure 2B.

In the full condition shown in Figure 2, positive priming was observed in the condition with no attentional task (“w/o task”), as predicted in our previous studies (Yoshimoto et al., 2014a; Yoshimoto et al., 2014b; Table 1). The clear difference here in relation to the results of the spatiotopic condition is that positive priming was also conspicuous at both attentional (“Identical” and “Different”) conditions. In all of the conditions, the strength of positive priming was prominent when ISI was as short as 400 ms but was reduced as ISI became longer. Thus, no effect of attentional manipulation was observed in the full condition.

In the retinotopic and unmatched conditions, no priming effect was observed in the “w/o task” condition, which also accorded with our prediction (Table 1). Attentional manipulation had no effect for both conditions.

Conditions in which negative priming was predicted: Figure 3 shows the group-averaged results for each coordinate condition. In Figure 3A, the duration of the priming stimulus is 167 ms and the velocity is 4 Hz; in Figure 3B, the values are 1,000 ms and 3 Hz, respectively (the predictions for these parameters are shown in Table 1). For both sets of parameters, for the no attentional task (“w/o task”), negative motion priming was dominant in both the retinotopic and full conditions, whereas no priming effect was observed in the spatiotopic and unmatched conditions, as predicted (Table 1). Negative priming was also observed in both the “Identical” and “Different” attentional conditions. The strength of negative priming was prominent when ISI was as short as 400 ms and was reduced as ISI became longer and converged to 50%. A two-way ANOVA showed that at a primer duration of 167 ms and a velocity of 4 Hz (Figure 3A), the main effect of the attentional task was not significant, \( F(2, 46) = 0.01, ns \), whereas that of the ISI was significant, \( F(7, 161) = 184.9, p < 0.0001, \eta^2_G = 0.56 \). The interaction between the attentional task and the ISI was not significant, \( F(14, 322) = 0.73, ns \). At a primer duration of 1,000 ms and a velocity of 3 Hz (Figure 3B), the main effect of the attentional task was not significant, \( F(2, 46) = 0.07, ns \), whereas that of the ISI was significant, \( F(7, 161) = 172.4, p < 0.0001, \eta^2_G = 0.70 \). Meanwhile, the interaction between the attentional task and ISI was not significant, \( F(14, 322) = 0.94, ns \). Thus, it is concluded that no effect of attentional manipulation was observed in the retinotopic and full conditions.
In accordance with our prediction (Table 1), no priming effect was observed in the “w/o task” in the spatiotopic and unmatched conditions. Furthermore, attentional manipulation had no effect on the perception of visual motion priming.

Summary of the results

Following is a summary of the main findings of Experiment 1:

1. In the condition with no attentional task (“w/o task”), positive priming was observed in the spatiotopic and full conditions but not in the retinotopic and unmatched conditions (Figure 2). Meanwhile, negative priming was observed in the retinotopic and full conditions but not in the spatiotopic and unmatched conditions (Figure 3). These results are a replication of our previous studies’ results (Yoshimoto et al., 2014a; Yoshimoto et al., 2014b).

2. The attentional task only modulated the positive priming effect in the spatiotopic condition (upper right of the Figures 2A and B). In the “Identical” condition, the positive priming became prominent at the short ISIs, where none or less positive priming was observed in the “w/o task” condition. The priming effect completely disappeared in the “Different” condition. No effect of attentional task was found when the negative priming was observed (Figure 3).

Discussion

The results obtained in the “w/o task” conditions are consistent with our previous results (Yoshimoto et al., 2014a; Yoshimoto et al., 2014b), even though there are several differences between this and the previous experiments, such as the number of participants (four vs. 24) and the monitor used (CRT vs. LCD). Thus, when a saccade after the offset of the primer was required, positive priming was observed for the spatiotopic condition, whereas negative priming was observed for the retinotopic condition. Pronounced
positive priming in the spatiotopic condition was observed only when the ISI was longer than 600 ms. Because no priming was observed in the unmatched condition, it can be surmised that the positive priming observed in the spatiotopic condition was not the by-product of the spatiotemporal summation of motion information over a larger area.

