

# The reference frame of visual motion priming depends on underlying motion mechanisms

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Several different types of motion mechanisms function in the human visual system. The purpose of this study was to clarify the type of reference frame, such as retinotopic and spatiotopic frames of reference, at which those different motion mechanisms function. To achieve this, we used a phenomenon called visual motion priming, in which the perceived direction of a directionally ambiguous test stimulus is influenced by the moving direction of a preceding stimulus. Previous studies have indicated that negative motion priming is induced by a low-level motion mechanism, such as a first-order motion sensor, whereas positive motion priming is induced by a high-level motion mechanism, such as a feature-tracking system. In the experiments, subjects made a saccade after the termination of a smoothly drifting priming stimulus and judged the perceived direction of a 180° phase-shifted sine-wave grating presented subsequently in retinotopic or screen-based spatiotopic coordinates. By manipulating the stimulus parameters, such as primer duration, velocity, and contrast, both positive and negative priming were observed. We found that positive priming was observed in spatiotopic coordinates, whereas negative priming was observed in retinotopic coordinates. Prominent positive priming in spatiotopic coordinates was observed only when the interval between the priming and test stimuli was longer than around 600 ms. This delayed priming effect was not caused by saccadic eye movements. These results suggest that a low-level motion mechanism functions in retinotopic coordinates, whereas a high-level motion mechanism functions in spatiotopic coordinates, in which the representation builds up slowly.

## Introduction

The visual system continuously receives varied spatiotemporal visual inputs. How does the visual system extract motion information from those visual inputs? The visual system contains specialized mechanisms to analyze the velocity of moving objects (Anstis, 1980; Braddick, 1980). Several different types of motion sensors have been described (e.g., Burr & Thompson, 2011; Cavanagh & Mather, 1989; Lu & Sperling, 1995; Nishida, 2011). A first-order motion mechanism, presumably operating at a low anatomical level, essentially acts as a spatiotemporal orientation detector that extracts velocity information from the luminance flow (Adelson & Bergen, 1985; Burr, Ross, & Morrone, 1986; De Valois, Cottaris, Mahon, Elfar, & Wilson, 2000; Emerson, Bergen, & Adelson, 1992; van Santen & Sperling, 1984, 1985; Watson & Ahumada, 1985). Higher order motion detectors, such as second-order and feature-tracking (or third-order) mechanisms, have also been postulated. Second-order motion may be extracted by a nonlinear transformation of spatiotemporal information (Chubb & Sperling, 1988; Smith, 1994). A feature-tracking mechanism, or third-order motion mechanism, is believed to detect changes in the position of identifiable pattern features over time (Bowns, 2002; Cavanagh, 1992, 1994; Dawson, 1991; Del Viva & Morrone, 1998; Derrington, Allen, & Delicato, 2004; Lu & Sperling, 1995; Seiffert & Cavanagh, 1998; Ullman, 1979). The purpose of this study was to determine the type of reference frame, namely, retinotopic and spatiotopic coordinates, in which the different motion mechanisms operate. It

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should be noted that our study focused on a first-order motion mechanism and a feature-tracking mechanism by using a luminance-modulated translational motion stimulus. Reference frames of motion mechanisms driven by complex moving stimuli, such as an expansion/contraction or rotation (e.g., Morrone et al., 2000), or by second-order motion stimuli such as a contrast-modulated moving grating, are beyond the scope of this study. We will discuss these points in the General discussion.

In many circumstances, we detect and perceive object motion veridically, regardless of eye/head/body movements that induce retinal image changes in a complex way. Therefore, the clarification of the reference frames of the motion mechanisms is one of the fundamental questions in the field of research in human vision. In early visual areas, such as in the primary visual cortex (V1), information is encoded retinotopically (e.g., Wandell, Brewer, & Dougherty, 2005). However, there must also be a mechanism that allows a nonretinotopic representation, as we perceive the world as being stable despite changes in retinal position every time we make an eye movement.

Turi and Burr (2012) showed that two forms of motion aftereffects, which probably act at different neural levels of processing, are observed in different reference frames: when the saccades are involved between the adaptation and test stimuli, the lower level adaptation, such as motion aftereffect (in which prolonged exposure to a moving stimulus makes a stationary stimulus viewed subsequently appear to move in the opposite direction), is eye based (i.e., encoded in retinotopic coordinates that shift with each eye movement), whereas the higher level analysis tapped by the positional motion aftereffect (in which apparent position changes by adaptation to motion) is spatiotopic (i.e., encoded in nonretinotopic screen-based coordinates). With one exception (Ezzati, Golzar, & Afraz, 2008), there is a consensus among studies that motion aftereffect occurs largely in the retinotopic frame of reference (Biber & Ilg, 2011; Boi, Ögmen, & Herzog, 2011; Cavanagh, Hunt, Afraz, & Rolfs, 2010; Knapen, Rolfs, & Cavanagh, 2009; Wenderoth & Wiese, 2008).

Hein and Cavanagh (2012) studied the motion correspondence problem by using the Ternus display and showed that high-level analysis of feature information contributes to correspondence over a limited spatial range, and that the range is imposed in spatiotopic, and not retinotopic, coordinates. According to Morrone, Cicchini, and Burr (2010), a higher order adaptation is in fact spatiotopic, remaining fixed in space during head turns. Those authors showed that adaptation to a fast-moving spatially localized grating decreases the perceived duration of the test grating

presented at a spatiotopically matched location (see also Morrone & Burr, 2008).

Based on these previous studies, we speculated that a higher level motion mechanism, such as feature tracking, might be spatially selective in external, rather than retinal, coordinates, whereas a lower level directionally selective, and presumably energy-based first-order motion system, may be selective in retinotopic coordinates. In this study, we examined this prediction by using visual motion priming.

Visual motion priming is a phenomenon in which the perceived direction of a directionally ambiguous stimulus is influenced by the movement direction of the preceding stimulus (Anstis & Ramachandran, 1987; Campana, Pavan, & Casco, 2008; Jiang, Luo, & Parasuraman, 2002; Jiang, Pantle, & Mark, 1998; Kanai & Verstraten, 2005; Pantle, Gallogly, & Piehler, 2000; Pavan, Campana, Guerreschi, Manassi, & Casco, 2009; Piehler & Pantle, 2001; Pinkus & Pantle, 1997; Ramachandran & Anstis, 1983; Raymond, O'Donnell, & Tipper, 1998; Takeuchi, Tuladhar, & Yoshimoto, 2011; Yoshimoto & Takeuchi, 2013). Ramachandran and Anstis (1983) reported that a preceding moving dot stimulus induces visual inertia, in which a subsequent directionally ambiguous bistable long-range stimulus is perceived to move in the same direction as the preceding one. Pinkus and Pantle (1997) used a moving sine-wave grating to show that visual inertia occurs with a periodic pattern. The subsequent presentation of a directionally ambiguous test pattern that was made of a 180°-shifted grating was perceived to move in the same direction as that of the priming grating when the presentation duration of the primer was less than approximately 300 ms. Those authors named this phenomenon positive motion priming. Pantle et al. (2000) showed that positive motion priming is perceived when the presentation duration of the priming stimulus is shorter, whereas the so-called negative motion priming is perceived when a subsequent test pattern is perceived to move in the opposite direction of the priming stimulus when its presentation duration is longer. In addition, Kanai and Verstraten (2005) showed that the strength of positive motion priming is reduced as the duration of the presentation of the priming stimulus increases, and the perceived direction of the test pattern is reversed by a priming stimulus of 640 ms. Those authors called this negative priming phenomenon the rapid form of motion aftereffects (e.g., Mather, Pavan, Campana, & Casco, 2008; Mather, Verstraten, & Anstis, 1998). These previous studies have shown that positive priming switches to negative priming as the primer duration lengthens. Note that, as explained below, the perceived direction of the test stimulus is not determined only by the primer duration; it also depends on the velocity and contrast of the stimulus.

Pantle et al. (2000) suggested that the motion mechanism that is responsible for positive priming would be different from the one that induces negative priming, because the two priming effects are observed antagonistically. There is evidence that different motion mechanisms have different sensitivities to the velocity/temporal frequency and luminance contrast of moving patterns (e.g., Hawken, Gegenfurtner, & Tang, 1994; Lu & Sperling, 1995). The contrast sensitivity of an energy-based first-order motion system is relatively higher than that of other motion mechanisms (Doshier, Landy, & Sperling, 1989; Lu & Sperling, 1995; Nishida, 1993; Smith, Hess, & Baker, 1994; Solomon & Sperling, 1994; Sperling, 1989; Takeuchi & De Valois, 1997, 2009). A plausible candidate for a directionally selective motion detector that is sensitive to high velocity would be energy based (Burr & Ross, 1982; Burr, Ross, & Morrone, 1986; Lappin, Tadin, Nyquist, & Corn, 2009; Lu & Sperling, 1995). In contrast, higher order motion mechanisms are insensitive to higher velocities (Lu & Sperling, 1995).

