

# Common and independent processing of visual motion perception and oculomotor response

Sanae Yoshimoto

School of Integrated Arts and Sciences,  
Hiroshima University, Hiroshima, Japan



Tomoyuki Hayasaka

School of Integrated Arts and Sciences,  
Hiroshima University, Hiroshima, Japan



**Visual motion signals are used not only to drive motion perception but also to elicit oculomotor responses. A fundamental question is whether perceptual and oculomotor processing of motion signals shares a common mechanism. This study aimed to address this question using visual motion priming, in which the perceived direction of a directionally ambiguous stimulus is biased in the same (positive priming) or opposite (negative priming) direction as that of a priming stimulus. The priming effect depends on the duration of the priming stimulus. It is assumed that positive and negative priming are mediated by high- and low-level motion systems, respectively. Participants were asked to judge the perceived direction of a  $\pi$ -phase-shifted test grating after a smoothly drifting priming grating during varied durations. Their eye movements were measured while the test grating was presented. The perception and eye movements were discrepant under positive priming and correlated under negative priming on a trial-by-trial basis when an interstimulus interval was inserted between the priming and test stimuli, indicating that the eye movements were evoked by the test stimulus per se. These findings suggest that perceptual and oculomotor responses are induced by a common mechanism at a low level of motion processing but by independent mechanisms at a high level of motion processing.**

level, a first-order motion mechanism detects the local spatiotemporal orientation of luminance-based motion (Adelson & Bergen, 1985; Burr, Ross, & Morrone, 1986; Watson & Ahumada, 1985). The motion perception elicited by other features (e.g., contrast and flicker) can be detected by different motion mechanisms operating at a higher level of motion processing, such as a second-order motion mechanism (Chubb & Sperling, 1988) and a feature-tracking mechanism (Cavanagh, 1992; Lu & Sperling, 1995). Here, we aimed to determine whether perceptual and oculomotor processing are shared or independent in the lower and higher levels of the visual motion hierarchy.

Motion signals drive, not only motion perception, but oculomotor responses. It has been shown that motion perception and smooth tracking eye movements, in particular, are closely linked (Schütz, Braun, Kerzel, & Gegenfurtner, 2008; Spering & Carrasco, 2015; Spering & Montagnini, 2011). For example, the direction of pursuit eye movements tends to align with the perceived direction rather than the actual direction of motion (Beutter & Stone, 1998, 2000; Braun, Pracejus, & Gegenfurtner, 2006; Krauzlis & Stone, 1999; Stone, Beutter, & Lorenceau, 2000; Stone & Krauzlis, 2003). Braun et al. (2006) demonstrated that pursuit eye movements can be elicited even by the illusory motion of motion aftereffect (MAE) with stationary test patterns and its direction corresponded with the perceived direction. The similarities between perception and ocular following response (OFR) are also reported. The OFR is a small involuntary eye movement that can occur rapidly because of the sudden motion of large patterns (Gellman, Carl, & Miles, 1990; Masson & Perrinet, 2012; Miles, Kawano, & Optican, 1986; Sheliga, FitzGibbon, & Miles, 2008). Illusory motion reversal, in which the perceived direction of motion was reversed when 1/4-wavelength steps were applied to the missing fundamental square-wave gratings (Adelson & Bergen, 1985; Baro & Levinson, 1988; Brown & He, 2000; Georgeson & Harris, 1990; Georgeson & Shackleton, 1989) or when a brief blank interval was

## Introduction

Visual motion perception is a crucial component of human behavior, and how the visual system serves motion information from various visual inputs is a fundamental problem in visual processing. The visual system is assumed to have a hierarchical structure to process motion, in which multiple motion mechanisms conceptually operate at different levels (Nishida, 2011; Nishida, Kawabe, Sawayama, & Fukiage, 2018). Motion signals are detected by directionally selective neurons in the primary visual cortex (V1). At the lower

Citation: Yoshimoto, S., & Hayasaka, T. (2022). Common and independent processing of visual motion perception and oculomotor response. *Journal of Vision*, 22(4):6, 1–20, <https://doi.org/10.1167/jov.22.4.6>.



inserted between two-frame motion (Boulton & Baker, 1993; Braddick, 1980; Pantle & Turano, 1992; Shioiri & Cavanagh, 1990; Takeuchi & De Valois, 1997; Takeuchi & De Valois, 2009), can be reflected in the direction of the OFR (Masson, Yang, & Miles, 2002; Sheliga, Chen, FitzGibbon, & Miles, 2005; Sheliga, Chen, FitzGibbon, & Miles, 2006). These studies suggest that motion reversals of the perceived direction and the OFR are both mediated by the first-order mechanism, indicating a common processing of motion information for perception and OFR at the lower level.

However, there is increasing evidence that oculomotor responses are dissociated from motion perception (Badler, Lefèvre, & Missal, 2012; Blum & Price, 2014; Boström & Warzecha, 2010; Gegenfurtner, Xing, Scott, & Hawken, 2003; Glasser & Tadin, 2014; Kuhn & Land, 2006; Naber, Frässle, & Einhäuser, 2011; Price & Blum, 2014; Simoncini, Perrinet, Montagnini, Mamassian, & Masson, 2012; Spering & Carrasco, 2012; Spering & Gegenfurtner, 2007; Spering, Pomplun, & Carrasco, 2011; Tavassoli & Ringach, 2010; van der Steen & Dits, 2012). Glasser and Tadin (2014) measured the OFR while participants judged the motion direction of large high-contrast drifting gratings presented for brief durations. They found that in some cases the OFR could reliably discriminate the motion direction even when the performance of perceptual discrimination tasks were near chance level (so-called spatial suppression phenomenon), and a trial-by-trial analysis indicated independent dissociable mechanisms responsible for the perceptual and oculomotor responses. The spatial suppression is considered to be mediated by center-surround antagonistic mechanisms, not in early visual areas but in middle temporal (MT) cortical area (Churan, Richard, & Pack, 2009; Pack, Hunter, & Born, 2005; Tadin & Lappin, 2005; Tadin, Lappin, Gilroy, & Blake, 2003; Tadin, Silvanto, Pascual-Leone, & Battelli, 2011). Blum and Price (2014) reported that the perceived direction and the OFR for random-dot patterns, for which the response magnitude of MT neurons increases with increasing motion coherence (Bisley, Zaksas, Droll, & Pasternak, 2004; Britten, Newsome, Shadlen, Celebrini, & Movshon, 1996; Zaksas & Pasternak, 2005), were correlated across but not within trials. These findings suggest that perceptual and oculomotor responses can be processed via different mechanisms at the higher level of motion processing such as MT, in contrast to the lower level where perceptual and oculomotor responses may be processed via a common mechanism.

To test these hypotheses, we used a phenomenon termed visual motion priming where the direction of a moving pattern affects the perceived direction of a subsequent ambiguous apparent motion (Akyuz, Pavan, Kaya, & Kafaligonul, 2020; 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, 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; Yoshimoto, Uchida-Ota, & Takeuchi, 2014). Pantle et al. (2000) demonstrated that a  $\pi$ -phase-shifted directionally ambiguous sine-wave grating (test stimulus) appeared to move in the same direction as the preceding drift grating (priming stimulus) presented briefly (<300 ms), named positive motion priming. Conversely, when the priming stimulus was presented for a longer duration, the perceived direction of the test stimulus was biased in the opposite direction of the priming stimulus, named negative motion priming. Kanai and Verstraten (2005) referred to this negative priming effect as a rapid form of motion aftereffect. In addition to the duration of the presentation of the priming stimulus, velocity and luminance contrast of the stimuli influence the priming effects. With high-contrast stimuli moving slowly, positive priming remained dominant and did not switch to negative priming with an increase in the duration of the priming stimulus. Conversely, when the contrast was low or the velocity was high, only negative priming was observed, irrespective of priming duration (Heller & Davidenko, 2018; Takeuchi et al., 2011; Yoshimoto & Takeuchi, 2013; Yoshimoto et al., 2014).

Positive and negative motion priming are antagonistic phenomena so different motion mechanisms, presumably operating at different stages of motion processing, are thought to underlie the two priming effects. It has been demonstrated that an energy-based first-order motion mechanism is more sensitive to low contrast and to high velocity than the other motion mechanisms are (Burr & Ross, 1982; Burr et al., 1986; Doshier, Landy, & Sperling, 1989; Lappin, Tadin, Nyquist, & Corn, 2009; Lu & Sperling, 1995; Nishida, 1993; Smith, Hess, & Baker, 1994; Solomon & Sperling, 1994; Sperling, 1989; Takeuchi & De Valois, 1997; Takeuchi & De Valois, 2009). Because negative motion priming is facilitated in low-contrast and high-velocity conditions, the first-order motion mechanism is a good candidate for negative motion priming. On the other hand, positive motion priming is prominent in high-contrast, low-velocity conditions, which can be the basis for a feature-tracking mechanism that tracks salient features in motion. Therefore positive motion priming can be processed by the feature-tracking mechanism (Takeuchi et al., 2011; Yoshimoto & Takeuchi, 2013; Yoshimoto et al., 2014). These conjectures are supported by neurophysiological and brain imaging studies. For negative motion priming, the rapid change in the adaptation state of directionally selective neurons in V1 by a moving stimulus with a duration as short as

several hundred milliseconds (Lisberger & Movshon, 1999; Priebe & Lisberger, 2002) is considered to be an underlying neuronal mechanism (Glasser, Tsui, Pack, & Tadin, 2011; Kanai & Verstraten, 2005; Pantle et al., 2000; Pavan et al., 2009), whereas positive motion priming may involve modulated neuronal responses in later stages of motion processing, such as MT (Ashida, Lingnau, Wall, & Smith, 2007; Brascamp, Kanai, Walsh, & Van Ee, 2010; Campana, Cowey, & Walsh, 2002; Jiang et al., 2002). The finding by Yoshimoto et al. (2014) that negative and positive motion priming were respectively observed in retinotopic and spatiotopic coordinates also corresponds to these assumptions because functional imaging studies have shown that neuronal responses in V1 are tuned to retinotopic coordinates and those in MT are tuned to spatiotopic coordinates (Crespi, Biagi, D'Avossa, Burr, Tosetti, & Morrone, 2011; d'Avossa, Tosetti, Crespi, Biagi, Burr, & Morrone, 2007).

In this study, we examined the trial-by-trial correspondence between perceptual and oculomotor responses in lower and higher levels of motion processing by measuring the tracking eye movements when positive and negative motion priming were perceived. The trial-by-trial analysis can reveal the existence of shared neural correlates and indicate the extent to which the two responses are driven by shared neural signals (Glasser & Tadin, 2014; Stone & Krauzlis, 2003). Although whether the priming stimulus influences the eye movements derived from the directionally ambiguous test stimulus is unclear, the priming effects on the direction of eye movements can be seen in the same manner as those in the perceived direction if perceptual and oculomotor process share neural signals. Furthermore, the trial-by-trial correspondence between the perceived and eye movement directions will be high. If different neural pathways mediate perceptual and oculomotor responses, they will not covary on a trial-by-trial basis even when the average priming effect for perceived direction and for eye movement direction are identical. Based on the assumption that perceptual and oculomotor responses are processed by a common mechanism at the low level while by different mechanisms at the high level, we predicted that the perceived direction would correlate with the direction of eye movements not only on average but on a trial-by-trial basis during the negative priming, whereas there would be no trial-by-trial correlation between the perceived and eye movement directions during the positive priming.

## Experiment 1

In [Experiment 1](#), we measured the perceived direction of the test stimulus with various durations of priming

stimulus by recording the tracking eye movements. Similar to previous studies on visual motion priming (e.g., Kanai & Verstraten, 2005; Takeuchi et al., 2011; Yoshimoto et al., 2014), a luminance-based (first-order) motion stimulus, a crucial factor for inducing the OFR (Sheliga et al., 2005), was adopted. As mentioned above, whether positive or negative motion priming is perceived depends not only on the duration of presentation of priming stimulus but on the other stimulus parameters; although the velocity and contrast influence the priming effect, the parameter of test stimulus differs for the conditions of positive priming dominant (low-velocity and high-contrast) from the one for negative priming dominant (high-velocity or low-contrast). Here we focused on the eye movements during the test stimulus to gauge when the positive or negative priming would be perceived. Therefore only the duration of the presentation of the priming stimulus was manipulated to switch the motion priming effect from positive to negative, whereas the parameter of the test stimulus was constant.

## Methods

### Participants

Three naïve students and two authors (one male and four females; age range 21–32 years) participated in both Experiments 1 and 2; all had normal or corrected-to-normal vision. The study followed protocols approved by the ethics committee of the Institutional Review Board at Hiroshima University and was performed in accordance with the Helsinki Declaration. All participants provided written informed consent prior to commencing the study.