Tests of the effect of spatial attention, controlled by the concurrent dot contrast-change detection task, revealed that only the perception of positive priming in spatiotopic reference frames depended on the attended location (Figures 2A and 2B). When spatial attention was explicitly directed to the location where the test stimulus would be presented ("Identical" condition), the positive priming became conspicuous at shorter ISIs compared with that obtained in the no attentional task ("w/o task") condition. However, when spatial attention was directed away from the test stimulus location, in the "Different" condition, the spatiotopic positive priming completely disappeared. In the other reference frame conditions, such an effect of spatial attention was not observed at all. These results suggest that attributing spatial attention to the location where the stimulus will appear is an important factor for perceiving spatiotopic visual motion. However, before drawing this conclusion, we conducted another experiment (Experiment 2) to examine the effect of saccade per se on spatiotopic perception.

**Experiment 2**

In Experiment 1, the perception of positive priming was modulated by spatial attention in the spatiotopic condition but not in the full condition (Figures 2A and B). One obvious difference between these two conditions is the presence of saccades. If saccadic eye movements per se caused the effect of spatial attention in the spatiotopic condition, priming effects would also be affected by manipulating spatial attention in the full condition when participants performed saccadic eye movements. We examined this possibility in Experiment 2. Such a control experiment for examining the effect of eye movements per se has been recommended for experiments of spatiotopic visual perception (Knapen et al., 2009; Knapen, Rolfs, Wexler, & Cavanagh, 2010; Marino & Mazer, 2016; Nieman, Hayashi, Andersen, & Shimojo, 2005).

**Methods**

**Participants**

We conducted the experiment with two different groups of participants. First, 21 individuals (8 men and 13 women; average age = 21.4 years, range 19–25 years) with normal or corrected-to-normal vision participated in Experiment 2; all had participated in Experiment 1 previously. To test whether the task experience of Experiment 1 influenced participants' performance in Experiment 2, the remaining 20 individuals (eight men and 12 women; average age = 20.7 years, range 19–24 years) with normal or corrected-to-normal vision were also recruited from Hiroshima University to participate only in Experiment 2. These participants who were undergraduate and graduate students were new observers and naive to the purpose of the experiment. One participant was excluded because of his low performance on the attentional task. The reported results were thereby derived from 19 participants for the second group (seven men and 12 women; average age = 20.8 years, range 19–24 years).

**Stimuli**

Figure 4 shows a schematic description of the stimuli used in one of the trials from Experiment 2. As in Experiment 1, we examined the manner in which a priming stimulus modulated the perceived direction of a directionally ambiguous test stimulus. The stimulus configuration was similar to that in the full condition in Experiment 1 (Figure 1C), with the exception that the fixation dot shifted; specifically, the fixation dot shifted 6.7° to the upper region of the screen immediately after the offset of the priming stimulus, remained there for 200 ms, and then returned to its original position (Figure 4). Thus, the participants performed two saccadic eye movements to track the fixation dot. We did not expect the saccades to be completed within 200 ms. This duration was arbitrarily determined to assist the participants when performing the saccadic eye movements. The ISIs between the offset of the primer and onset of the test stimulus were the same as those used in Experiment 1; however, our previous studies, in addition to the preliminary observations in this study, showed that an ISI of 400 ms is not sufficiently long for participants to perform two saccades. Therefore, we examined a range of ISIs, from 600 to 3,000 ms.

In the attentional condition, another small dark-gray dot was presented 3.3° above ("Identical" condition) or below ("Different" condition) the initial fixation point during the ISIs. The dot contrast was increased or decreased by 30%. To avoid an effect of saccadic inhibition, the dot contrast was changed at least 300 ms after the fixation dot had returned to the initial fixation point. In the "w/o task" condition, dot contrast-change detection was not required. To induce positive priming, the primer duration and velocity were set to 167 ms and 3 Hz or 1,000 ms and 2 Hz, respectively (Table 1; Figure 2). The luminance contrast of the stimuli was 50%. We did not examine the conditions in which negative priming would be expected, such as in 167-ms
duration and 4-Hz velocity, or 1,000-ms duration and 3-Hz velocity conditions (Table 1), as no effect of attention was found in these conditions (Figure 3).