The perceived direction of motion priming depends on the velocity and contrast of the stimulus, as well as on the duration of the priming stimulus. Takeuchi et al. (2011) reported that positive priming is prominent at the primer velocity of less than 3 Hz, whereas only negative priming was observed at a higher velocity, regardless of primer duration. Yoshimoto and Takeuchi (2013) found that positive priming was observed when the velocity of the primer was as low as 2 Hz and the contrast of the primer was as high as eight times the direction-discrimination threshold. Negative priming was dominant at velocities as high as 4 Hz, or at the low contrast of two times the threshold. In summary, negative priming is prominent in high-velocity or low-contrast conditions, whereas positive priming is prominent in low-velocity and high-contrast conditions. Basically, a longer primer induces negative priming, but both velocity and contrast influence perception. The velocity/contrast dependences of visual motion priming observed psychophysically suggest that a low-level motion mechanism, such as a first-order motion mechanism, is responsible for the induction of negative priming, whereas a high-level motion mechanism, such as feature tracking, is responsible for positive priming (Takeuchi et al., 2011; Yoshimoto & Takeuchi, 2013).

Other evidences regarding the underlying motion mechanisms for positive and negative motion priming are as follows. Neurophysiological studies have shown that a moving stimulus with a very short duration, such as several hundred milliseconds, is sufficient to change the adaptation status of directionally selective neurons located at as early as the V1 (Lisberger & Movshon, 1999; Priebe, Churchland, & Lisberger, 2002). Psychophysical studies have indicated that the rapid adaptation of directionally selective neurons is an underlying

neural mechanism of negative motion priming or rapid-type motion aftereffect (Glasser, Tsui, Pack, & Tadin, 2011; Kanai & Verstraten, 2005; Pantle et al., 2000; Pavan et al., 2009). By applying repetitive transcranial magnetic stimulation (rTMS), Campana, Pavan, Mangià, and Casco (2011) found larger involvement of visual areas V1/V2 than V5/MT when negative motion priming was induced. In addition, Jiang et al. (2002) measured event-related potentials from human subjects while they observed positive motion priming and concluded that higher order motion mechanisms are responsible for the induction of positive priming. The spatial localization of the prominent visual features is crucial for tracking moving patterns in feature-tracking mechanisms or third-order motion mechanisms. As positional acuity is degraded under low retinal illuminance (Livingstone & Hubel, 1994), it has been predicted that positive motion priming is reduced under low retinal illuminance. This prediction has been confirmed (Takeuchi et al., 2011, Yoshimoto & Takeuchi, 2013). In those experiments, negative priming became dominant when the subjects observed the visual stimuli through a neutral density filter, so that their retinal illuminance was reduced to mesopic or scotopic levels.

In this study, we investigated the reference frames associated with motion mechanisms by using visual motion priming. For this purpose, we followed the experimental method described in previous studies (Knapen et al., 2009; Turi & Burr, 2012) and estimated the strength of visual motion priming in retinotopic and spatiotopic coordinates. To distinguish between the two conditions, the test stimulus was shifted in the same retinal location relative to fixation after a vertical saccade in the retinotopic condition; in contrast, the test stimulus was kept at the same location on the display in the spatiotopic condition (Figure 1). Based on the results of Turi and Burr (2012), we predicted that negative motion priming, presumably induced by a low-level energy-based first-order motion mechanism, would be observed in retinotopic coordinates, whereas positive motion priming, presumably induced by a high-level motion system (such as a feature-tracking mechanism) would be observed in spatiotopic coordinates. To examine this prediction, we manipulated the three stimulus parameters (duration of the priming stimulus, velocity, and luminance contrast) that influence the effects of motion priming.

We also modified the duration of the interstimulus interval (ISI) between the priming and test stimuli. Recent studies showed that a spatiotopic (or non-retinotopic) representation is not available instantaneously (Burr & Morrone, 2011, 2012; Golomb, Marino, Chun, & Mazer, 2011; Golomb, Pulido, Albrecht, Chun, & Mazer, 2010; Morrone et al., 2010; Wurtz, 2008; Zimmermann, Morrone, Fink, & Burr,

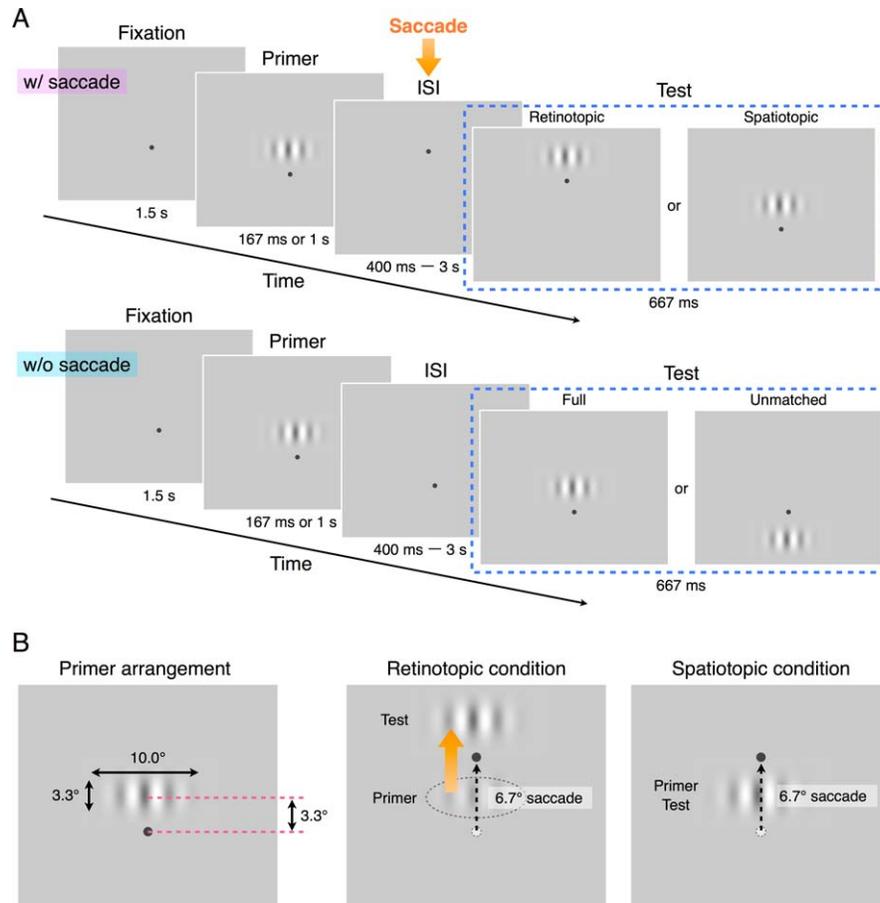


Figure 1. Schematic description of the trial sequence and the stimulus arrangement. (A) Trial sequence in the four different experimental conditions. A small black dot (as a fixation point) was displayed for 1.5 s, followed by the 167-ms or 1000-ms primer. In the retinotopic and spatiotopic conditions, the fixation point jumped  $6.7^\circ$  to the upper region of the screen after the termination of the primer, and subjects made a saccade to the new fixation point. After the ISI varied from 400 to 3000 ms, the test stimulus was presented above (retinotopic condition) or below (spatiotopic condition) the fixation point for 667 ms. In the spatiotopic condition, the priming and test stimuli occupied the same position on the display. In the full and unmatched conditions, the position of the fixation point was not changed; thus, saccades were not required. After the ISI, the test stimulus was presented above (full condition) or below (unmatched condition) the fixation point. In the full condition, the priming and the test stimuli occupied the same position on the display. Subjects were asked to judge whether the perceived direction of the test stimulus was leftward or rightward. (B) Details of the stimulus arrangements in the retinotopic and spatiotopic conditions. The primer was presented at the center of the screen and the fixation point was displayed  $3.3^\circ$  below the center of the primer. In the retinotopic condition, the fixation point jumped to the upper region of the screen, and the test stimulus was presented in the same retinotopic position relative to the fixation point as the primer. In the spatiotopic condition, the fixation point jumped to the upper region of the screen, and the test stimulus was presented in the same screen position as the primer.

2013). Zimmermann et al. (2013) found that a tilt aftereffect, in which the apparent orientation of a line or grating of fixed physical orientation is altered after the inspection of a different orientation, has spatiotopic coordinates only after the saccadic target has been displayed for at least 500 ms before gaze change. Those authors pointed out that the results of the report that did not show spatiotopy (Boi et al., 2011; Knapen, Rolfs, Wexler, & Cavanagh, 2010) might stem from a lack of sufficient time for the spatiotopy to build. If this argument is applied to the case of motion perception, it

will take a certain time to observe the positive motion priming if it occurs in spatiotopic coordinates.

We found that negative motion priming was dominant in retinotopic coordinates, whereas positive motion priming was dominant in spatiotopic coordinates. Although the retinotopic negative priming was prominent at the shortest ISI examined, the spatiotopic positive priming was not observed instantaneously; rather, it became conspicuous only when the ISI was longer than around 600 ms. We also found that the delayed priming effect in spatiotopic coordinates was

not caused by the eye movement. These results led us to conclude that the low-level motion analysis is processed in retinotopic coordinates, whereas the high-level motion mechanism functions in spatiotopic coordinates, in which the representation builds up slowly.