### Apparatus

Stimuli were created using MATLAB (The MathWorks, Inc., Natick, MA, USA) with the Psychophysics Toolbox (Brainard, 1997; Kleiner, Brainard, Pelli, Ingling, Murray, & Broussard, 2007; Pelli, 1997) and presented on a 24-inch flat screen LCD monitor (BenQ ZOWIE XL2411P; BenQ Co., Taipei, Taiwan). This monitor is a model that can be used for millisecond precise presentation comparable to a CRT monitor (Rohr & Wagner, 2020). The monitor had an eight-bit gray-level spatial resolution of 1920 × 1080 pixels with a refresh rate of 120 Hz, and its output was gamma-corrected based on calibrations with a ColorCAL MKII colorimeter (Cambridge Research Systems Ltd., Rochester, UK). Participants viewed the monitor binocularly from a distance of 63 cm in a room darkened, with no other light source present. Their head positions were maintained with chin and head rests. We recorded each participant's eye movements

using an infrared-video-based eye-tracking device (Tobii Pro Fusion; Tobii Technology Inc., Stockholm, Sweden) with a 120 Hz sampling rate. Blinks and saccades were detected with the Tobii I-VT filter (Olsen, 2012; Salvucci & Goldberg, 2000).

### Visual stimulus

The priming stimulus was an achromatic vertical sine-wave grating (spatial frequency =  $0.5\text{ c/}^\circ$ , Michelson contrast = 99%) presented in a rectangular window of size  $20^\circ$  (width)  $\times$   $4^\circ$  (height) on a uniform gray background with the same chromaticity (CIE 1931;  $x = 0.33$ ,  $y = 0.33$ ) and space-averaged luminance ( $101.6\text{ cd/m}^2$ ). The vertical edges of the stimulus were tapered by a Gaussian filter. The priming stimulus smoothly drifted either to the left or right at 3 Hz. The duration that the priming stimulus appeared was varied in 11 steps: 67, 100, 167, 300, 400, 600, 800, 1067, 1600, 2133, and 3200 ms.

The test stimulus was the same as the priming stimulus, except that the phase of the grating was shifted by  $\pi$  in each of four frames; thus the direction of motion was ambiguous. To match the velocities of the priming and test stimuli, each frame of the test stimulus was replaced by the next frame every 167 ms, which was necessary for the priming stimulus to reach the  $\pi$  phase shift. The duration of the presentation of the test stimulus was therefore 667 ms in total.

### Procedure

A beep signaled the beginning of each trial and a fixation black cross ( $1^\circ \times 1^\circ$ ) was presented at the center of the screen for one second. Subsequently, the priming stimulus was presented for a certain duration and then immediately replaced by the test stimulus. After the offset of the test stimulus, participants judged the direction the test stimulus appeared to move in by pressing appropriate arrow keys (left or right) on the keyboard. Their responses were followed by a one-second intertrial interval with a blank screen to eliminate the effect of the former trial. Each session comprised 88 trials, in which four trials for each of the 11 priming durations and for the two drifting directions of the priming stimulus were presented in random order. Each participant completed four sessions (16 trials in each session and 352 trials in total) after 22 practice trials, comparable to previous studies (e.g., Kanai & Verstraten, 2005; Takeuchi et al., 2011; Yoshimoto et al., 2014). Before data acquisition, participants were informed that their eye movements were recorded during each trial, and they were asked to view the fixation cross or the central part of the stimuli.

### Data analysis

*Psychometric analysis:* We counted the number of trials where the perceived direction of the test stimulus was the same as the drifting direction of the priming stimulus (positive priming) for each priming duration. Participants judged the perceived direction; 16 trials for each of two priming directions. The responses were pooled together when the priming stimulus drifted leftward and rightward so the minimum and maximum counts are 0 and 32. These counts were then converted into a percentage of positive priming. The percentage value decreases with an increase in the number of trials when the perceived direction of the test stimulus is the opposite of the drifting direction of the priming stimulus (negative priming). To represent the results in a more convenient way, the percentage value was rescaled from  $-1$  (corresponding to 100% negative priming) to 1 (corresponding to 100% positive priming); 0 indicated no priming effect.

*Oculometric analysis:* For each trial, the average horizontal displacements of the dominant eye during the presentation of a test stimulus were used as the eye movement induced by the test stimulus. The eye positions were normalized by subtracting the initial value at the onset of the test stimulus before averaging. A positive value ( $>0$ ) indicates eye displacement in the rightward direction after the onset of the test stimulus; a negative value ( $<0$ ), indicates eye displacement in the leftward direction. Before the analysis, the trials that included blinks and saccades from 200 ms before the onset of the test stimulus until the offset of test stimulus were omitted. Furthermore, the trials where the eye position was outside of the stimulus window were excluded from the analysis.

Like the perceptual motion direction judgement, the probability that the direction of the eye movements, while viewing the test stimulus, were the same as the drifting direction of the priming stimulus was computed as “positive priming” in the oculomotor domain. Figure 1 shows an example of the analysis. Similar to Glasser and Tadin (2014), we used a receiver operating characteristics analysis to measure the discrimination accuracy as derived from a signal detection theory (Green & Swets, 1966). The area under the receiver operating characteristic curve (AUC) represents the probability that the eye displacements during the test stimulus presentation following the leftward priming stimulus are different from those following the rightward priming stimulus. For the priming duration where the mean eye displacement, during the test stimulus period, was biased in the same direction as the priming stimulus (Figure 1A), the AUC value was used as an index of positive priming (Figures 1C and 1E). The discriminability of eye displacements also increases when the eye moves in the opposite direction of the priming stimulus in most

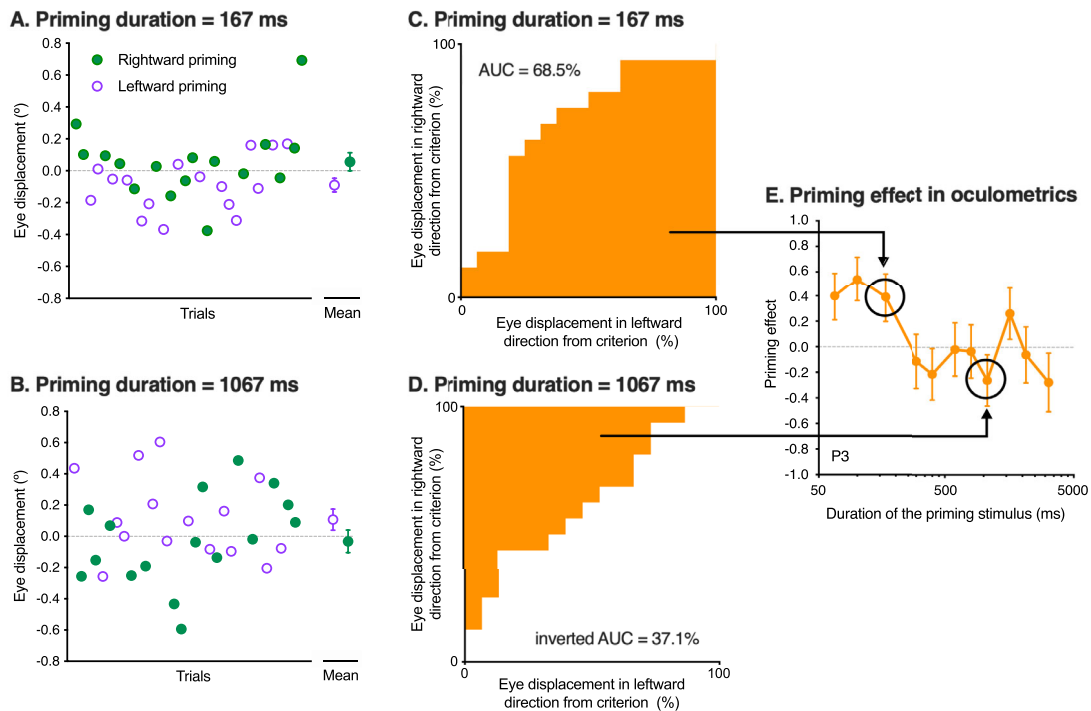


Figure 1. Computation of the percentage of positive priming for the oculomotor responses from a participant (P3). A and B indicate the individual and mean horizontal eye displacements during the test stimulus following the rightward (*filled green symbols*) or leftward (*open purple symbols*) priming stimulus. The positive and negative displacements indicate rightward and leftward eye movements, respectively. The *error bars* for the mean values represent standard error of the mean (SEM). In C and D to convert the eye displacements into discrimination accuracy, the receiver operating characteristic analysis was applied, which compares the percentage of trials that exceed a criterion for each direction (leftward or rightward) for each possible criterion. When the mean eye displacement was biased in the same direction as the priming stimulus (A), the AUC was used as an index of positive priming (C), whereas when the mean eye displacement was biased in the opposite direction of the priming stimulus (B), the inverted AUC was used as an index of positive priming (D). In E the results of repeating calculations for each priming duration with rescaling data from  $-1$  (negative priming) to  $1$  (positive priming), is indicated. The *circles* mark the priming duration of 167 ms (corresponding to A and C) and 1067 ms (corresponding to B and D). The *error bars* represent SEM.

trials. Therefore, for the priming duration where the mean eye displacement during the test stimulus period was biased in the direction opposite to the priming stimulus (Figure 1B), the inverted AUC was calculated as an index of positive priming (Figures 1D and 1E). Both noninverted and inverted AUC values were again rescaled to range from  $-1$  to  $1$ , corresponding to negative and positive priming (Figure 1E).

#### Correspondence between psychometrics and oculometrics:

The subsequent analysis was performed to determine whether the perceptual and oculomotor responses are processed by a common mechanism or not, based on a trial-by-trial basis. The proportion of trials in which the perceived direction and eye movement directions were the same ( $p_{\text{same}}$ ) indicates how much a common mechanism contributes to those responses. The  $p_{\text{same}}$  can be compared to the proportions in which coin-flip results reported by two individuals are the same (Glasser & Tadin, 2014; Stone & Krauzlis, 2003). If the perceptual and oculomotor processes

are entirely independent, similar to a situation where two individuals flip two different coins and report the result independently, the  $p_{\text{same}}$  should be 50%. Meanwhile, if the perceptual and oculomotor responses are completely processed by a common mechanism, similar to a situation where two individuals report the same coin-flip result, the  $p_{\text{same}}$  should be 100%.

Similar to way reported by Glasser and Tadin (2014) and Stone and Krauzlis (2003), we calculated the  $p_{\text{same}}$  for each priming duration, and then compared  $p_{\text{same}}$  to predictions by the chance correlation between the two variables, with the following equation:

$$P_{\text{same}} = P_{\text{psychometric}}P_{\text{oculometric}} + (1 - P_{\text{psychometric}})(1 - P_{\text{oculometric}}), \quad (1)$$

where  $p_{\text{psychometric}}$  and  $p_{\text{oculometric}}$  are proportions of the positive priming in the perceptual and oculomotor domains for each priming duration. If the perceived direction of the test stimulus and the direction of eye

movement are mediated by independent mechanisms, the positive (or negative) priming in the perceptual domain occurs, irrespective of that in the oculomotor domain. For example, when the  $p_{\text{psychometric}}$  and  $p_{\text{oculometric}}$  are 50% respectively, the  $p_{\text{same}}$  corresponding to the percentage of the trials where the priming effects in the two domains are matched (both positive or both negative), should be 50%.

Meanwhile, if the directions of perception and eye movement are mediated by common mechanisms, the perceptual responses correlate with the oculomotor responses. Therefore the  $p_{\text{same}}$  becomes higher with the increase in the correspondence between the  $p_{\text{psychometric}}$  and  $p_{\text{oculometric}}$ , as in:

$$p_{\text{same}} = 1 - |p_{\text{psychometric}} - p_{\text{oculometric}}|. \quad (2)$$

We also compared the  $p_{\text{same}}$  to that predicted by this equation.

Furthermore, the analyses described above were repeated using the eye displacements during the test stimulus presentation divided into three successive time windows of 222 ms each (early, middle, and late parts) to assess the temporal dynamics of oculomotor responses. OFRs can be influenced by the history of visual stimulation. Given that a brief motion signal (100 ms) can suppress the OFR for the subsequent stimulus (Sheliga, Quaia, FitzGibbon, & Cumming, 2021), the OFR in the early part of the test stimulus could be attenuated by the presence of a priming stimulus. The divided time window was similar to the one used by Glasser and Tadin (2014), where they confirmed that the analysis using shorter time windows did not qualitatively affect the results.