Procedure

Each trial began with the presentation of a 1.5-s fixation point, followed by the primer (Figure 4). Participants were asked to perform two saccades in response to the movements of the fixation dot during the variable ISI between the termination of the primer and onset of the test stimulus and subsequently judge whether the direction of the test stimulus was rightward or leftward. In the attentional condition (“Identical” and “Different”), soon after the motion direction judgment, the participants also judged whether the contrast of the dot that appeared after the saccades was higher or lower than that of the original dot. Each session consisted of 56 trials: four trials for each of the...
seven ISIs between the priming and test stimuli (600, 800, 1,000, 1,200, 1,600, 2,000, or 3,000 ms) and for the two directions of the primer (leftward or rightward). The trials were presented in a random order. In each session, the durations and velocities of the primer were fixed. The two parameter combinations (167-ms duration and 3-Hz velocity; 1,000-ms duration and 2-Hz velocity) were examined. Each participant completed four sessions for each of the two parameter combinations, with each of the three attentional task conditions in random order. Therefore, each participant completed 32 trials per condition through 24 sessions in total within a month. Each session took about 5 min to complete. Eye movements were recorded during trials.

Results and Discussion

We verified whether the saccade was executed twice synchronous to the shifts of the fixation point (the red-colored dot in Figure 4). In all trials, both participant groups (the participants in Experiment 1 and the new participants) made two saccades within 500 ms after the offset of the primer (the duration for the two saccades ranged from 233–489 ms for the participants in Experiment 1 and from 267–477 ms for the new participants). Therefore, in the “Identical” and “Different” attentional conditions, the dot contrast was changed after the end of the second saccade. Some trials in which the eye position was more than 1.5% away from the fixation dot were excluded from the subsequent analysis (6.3% of trials across participants). In the attentional conditions (for both “Identical” and “Different”), participants correctly judged whether the dot contrast had decreased or increased relative to the original one (average of 95.1% correct for the participants in Experiment 1; 94.7% correct for the new participants) in most of the trials. In the new participant group, one participant correctly judged only 69% of the trials; therefore, his data were excluded from the analysis.

Figure 5 shows the group-averaged results for each participant group and for each condition. For both primer duration and velocity combinations, the results were similar to those obtained for the full condition in Experiment 1, in which no saccade was required: The positive priming was prominent, irrespective of whether participants performed the attentional task (Figure 2). The priming effect was gradually reduced as the length of the ISIs increased. These results were robust as to whether or not participants engaged in Experiment 1. For a primer duration of 167 ms and velocity of 3 Hz (Figure 5A), a two-way ANOVA for repeated measures revealed that the main effect of the attentional task was not significant, $F(2, 40) = 2.01, ns$ for the participants in Experiment 1; $F(2, 36) = 0.80, ns$ for the new participants, whereas that of the ISI was significant, $F(6, 120) = 72.72, p < 0.0001, \eta^2_p = 0.58,$ for the participants in Experiment 1 and $F(6, 108) = 39.24, p < 0.0001, \eta^2_p = 0.44$ for the new participants. Furthermore, the interaction between the attentional task and ISI was not significant, $F(12, 240) = 1.00, ns$ for the participants in Experiment 1 and $F(12, 216) = 1.65, ns$ for the new participants. At a primer duration of 1,000 ms and velocity of 2 Hz (Figure 5B), the main effect of the attentional task was not significant, $F(2, 40) = 0.33, ns$ for the participants in Experiment 1 and $F(2, 36) =$...
to construct spatiotopic representation, as suggested by Melcher and Morrone (2013). This suggests that attributing spatial attention to the future location of a test stimulus is requisite for inducing the effect of spatial attention observed in the spatiotopic condition in Experiment 1.

### General discussion

#### Attentional modulation of spatiotopic motion perception

Table 2 shows the summary of the results of Experiments 1 and 2. We replicated the results of our previous study (Yoshimoto et al., 2014b), specifically, that positive priming is dominant in the spatiotopic condition, whereas negative priming is prominent in the retinotopic condition. To understand the effect of spatial attention on spatiotopic motion perception, we conducted a concurrent dot contrast-change detection task after the saccade and found that spatial attention modifies only spatiotopic motion perception. This conclusion is supported by the findings that spatial attention did not affect priming effects in the full condition in Experiment 2. The results affected by the attentional task are depicted in boldface font.

Table 2. The summary of the results in Experiments 1 and 2. Notes: The first row indicates the combination of the primer duration and velocity. The second row indicates three attentional conditions. The fourth, fifth, sixth, and seventh rows indicate the priming effect under the retinotopic, spatiotopic, full, and unmatched conditions in Experiment 1, respectively. The bottom row indicates the priming effect under the full condition in Experiment 2. The results affected by the attentional task are depicted in boldface font.