## Experiment 1

In Experiment 1, we measured the strength of the effect of the duration-varying priming stimulus on a test stimulus presented after saccades in retinotopic or spatiotopic frames of reference. As mentioned in the Introduction, it has been reported that both positive and negative motion priming are highly dependent on the duration of the presentation of the priming stimulus when the velocity and contrast of the stimuli are fixed (Kanai & Verstraten, 2005; Pantle et al., 2000; Pavan et al., 2009; Pinkus & Pantle, 1997; Takeuchi et al., 2011; Yoshimoto & Takeuchi, 2013). Those studies showed that positive priming was observed when the priming stimulus was presented for periods as short as 100–200 ms. Positive priming switched to negative priming at a duration of the presentation of the priming stimulus of around 300 ms. If positive and negative priming are induced by high- and low-level motion mechanisms, respectively (Pantle et al., 2000; Takeuchi et al., 2011; Yoshimoto & Takeuchi, 2013), then positive priming at a short duration of primer presentation will be observed in spatiotopic coordinates, whereas negative priming observed at a longer duration of primer presentation will be observed in retinotopic coordinates.

## Methods

### Subjects

Four subjects (EA, SY, TT, and YI) participated in the experiments. Two of them were authors (SY and TT), and the other two were naïve to the purpose of the experiments. All had normal or corrected-to-normal vision. All subjects gave informed consent before their inclusion in the study.

### Apparatus

The stimuli were generated by MATLAB (The MathWorks, Inc., Natick, MA, USA) using the Psychophysics Toolbox version 3.0 extension (Brainard, 1997; Pelli, 1997) on a computer (MacPro, Apple Inc., Cupertino, CA, USA), and were displayed on a 21-in. RGB monitor (SONY GDM F520, Sony Corporation, Tokyo, Japan). The monitor frame rate was 120 Hz, with a spatial resolution of  $1024 \times 768$

pixels and 12-bit gray-level resolution. The monitor output was linearized (gamma corrected) under software control. For all experiments using luminance-varying stimuli, the space-averaged chromaticity (CIE 1931) of the display had an  $x$  value of 0.31 and a  $y$  value of 0.33. The averaged luminance of the screen was  $46.8 \text{ cd/m}^2$ . Subjects observed the display while their head position was maintained by a chin and head rest. Patterns were viewed binocularly at a viewing distance of 57 cm. The movements of the right eye of each subject were monitored with a ViewPoint Eye-Tracker 220 fps USB system (Arrington Research, Inc., Scottsdale, AZ, USA) that was controlled by the same PC during the whole period of the experiments. The sampling rate of this infrared-video-based eye tracker was 220 Hz. Saccades were detected by applying a set of velocity and acceleration criteria (Krauzlis & Miles, 1996).

### Stimuli

Figure 1 provides a schematic description of the trial sequence and stimulus arrangement. To allow comparisons with previous studies of motion priming, we used a stimulus that was similar to that used by Kanai and Verstraten (2005) and Takeuchi et al. (2011). An achromatic vertical sine-wave grating was displayed in a rectangular window that measured  $10.0^\circ \times 3.3^\circ$  (H  $\times$  V). The edges of the stimulus were tapered by a Gaussian function with a sigma value of  $1.0^\circ$ . The spatial frequency of the stimulus was set to  $0.5 \text{ c/}^\circ$ . The stimulus was presented on a uniform gray-colored background (CIE1931;  $x = 0.31$ ,  $y = 0.33$ ) that had a luminance that was the same as the space-averaged luminance of the sine-wave grating.

The direction of motion of the priming stimulus was either to the right or to the left. Takeuchi et al. (2011) showed that, at a velocity of the stimulus of 3 Hz and a contrast as high as 10 times the direction-discrimination threshold, positive priming was prominent when the primer duration was set to 150 ms, whereas negative priming was dominant when the primer duration was longer than 600 ms (see Takeuchi et al., 2011, figure 2). Based on that study and our preliminary observations, the duration of the presentation of the priming stimulus was set to 167 or 1000 ms, to induce both positive and negative priming effects. The velocity of the priming stimulus was set at 3 Hz. The Michelson contrast of the priming stimulus was set at 50%.

Similar to previous studies (Kanai & Verstraten, 2005; Pantle et al., 2000; Pinkus & Pantle, 1997; Takeuchi et al., 2011; Yoshimoto & Takeuchi, 2013), an ambiguous test stimulus was generated by shifting the phase of the grating by  $180^\circ$ . The spatial frequency was set at  $0.5 \text{ c/}^\circ$ , which was the same as that of the priming stimulus. To equate the velocities of the

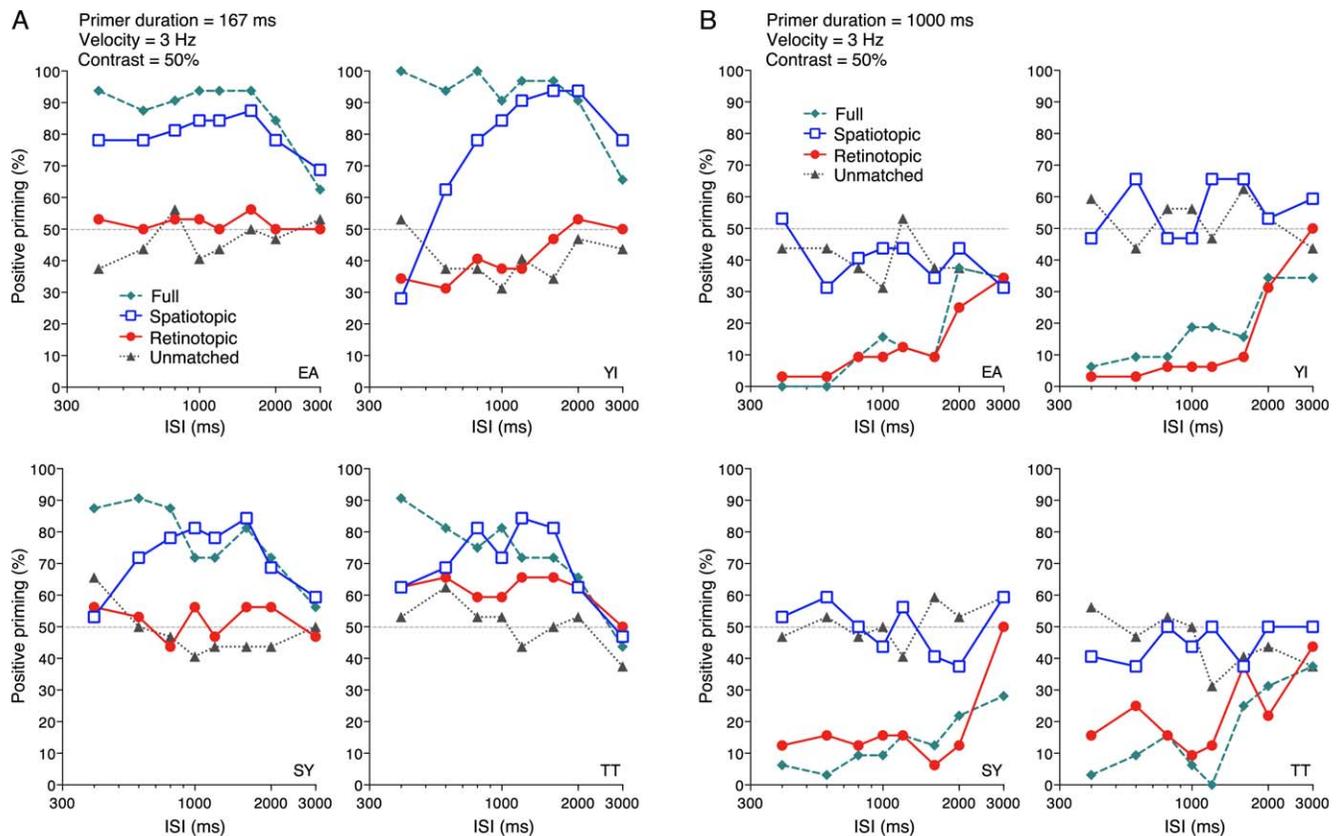


Figure 2. Results of Experiment 1 for the four subjects. In each graph, the percentage response of positive priming (motion of test stimulus in the same direction as the primer) is plotted as a function of the ISI between the primer and test stimulus (in ms). Each curve represents the data that were collected in different experimental conditions (retinotopic, spatiotopic, full, and unmatched conditions). The velocity of the stimulus was set at 3 Hz. The luminance contrast was set at 50%. (A) The primer duration was set at 167 ms. (B) The primer duration was set at 1000 ms.

priming and test stimuli, the duration of one frame of the test stimulus was set to 167 ms (it was set to a duration that was equal to that required for the priming stimulus to shift 180°). A total of four frames were presented for the test stimulus; thus, the duration of the test stimulus was set at 667 ms. The luminance contrast of the test stimulus was 50%, which was the same as that of the priming stimulus.