## Results

Based on the data exclusion criteria mentioned above, 6.1% of the trials were excluded from the subsequent analyses. Figure 2 illustrates the results for each participant. The analysis output using oculomotor responses during the overall duration of the test stimulus and each of the three divided periods (early, middle, and last) are shown from the leftmost to the rightmost panels, respectively. For each participant, the top panels illustrate the perceptual and oculomotor responses to the directionally ambiguous test stimulus. The value indicating the strength of the priming effect is plotted as a function of the duration of the presentation of the priming stimulus. For the perceptual responses (psychometric curve), more than 0 indicates that the test stimulus appeared to move in the same direction as the priming stimulus in most trials (positive priming), whereas less than 0 indicates that the test

stimulus appeared to move in the opposite direction of the priming stimulus (negative priming). For the oculometric responses (oculometric curve), more than 0 indicates that the eye was biased to move in the same direction as the priming stimulus while viewing the test stimulus, whereas less than 0 indicates that the eye was biased to move in the opposite direction of the priming stimulus while viewing the test stimulus.

The perceived direction of the test stimulus was the same as the direction of the priming stimulus for all participants in most of the trials (psychometric positive priming) when the priming stimulus drifted briefly. As the duration of the presentation of the priming stimulus was increased, the psychometric positive priming gradually weakened, and the perceived direction of the test stimulus was inverted (psychometric negative priming). These results concurred with previous findings (Kanai & Verstraten, 2005; Pantle et al., 2000; Takeuchi et al., 2011). Except for P4, the participants' eyes tended to move in the same direction as the priming stimulus when the duration of the presentation of the priming stimulus was short (oculometric positive priming). The increase in the duration of the presentation of the priming stimulus reduced the oculometric positive priming to 50% (i.e., the discriminability of the eye movements was low [P1, P2, and P3]). Unlike with perceptual responses, their eyes were not biased to move in the opposite direction of the test stimulus even when the priming stimulus was presented at 3200 ms. P5's eyes kept moving in the same direction as the priming stimulus, irrespective of the duration of the presentation of the priming stimulus. Repeating the oculometric analysis with different time windows showed that these results were not greatly altered through the time course of the test stimulus.

Subsequently, we examined whether the mechanisms underlying perceptual and oculomotor responses are common or independent. The bottom panels for each participant in Figure 2 show the observed  $p_{\text{same}}$  (proportion of the trials where the perceived direction of the test stimulus and the direction of eye movement were matched) plotted with filled red circles for each duration of the presentation of the priming stimulus for each time window. The dashed and solid lines represent the  $p_{\text{same}}$  predicted by independent mechanisms (Equation 1) and common mechanisms (Equation 2), respectively. For all participants, the observed  $p_{\text{same}}$  approximated the predicted curve from independent mechanisms for any duration of the priming stimulus in any time windows. This approximation existed even when the psychometric and oculometric curves of positive priming were overlapped (e.g., at the priming duration of 67–600 ms in P3).

Although some individual differences were found, the overall trends were similar for all participants. Thus we pooled the individual data and performed one sample  $t$  test to compare the observed  $p_{\text{same}}$  with the predicted

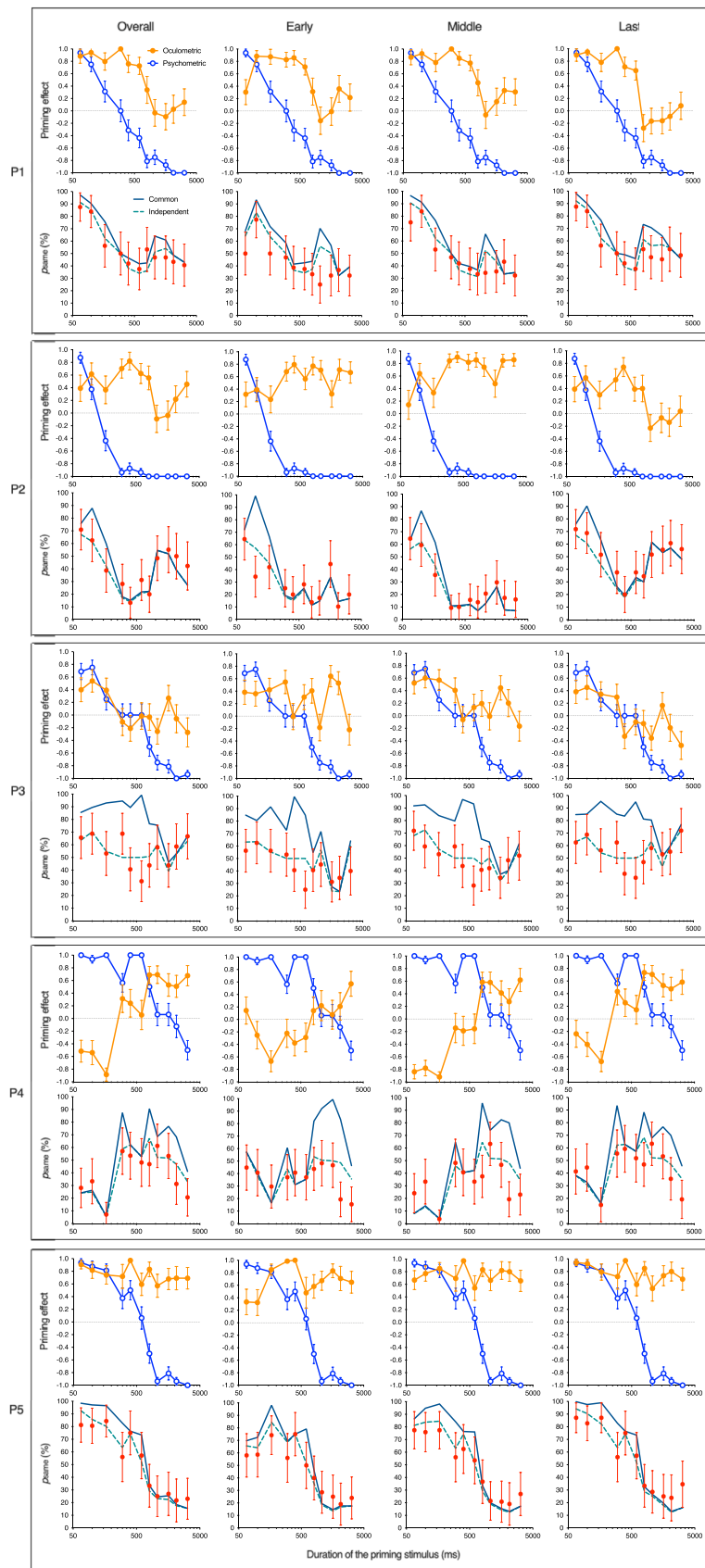


Figure 2. Results of Experiment 1 for each participant. The data during the overall duration of the test stimulus and each of the three divided periods (early, middle, and last) are shown from the leftmost to the rightmost panels, respectively. Each of the top panels



← shows the psychometric and oculometric curves of priming effect as a function of the duration of the presentation of the priming stimulus. The *error bars* represent standard error of the mean. Each of the bottom panels demonstrates the observed  $p_{\text{same}}$  (correspondence between the perceived direction and the direction of eye movement) for each duration of the priming stimulus (*filled red circles*). The dashed line indicates the  $p_{\text{same}}$  predicted by Equation 1, assuming that the perceptual and oculomotor responses are mediated by independent mechanisms. The *solid line* indicates the  $p_{\text{same}}$  predicted by Equation 2, assuming that the perceptual and oculomotor responses are mediated by common mechanisms. The *error bars* represent 95% confidence intervals.

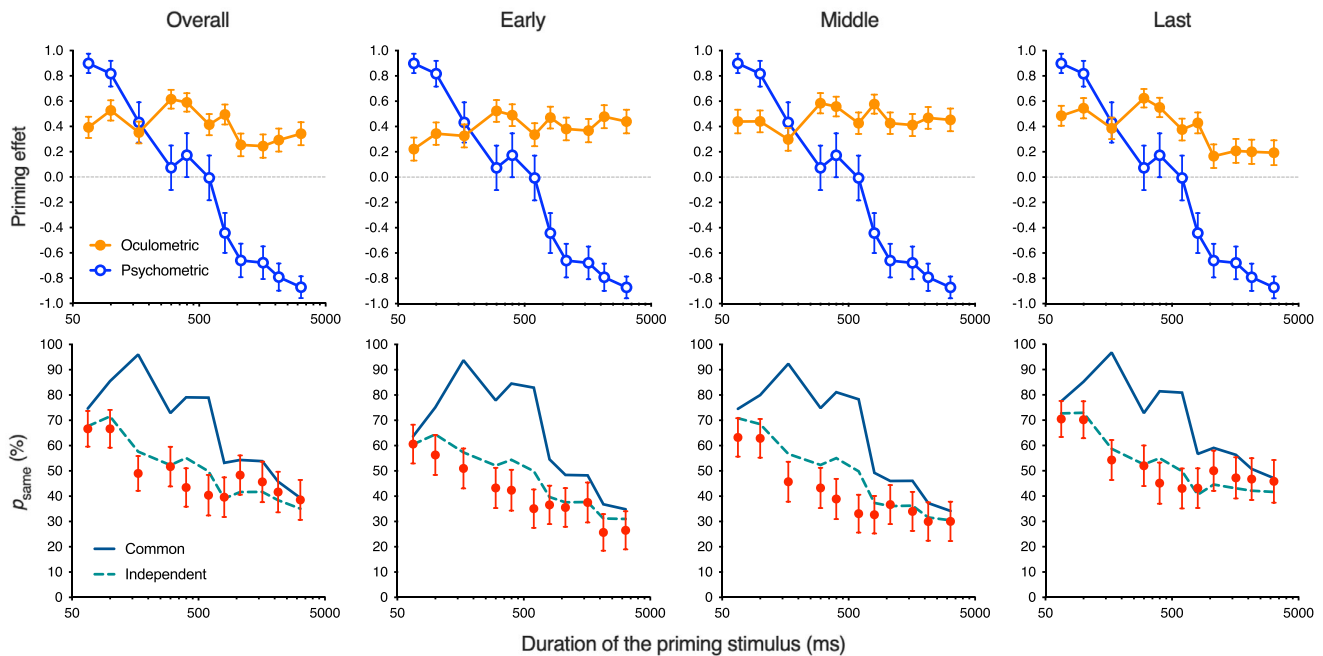


Figure 3. Pooled data from the five participants shown in Figure 2 during the overall duration of the test stimulus and each of the three divided periods, namely early, middle, and last, respectively, from the leftmost to the rightmost panels. The top panel indicates the psychometric and oculometric curves of priming effect as a function of the duration of the presentation of the priming stimulus. The *error bars* represent standard error of the mean. The bottom panel shows the observed  $p_{\text{same}}$  for each duration of the priming stimulus (*filled red circles*). The dashed line indicates the  $p_{\text{same}}$  predicted by Equation 1, assuming that the perceptual and oculomotor responses are mediated by independent mechanisms. The *solid line* indicates the  $p_{\text{same}}$  predicted by Equation 2, assuming that the perceptual and oculomotor responses are mediated by common mechanisms. The *error bars* represent clustered robust standard errors.

curve from independent and common mechanisms. The  $t$  test was applied only to the results using the oculomotor responses during the overall duration of the test stimulus because the analogous tendencies were found in any time windows. Because the  $t$  test was applied twice for each of 11 priming durations, the likelihood of false-positive significant results could have been increased. To avoid this problem,  $p$  values were multiplied by 22 (Bonferroni's correction). The corrected  $p$  values greater than 1 were set equal to 1. An angular transformation was used on proportions before conducting the  $t$  test with Bonferroni's correction. To reduce the concern regarding the independence assumption of the  $t$  test by pooling the individual data, clustered robust standard errors were used (Stock &

Watson, 2012). Figure 3 illustrates the pooled result of the priming effect in the perception and oculomotor domains (top panels) and the observed and predicted  $p_{\text{same}}$  (bottom panels) for the five participants (Figure 2). Again, the priming effect on the perceived direction of the test stimulus shifted from positive to negative with an increase in the priming duration. Meanwhile, the eye generally moved in the same direction as the priming stimulus. For a priming duration shorter than 300 ms where a positive priming was observed in the majority of trials, the observed  $p_{\text{same}}$  was significantly different from the predicted curve based on common mechanisms ( $t(152) = 3.94$ , corrected  $p < 0.01$  for 100-ms priming duration;  $t(154) = 11.21$ , corrected  $p < 0.0001$  for 167-ms priming duration) except for 67-ms



priming duration ( $t(158) = 1.60$ , corrected  $p = 1.00$ ), but not from the predicted curve based on independent mechanisms ( $t(158) = 0.19$ , corrected  $p = 1.00$  for 67-ms priming duration;  $t(152) = 0.90$ , corrected  $p = 1.00$  for 100-ms priming duration;  $t(154) = 1.47$ , corrected  $p = 1.00$  for 167-ms priming duration). For a priming duration longer than 600 ms in which the negative priming was dominant, the observed  $p_{\text{same}}$  was not significantly different from the predicted curves based on both common ( $t(153) = 1.96$ , corrected  $p = 0.56$  for 1067-ms priming duration;  $t(152) = 0.87$ , corrected  $p = 1.00$  for 1067-ms priming duration;  $t(148) = 1.18$ , corrected  $p = 1.00$  for 1600-ms priming duration;  $t(143) = 0.57$ , corrected  $p = 1.00$  for 2133-ms priming duration;  $t(139) = 0.10$ , corrected  $p = 1.00$  for 3200-ms priming duration) and independent mechanisms ( $t(153) = 0.07$ , corrected  $p = 1.00$  for 800-ms priming duration;  $t(152) = 0.97$ , corrected  $p = 1.00$  for 1067-ms priming duration;  $t(148) = 0.55$ , corrected  $p = 1.00$  for 1600-ms priming duration;  $t(143) = 0.44$ , corrected  $p = 1.00$  for 2133-ms priming duration;  $t(139) = 0.47$ , corrected  $p = 1.00$  for 3200-ms priming duration).