<table>
<thead>
<tr>
<th>Experiment 1</th>
<th>Retinotopic</th>
<th>Spatiotopic</th>
<th>Full</th>
<th>Unmatched</th>
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<tr>
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<td>Positive</td>
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</tr>
<tr>
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<td>No priming</td>
<td>No priming</td>
<td></td>
</tr>
<tr>
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<td>Negative</td>
<td>Negative</td>
<td></td>
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<td>No priming</td>
<td></td>
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<td>Different</td>
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<td>No priming</td>
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<td>Negative</td>
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</tr>
<tr>
<td>Identical</td>
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<td>No priming</td>
<td>No priming</td>
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<tr>
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<table>
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<th>Full</th>
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<td>Identical</td>
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<tr>
<td>Different</td>
<td>—</td>
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</table>

Notes: The first row indicates the combination of the primer duration and velocity. The second row indicates three attentional conditions. The fourth, fifth, sixth, and seventh rows indicate the priming effect under the retinotopic, spatiotopic, full, and unmatched conditions in Experiment 1, respectively. The bottom row indicates the priming effect under the full condition in Experiment 2. The results affected by the attentional task are depicted in boldface font.

0.08, ns for the new participants, whereas that of the ISI was significant, $F(6, 120) = 113.8, p < 0.0001$, $\eta^2_G = 0.62$ for the participants in Experiment 1 and $F(6, 108) = 63.44, p < 0.0001$, $\eta^2_G = 0.52$ for the new participants. Meanwhile, the interaction between the attentional task and ISI was not significant, $F(12, 240) = 0.12, ns$ for the participants in Experiment 1 and $F(12, 216) = 1.51, ns$ for the new participants. These results indicate that the saccade per se between the priming and test stimuli cannot be the main factor for inducing the effect of spatial attention observed in the spatiotopic condition in Experiment 1.

### General discussion

#### Attentional modulation of spatiotopic motion perception

Table 2 shows the summary of the results of Experiments 1 and 2. We replicated the results of our previous study (Yoshimoto et al., 2014b), specifically, that positive priming is dominant in the spatiotopic condition, whereas negative priming is prominent in the retinotopic condition. To understand the effect of spatial attention on spatiotopic motion perception, we conducted a concurrent dot contrast-change detection task after the saccade and found that spatial attention modifies only spatiotopic motion perception. This conclusion is supported by the findings that spatial attention did not affect priming effects in the full condition in Experiment 2. The results affected by the attentional task are depicted in boldface font.

As discussed in the Introduction section, whether the blood oxygen level–dependent response of the visual cortex is tuned to spatiotopic coordinates or retinotopic coordinates is a matter of debate (Crespi et al., 2011; d’Avossa et al., 2007; Gardner et al., 2008), and it is likely that the current conflicting reports are due to the presence or absence of spatial attention to the moving stimulus or its future location (Melcher & Morrone, 2015; Zimmermann et al., 2014). Our results predict that when attention is not directed to the upcoming stimulus’s location, spatiotopic fMRI responses at the motion-related area may not appear; in other words, spatial attention is necessary to induce representation for spatiotopic motion perception.

In the “w/o task” condition, in which the participants were not required to perform an attentional task, positive priming was observed for the intermediate ISIs (Figure 2). The emergence of positive priming in this condition suggests that the participants did attend to the location where the test stimulus would appear, even though they were not explicitly instructed to attend to that location. A similar argument could be applied to the condition used in Crespi et al. (2011), in which the participants freely viewed a moving stimulus.

When spatial attention was directed away from the future test stimulus location (“Different” condition), no positive priming was observed at all in the spatiotopic condition. This suggests that attributing spatial attention to the future location of a test stimulus is requisite to construct spatiotopic representation, as suggested by Crespi et al. (2011). No effect of spatial attention was observed on positive priming at the full condition (Figures 2 and 5). This indicates that not the positive priming per se but the spatiotopic motion perception is modulated by the spatial attention. In other words, only the stimulus configurations that contain only a spatiotopic component combined with eye movement but do not contain a retinotopic component were affected by the attentional manipulation.
below, the delayed priming effect is consistent with the findings that spatiotopic representation develops slowly and requires at least approximately 500 ms (e.g., Zimmermann et al., 2014). However, when observers were forced to attend to the future location of the test stimulus, the delay observed in the “w/o task” condition almost disappeared. The results for the “Identical” condition indicate that the amount of delay observed in spatiotopic motion perception is not fixed but is susceptible to the attentional condition of the observers, as discussed below.