The priming stimulus was presented in the center of the screen, and the position of the test stimulus and the fixation point were changed. We ran four experimental conditions, as described in Figure 1A: (a) retinotopic condition, in which the fixation point jumped to the upper region of the screen soon after the offset of the priming stimulus, and the test stimulus was presented with a variable ISI in the same retinotopic position relative to fixation as the priming stimulus; (b) spatiotopic condition, which was similar to the retinotopic condition, with the exception that the test stimulus was presented in the same screen position as the priming stimulus; (c) full condition, in which the test stimulus was presented with a variable ISI at the same location as that used during the priming stimulus,

with no shift in the fixation point (i.e., this condition represented both retinotopic and spatiotopic coordinates); and (d) unmatched condition, in which the test stimulus was presented with a variable ISI at the position that matched neither the spatiotopic nor retinotopic location of the priming stimulus, with no shift in the fixation point. Subjects made saccades in conditions (a) and (b), but not in conditions (c) and (d). The unmatched condition (d) was adopted to examine the possibility that the effects of motion priming could result from a motion integration over a large spatial region in the spatiotopic condition (b), in which the priming and test stimuli were separated retinotopically.

To investigate the temporal properties of the representation process in retinotopic and spatiotopic coordinates, the time from the offset of the priming stimulus to the onset of the test stimulus (i.e., ISI between the priming and test stimuli) was changed from 400 to 3000 ms. The ISI was also changed in the full and unmatched conditions, in which no saccade was required, in the same manner as that used for the retinotopic and spatiotopic conditions.

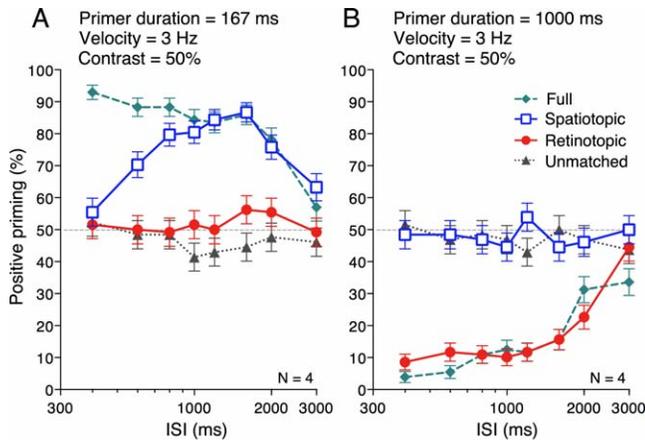


Figure 3. Averaged data for the four subjects in Experiment 1. Each curve represents the data that were collected in different experimental conditions (retinotopic, spatiotopic, full, and unmatched conditions). Error bars represent  $\pm 1$  standard error of the mean. The velocity of the stimulus was set at 3 Hz. The luminance contrast was set at 50%. (A) The primer duration was set at 167 ms. (B) The primer duration was set at 1000 ms.

Figure 1B illustrates the details of the stimulus arrangement in the retinotopic and spatiotopic conditions. In all conditions, the spatial distance between the center of the priming stimulus and the fixation point was set at  $3.3^\circ$ . A black dot with a radius of  $0.25^\circ$  was displayed to assist subjects in maintaining fixation while the grating was presented in the parafovea. Subjects made a  $6.7^\circ$  upward saccade with the shift of the fixation point in the retinotopic and spatiotopic conditions.

In preliminary observations, we collected data both when the priming stimulus was presented in the upper peripheral retina (above the fixation point) and in the lower peripheral retina (below the fixation point), and did not find any systematic difference between the data collected from lower and upper retinas. Therefore, the priming stimulus was presented only in the upper peripheral retina in the main experiment, as shown in Figure 1.

### Procedure

The trial sequence used is illustrated in Figure 1A. Each trial began with the presentation of a small dot, which appeared at fixation for 1.5 s, followed by the priming sine-wave stimulus. In the retinotopic and spatiotopic conditions, the fixation point immediately jumped by  $6.7^\circ$  to the upper region of the screen after the termination of the priming stimulus, and the subjects executed a saccade to the new fixation point. After a variable ISI, during which the display was blank (but containing the fixation point), a directionally ambiguous test stimulus was presented. The

subjects' task was to judge whether the perceived direction of the test stimulus was leftward or rightward by pressing the appropriate arrow key. The subjects were instructed to view the fixation point continuously throughout the trial. After a button was pressed, 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. The saccade conditions (retinotopic and spatiotopic) and the no-saccade conditions (full and unmatched) were carried out in separate sessions. Each session consisted of 128 trials: four trials for each of the two types of presentation of the test stimulus (retinotopic and spatiotopic conditions in the saccade session; full and unmatched conditions in the no-saccade session), for each of the eight ISIs between the priming and test stimuli (400, 600, 800, 1000, 1200, 1600, 2000, and 3000 ms), and for the two directions of the priming stimulus (rightward or leftward), which were presented in a random order. In each session, the duration of the presentation of the priming stimulus (167 or 1000 ms) was fixed. Each subject completed four saccade sessions and four no-saccade sessions for each of the duration conditions of the priming stimulus (16 sessions in total), in a random order. Subjects underwent at least 20 practice trials in each condition prior to the actual data acquisition.

### Results and discussion

Eye position was monitored during the experiment. In the retinotopic and spatiotopic conditions, all subjects made saccades normally. The latencies ranged from 141 to 277 ms, so that the ISI of 400 ms was sufficiently long to make a  $6.7^\circ$  saccade. In a small number of trials, subjects looked more than  $1.5^\circ$  away from the fixation point (both pre- and post-saccade) through a single trial (3.3% on average). We excluded those trials from the subsequent analyses.

Figure 2 shows the results of Experiment 1 for each subject at each primer duration and experimental condition. The percentage response to positive motion priming is plotted as a function of the ISI between the priming and test stimuli (in milliseconds). Thus, when more than 50% of the responses represented positive motion priming, subjects reported that the perceived direction of the test stimulus was in the same direction as that of the priming stimulus in the majority of the trials. When fewer than 50% of the responses were scored as positive priming, subjects reported that the motion of the test stimulus was in the direction opposite to the priming stimulus (negative motion priming) in the majority of the trials.

Although there was some intersubject variability, the results were essentially consistent across subjects. Thus,

the averaged data were used in our analyses. Figure 3 presents the averaged data for the four subjects. In the full condition, we replicated the results that were reported previously by Kanai and Verstraten (2005), Pantle et al. (2000), and Takeuchi et al. (2011), who showed that positive priming switches to negative priming depending on the duration of the priming stimulus. Positive priming was observed in the majority of the trials at the primer duration of 167 ms (Figure 3A), whereas negative priming was dominant at the duration of 1000 ms (Figure 3B). We found that the frequency of the perception of motion priming decayed as the ISI between the priming and test stimuli became longer; thus, the percentage response converged to 50%. This is consistent with the results reported by Kanai and Verstraten (2005).

Our prediction was that positive and negative priming would be observed in spatiotopic and retinotopic coordinates, respectively. We found that positive priming was dominant in the spatiotopic condition, and disappeared in the retinotopic condition (Figure 3A), whereas negative priming was dominant in the retinotopic condition, but not in the spatiotopic condition (Figure 3B).

We also found that the effect of the ISI was different between the spatiotopic positive priming and the retinotopic negative priming. The negative priming in the retinotopic condition was dominant at the short ISI, similar to that observed in the full condition (Figure 3B). Conversely, the positive priming function in the spatiotopic condition had a flattened inverted V shape (Figure 3A): the positive priming became conspicuous at the ISI of around 600–2000 ms, but not at shorter and longer ISIs. These results suggest that a longer time is required for the effects of motion priming to be available in spatiotopic coordinates compared with retinotopic coordinates.

It should be noted that neither positive nor negative priming was conspicuous in the unmatched condition, regardless of primer duration. Thus, the positive priming observed in the spatiotopic condition (Figure 3A) cannot be explained by the hypothesis that spatially separated priming and test stimuli are integrated by a spatially large receptive field of motion mechanism to induce a priming effect.

These interpretations were supported by the statistical analyses. At the primer duration of 167 ms (Figure 3A), a within-subject two-way analysis of variance (ANOVA) showed that the main effects of experimental condition and ISI between the priming and test stimuli were significant,  $F(3, 9) = 16.85$ ,  $p < 0.001$  for the experimental condition;  $F(7, 21) = 4.86$ ,  $p < 0.01$  for the ISI. The interaction between the experimental condition and ISI was also significant,  $F(21, 63) = 5.48$ ,  $p < 0.0001$ . At the primer duration of 1000 ms (Figure 3B), a within-subject two-way ANOVA showed that

the main effects of experimental condition and ISI were significant,  $F(3, 9) = 77.67$ ,  $p < 0.0001$  for the experimental condition;  $F(7, 21) = 7.13$ ,  $p < 0.001$  for the ISI. The interaction between the experimental condition and ISI was also significant,  $F(21, 63) = 4.74$ ,  $p < 0.0001$ .

Based on the assumption that positive and negative priming would be induced by higher and lower order motion mechanisms, respectively (Jiang et al., 2002; Pantle et al., 2000; Takeuchi et al., 2011; Yoshimoto & Takeuchi, 2013), these results can be interpreted in the following manner: a higher order motion mechanism functions in spatiotopic coordinates, whereas a lower order motion mechanism functions in retinotopic coordinates.

However, before reaching this conclusion, we need to examine whether the observed effect of the coordinate (retinotopic or spatiotopic) was actually related to the resulting priming effects, negative or positive priming per se, and not to the duration of presentation of the priming stimulus, as we only manipulated primer duration in Experiment 1. As described above, the priming effects depended not only on the duration of the presentation of the priming stimulus, but also on its velocity and the luminance contrast. In Experiment 2, we examined further the reference frame of visual motion priming by changing the velocity and the contrast of the stimulus.