## Discussion

The test stimulus appeared to move in the same direction as the priming stimulus (positive priming) when the duration was shorter than approximately 300 ms; otherwise, the perceived direction of the test stimulus was opposite to that of the priming stimulus (negative priming). This result replicated previous findings (Pantle et al., 2000; Takeuchi et al., 2011). When the positive priming was observed, the eye movements were also biased in the same direction as the priming stimulus (Figure 3). In accordance with our expectation, the trial-by-trial correspondence between

perception and eye movements overlapped on the curve calculated from Equation 1, which assumes that the perceptual and oculomotor responses are mediated by different mechanisms (Glasser & Tadin, 2014; Stone & Krauzlis, 2003). Based on the assumption that positive priming is induced by a higher order motion system (Heller & Davidenko, 2018; Jiang et al., 2002; Takeuchi et al., 2011; Yoshimoto et al., 2014), this result indicates that perceptual and oculomotor processes are dissociated at the higher levels of motion processing. However, contrary to our expectation, the eyes tended to move in the same direction as the priming stimulus presented for 800 to 3200 ms; hence, the negative priming was conspicuously perceived (Figure 3). The trial-by-trial correspondences were again predicted from Equation 1 rather than from Equation 2, which assumes that the perceptual and oculomotor responses are mediated by common mechanisms.

One possibility for these findings is that the eye movements derived from the priming stimulus influenced those derived from the test stimulus because the test stimulus was presented soon after the offset of the priming stimulus. Figure 4 illustrates examples of eye displacements of a typical participant (P3) during the test stimulus for each direction and duration of the priming stimulus. The positive and negative values indicate rightward and leftward eye displacements, respectively. When the duration of the priming stimulus was 100 ms, and the participant perceived positive priming in most trials (Figure 2), the eye displacements are biased in the same direction as the priming stimulus (Figure 4A). On the other hand, when the duration of the priming stimulus was 2133 ms and the participant perceived negative priming in most of the trials (Figure 2), the eye initially tended to move in the same direction as the priming stimulus and then gradually in the opposite direction (Figure 4B). These observations suggest that the eye movements during the test stimulus

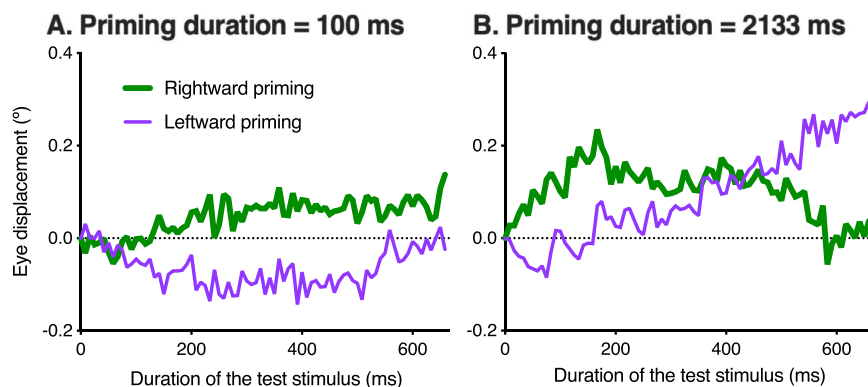


Figure 4. Eye displacements of a typical participant (P3) during the test stimulus for the priming durations of 100 ms (A) and 2133 ms (B). The horizontal eye displacements during the test stimulus following the rightward (*bold green line*) or leftward (*thin purple line*) directions; priming stimulus was plotted as a function of the duration of the test stimulus. The positive and negative displacements indicate rightward and leftward eye movements, respectively.

might contain those derived not only from the test stimulus per se but also from the priming stimulus. This resulted in a trial-averaged eye movements' bias in the same direction as the priming stimulus and the correspondence between the perceived and eye movement directions was traced on the predicted curve based on different mechanisms, irrespective of the priming duration (Figure 3). The degree and timing of direction changes of eye movements varied with both trial-to-trial and participant-to-participant, and thus the eye movements that originated from the test stimulus per se could not be captured by simply dividing the analysis time windows into shorter ones. We tested this possibility in Experiment 2.

## Experiment 2

In this experiment, we replicated Experiment 1 with the exception that a certain interstimulus interval (ISI) between the priming and test stimuli was inserted. Although the presence of ISI would weaken the priming effect (Kanai & Verstraten, 2005; Yoshimoto et al., 2014), we expected to obtain the eye movements induced by the test stimulus per se.

## Methods

The participants were identical to those in Experiment 1. The apparatus and stimuli from

Experiment 1 were reused in Experiment 2. An ISI was inserted between the priming and test stimuli. The ISI was varied in seven steps: 100, 200, 400, 800, 1200, 2000, and 3000 ms. The duration of the presentation of the priming stimulus was set to 67 or 3200 ms, which induced prominent positive or negative priming in Experiment 1 (the top panel of Figure 3). All other stimulus parameters were the same as those in Experiment 1.

The procedure was the same as in Experiment 1, except that an ISI was inserted between the priming and test stimuli. Each session comprised 112 trials in which four trials for each of seven ISI for the two priming durations and for the two drift directions of the priming stimulus was presented in random order. Each participant completed four sessions (16 trials at each session and 448 trials in total) after 28 practice trials. After the data acquisition, we performed the same analyses as in the Experiment 1. The data during the overall duration of the test stimulus were used in Experiment 2 as the analyses with divided time windows did not alter the results of Experiment 1.

One participant (P3) performed an additional four sessions with catch-trials where a blank screen was presented after the priming stimulus offset. We smoothed the eye position data using a cubic spline basis and computed eye velocity profiles before conducting the analyses described in Experiment 1. The subtraction of velocity profiles for a catch-trial from mean velocity profiles for each condition could remove any spurious ocular drift (Barthélemy, Vanzetta, & Masson, 2006). We confirmed that our main results

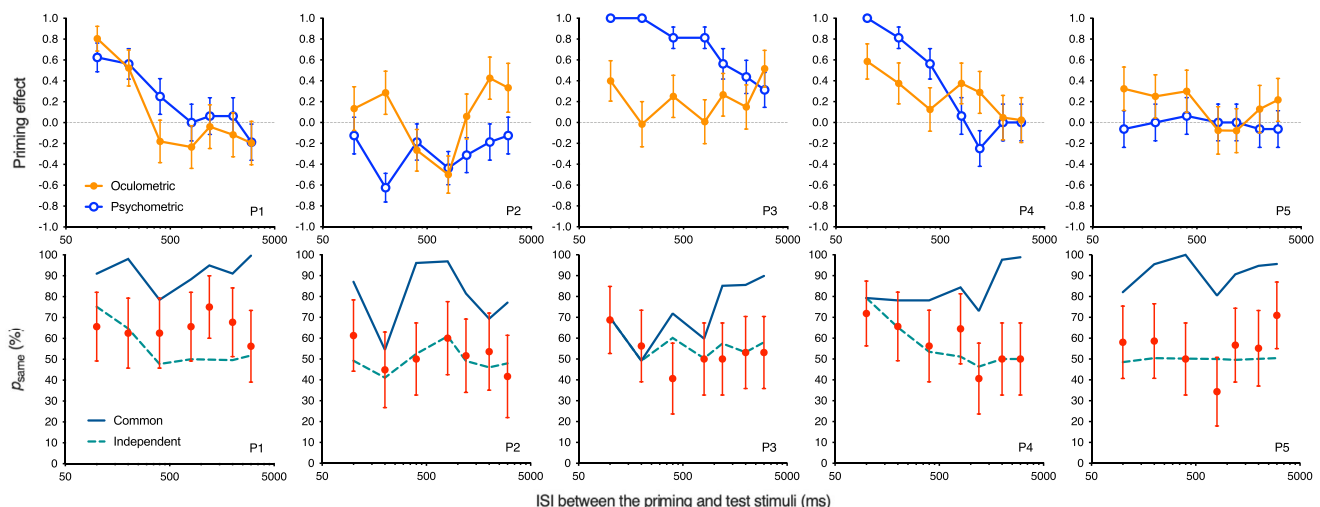


Figure 5. Results for the 67-ms priming duration in Experiment 2 for each participant. The top panels show the psychometric and oculometric curves of the priming effect as a function of the ISI between the priming and test stimuli. The error bars represent standard error of the mean. The bottom panels show the observed  $p_{\text{same}}$  for each ISI (filled red circles). The dashed line indicates the  $p_{\text{same}}$  predicted by Equation 1, assuming that the perceptual and oculomotor responses are mediated by independent mechanisms. The solid line indicates the  $p_{\text{same}}$  predicted by Equation 2, assuming that the perceptual and oculomotor responses is mediated by common mechanisms. The error bars represent 95% confidence intervals.

were not significantly influenced by this analysis, even in the shorter ISI conditions (for details, please see the Supplementary Material).

## Results

### Short priming duration that can induce positive priming

The data exclusion criteria described in Experiment 1 was applied and 4.2% of the trials were excluded from the subsequent analyses. The top panels of Figure 5 illustrate the perceptual and oculomotor responses of each participant to the directionally ambiguous test stimulus when the duration of the priming stimulus was set to 67 ms. The value indicating the strength of the priming effect is plotted as a function of the ISI between the priming and test stimuli. Regarding the psychometric function, the positive priming was prominently observed at the shortest ISI and gradually reduced by increasing the ISI for three of the participants (P1, P3, and P4). No positive priming was observed at any ISI for the other participants (P2 and P5). The pattern of the oculometric function was similar to that of the psychometric function for each participant, except for P3. The bottom panels of Figure 5 indicate the observed  $p_{\text{same}}$  (filled red circles) for each ISI for each participant when the duration of the priming stimulus is 67 ms. The dashed and solid lines represent the  $p_{\text{same}}$  predicted by independent (Equation 1) and common mechanisms (Equation 2), respectively. For all participants and at all ISIs, the observed  $p_{\text{same}}$  were generally closer to the predicted curve from independent mechanisms than that from common mechanisms.

Figure 6 shows the pooled result of the priming effect on perception and eye movement (top panel) and the observed and predicted  $p_{\text{same}}$  (bottom panel) for the 67-ms priming duration for the five participants (Figure 5). At the shortest ISI (100 ms), positive priming was observed in the majority of the trials. The priming effect became less pronounced and eventually disappeared, as the ISI increased. The psychometric and oculometric functions were overlapped: both perceived and eye movement directions were biased in the same direction as the priming stimulus at the shorter ISIs. However, the observed  $p_{\text{same}}$ , the trial-by-trial correspondence between the perceived and eye movement directions, approximated the predicted curve from independent mechanisms ( $t \leq 1.76$ , corrected  $p \geq 0.57$ ) and significantly differed from the predicted curve of common mechanisms at any ISI ( $t \geq 5.88$ , corrected  $p < 0.0001$ ).