Developing spatiotopic representation through attention

It has been argued that explicit spatiotopic representation may not be necessary, because a mechanism that updates retinotopic information is sufficient to integrate visual information across saccades (e.g., Cavanagh et al., 2010; Gardner et al., 2008; Merriam, Gardner, Movshon, & Heeger, 2013; Wurtz, 2008). However, as described above, evidence for the existence of slowly developing spatiotopic representation has also been amassed (Burr & Morrone, 2012; Zimmermann et al., 2014). For example, Zimmermann et al. (2013) showed that a tilt aftereffect occurs in both retinotopic and spatiotopic conditions. They also found that an adaptation of tilt in the spatiotopic condition became effective only when the saccadic target was presented for 500–1,000 ms before changing gaze. Further, Golomb et al. (2011) showed that 500–600 ms is required to update spatiotopic information for each saccade.

Meanwhile, Zimmerman et al. (2014) indicated that this kind of slow mechanism is relatively unrelated to the classical problem of keeping vision stable during each saccade. They suggested, rather, that the function is to store object information, including motion, in a gaze-invariant visual memory representation. Our data seem to support this view, as clear positive priming, which is the outcome of solving the correspondence problem between the primer and test stimulus, occurs after 600 ms without explicit manipulation of spatial attention. Even when the attention is allocated, our data demonstrated a gradual increase of positive priming from 400 ms of ISI. This time scale seems to be too slow to accomplish visual stability through mechanisms such as efference copy or corollary discharge (e.g., Wurtz, 2008). Recently, Zimmermann, Weidner, Abdollahi, and Fink (2016) used a tilt aftereffect and found both retinotopic and spatiotopic representations in visual areas such as V3, V4, and VO, which they examined using fMRI adaptation. Our study provided evidence that an attentional resource is requisite for developing spatiotopic representation and also that spatial attention can accelerate this process.

As shown in Figure 2, the full condition was not affected by the attention manipulation, even though it induced positive priming. One clear difference between the full and the spatiotopic conditions in Figure 2 is that positive priming was clearly observed at 400 ms of ISI in the full condition, whereas it was not observed in the spatiotopic condition in the “w/o task” attentional condition. In the spatiotopic condition, attentional modulation is needed to induce positive priming, as shown in the “Identical” condition with a short ISI of 400 or 600 ms. If the ISI-dependent positive priming effect in the spatiotopic condition indicates a slowly developing spatiotopic representation as previously discussed, it could be argued that spatiotopic representation had been already constructed in the visual pathway of participants while conducting the full condition. Because participants did not have to move their eye (the full condition in Experiment 1), or because they always moved their eyes back to the original position (Experiment 2), spatiotopic representation did not have to be updated in those conditions, which is different from the spatiotopic condition in Experiment 1. Thus, we speculate that the needs for temporally developing spatiotopic representation would determine the effect of attentional modulation, and the different effects of attention between the spatiotopic condition and full condition (in Experiment 1) might reflect this point.

Relationship with lower- and higher-order motion mechanisms

The attentional effect appeared only in the spatiotopic condition, and no difference was observed between the “Identical” and “Different” conditions in the other reference frame conditions (Figures 2 and 3). The reason for this absence of the attentional effect is not yet clear. It can be supposed that the strength of the attentional modulation induced by the dot contrast-change detection task was sufficient to intervene in the computation of spatiotopic motion perception but was not sufficient for retinotopic perception. This speculation indicates that the processing levels for spatiotopic and retinotopic visual motion differ, which we discuss below.

Because positive and negative priming are observed antagonistically, these two priming effects should be induced by separate visual motion mechanisms (Kanai & Verstraten, 2005; Pantle et al., 2000). In our previous experiment, negative priming became prominent in the high-velocity and low-contrast conditions, in which the contribution of a first-order motion system (Adelson & Bergen, 1985; Lu & Sperling, 1995) increased. On the
other hand, positive priming became dominant in the low-velocity and high-contrast conditions, in which the high accuracy of spatial localization facilitated the tracking of prominent visual features (Takeuchi et al., 2011). Yoshimoto et al. (2014b) concluded that a first-order system functions in retinotopic coordinates, whereas a higher-order system, such as a feature-tracking mechanism, functions in spatiotopic coordinates.