## Experiment 2

The primer duration value at which the transition from positive to negative motion priming occurs depends on the velocity and luminance contrast of the stimulus. Takeuchi et al. (2011) found that, at velocities of the stimulus lower than 3 Hz, positive priming was dominant, regardless of the duration of the priming stimulus. Conversely, at velocities of the stimulus higher than 3 Hz, negative priming became conspicuous, even when the primer duration was as short as 150 ms. Yoshimoto and Takeuchi (2013) showed that, when the contrast of the stimulus was as high as eight times the direction-discrimination threshold, both positive and negative priming were observed, depending on the primer duration and the velocity; conversely, when the contrast was as low as two times the threshold, negative priming was dominant, regardless of the other stimulus parameters.

It should be noted that, in the full condition, the perceived direction of the test stimulus that was modulated by the 167-ms priming stimulus with a 3-Hz velocity and 50% luminance contrast was positive (Figure 3A). Based on the previous studies described above, we expected that the priming effect would

Experiment 1	Primer duration (ms)	Velocity (Hz)	Contrast (%)	Observed priming effects in the full condition
	167	3	50	Positive
	1000	3	50	Negative
Experiment 2	Primer duration (ms)	Velocity (Hz)	Contrast (%)	Predicted priming effects in the full condition
	167	4	50	Negative
	167	3	5	Negative
	1000	2	50	Positive

Table 1. Stimulus parameters examined in Experiments 1 and 2 coupled with the observed or predicted priming effects in the full condition.

change from positive to negative by increasing the velocity from 3 Hz to 4 Hz, or by decreasing the luminance contrast from 50% to 5%, while maintaining the primer duration at 167 ms. Similarly, the perceived direction of the test stimulus that was modulated by a 1000-ms priming stimulus was expected to switch from negative (Figure 3B) to positive by decreasing the velocity from 3 Hz to 2 Hz. In Experiment 2, we used these dependencies of the priming effect on stimulus parameters to examine further the reference frame of motion mechanisms. The stimulus parameters used and the predictions regarding the perceived direction of the motion priming are summarized in Table 1.

If the reference frame of visual motion priming is determined by the duration of the presentation of the priming stimulus regardless of the direction of the priming effects, short and long priming stimuli will induce motion priming in spatiotopic and retinotopic coordinates, respectively, as in Experiment 1. In contrast, if lower and higher order motion mechanisms function in the different reference frames, positive priming will be observed in spatiotopic coordinates, whereas negative priming will be observed in retinotopic coordinates, regardless of the stimulus parameters of the primer.

## Methods

### Stimuli

As in Experiment 1, we examined the manner in which the preceding moving grating modulates the perceived direction of a 180° phase-shifted test gratings. Subjects judged the perceived directions of a test stimulus presented after a variable ISI (from the offset of the priming stimulus to the onset of the test stimulus) in the four experimental conditions (Figure 1A). The duration of one frame of the test stimulus was calculated based on the velocity of the priming stimulus. The velocity and the luminance contrast of the stimuli, coupled with the predicted perceived direction of the test stimulus, are shown in Table 1.

In preliminary observations, we confirmed that neither positive nor negative priming was reported when the velocity of the priming stimulus increased to 5 Hz or decreased to 1 Hz. Therefore, we restricted the range of velocity of the priming stimulus from 2 to 4 Hz, similar to our previous study (Yoshimoto & Takeuchi, 2013). When the contrast of the 1000-ms priming stimulus was increased to 100% in the preliminary observations, negative priming was still dominant, and no transition to positive priming was observed. Thus, we did not run the contrast-increment condition for the 1000-ms priming stimulus in the main experiment.

### Procedure

As in Experiment 1, each trial began with the presentation of a small dot, which appearing at fixation for 1.5 s, followed by the priming sine-wave stimulus (Figure 1). In the retinotopic and spatiotopic conditions, the fixation point immediately jumped by 6.7° to the upper region of the screen after termination of the priming stimulus, and the subjects executed a saccade to the new fixation point. After a variable ISI, a directionally ambiguous test stimulus was presented. Subjects were asked to judge whether the perceived direction of the test stimulus was leftward or rightward. The saccade conditions (retinotopic and spatiotopic) and the no-saccade conditions (full and unmatched) were carried out in separate sessions. Each session consisted of 128 trials: four trials for each of the two types of presentation of the test stimulus (retinotopic and spatiotopic conditions in the saccade session; full and unmatched conditions in the no-saccade session), for each of the eight ISI between the priming and test stimuli (400, 600, 800, 1000, 1200, 1600, 2000, and 3000 ms), and for the two directions of the priming stimulus (rightward or leftward), which were presented in a random order. In each session, the duration of presentation of the priming stimulus, the velocity, and the contrast were fixed. The three stimulus parameter combinations shown in Table 1 (167-ms primer duration, 4-Hz velocity, and 50% contrast; 167-ms

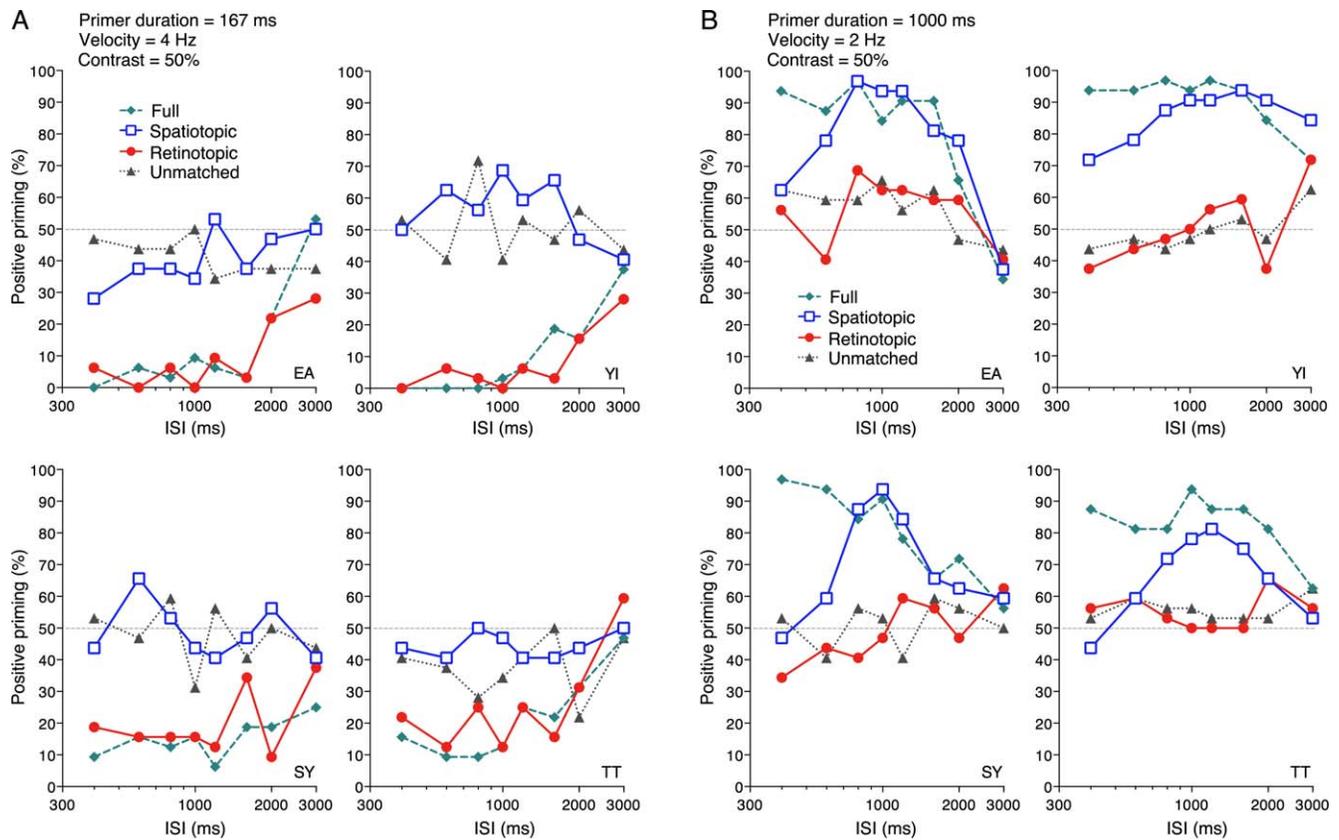


Figure 4. Results of Experiment 2 for the four subjects. In each graph, the percentage response of positive priming (motion of test stimulus in the same direction as the primer) is plotted as a function of the ISI between the primer and test stimulus (in ms). Each curve represents the data that were collected in different experimental conditions (retinotopic, spatiotopic, full, and unmatched conditions). The luminance contrast was set at 50%. (A) The primer duration and velocity were set at 167 ms and 4 Hz, respectively. (B) The primer duration and velocity were set at 1000 ms and 2 Hz, respectively.

primer, 3-Hz velocity, and 5% contrast; 1000-ms primer duration, 2-Hz velocity, and 50% contrast) were examined. Each subject completed four saccade sessions and four no-saccade sessions for each of the three stimulus parameter combinations (24 sessions in total), in a random order. The same subjects that performed Experiment 1 participated in Experiment 2.