### Long priming duration that can induce negative priming

The top panels of Figure 7 show the priming effect on the perceptual and oculomotor responses of each

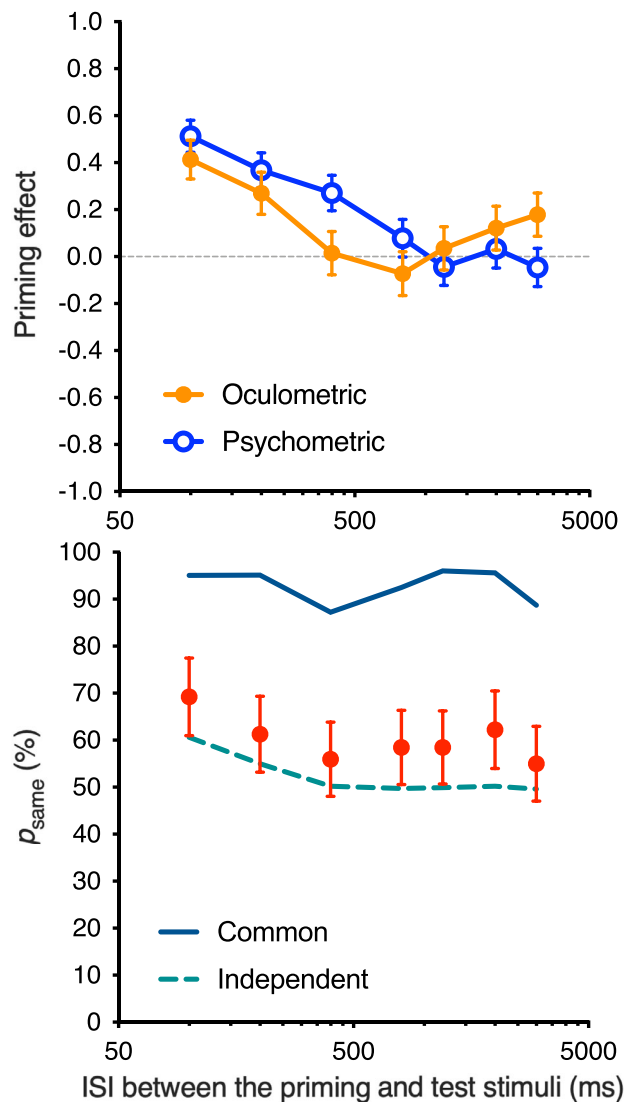


Figure 6. Pooled data from the five participants shown in Figure 4, when the duration of the presentation of the priming stimulus was 67 ms. The top panel shows the psychometric and oculometric curves of the priming effect as a function of the ISI between the priming and test stimuli. The error bars represent standard error of the mean. The bottom panel shows the observed  $p_{\text{same}}$  for each ISI (filled red circles). The dashed line indicates the  $p_{\text{same}}$  predicted by Equation 1, assuming that the perceptual and oculomotor responses are mediated by independent mechanisms. The solid line indicates the  $p_{\text{same}}$  predicted by Equation 2, assuming that the perceptual and oculomotor responses are mediated by common mechanisms. The error bars represent clustered robust standard errors.

participant when the duration of the priming stimulus was set to 3200 ms. The value indicating the strength of the priming effect is plotted as a function of the ISI. Contrary to a short priming duration, the participants reported negative priming in most trials. The priming

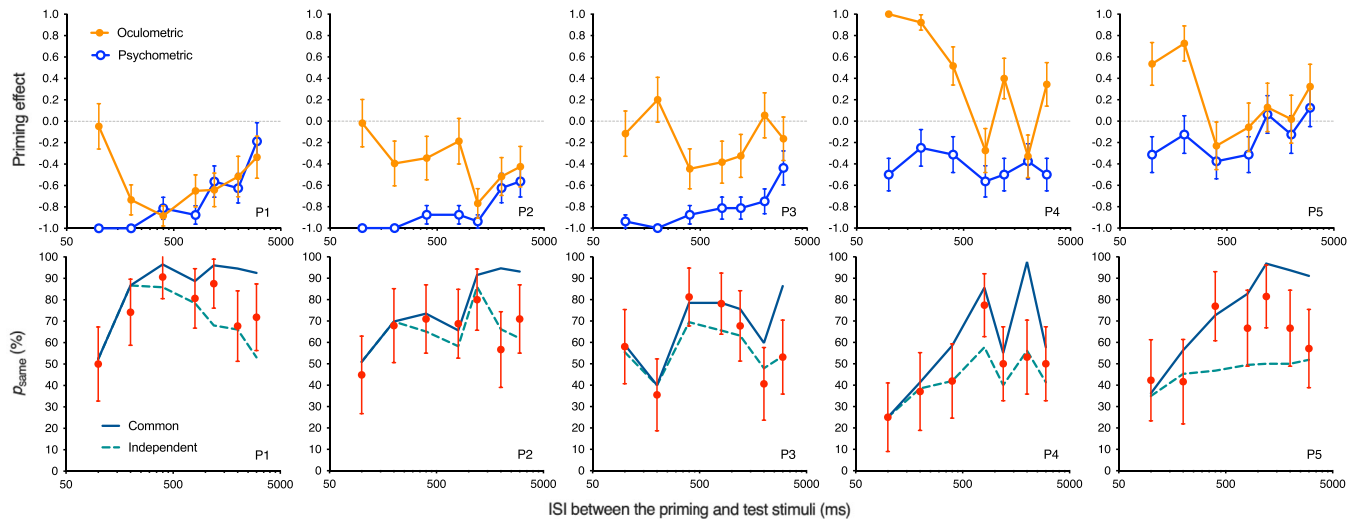


Figure 7. Results for the 3200-ms priming duration in Experiment 2 for each participant. The top panels show the psychometric and oculometric curves of the priming effect as a function of the ISI between the priming and test stimuli. The error bars represent standard error of the mean. The bottom panels show the observed  $p_{\text{same}}$  for each ISI (filled red circles). The dashed line indicates the  $p_{\text{same}}$  predicted by Equation 1, assuming that the perceptual and oculomotor responses are mediated by independent mechanisms. The solid line indicates the  $p_{\text{same}}$  predicted by Equation 2, assuming that the perceptual and oculomotor responses are mediated by common mechanisms. The error bars represent 95% confidence intervals.

effect was reduced when the ISI was prolonged to 3000 ms, except for P4. At an ISI shorter than 200 ms, the direction of eye movement was neither the same nor in the opposite direction of the priming stimulus (P1, P2, and P3), or the same direction as the priming stimulus (P4 and P5). At the longer ISIs (400–3000 ms), the participants' eyes tended to move in the opposite direction of the priming stimulus and the patterns of oculometric functions became similar to those of psychometric functions. The bottom panels of Figure 7 show the observed  $p_{\text{same}}$  (filled red circles) for each ISI for each participant when the duration of the priming stimulus was 3200 ms. The dashed and solid lines represent the  $p_{\text{same}}$  predicted by independent (Equation 1) and common mechanisms (Equation 2), respectively. When the ISI was shorter than 200 ms, the observed  $p_{\text{same}}$  was on the predicted curves from both common and different mechanisms. At the middle ISIs (400–1200 ms), the observed  $p_{\text{same}}$  were approached to the predicted values from common mechanisms compared to those from different mechanisms for most of the participants. As the ISI increased, the observed  $p_{\text{same}}$  neared the predicted curve from different mechanisms.

Figure 8 shows the pooled result of the priming effect on perception and eye movement (top panel) and the observed and predicted  $p_{\text{same}}$  (bottom panel) for the 3200-ms priming duration for the five participants (Figure 7). For the perceptual responses, negative priming was dominant, but reduced with an increase

in the ISI. For the oculomotor responses, the eye movements were biased in the same direction as the priming stimulus at the shorter ISIs (100–200 ms), whereas the direction of the eye movement was reversed at the ISI longer than 400 ms. At the shorter ISIs where the priming effect on the perceptual and oculometric responses were different (psychometric negative priming and oculometric positive priming), no significant differences were found among the observed  $p_{\text{same}}$ , the predicted values from common mechanisms ( $t(149) = 0.38$ , corrected  $p = 1.00$  for 100-ms ISI;  $t(141) = 0.11$ , corrected  $p = 1.00$  for 200-ms ISI) and those from different mechanisms ( $t(149) = 1.47$ , corrected  $p = 1.00$  for 100-ms ISI;  $t(141) = 1.61$ , corrected  $p = 0.77$  for 200-ms ISI). At the middle ISIs where negative priming appeared in both perceptual and oculometric domains, the observed  $p_{\text{same}}$  approximated the values predicted by common mechanisms ( $t(152) = 1.17$ , corrected  $p = 1.00$  for 400-ms ISI;  $t(153) = 0.46$ , corrected  $p = 1.00$  for 800-ms ISI), but not those predicted by different mechanisms ( $t(152) = 2.80$ , corrected  $p < 0.05$  for 400-ms ISI;  $t(153) = 2.97$ , corrected  $p < 0.05$  for 800-ms ISI). When the ISI was longer than 1200 ms, however, the observed  $p_{\text{same}}$  approached the values predicted by different mechanisms ( $t(153) = 0.33$ , corrected  $p = 1.00$  for 2000-ms ISI;  $t(154) = 1.50$ , corrected  $p = 0.95$  for 3000-ms ISI), and significantly differed from those predicted by common mechanisms ( $t(153) = 5.23$ , corrected  $p < 0.0001$  for 2000-ms ISI;  $t(154) = 4.25$ , corrected  $p < 0.001$  for 3000-ms ISI).

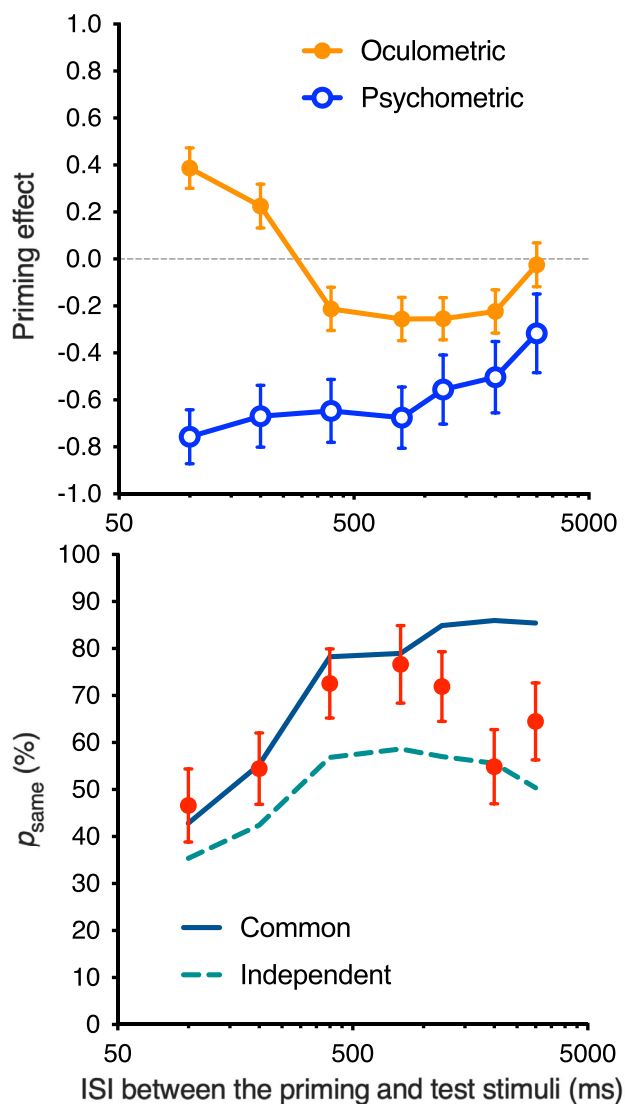


Figure 8. Pooled data from the five participants shown in Figure 6, where the duration of the presentation of the priming stimulus was 3200 ms. The top panel shows the psychometric and oculometric curves of the priming effect as a function of the ISI between the priming and test stimuli. The error bars represent SEM. The bottom panel shows the observed  $p_{\text{same}}$  for each ISI (filled red circles). The dashed line indicates the  $p_{\text{same}}$  predicted by Equation 1, assuming that the perceptual and oculomotor responses are mediated by independent mechanisms. The solid line indicates the  $p_{\text{same}}$  predicted by Equation 2, assuming that the perceptual and oculomotor responses are mediated by common mechanisms. The error bars represent clustered robust standard errors.

## Discussion

We replicated the previous finding of decreasing motion priming effect with increasing ISI between the priming and test stimuli (Kanai & Verstraten, 2005). Analogous results were also obtained for

the eye movements. For the short priming duration of 67 ms (Figure 6), the averaged perceptual and oculomotor responses were similar: both perceived and eye movement directions were biased in the same direction as the priming stimulus. However, those responses were not covariant on a trial-by-trial basis irrespective of the ISI and was well predicted from Equation 1. These results again suggest that the perceptual and oculomotor responses are mediated by different mechanisms when the positive priming is dominant, in which the higher order motion mechanism can operate. For the long priming duration of 3200 ms (Figure 8), the results were similar to those obtained in Experiment 1 (Figure 3) when the ISI was shorter than 200 ms. By contrast, at ISIs of 400 to 1200 ms, negative priming was observed not only on perceived direction but on eye movement direction, and the trial-by-trial correspondence between those directions was consistent with the prediction from Equation 2. These observations indicate that the eye movements around 400 ms, after the offset of the priming stimulus, would be derived from the test stimulus per se and support the idea that the perceptual and oculomotor responses are mediated by common mechanisms at the lower level of motion processing that is assumed to be associated with the negative priming.

It should be noted that although positive and negative motion priming effects were observable in oculomotor responses in a similar pattern as perceptual responses, the effects on oculomotor responses were less prominent than those on perceptual responses (Figures 6 and 8). This may be because oculomotor responses can more reliably reflect the actual motion than perceptual responses. Previous studies demonstrated that involuntary tracking eye movements, which is supposed here, can trace the physical motion direction even when the perceived direction is dissociated from it (Spring & Carrasco, 2012; Spring et al., 2011). Consistent with these findings, the eyes moved in neither the same nor the opposite direction of the priming stimulus, on average, while viewing the test stimulus, when the ISI between the priming and test stimulus was long enough to reduce the priming effect (Figures 6 and 8). Again, the test stimulus was composed of counterphase grating patterns, and thus its direction of motion was physically ambiguous.