This argument seems to be supported by several existing studies that examined the relationship between visual motion perception and reference frames (Biber & Ilg, 2011; Boi, Ögmen, & Herzog, 2011; Cavanagh et al., 2010; Hein & Cavanagh, 2012; Knapen et al., 2009; Melcher & Morrone, 2003; Turi & Burr, 2012; Wenderoth & Wiese, 2008). For example, Turi and Burr (2012) showed that lower and higher levels of visual information processing have different coordinate bases by using motion aftereffect and positional motion aftereffect. The former, which is assumed to be processed through a first-order system, is perceived in retinotopic coordinates, whereas the latter, which is assumed to require higher-order processing, is perceived in spatiotopic coordinates. From the results of this study, it is indicated that an attentional mechanism that modulates positive motion priming in spatiotopic coordinates functions only in the higher-order streams of visual motion processing.

Future studies and the relation to daily environment

As described above, negative motion priming becomes prominent by increasing the velocity and presentation duration or decreasing the luminance contrast of the primer, whereas positive motion priming becomes conspicuous in the lower-velocity, higher-contrast, and shorter-duration priming stimulus conditions. Other visual phenomena such as binocular rivalry or Necker cube rivalry show similar characteristics to the visual motion priming (Brascamp, Knapen, Kanai, van Ee, & van den Berg, 2007; Huber & O’Reilly, 2003; Long, Toppino, & Mondin, 1992). In the case of binocular rivalry, short-duration and/or low-contrast prior stimulus induces flash facilitation, whereas long-duration and/or high-contrast prior stimulus induces flash suppression (Brascamp et al., 2007). In the Necker cube rivalry, unambiguous priming cube and ambiguous Necker pattern are perceived as having the same configuration when the exposure time of the primer is short. When the exposure time of the primer is long, the Necker pattern is perceived to be the opposite to that of the priming cube (Long et al., 1992). For now, we do not know whether the motion priming, the binocular rivalry, and the Necker cube rivalry reflect a common mechanism that solves ambiguity by using the information of the priming stimulus. To understand the effects of spatial attention under different coordinates such as retinotopic or spatiotopic, it would be promising to clarify the kind of mechanism that is functioning for these three phenomena.

Burr and Morrone (2012) discussed that spatiotopic representation would be connected to action and guide our physical interaction with the world. For taking appropriate actions, an internal model of the external world must be constructed and updated as we move through the world (Land, 2012). After conducting body movements, performing actions such as pointing precisely was possible even without visual input (Byrne, Becker, & Burgess, 2007), probably by virtue of the spatiotopic representations of the environment constructed in our brain. In our previous study (Yoshimoto et al., 2014a), we found that in a spatiotopic condition similar to the one in Figure 1, the positive priming effect disappeared at dim (mesopic) light levels. We speculated that these results might indicate that proper spatiotopic representation was not constructed under mesopic vision, and this kind of failure would be related to several problems regarding the actions during dusk (Yoshimoto et al., 2014a). For example, Oudejans, Michaels, Bakker, and Davids (1999) showed that in both experimental settings and actual games, a baseball outfielder is more likely to lose sight of a flying ball during dusk and commit errors. The number of motor vehicle accidents increases at dusk both in Japan (Yamadaya, 2010) and the United States (Owens, Wood, & Owens, 2007).

The current study demonstrated that positive priming at the spatiotopic condition disappeared not only under mesopic conditions but also under photopic conditions in which spatial attention was not directed to the stimulus. If our experimental results reflect the function of representing object memory information in a gaze-invariant manner, as suggested by Zimmermann et al. (2014), losing memory of objects in the environment by the failure of constructing memory representation in the spatiotopic coordinates would induce improper actions such as making errors in catching a ball or while driving. Further studies are needed to clarify the relationship between action, spatiotopic representations, and spatial attention. In such studies, we would need participants to take actions, because viewed actions such as grasping by hand are shown to be mapped retinotopically in the visual pathway (Porat, Pertzov, & Zohary, 2011).

Keywords: visual motion perception, reference frames, spatiotopic coordinate, retinotopic coordinate, spatial attention, motion priming
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