### Results and discussion

For clarity, we separately the present data into Figures 4 and 5, in which the contrast was 50%, and into Figures 6 and 7, in which the contrast was 5%. Figures 4 and 5 present the individual and group-averaged results, respectively. The primer duration was 167 ms and the velocity was 4 Hz in Figures 4A and 5A, and 1000 ms and 2 Hz in Figures 4B and 5B. The averaged data shown in Figure 5 was used in the subsequent analyses, because the results were essentially consistent across subjects.

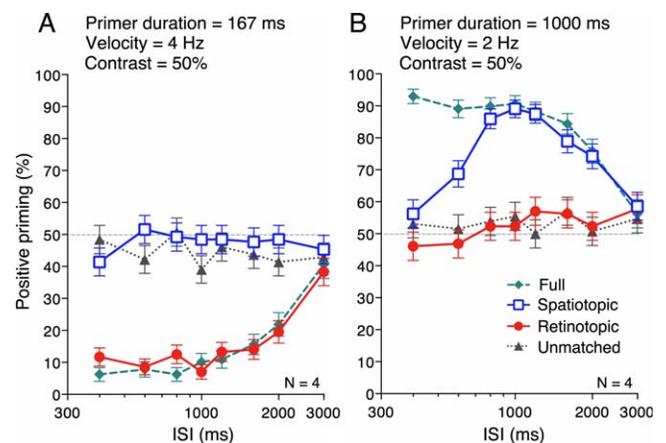


Figure 5. Averaged data for the four subjects shown in Figure 4. Each curve represents the data that were collected in different experimental conditions (retinotopic, spatiotopic, full, and unmatched conditions). Error bars represent  $\pm 1$  standard error of the mean. The luminance contrast was set at 50%. (A) The primer duration and velocity were set at 167 ms and 4 Hz, respectively. (B) The primer duration and velocity were set at 1000 ms and 2 Hz, respectively.

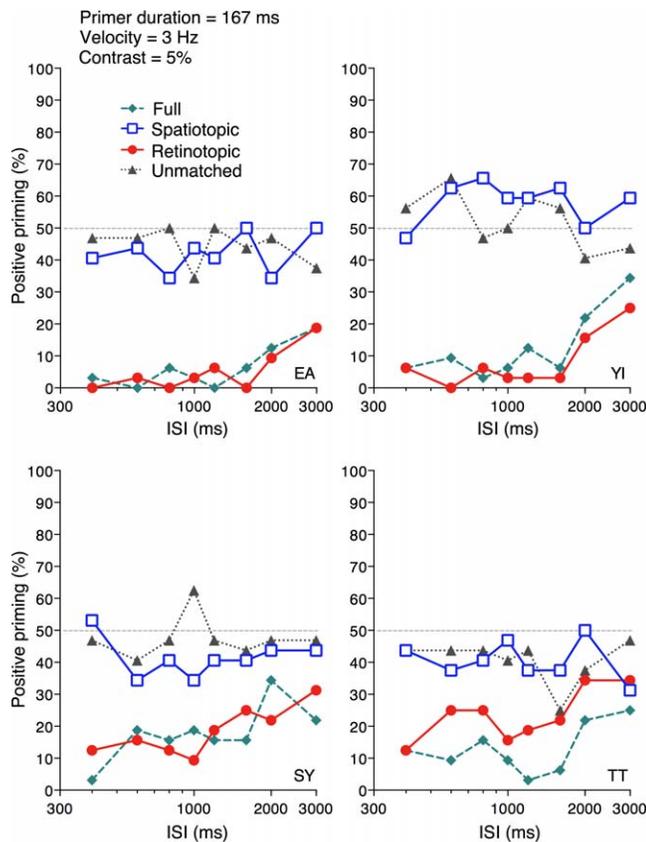


Figure 6. Results of Experiment 2 for the four subjects. The luminance contrast of the stimulus was 5%. The primer duration and velocity were set at 167 ms and 3 Hz, respectively. In each graph, the percentage response of positive priming (motion of test stimulus in the same direction as the primer) is plotted as a function of the ISI between the primer and test stimuli (in ms). Each curve represents the data that were collected in different experimental conditions (retinotopic, spatiotopic, full, and unmatched conditions).

In the full condition, negative priming was dominant at the primer duration of 167 ms (Figure 5A), whereas positive priming was observed in the majority of the trials at the duration of 1000 ms (Figure 5B). The strength of the motion priming was reduced as the ISI between the priming and test stimuli became longer. Positive priming was prominent in the spatiotopic condition, and disappeared in the retinotopic condition in Figure 5B, whereas negative priming was dominant in the retinotopic condition, but not in the spatiotopic condition in Figure 5A. Positive priming became conspicuous when the ISI was longer than around 600 ms. Conversely, negative priming in the retinotopic condition was observed in nearly 90% of the trials at the ISI of 400 ms, and the percentage decreased gradually to 50% when no priming effect was induced. Neither positive nor negative priming was observed in the unmatched condition.

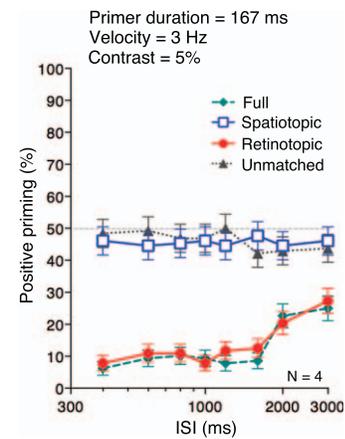


Figure 7. Averaged data for the four subjects shown in Figure 6. Each curve represents the data that were collected in different experimental conditions (retinotopic, spatiotopic, full, and unmatched conditions). Error bars represent  $\pm 1$  standard error of the mean. The primer duration, velocity, and luminance contrast were set at 167 ms, 3 Hz, and 5%, respectively.

It should be noted that the negative priming observed in the retinotopic condition appeared both when the priming duration was 1000 ms (Figure 3B) or 167 ms (Figure 5A). Similarly, the positive priming observed in the spatiotopic condition appeared both when the priming duration was 167 ms (Figure 3A) and 1000 ms (Figure 5B). These data indicate that the duration of the presentation of the priming stimulus was not the sole predictor of motion priming in the retinotopic and spatiotopic conditions. Rather, these results support the idea that the perceived direction of the motion priming per se, regardless of whether it is positive or negative, is related to the reference frame of motion priming.

These interpretations were supported by the statistical analyses. At the velocity of 4 Hz and the primer duration of 167 ms (Figure 5A), a within-subject two-way ANOVA showed that the main effects of experimental condition and ISI between the priming and test stimuli were significant,  $F(3, 9) = 21.54$ ,  $p < 0.001$  for the experimental condition;  $F(7, 21) = 7.33$ ,  $p < 0.001$  for the ISI. The interaction between the experimental condition and ISI was also significant,  $F(21, 63) = 3.87$ ,  $p < 0.0001$ . At the velocity of 2 Hz and primer duration of 1000 ms (Figure 5B), a within-subject two-way ANOVA showed that the main effects of experimental condition and ISI were significant,  $F(3, 9) = 30.43$ ,  $p < 0.0001$  for the experimental condition;  $F(7, 21) = 3.43$ ,  $p < 0.05$  for the ISI. The interaction between the experimental condition and ISI was also significant,  $F(21, 63) = 7.05$ ,  $p < 0.0001$ .

Other data supported our interpretation. Figures 6 and 7 present the individual and group-averaged results, respectively, for the four subjects at the

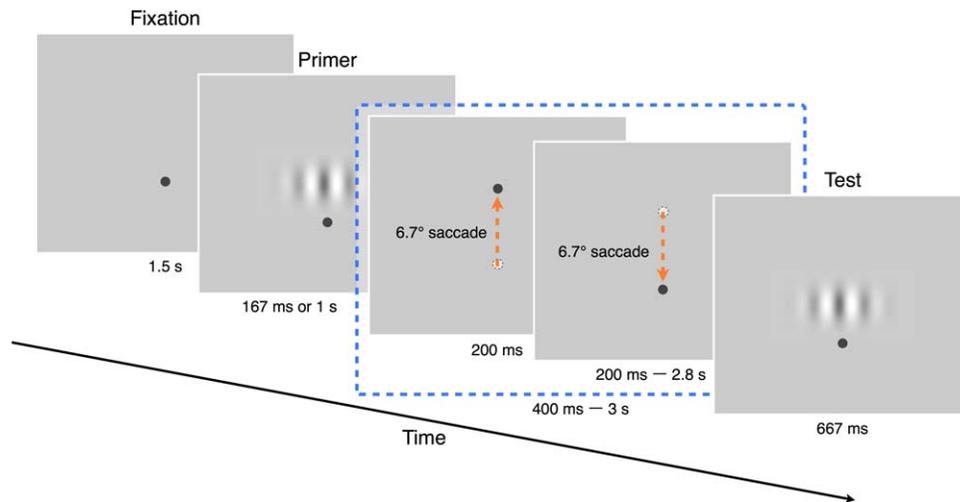


Figure 8. Schematic illustration of the stimuli in a single trial in Experiment 3. A small black dot (fixation point) was displayed for 1.5 s, followed by a 167-ms or 1000-ms primer. The fixation point jumped  $6.7^\circ$  to the upper region of the screen after the termination of the primer, stayed on for 200 ms, and then returned to the original position. Thus, subjects made two saccades to track the shift in the location of the fixation point. After a variable ISI (400–3000 ms), the test stimulus was presented in the same screen position as the primer. Subjects were asked to judge whether the perceived direction of the test stimulus was leftward or rightward.

stimulus contrast of 5%, the velocity of 3 Hz, and the primer duration of 167 ms. In the full condition (shown in Figure 7), negative priming was prominent. It should be noted that, in a condition that was similar with the exception of a higher contrast (50%), the effect of the priming was just the opposite (Figure 3A). In Figure 7, negative priming was observed in the retinotopic condition, but not in the spatiotopic and unmatched conditions. The strength of the negative priming was diminished as the ISI was increased. In addition to the results shown in Figure 5, these results suggest that the reference frame of the motion priming is related to the perceived direction of the motion priming per se.