Finally, we address the variability within and between participants in perceptual and oculomotor responses. For P2 and P5, although the short priming duration of 67 ms produced a strong positive priming on both perceived and eye movement directions in Experiment 1 (Figure 2), such a priming effect was eliminated in Experiment 2 (Figure 5). This variability may be due to individual differences in the effect of the ISI on positive motion priming, potentially linked to the differences in the excitatory process in the supra-sensory areas

(Takeuchi, Yoshimoto, Shimada, Kochiyama, & Kondo, 2017). For P4, the oculomotor responses after the priming stimulus with shorter duration were inverted between Experiments 1 and 2 whereas positive priming was robustly perceived in both experiments (Figures 2 and 5). It was unclear why P4 eye was biased to move in the opposite direction of the priming stimulus when its duration was shorter than 167 ms in Experiment 1. We speculate that in some cases, the relative motion between a brief priming stimulus and after image of the fixation point might elicit the eye movements shifted to the opposite direction of the priming stimulus. This may be because a longer priming stimulus or inserting ISI eliminated the peculiar pattern of eye movements of P4.

## General discussion

In this study, we tested the correspondence between perception and eye movements for the directionally ambiguous test stimulus when the motion priming effect was present. We assumed reflexive tracking eye movements since participants were instructed not to follow the moving stimuli but to maintain central fixation. A typical pattern was observed: the motion priming effect changed from positive to negative with the increase in the duration of priming stimulus. A trial-by-trial analysis showed that when the ISI between the priming and test stimuli was shorter than 200 ms, the perceived direction did not correspond to eye movement irrespective of whether the motion priming effect was positive or negative. However, when the ISI was extended to 400 or 800 ms, the perceived direction tended to covary with the eye movement on a trial-by-trial basis in the condition where the negative priming was dominant but not in the condition where the positive priming was dominant. Within the range of the ISI, the eye movement and the perceived direction of the test stimulus were opposite to the direction of the priming stimulus with the 3200-ms duration (negative priming), assuming that the eye movements were derived from the test stimulus per se, and not from the priming stimulus.

As described in the Introduction, negative priming is regarded as a rapid form of MAE and believed to be processed by a low-level motion mechanism that is sensitive to first-order motion energy (Kanai & Verstraten, 2005; Takeuchi et al., 2011; Yoshimoto & Takeuchi, 2013; Yoshimoto et al. 2014), which is known to drive the OFR (Masson et al., 2002; Sheliga et al., 2005; Sheliga et al., 2006). Our observations that the trial-by-trial correlation between the perceived and eye movement directions during negative priming corresponded to the prediction

using Equation 2, support the hypothesis that the perceptual and oculomotor responses are mediated by shared mechanisms at the lower level of visual motion processing. By contrast, it has been considered that positive priming is mediated by a high-level motion mechanism such as feature-tracking because the stimulus parameters that may be important to detect the changes in position of salient features in motion (e.g., high-contrast and low-velocity) are crucial cues for positive priming (Takeuchi et al., 2011; Yoshimoto & Takeuchi, 2013; Yoshimoto et al., 2014). When positive priming was dominant, the perceived direction did not covary with the eye movement on a trial-by-trial basis, consistent with the prediction from Equation 1. This tendency was found even when the ISI between the priming and test stimuli was present to negate the eye movements derived from the priming stimulus. These results bear out the hypothesis that the perceptual and oculomotor responses are independently processed at the high-level of visual motion processing. Our conjecture agrees with the previous studies that the perceived direction of a moving stimulus was dissociated from the OFR using spatial suppression phenomenon (Glasser & Tadin, 2014) and random dot patterns (Blum & Price, 2014), presumably involving a higher level of visual processing.

A study using electroencephalography and functional magnetic resonance imaging demonstrated that positive motion priming involves the modulation of neural responses in MT (Jiang et al., 2002). MT neurons are known to play an important role in the control of both pursuit and OFR, and there may be common neural substrates for motion perception and eye movements (Kawano, Shidara, Watanabe, & Yamane, 1994; Lisberger, 2010; Lisberger & Movshon, 1999; Newsome, Wurtz, Dursteler, & Mikami, 1985; Spering & Montagnini, 2011). Nevertheless, perceptual and oculomotor responses were dissociated when positive motion priming was dominant. Glasser and Tadin (2014), who demonstrated a discrepancy between perceptual and oculomotor sensitivities to motion direction using spatial suppression phenomenon, argued that different populations of MT neurons provide motion signals for perception and reflexive ocular following eye movements. Previous neurophysiological studies have identified subpopulations of MT neurons with different receptive field characteristics and contrast sensitivities (Allman, Miezin, & McGuinness, 1985; Born, Groh, Zhao, & Lukaszewicz, 2000; Born & Tootell, 1992; Churan, Khawaja, Tsui, & Pack, 2008; Pack et al., 2005). The eye movements may be mediated by “wide-field” neurons that integrate motion information over large parts of a visual field whereas motion perception may be mediated by the neurons having a receptive field with antagonistic center-surround structure. This assumption is consistent

with the finding that spatial summation mechanisms trigger OFRs (Barthélemy et al., 2006). The observation that positive motion priming is likely to be induced by briefly presented priming stimuli at high contrast would also match this idea because center-surround MT neurons respond to high-contrast brief motion better than to wide-field neurons (Churan et al., 2008; Pack et al., 2005).

Meanwhile, the perceived and eye movement directions tended to covary when negative motion priming was dominant. A rapid change in the adaptation state of directionally selective V1 neurons is a candidate for the underlying mechanism of negative motion priming (Glasser et al., 2011; Kanai & Verstraten, 2005; Lisberger & Movshon, 1999; A. J. Pantle et al., 2000; Pavan et al., 2009; Priebe & Lisberger, 2002). Our results thus suggest that perceptual and oculomotor responses are mediated by common mechanisms at visual areas as early as V1, consistent with the evidence for shared brain pathways for perception and eye movements (Lisberger, 2010; Spering & Montagnini, 2011). In the current study, however, the two responses were not perfectly correlated: the trial-by-trial correspondence between perception and eye movements was up to about 80% (Figure 8). This may be because our stimuli were not optimized to produce a strong oculomotor response and the resultant eye movements were small. As mentioned in Experiment 1, the stimulus velocity used here was set at 3 Hz to induce both positive and negative priming while the test stimulus parameter was constant. It has been shown that negative priming was dominant when the velocity was higher than around 3 Hz irrespective of the duration of the priming stimulus (Takeuchi et al., 2011; Yoshimoto & Takeuchi, 2013). The optimal velocity of drifting gratings for the human OFR was estimated to be 10 to 20 Hz (Gellman et al., 1990). Boosting the stimulus velocity may therefore increase the trial-by-trial correspondence between perception and eye movements during the appearance of negative priming, whereas positive priming will disappear. Alternatively, the imperfect correlation may reflect that perception and eye movements are in part affected by different noise sources (Blum & Price, 2014; Boström & Warzecha, 2010; Gegenfurtner et al., 2003; Stone & Krauzlis, 2003). Although perceptual and oculomotor systems may share common motion signals and sensory noise, additional noise may be added to oculomotor areas such as the frontal eye field or the cerebellum (Lisberger, 2010). This explanation can account for variability differences in spite of similar sensitivities between perception and eye movements (Spering & Carrasco, 2015).

Negative motion priming, or a rapid form of MAE, is thought to occur at the lower level of visual motion processing. It is notable that MAE is quite a complex phenomenon that can be processed at different

levels in the hierarchy of visual motion (Campana, Maniglia, & Pavan, 2013; Mather, Pavan, Campana, & Casco, 2008). A type of MAE in which test stimuli were temporally varying patterns like those used in this study have been suggested to involve both low- and high-levels of motion processing (Campana, Pavan, Maniglia, & Casco, 2011; Culham, Verstraten, Ashida, & Cavanagh, 2000; Nishida & Sato, 1995; Pavan et al., 2009; Pavan, Campana, Maniglia, & Casco, 2010; Pavan & Skujevskis, 2013). Akyuz et al. (2020) measured electroencephalography activity while participants experienced the MAE induced by the adaptation stimulus drifting for short (640 ms) or long (6.4-second) duration. They found that the average event-related potentials of short-duration adaptation were significantly different only for the occipital scalp sites whereas the long-duration adaptation led to changes in the potentials over both occipital and parietal scalp sites corresponding to low- and high-levels of motion hierarchy, such as V1 and MT. In line with these findings, negative motion priming can be assumed to tap low-level motion processing. Braun et al. (2006) reported no trial-by-trial covariation between perception and eye movements despite good agreement in the magnitude of a long-term form of MAE for both. Given that the MAE induced by a long-duration adaptation might involve later stages of motion processing, their results are consistent with the hypothesis that perceptual and oculomotor responses are mediated by different mechanisms in those stages. It would be meaningful to test the validity of our conclusions regarding the relationship between perceptual and oculomotor responses at the different levels of the motion hierarchy using priming or adapting stimulus with a wider range of durations to induce negative motion priming or MAE.

*Keywords:* visual motion perception, eye movements, motion priming, oculomotor response, ocular following response

## Acknowledgments

The authors thank Editage ([www.editage.com](http://www.editage.com)) for English language editing.

Supported by JSPS KAKENHI Grant Number 20K14257 and 20H01788.

Commercial relationships: none.

Corresponding author: Sanae Yoshimoto.

Email: [syoshimo@hiroshima-u.ac.jp](mailto:syoshimo@hiroshima-u.ac.jp).

Address: School of Integrated Arts and Sciences, Hiroshima University, Hiroshima, Japan.

## References

- Adelson, E. H., & Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America A*, 2(2), 284–299, <https://doi.org/10.1364/josaa.2.000284>.
- Akyuz, S., Pavan, A., Kaya, U., & Kafaligonul, H. (2020). Short- and long-term forms of neural adaptation: An ERP investigation of dynamic motion aftereffects. *Cortex*, 125, 122–134, <https://doi.org/10.1016/j.cortex.2019.12.015>.
- Allman, J., Miezin, F., & McGuinness, E. (1985). Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT). *Perception*, 14(2), 105–126, <https://doi.org/10.1068/p140105>.
- Anstis, S., & Ramachandran, V. S. (1987). Visual inertia in apparent motion. *Vision Research*, 27(5), 755–764, [https://doi.org/10.1016/0042-6989\(87\)90073-3](https://doi.org/10.1016/0042-6989(87)90073-3).
- Ashida, H., Lingnau, A., Wall, M. B., & Smith, A. T. (2007). fMRI adaptation reveals separate mechanisms for first-order and second-order motion. *Journal of Neurophysiology*, 97(2), 1319–1325, <https://doi.org/10.1152/jn.00723.2006>.
- Badler, J. B., Lefèvre, P., & Missal, M. (2012). Divergence between oculomotor and perceptual causality. *Journal of Vision*, 12(5):3, 1–15, <https://doi.org/10.1167/12.5.3>.
- Baro, J. A., & Levinson, E. (1988). Apparent motion can be perceived between patterns with dissimilar spatial frequencies. *Vision Research*, 28(12), 1311–1313, [https://doi.org/10.1016/0042-6989\(88\)90062-4](https://doi.org/10.1016/0042-6989(88)90062-4).
- Barthélemy, F. V., Vanzetta, I., & Masson, G. S. (2006). Behavioral receptive field for ocular following in humans: Dynamics of spatial summation and center-surround interactions. *Journal of Neurophysiology*, 95(6), 3712–3726, <https://doi.org/10.1152/jn.00112.2006>.
- Beutter, B. R., & Stone, L. S. (1998). Human motion perception and smooth eye movements show similar directional biases for elongated apertures. *Vision Research*, 38(9), 1273–1286, [https://doi.org/10.1016/S0042-6989\(97\)00276-9](https://doi.org/10.1016/S0042-6989(97)00276-9).
- Beutter, B. R., & Stone, L. S. (2000). Motion coherence affects human perception and pursuit similarly. *Visual Neuroscience*, 17(1), 139–153, <https://doi.org/10.1017/S0952523800171147>.
- Bisley, J. W., Zaksas, D., Droll, J. A., & Pasternak, T. (2004). Activity of neurons in cortical area mt during a memory for motion task. *Journal of Neurophysiology*, 91(1), 286–300, <https://doi.org/10.1152/jn.00870.2003>.
- Blum, J., & Price, N. S. C. (2014). Reflexive tracking eye movements and motion perception: One or two neural populations? *Journal of Vision*, 14(3):23, 1–14, <https://doi.org/10.1167/14.3.23>.
- Born, R. T., Groh, J. M., Zhao, R., & Lukasewycz, S. J. (2000). Segregation of object and background motion in visual area MT: Effects of microstimulation on eye movements. *Neuron*, 26(3), 725–734, [https://doi.org/10.1016/S0896-6273\(00\)81208-8](https://doi.org/10.1016/S0896-6273(00)81208-8).
- Born, R. T., & Tootell, R. B. H. (1992). Middle temporal visual area. *Nature*, 357, 497–499.
- Boström, K. J., & Warzecha, A. K. (2010). Open-loop speed discrimination performance of ocular following response and perception. *Vision Research*, 50(9), 870–882, <https://doi.org/10.1016/j.visres.2010.02.010>.
- Boulton, J. C., & Baker, C. L. (1993). Dependence on stimulus onset asynchrony in apparent motion: Evidence for two mechanisms. *Vision Research*, 33(14), 2013–2019, [https://doi.org/10.1016/0042-6989\(93\)90024-Q](https://doi.org/10.1016/0042-6989(93)90024-Q).
- Braddick, O. J. (1980). Low-level and high-level processes in apparent motion. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, 290(1038), 137–151, <https://doi.org/10.1098/rstb.1980.0087>.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10(4), 433–436, <https://doi.org/10.1163/156856897X00357>.
- Brascamp, J. W., Kanai, R., Walsh, V., & Van Ee, R. (2010). Human middle temporal cortex, perceptual bias, and perceptual memory for ambiguous three-dimensional motion. *Journal of Neuroscience*, 30(2), 760–766, <https://doi.org/10.1523/JNEUROSCI.4171-09.2010>.
- Braun, D. I., Pracejus, L., & Gegenfurtner, K. R. (2006). Motion aftereffect elicits smooth pursuit eye movements. *Journal of Vision*, 6(7), 671–684, <https://doi.org/10.1167/6.7.1>.
- Britten, K. H., Newsome, W. T., Shadlen, M. N., Celebrini, S., & Movshon, J. A. (1996). A relationship between behavioral choice and the visual responses of neurons in macaque MT. *Visual Neuroscience*, 13(1), 87–100, <https://doi.org/10.1017/S09525238000715X>.
- Brown, R. O., & He, S. (2000). Visual motion of missing-fundamental patterns: Motion energy versus feature correspondence. *Vision Research*, 40(16), 2135–2147, [https://doi.org/10.1016/S0042-6989\(00\)00080-8](https://doi.org/10.1016/S0042-6989(00)00080-8).
- Burr, D. C., & Ross, J. (1982). Contrast sensitivity at high velocities. *Vision Research*, 22(4), 479–484, [https://doi.org/10.1016/0042-6989\(82\)90196-1](https://doi.org/10.1016/0042-6989(82)90196-1).