These interpretations were supported by the statistical analyses. A within-subject two-way ANOVA showed that the main effects of experimental condition and ISI between the priming and test stimuli were significant,  $F(3, 9) = 23.33$ ,  $p < 0.001$  for the experimental condition;  $F(7, 21) = 11.52$ ,  $p < 0.0001$  for the ISI. The interaction between the experimental condition and ISI was also significant,  $F(21, 63) = 2.52$ ,  $p < 0.01$ .

In summary, none of the three stimulus parameters (duration of the priming stimulus, velocity, and luminance contrast) was a sole determinant of the reference frame of motion priming. Rather, the results imply that the perceived direction of the motion priming, which was determined by a specific combination of the three parameters described above, is key to understanding the reference frame of motion priming. Based on the assumption that the negative and positive motion priming are induced by lower and higher order

motion mechanisms, respectively (Jiang et al., 2002; Pantle et al., 2000; Takeuchi et al., 2011; Yoshimoto & Takeuchi, 2013), our results suggest that a different motion mechanism functions under a different reference frame.

## Experiment 3

In Experiments 1 and 2, positive priming was dominant in the full condition, but not in the spatiotopic condition, when the ISI was 400 ms. Prominent positive priming in the spatiotopic condition was observed only when the ISI was longer than 600 ms (Figures 3A and 5B). One obvious difference between the full and spatiotopic conditions is the presence of saccadic eye movements. If eye movements cause the delayed priming effect in the spatiotopic condition, positive priming effects will take time to emerge in the full condition if subjects make saccades before judging the perceived direction of the test stimulus. We examined this possibility in Experiment 3.

## Methods

### Stimuli

Figure 8 provides a schematic illustration of the stimuli in a single trial in Experiment 3. As in Experiment 1, we examined the manner by which a moving grating modulates the perceived motion direction of a subsequently presented  $180^\circ$  phase-shifted test

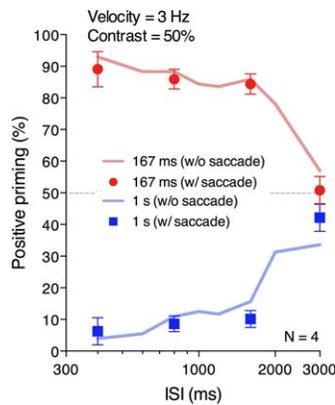


Figure 9. Averaged data for the four subjects in Experiment 3. The percentage of positive priming responses (motion of the test stimulus in the same direction as the primer) is plotted as a function of the primer-test ISI (in ms). Each symbol represents a different primer duration condition (167 or 1000 ms). The velocity and luminance contrast were 3 Hz and 50%, respectively. The curves are re-plots of the data from the full condition in Figure 3 (the red curve from Figure 3A and the blue curve from Figure 3B).

grating. Stimulus configuration was similar to the full condition shown in Figure 1A, with the exception that the fixation point shifted (Figure 8). The fixation point jumped to the upper region of the screen after the offset of the priming stimulus, and then returned to the original position. Thus, the subjects executed two saccades in Experiment 3. The duration of the priming stimulus was set to 167 or 1000 ms. The velocity and the luminance contrast of the stimuli were set to 3 Hz and 50%, respectively.

### Procedure

As in Experiment 1, each trial began with the presentation of a small dot, which appeared at fixation for 1.5 s, followed by the priming sine-wave stimulus (Figure 8). The fixation point immediately jumped  $6.7^\circ$  to the upper region of the screen after termination of the priming stimulus, stayed on for 200 ms, and then returned to the original fixation position. Thus, subjects made two saccades to track the position of the fixation point. After a variable ISI between the offset of the priming stimulus and the onset of the test stimulus, a directionally ambiguous test stimulus was presented in the same screen position as the priming stimulus. Subjects were asked to judge whether the perceived motion direction of the test stimulus was leftward or rightward. Each session consisted of 64 trials presented in a random order. There were eight trials for each combination of primer-test ISI (400, 800, 1600, or 3000 ms), and primer motion direction

(rightward or leftward). In each session, the primer duration (167 or 1000 ms) was fixed. Each subject completed two sessions for each of the primer duration conditions (four sessions in total) in a random order. Subjects were the same as Experiments 1 and 2.

### Results and discussion

As in the previous experiments, eye position was monitored during the experiment. We confirmed whether all subjects made two proper saccades in each trial. The total duration from the beginning of the first saccade to the end of the second saccade was 242–485 ms. In some number of trials, the time needed to finish the second saccade was greater than 400 ms in the 400-ms ISI condition (17.2% on average). In addition, subjects looked more than  $1.5^\circ$  away from the fixation point in an average of 3.7% trials. We excluded those trials from the subsequent analyses.

Figure 9 shows the averaged data for the four subjects. Results were quite similar to those in the full condition in Experiment 1, where no saccade was required. Irrespective of eye movements, when the ISI was 400–1600 ms, positive priming was prominent when the primer duration was 167 ms, whereas negative priming was observed in the majority of the trials when the primer duration was 1000 ms. The strength of the motion priming was reduced when the ISI was 3000 ms. These data indicate that the delayed priming effect in the spatiotopic conditions (Figures 3A and 5B) were not the due to eye movements per se. Rather, these results further support the hypothesis that the development of spatiotopic (or nonretinotopic) representations requires time (Burr & Morrone, 2011, 2012; Golomb et al., 2011; Golomb et al., 2010; Morrone et al., 2010; Wurtz, 2008; Zimmermann et al., 2013), as will be discussed.

These interpretations were supported by the statistical analyses. We compared the results of Experiment 3 with the full condition of Experiment 1 using the data for the ISIs examined in both Experiments 1 and 3 (400, 800, 1600, and 3000 ms) When the primer duration was 167 ms (red curve and circle symbol), a within-subject two-way ANOVA showed no significant main effect of saccade presence,  $F(1, 3) = 1.16$ , *n.s.*, and a significant main effect of ISI between the priming and test stimuli was significant,  $F(3, 9) = 48.99$ ,  $p < 0.0001$ . The interaction between saccade presence and ISI was not significant,  $F(3, 9) = 0.19$ , *n.s.* When the primer duration was 1000 ms (blue curve and square symbol), a within-subject two-way ANOVA showed no significant main effect of saccade presence,  $F(1, 3) = 0.11$ , *n.s.*, and a significant main effect of ISI,  $F(3, 9) = 50.62$ ,  $p <$

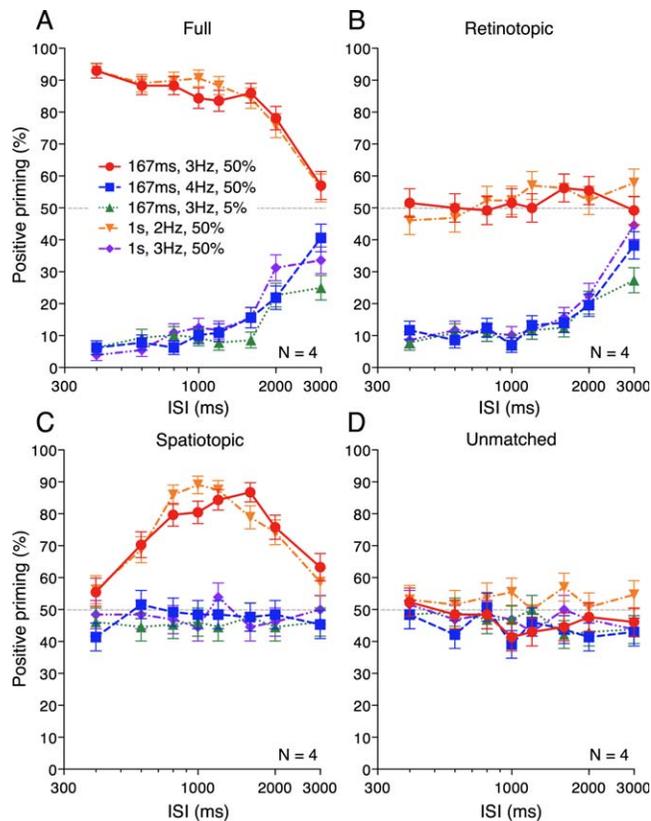


Figure 10. Combined data in Figures 3, 5, and 7. Each curve represents the data for the different stimulus parameter combinations (the primer duration, velocity, and luminance contrast). Each graph shows the data for the full condition (A), the retinotopic condition (B), the spatiotopic condition (C), and the unmatched condition (D).