- Burr, D. C., Ross, J., & Morrone, M. C. (1986). Seeing objects in motion. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, 227(1247), 249–265, <https://doi.org/10.1098/rspb.1986.0022>.
- Campana, G., Cowey, A., & Walsh, V. (2002). Priming of motion direction and area V5/MT: A test of perceptual memory. *Cerebral Cortex*, 12(6), 663–669, <https://doi.org/10.1093/cercor/12.6.663>.
- Campana, G., Maniglia, M., & Pavan, A. (2013). Common (and multiple) neural substrates for static and dynamic motion after-effects: A rTMS investigation. *Cortex*, 49(9), 2590–2594, <https://doi.org/10.1016/j.cortex.2013.07.001>.
- Campana, G., Pavan, A., & Casco, C. (2008). Priming of first- and second-order motion: Mechanisms and neural substrates. *Neuropsychologia*, 46(2), 393–398, <https://doi.org/10.1016/j.neuropsychologia.2007.07.019>.
- Campana, G., Pavan, A., Maniglia, M., & Casco, C. (2011). The fastest (and simplest), the earliest: The locus of processing of rapid forms of motion aftereffect. *Neuropsychologia*, 49(10), 2929–2934, <https://doi.org/10.1016/j.neuropsychologia.2011.06.020>.
- Cavanagh, P. (1992). Attention-based motion perception. *Science*, 257(5076), 1563–1565, <https://doi.org/10.1126/science.1523411>.
- Chubb, C., & Sperling, G. (1988). Drift-balanced random stimuli: A general basis for studying non-Fourier motion perception. *Journal of the Optical Society of America A*, 5(11), 1986–2007, <https://doi.org/10.1364/josaa.5.001986>.
- Churan, J., Khawaja, F. A., Tsui, J. M. G., & Pack, C. C. (2008). Brief motion stimuli preferentially activate surround-suppressed neurons in macaque visual area MT. *Current Biology*, 18(22), 1051–1052, <https://doi.org/10.1016/j.cub.2008.10.003>.
- Churan, J., Richard, A. G., & Pack, C. C. (2009). Interaction of spatial and temporal factors in psychophysical estimates of surround suppression. *Journal of Vision*, 9(4):15, 1–15, <https://doi.org/10.1167/9.4.15>.
- Crespi, S., Biagi, L., D’Avossa, G., Burr, D. C., Tosetti, M., & Morrone, M. C. (2011). Spatiotopic coding of BOLD signal in human visual cortex depends on spatial attention. *PLoS ONE*, 6(7), e21661, <https://doi.org/10.1371/journal.pone.0021661>.
- Culham, J. C., Verstraten, F. A. J., Ashida, H., & Cavanagh, P. (2000). Independent aftereffects of attention and motion. *Neuron*, 28(2), 607–615, [https://doi.org/10.1016/S0896-6273\(00\)00137-9](https://doi.org/10.1016/S0896-6273(00)00137-9).
- d’Avossa, G., Tosetti, M., Crespi, S., Biagi, L., Burr, D. C., & Morrone, M. C. (2007). Spatiotopic selectivity of BOLD responses to visual motion in human area MT. *Nature Neuroscience*, 10(2), 249–255, <https://doi.org/10.1038/nn1824>.
- Dosher, B. A., Landy, M. S., & Sperling, G. (1989). Kinetic depth effect and optic flow-I. 3D shape from Fourier motion. *Vision Research*, 29(12), 1789–1813, [https://doi.org/10.1016/0042-6989\(89\)90161-2](https://doi.org/10.1016/0042-6989(89)90161-2).
- Gegenfurtner, K. R., Xing, D., Scott, B. H., & Hawken, M. J. (2003). A comparison of pursuit eye movement and perceptual performance in speed discrimination. *Journal of Vision*, 3(11):19, 865–876, <https://doi.org/10.1167/3.11.19>.
- Gellman, R. S., Carl, J. R., & Miles, F. A. (1990). Short latency ocular-following responses in man. *Visual Neuroscience*, 5(2), 107–122, <https://doi.org/10.1017/S095252380000158>.
- Georgeson, M. A., & Harris, M. G. (1990). The temporal range of motion sensing and motion perception. *Vision Research*, 30(4), 615–619, [https://doi.org/10.1016/0042-6989\(90\)90072-S](https://doi.org/10.1016/0042-6989(90)90072-S).
- Georgeson, M. A., & Shackleton, T. M. (1989). Monocular motion sensing, binocular motion perception. *Vision Research*, 29(11), 1511–1523, [https://doi.org/10.1016/0042-6989\(89\)90135-1](https://doi.org/10.1016/0042-6989(89)90135-1).
- Glasser, D. M., & Tadin, D. (2014). Modularity in the motion system: Independent oculomotor and perceptual processing of brief moving stimuli. *Journal of Vision*, 14(3):28, 1–13, <https://doi.org/10.1167/14.3.28>.
- Glasser, D. M., Tsui, J. M. G., Pack, C. C., & Tadin, D. (2011). Perceptual and neural consequences of rapid motion adaptation. *Proceedings of the National Academy of Sciences of the United States of America*, 108(45), E1080–E1088, <https://doi.org/10.1073/pnas.1101141108>.
- Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. New York: John Wiley and Sons.
- Heller, N. H., & Davidenko, N. (2018). Dissociating higher and lower order visual motion systems by priming illusory apparent motion. *Perception*, 47(1), 30–43, <https://doi.org/10.1177/0301006617731007>.
- Jiang, Y., Luo, Y. J., & Parasuraman, R. (2002). Neural correlates of perceptual priming of visual motion. *Brain Research Bulletin*, 57(2), 211–219, [https://doi.org/10.1016/S0361-9230\(01\)00743-2](https://doi.org/10.1016/S0361-9230(01)00743-2).
- Jiang, Y., Pantle, A. J., & Mark, L. S. (1998). Visual inertia of rotating 3-D objects. *Perception and Psychophysics*, 60(2), 275–286, <https://doi.org/10.3758/BF03206036>.
- Kanai, R., & Verstraten, F. A. J. (2005). Perceptual manifestations of fast neural plasticity: Motion priming, rapid motion aftereffect and perceptual sensitization. *Vision Research*, 45(25–26), 3109–3116, <https://doi.org/10.1016/j.visres.2005.05.014>.

- Kawano, K., Shidara, M., Watanabe, Y., & Yamane, S. (1994). Neural activity in cortical area MST of alert monkey during ocular following responses. *Journal of Neurophysiology*, *71*(6), 2305–2324, <https://doi.org/10.1152/jn.1994.71.6.2305>.
- Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R., & Broussard, C. (2007). What's new in psychtoolbox-3. *Perception*, *36*(14), 1–16.
- Krauzlis, R. J., & Stone, L. S. (1999). Tracking with the mind's eye. *Trends in Neurosciences*, *22*(12), 544–550, [https://doi.org/10.1016/S0166-2236\(99\)01464-2](https://doi.org/10.1016/S0166-2236(99)01464-2).
- Kuhn, G., & Land, M. F. (2006). There's more to magic than meets the eye. *Current Biology*, *16*(22), 950–951, <https://doi.org/10.1016/j.cub.2006.10.012>.
- Lappin, J. S., Tadin, D., Nyquist, J. B., & Corn, A. L. (2009). Spatial and temporal limits of motion perception across variations in speed, eccentricity, and low vision. *Journal of Vision*, *9*(1), 1–14, <https://doi.org/10.1167/9.1.30>.
- Lisberger, S. G. (2010). Visual guidance of smooth-pursuit eye movements: Sensation, action, and what happens in between. *Neuron*, *66*(4), 477–491, <https://doi.org/10.1016/j.neuron.2010.03.027>.
- Lisberger, S. G., & Movshon, J. A. (1999). Visual motion analysis for pursuit eye movements in area MT of Macaque monkeys. *Journal of Neuroscience*, *19*(6), 2224–2246, <https://doi.org/10.1523/jneurosci.19-06-02224.1999>.
- Lu, Z. L., & Sperling, G. (1995). The functional architecture of human visual motion perception. *Vision Research*, *35*(19), 2697–2722, [https://doi.org/10.1016/0042-6989\(95\)00025-U](https://doi.org/10.1016/0042-6989(95)00025-U).
- Masson, G. S., Yang, D.-S., & Miles, F. A. (2002). Reversed short-latency ocular following. *Vision Research*, *42*(17), 2081–2087, [https://doi.org/10.1016/s0042-6989\(02\)00082-2](https://doi.org/10.1016/s0042-6989(02)00082-2).
- Masson, G. S., & Perrinet, L. U. (2012). The behavioral receptive field underlying motion integration for primate tracking eye movements. *Neuroscience and Biobehavioral Reviews*, *36*(1), 1–25, <https://doi.org/10.1016/j.neubiorev.2011.03.009>.
- Mather, G., Pavan, A., Campana, G., & Casco, C. (2008). The motion aftereffect reloaded. *Trends in Cognitive Sciences*, *12*(12), 481–487, <https://doi.org/10.1016/j.tics.2008.09.002>.
- Miles, F. A., Kawano, K., & Optican, L. M. (1986). Short-latency ocular following responses of monkey. I. Dependence on temporospatial properties of visual input. *Journal of Neurophysiology*, *56*(5), 1321–1354, <https://doi.org/10.1152/jn.1986.56.5.1321>.
- Naber, M., Frässle, S., & Einhäuser, W. (2011). Perceptual rivalry: Reflexes reveal the gradual nature of visual awareness. *PLoS ONE*, *6*(6), e20910, <https://doi.org/10.1371/journal.pone.0020910>.
- Newsome, W. T., Wurtz, R. H., Dursteler, M. R., & Mikami, A. (1985). Deficits in visual motion processing following ibotenic acid lesions of the middle temporal visual area of the macaque monkey. *Journal of Neuroscience*, *5*(3), 825–840, <https://doi.org/10.1523/jneurosci.05-03-00825.1985>.
- Nishida, S. (1993). Spatiotemporal properties of motion perception for random-check contrast modulations. *Vision Research*, *33*(5–6), 633–645, [https://doi.org/10.1016/0042-6989\(93\)90184-X](https://doi.org/10.1016/0042-6989(93)90184-X).
- Nishida, S. (2011). Advancement of motion psychophysics: Review 2001–2010. *Journal of Vision*, *11*(5):11, 1–53, <https://doi.org/10.1167/11.5.11>.
- Nishida, S., Kawabe, T., Sawayama, M., & Fukiage, T. (2018). Motion perception: From detection to interpretation. *Annual Review of Vision Science*, *4*(1), 501–523, <https://doi.org/10.1146/annurev-vision-091517-034328>.
- Nishida, S., & Sato, T. (1995). Motion aftereffect with flickering test patterns reveals higher stages of motion processing. *Vision Research*, *35*(4), 477–490, [https://doi.org/10.1016/0042-6989\(94\)00144-B](https://doi.org/10.1016/0042-6989(94)00144-B).
- Olsen, A. (2012). The Tobii I-VT Fixation Filter: Algorithm description. *Tobii Technology*, Retrieved from <https://www.tobii.com/siteassets/tobii-pro/learn-and-support/analyze/how-do-we-classify-eye-movements/tobii-pro-i-vt-fixation-filter.pdf>.
- Pack, C. C., Hunter, J. N., & Born, R. T. (2005). Contrast dependence of suppressive influences in cortical area MT of alert macaque. *Journal of Neurophysiology*, *93*(3), 1809–1815, <https://doi.org/10.1152/jn.00629.2004>.
- Pantle, A. J., Gallogly, D. P., & Piehler, O. C. (2000). Direction biasing by brief apparent motion stimuli. *Vision Research*, *40*(15), 1979–1991, [https://doi.org/10.1016/S0042-6989\(00\)00071-7](https://doi.org/10.1016/S0042-6989(00)00071-7).
- Pantle, A., & Turano, K. (1992). Visual resolution of motion ambiguity with periodic luminance- and contrast-domain stimuli. *Vision Research*, *32*(11), 2093–2106, [https://doi.org/10.1016/0042-6989\(92\)90071-P](https://doi.org/10.1016/0042-6989(92)90071-P).
- Pavan, A., Campana, G., Guerreschi, M., Manassi, M., & Casco, C. (2009). Separate motion-detecting mechanisms for first- and second-order patterns revealed by rapid forms of visual motion priming and motion after effect. *Journal of Vision*, *9*(11):1, 1–16, <https://doi.org/10.1167/9.11.1>.
- Pavan, A., Campana, G., Maniglia, M., & Casco, C. (2010). The role of high-level visual areas in short- and longer-lasting forms of neural plasticity.

- Neuropsychologia*, 48(10), 3069–3079, <https://doi.org/10.1016/j.neuropsychologia.2010.06.018>.
- Pavan, A., & Skujevskis, M. (2013). The role of stationary and dynamic test patterns in rapid forms of motion after-effect. *Journal of Vision*, 13(1):10, 1–17, <https://doi.org/10.1167/13.1.10>.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10(4), 437–442, <https://doi.org/10.1163/156856897X00366>.
- Piehler, O. C., & Pantle, A. J. (2001). Direction-specific changes of sensitivity after brief apparent motion stimuli. *Vision Research*, 41(17), 2195–2205, [https://doi.org/10.1016/S0042-6989\(01\)00117-1](https://doi.org/10.1016/S0042-6989(01)00117-1).
- Pinkus, A., & Pantle, A. (1997). Probing visual motion signals with a priming paradigm. *Vision Research*, 37(5), 541–552, [https://doi.org/10.1016/S0042-6989\(96\)00162-9](https://doi.org/10.1016/S0042-6989(96)00162-9).
- Price, N. S. C., & Blum, J. (2014). Motion perception correlates with volitional but not reflexive eye movements. *Neuroscience*, 277, 435–445, <https://doi.org/10.1016/j.neuroscience.2014.07.028>.
- Priebe, N. J., & Lisberger, S. G. (2002). Constraints on the source of short-term motion adaptation in macaque area MT. II. Tuning of neural circuit mechanisms. *Journal of Neurophysiology*, 88(1), 370–382, <https://doi.org/10.1152/jn.2002.88.1.370>.
- Ramachandran, V. S., & Anstis, S. M. (1983). Extrapolation of motion path in human visual perception. *Vision Research*, 23(1), 83–85, [https://doi.org/10.1016/0042-6989\(83\)90044-5](https://doi.org/10.1016/0042-6989(83)90044-5).
- Raymond, J. E., O'Donnell, H. L., & Tipper, S. P. (1998). Priming reveals attentional modulation of human motion sensitivity. *Vision Research*, 38(19), 2863–2867, [https://doi.org/10.1016/S0042-6989\(98\)00145-X](https://doi.org/10.1016/S0042-6989(98)00145-X).
- Rohr, M., & Wagner, A. (2020). How monitor characteristics affect human perception in visual computer experiments: CRT vs. LCD monitors in millisecond precise timing research. *Scientific Reports*, 10(1), 1–10, <https://doi.org/10.1038/s41598-020-63853-4>.
- Salvucci, D. D., & Goldberg, J. H. (2000). Identifying fixations and saccades in eye-tracking protocols. *Proceedings of the Symposium on Eye Tracking Research & Applications - ETRA '00*, 10(3), 71–78. New York, New York, USA: ACM Press, <https://doi.org/10.1145/355017.355028>.
- Schütz, A. C., Braun, D. I., Kerzel, D., & Gegenfurtner, K. R. (2008). Improved visual sensitivity during smooth pursuit eye movements. *Nature Neuroscience*, 11(10), 1211–1216, <https://doi.org/10.1038/nn.2194>.
- Sheliga, B. M., Chen, K. J., FitzGibbon, E. J., & Miles, F. A. (2005). Initial ocular following in humans: A response to first-order motion energy. *Vision Research*, 45(25–26), 3307–3321, <https://doi.org/10.1016/j.visres.2005.03.011>.
- Sheliga, B. M., Chen, K. J., FitzGibbon, E. J., & Miles, F. A. (2006). The initial ocular following responses elicited by apparent-motion stimuli: Reversal by inter-stimulus intervals. *Vision Research*, 46(6–7), 979–992, <https://doi.org/10.1016/j.visres.2005.09.001>.
- Sheliga, B. M., FitzGibbon, E. J., & Miles, F. A. (2008). Spatial summation properties of the human ocular following response (OFR): Evidence for nonlinearities due to local and global inhibitory interactions. *Vision Research*, 48(17), 1758–1776, <https://doi.org/10.1016/j.visres.2008.05.017>.
- Sheliga, B. M., Quaia, C., FitzGibbon, E. J., & Cumming, B. G. (2021). Short-latency ocular following responses to motion stimuli are strongly affected by temporal modulations of the visual content during the initial fixation period. *Journal of Vision*, 21(5):8, 1–18, <https://doi.org/10.1167/jov.21.5.8>.
- Shioiri, S., & Cavanagh, P. (1990). ISI produces reverse apparent motion. *Vision Research*, 30(5), 757–768, [https://doi.org/10.1016/0042-6989\(90\)90101-P](https://doi.org/10.1016/0042-6989(90)90101-P).
- Simoncini, C., Perrinet, L. U., Montagnini, A., Mamassian, P., & Masson, G. S. (2012). More is not always better: Adaptive gain control explains dissociation between perception and action. *Nature Neuroscience*, 15(11), 1596–1603, <https://doi.org/10.1038/nn.3229>.
- Smith, A. T., Hess, R. F., & Baker, C. L. (1994). Direction identification thresholds for second-order motion in central and peripheral vision. *Journal of the Optical Society of America A*, 11(2), 506–514, <https://doi.org/10.1364/JOSAA.11.000506>.
- Solomon, J. A., & Sperling, G. (1994). Full-wave and half-wave rectification second-order motion perception. *Vision Research*, 34(17), 2239–2257, [https://doi.org/10.1016/0042-6989\(94\)90105-8](https://doi.org/10.1016/0042-6989(94)90105-8).
- Spering, M., & Carrasco, M. (2012). Similar effects of feature-based attention on motion perception and pursuit eye movements at different levels of awareness. *Journal of Neuroscience*, 32(22), 7594–7601, <https://doi.org/10.1523/JNEUROSCI.0355-12.2012>.
- Spering, M., & Carrasco, M. (2015). Acting without seeing: Eye movements reveal visual processing without awareness. *Trends in Neurosciences*, 38(4), 247–258, <https://doi.org/10.1016/j.tins.2015.02.002>.
- Spering, M., & Gegenfurtner, K. R. (2007). Contextual effects on smooth-pursuit eye movements.

- Journal of Neurophysiology*, 97(2), 1353–1367, <https://doi.org/10.1152/jn.01087.2006>.
- Spering, M., & Montagnini, A. (2011). Do we track what we see? Common versus independent processing for motion perception and smooth pursuit eye movements: A review. *Vision Research*, 51(8), 836–852, <https://doi.org/10.1016/j.visres.2010.10.017>.
- Spering, M., Pomplun, M., & Carrasco, M. (2011). Tracking without perceiving: A dissociation between eye movements and motion perception. *Psychological Science*, 22(2), 216–225, <https://doi.org/10.1177/0956797610394659>.
- Sperling, G. (1989). Three stages and two systems of visual processing. *Spatial Vision*, 4(2–3), 183–207, <https://doi.org/10.1163/156856889X00112>.
- Stock, J. H., & Watson, M. M., (2012). *Introduction to Econometrics* (3rd Ed.). Harlow, UK: Pearson Education.
- Stone, L. S., Beutter, B. R., & Lorenceau, J. (2000). Visual motion integration for perception and pursuit. *Perception*, 29(7), 771–787, <https://doi.org/10.1068/p2979>.
- Stone, L. S., & Krauzlis, R. J. (2003). Shared motion signals for human perceptual decisions and oculomotor actions. *Journal of Vision*, 3(11), 7, <https://doi.org/10.1167/3.11.7>.
- Tadin, D., & Lappin, J. S. (2005). Optimal size for perceiving motion decreases with contrast. *Vision Research*, 45(16), 2059–2064, <https://doi.org/10.1016/j.visres.2005.01.029>.
- Tadin, D., Lappin, J. S., Gilroy, L. A., & Blake, R. (2003). Perceptual consequences of centre-surround antagonism in visual motion processing. *Nature*, 424(6946), 312–315, <https://doi.org/10.1038/nature01800>.
- Tadin, D., Silvanto, J., Pascual-Leone, A., & Battelli, L. (2011). Improved motion perception and impaired spatial suppression following disruption of cortical area MT/V5. *Journal of Neuroscience*, 31(4), 1279–1283, <https://doi.org/10.1523/JNEUROSCI.4121-10.2011>.
- Takeuchi, T., & De Valois, K. K. (1997). Motion-reversal reveals two motion mechanisms functioning in scotopic vision. *Vision Research*, 37(6), 745–755, [https://doi.org/10.1016/S0042-6989\(96\)00207-6](https://doi.org/10.1016/S0042-6989(96)00207-6).
- Takeuchi, T., & De Valois, K. K. (2009). Visual motion mechanisms under low retinal illuminance revealed by motion reversal. *Vision Research*, 49(8), 801–809, <https://doi.org/10.1016/j.visres.2009.02.011>.
- Takeuchi, T., Tuladhar, A., & Yoshimoto, S. (2011). The effect of retinal illuminance on visual motion priming. *Vision Research*, 51(10), 1137–1145, <https://doi.org/10.1016/j.visres.2011.03.002>.
- Takeuchi, T., Yoshimoto, S., Shimada, Y., Kochiyama, T., & Kondo, H. M. (2017). Individual differences in visual motion perception and neurotransmitter concentrations in the human brain. *Philosophical Transactions of the Royal Society of London B*, 372, 20160111, <http://dx.doi.org/10.1098/rstb.2016.0111>.
- Tavassoli, A., & Ringach, D. L. (2010). When your eyes see more than you do. *Current Biology*, 20(3), 93–94, <https://doi.org/10.1016/j.cub.2009.11.048>.
- van der Steen, J., & Dits, J. (2012). Binocular eye movement control and motion perception: What is being tracked? *Investigative Ophthalmology and Visual Science*, 53(11), 7268–7275, <https://doi.org/10.1167/iovs.12-9809>.
- Watson, A. B., & Ahumada, A. J. (1985). Model of human visual-motion sensing. *Journal of the Optical Society of America A*, 2(2), 322–342, <https://doi.org/10.1364/JOSAA.2.000322>.
- Yoshimoto, S., & Takeuchi, T. (2013). Visual motion priming reveals why motion perception deteriorates during mesopic vision. *Journal of Vision*, 13(8):8, 1–21, <https://doi.org/10.1167/13.8.8>.
- Yoshimoto, S., Uchida-Ota, M., & Takeuchi, T. (2014). The reference frame of visual motion priming depends on underlying motion mechanisms. *Journal of Vision*, 14(1):10, 10–10, <https://doi.org/10.1167/14.1.10>.
- Zaksas, D., & Pasternak, T. (2005). Area MT neurons respond to visual motion distant from their receptive fields. *Journal of Neurophysiology*, 94(6), 4156–4167, <https://doi.org/10.1152/jn.00505.2005>.