0.0001. The interaction between saccade presence and ISI was not significant,  $F(3, 9) = 3.27$ , *n.s.*

## General discussion

In this study, we investigated the reference frame in which motion mechanisms function. Figure 10 shows the combined results from Figures 3, 5, and 7. The effects of visual motion priming depended on the stimulus parameters, as shown in Figure 10A. We found that positive motion priming was prominent in the spatiotopic condition (Figure 10C), whereas negative motion priming was dominant in the retinotopic condition (Figure 10B). These observations were related to the positive and negative effects of the motion priming per se, and not to a specific stimulus parameter, such as the duration of the presentation of the priming stimulus, velocity, or luminance contrast.

As shown by Takeuchi et al. (2011) and Yoshimoto and Takeuchi (2013), negative priming became dominant by increasing the velocity or decreasing the

contrast of the stimulus, which increased the contribution of a first-order motion mechanism. Therefore, we concluded that a low-level motion analysis could be processed in retinotopic coordinates. This argument seems to be supported by the fact that a motion aftereffect, presumably induced by a lower order motion mechanism (Pavan, Contillo, & Mather, 2013), was observed in retinotopic coordinates (Biber & Ilg, 2011; Boi et al., 2011; Cavanagh et al., 2010; Knapen et al., 2009; Turi & Burr, 2012; Wenderoth & Wiese, 2008).

Positive and negative priming are induced by separate visual motion mechanisms, because the two priming effects are observed antagonistically (Kanai & Verstraten, 2005; Pantle et al., 2000; Takeuchi et al., 2011). Here, positive priming became conspicuous in the lower velocity or higher contrast conditions, in which the accuracy of spatial localization became sufficiently high to allow tracking of prominent visual features. This suggests that a higher order motion system, such as a feature-tracking mechanism, functions in spatiotopic coordinates. Our argument is consistent with the findings of Hein and Cavanagh (2012), who showed that motion correspondence is solved in spatial, not retinal, coordinates. We speculate that an attentional mechanism, such as the one proposed by Cavanagh et al. (2010), functions not only in solving the motion correspondence problem, but also in perceiving positive motion priming in a spatiotopic coordinate. Melcher and Morrone (2003) found that motion signals were integrated across eye movements in a spatiotopic fashion. This may be due to the operation of such a higher order motion mechanism.

Turi and Burr (2012) showed that low and high levels of visual analyses have different coordinate bases by using motion aftereffect and positional motion aftereffect. The former is perceived in retinotopic coordinates, whereas the latter is perceived in spatiotopic coordinates. Although both phenomena are induced by motion stimuli, the resulting visual perceptions are qualitatively different: the former regards the motion perception, and the latter regards the perception of spatial position. Moreover, our study was based on a single motion task in which we estimated the perceived direction of a directionally ambiguous test stimulus. Therefore, in contrast with the conclusion of Turi and Burr (2012), we confine our argument to the visual motion hierarchy (e.g., Lu & Sperling, 1995), in which the processing stream for motion information is supposed to be divided into different stages.

Our conclusion that lower and higher order motion systems operate in retinotopic and spatiotopic coordinates, respectively, is consistent with the results of recent neurophysiological studies. Functional imaging studies have shown that blood oxygenation level-dependent (BOLD) responses in the primary visual

cortex are clearly tuned to retinotopic coordinates, whereas the response of area MT is tuned to spatiotopic coordinates, regardless of gaze shifts (Crespi et al., 2011; d'Avossa et al., 2007). Although this finding has been challenged by Gardner, Merriam, Movshon, and Heeger (2008), who found only retinotopic representations in the whole occipital cortex, these conflicting reports are supposed to be due to the presence or absence of a foveal attentive task (see Crespi et al., 2011). In addition, it has been reported that motion processing regarding a short-term memory in area MT could be carried out in spatiotopic coordinates (Ong, Hooshvar, Zhang, & Bisley, 2009).

We found that the effect of the motion priming disappeared in the unmatched condition, in which the priming and test stimuli were presented in separate spatial regions and no saccade was required. Thus, the positive priming observed in the spatiotopic condition was not simply due to spatial summation over a large visual field. Note that remote motion aftereffect has been reported, in which motion aftereffect can be translated across space, even in areas that were not directly stimulated during the adaptation phase (Arman, Ciaramitaro, & Boynton, 2006; Meng, Mazzoni, & Qian, 2006; von Grünau & Dubé, 1992). The lack of remote effect in negative motion priming (or a rapid-type of motion aftereffect) suggests that remote motion aftereffect could only be induced by a traditional prolonged adaptation to motion in a given direction.

In this study, we changed the ISI between the offset of the priming stimulus, at which subjects made a saccade, and the onset of the test stimulus. Prominent negative priming was observed in the retinotopic condition from an ISI of 400 ms, which was the lowest value examined here (Figure 10B). In contrast, positive priming in the spatiotopic condition was not observed at this ISI, but emerged when it was longer than 600 ms (Figure 10C). This delayed priming effect was not merely the result of saccadic eye movements (Figure 9). These results are consistent with the recent findings that the spatiotopic (or nonretinotopic) representation builds up slowly (Burr & Morrone, 2011, 2012; Golomb et al., 2011; Golomb et al., 2010; Morrone et al., 2010; Wurtz, 2008; Zimmermann et al., 2013). Golomb et al. (2011) showed that around 500–600 ms (including a saccade latency of ~250 ms) are necessary to update retinotopic coordinates with spatiotopic information with each saccade. Zimmermann et al. (2013) found that a tilt aftereffect occurred in both the retinotopic and spatiotopic coordinates; however, spatiotopic adaptation of orientation became prominent only after the saccadic target had been displayed for 500–1000 ms before gaze change. Those authors concluded that the build-up of spatiotopic representation requires at least 500 ms. Our results indicate that a

similar amount of time is needed to achieve spatiotopic representations of motion.

Burr and Morrone (2011) proposed a receptive field oriented in space-time to enable transient spatiotopy based on finding from neurons, which shift their receptive fields in anticipation of the upcoming saccades (Duhamel, Colby, & Goldberg, 1992). According to those authors, many transient processes occur when the eyes move, both in space and in time, leading to a spatiotemporal oriented mechanism that could provide a quick transient local spatiotopy for immediate interaction with the world (see also Burr & Morrone, 2012). We found that positive priming in the spatiotopic condition was only dominant when the ISI was around 600–2000 ms. This type of transient priming effect in spatiotopic coordinates seems to be consistent with the model of a spatiotemporally oriented receptive field for transient spatiotopy.

Our study indicates that a low-level motion system, such as first-order motion mechanism, functions in retinotopic coordinates, whereas a higher order motion mechanism, such as the feature-tracking function in spatiotopic coordinates, in which the representation could be achieved slowly. We should note that our method involved only eye movements and not head/body rotations. Thus, whether the high-level motion analysis is indeed spatiotopic or merely craniotopic (head centered) is yet to be determined, and future studies are needed.

Although we only used luminance-modulated translational moving patterns in this study (Figure 1), the visual system can handle different types of moving stimuli. Pavan, Campana, Maniglia, and Casco (2010) showed that positive motion priming (rVMP in their terminology) was not induced by an expanding or contracting priming stimulus. Because those complex motion types are known to be processed at a higher level of visual stream (e.g., Morrone et al., 2000), they argued that positive motion priming could be induced by a low-level motion mechanism, not by a high-level motion mechanism, as suggested by our study. As the combination of primer duration/velocity/contrast modulates the perceived direction of the subsequent test pattern, it is necessary to examine stimulus parameter combinations other than those used in Pavan et al. (2010) (velocity: 4.16 Hz; luminance contrast: 96%; primer duration: 80–640 ms) to determine whether positive priming can be observed with complex motion primers. At the same time, Campana et al. (2008) examined intertrial priming effects, and found that while first- or second-order positive motion priming showed characteristics of a low-level mechanism, cross-order motion priming could be mediated by high-level motion processing (see also Kristjánsson & Campana, 2010). Further studies are needed to determine whether the conclusions of this study can be

applied to the situations where mechanisms that are sensitive to the motion types other than first-order translational motion are operational.

Throughout this study, we assumed that negative motion priming (or rapid MAE) is processed at a low-level of the visual motion hierarchy. However, previous studies suggest that motion aftereffects (MAE) are a very complex phenomenon that can take place at different levels of visual motion processing (e.g., Mather et al., 2008). For example, by applying rTMS, Campana et al. (2011) and Campana, Maniglia, and Pavan (2013) showed that rMAE (negative motion priming in our terminology), static MAE, and dynamic MAE have different neural loci. Since complex motion is processed at a higher level than translational motion (Morrone et al., 2000), the MAEs induced by complex motion could have a different neural locus than MAEs induced by translational motion (Théoret, Kobayashi, Ganis, Di Capua, & Pascual-Leone, 2002). It would be useful to check the validity of our conclusions regarding the relationship between level of motion processing and reference frame using those different types of motion stimuli.

*Keywords: motion perception, visual motion priming, first-order motion mechanism, feature-tracking mechanism, spatiotopic processing, retinotopic processing*

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