Short Report

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Stationary Objects Flashed Periodically Appear to Move During Smooth Pursuit Eye Movement

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Abstract

We discovered that a white disc flashed twice at the same location appears to move during smooth pursuit eye tracking in the direction opposite to that of the eye movement. We called this novel phenomenon *movement-induced apparent motion* (MIAM). Using the method of constant stimuli, we measured the required displacement of the second appearance of the disc in the pursuit direction to null the effect during the closed-loop stage of smooth pursuit eye tracking. We observed a strong linear relationship between the points of subjective stationarity and the inter-stimuli intervals for four smooth pursuit eye movement speeds. The slopes and y-intercepts of these linear fits were well predicted by the hypothesis according to which subjects saw illusory motion from the first to the second retinal projections of the flashed disc during smooth pursuit eye movement, with no extra-retinal signal compensation.

Keywords

eye movements, motion, optic flow, perceptual organization, pursuit

When our eyes are still and two neighboring visible lights are flashed in rapid succession, we see movement when nothing is actually moving in the environment. This phenomenon is named beta or apparent motion; it was first thoroughly studied by Wertheimer in 1912. A similar situation occurs on the retina when an observer engages in smooth pursuit eye movement (SPEM) in front of a stationary light flashed periodically. In both cases, neighboring groups of retinal receptors are stimulated by light successively. Indeed, the two cases are indiscriminable *on the retina* if the following conditions are satisfied: (a) if the light is first flashed at the same retinal location in both cases, (b) if the period of the flashes is the same in both cases, and (c) if the displacement vector of the lights in the apparent motion case divided by the period of the flashes is equal to the SPEM velocity in the other case.

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As you would expect *qualitatively* from this retinal analysis, eye tracking the tip of a moving pencil or finger in front of Video 1 which displays stationary white discs flashed with periods increasing by steps of 16.67 ms from 0 ms, at the bottom, to 100 ms, at the top, results in the discs appearing to move in the direction opposite to that of the eyes. Importantly, *you need to pay attention to the flashing discs* while engaging in SPEM. As far as we know, this phenomenon—henceforth called *movement-induced apparent motion* (MIAM)—has never been reported in the literature. You might have noticed during this demonstration that the white discs align with one another. This indicates that the apparent disc displacement is *proportional* to the speed of SPEM times the period of the flashes. Again, this is compatible with the above retinal analysis which predicts that the apparent disc displacement should be *equal* to the speed of SPEM times the period of the flashes.

However, it is at odds with our ubiquitous experience that the *continuously illuminated* world around us is stable despite shifts of the images projected onto the retina during SPEM. Helmholtz (1925) suggested that this retinal displacement is cancelled by an 'effort of the will'. Sperry (1950) developed the idea and proposed that the retinal displacement is compared with the *corollary discharge* (also called *efference copy*; von Holst & Mittelstaedt, 1950)—a copy of the motor command that is sent to the muscles to produce an eye movement. Although our visual system comes close to this ideal, slight undercompensation can be revealed in the form of the perception of a tiny and usually non-disturbing movement of the stationary world opposite to eye movement. This illusionary motion of a *continuously illuminated* background induced by SPEM is referred to as the Filehne illusion (Filehne, 1920; Haarmeier, Thier, Repnow, & Petersen, 1997). Given the obvious similarities between MIAM and the Filehne illusion, it is tempting to argue that they are one and the same. However, the small undercompensation for retinal slip, which is believed to cause the Filehne illusion, should be identical for all the pulsating white discs in Video 1; therefore, the Filehne illusion cannot explain why the discs appear to move less and less from top to bottom. Moreover, the magnitude of the erroneous motion characterizing the Filehne illusion (e.g., that of the disc at the bottom of Video 1, which is presented continuously) is minuscule in comparison to that characterizing MIAM (e.g., that of the disc at the top, which is flashed with a period of 100 ms). Jumping the guns, we shall show in the following pages that MIAM is very well explained by the SPEM analog of apparent motion described earlier, *with no extra-retinal compensation* whatsoever.

Specifically, we will take a *quantitative* look at the atomic event in Video 1: two discs flashed during SPEM. Using the method of constant stimuli, we will find the displacement of the second disc in the pursuit direction required to null MIAM. We will do this for several inter-stimuli intervals (ISI) and SPEM speeds. Complete failure to compensate for the large retinal slip between the appearance of the two white discs would lead to a linear relationship between ISI and the nulling displacement with a slope equal to the tracking speed and a y-intercept equal to 0; and full compensation would lead to no nulling required at all.

Methods

Subjects

Six observers (three males) aged between 19 and 44 took part in the experiment. All participants had a normal or corrected-to-normal visual acuity. Written consent was obtained for all participants, and the study was approved by the Université de Montréal ethics committee.

Apparatus

The experimental programs were run on a MacPro computer in the Matlab environment, using the Psychophysics (Brainard, 1997; Pelli, 1997) and EyeLink toolboxes (Cornelissen, Peters, & Palmer, 2002). All stimuli were presented on an Asus VG278H at 60 Hz with a resolution of 1920 × 1080 pixels. Room lights were turned on so that natural background visual cues, such as the frame of the computer monitor, were available. A chin rest was used to maintain viewing distance at 66 cm. Eye movements were monitored at 250 Hz with an EyeLink II head-mounted eye-tracker (SR Research, Mississauga, Ontario). Only the dominant eye—as assessed by the Miles test (1930)—was tracked, but viewing was binocular.

Procedure

A nine-point calibration was performed with the eye-tracker at the beginning of each experimental session, and a drift-correction was performed every five trials. On each trial, a stationary red dot with a diameter of 6.50 arcmin was shown for 400 ms on a black background 0.95, 2.90, 3.87, or 9.69 deg to the left of the unmarked center of the computer monitor, depending on SPEM speed. Then the red dot began to move rightward at a constant speed of 1.95 deg/s (FG3, SFS3), 5.85 deg/s (FG2, SFS2, and WM), 7.80 deg/s (CAC, CBP, FG1, LN, and SFS1), or 19.50 deg/s (FG4 and SFS4). When the red dot reached the unmarked center of the computer monitor, it was superimposed on a centred white disc with a diameter of 0.43 deg presented for 16.67 ms. This was followed by an ISI which varied between 16.67 ms and 133.33 ms, depending on the experimental session. A second white disc, identical to the first one, was then presented for 16.67 ms with a horizontal offset relative to the center of the computer monitor +SPEM speed (deg/sec) × ISI (sec) of −0.22, −0.13, −0.04, 0.04, 0.13, or 0.22 deg (see Videos 2 and 3). Each subject completed one series of either four (for the 19.50 and 1.95 deg/s SPEM speeds) or seven (for the 7.80 and 5.85 deg/s SPEM speeds) experimental sessions of 120 trials. ISI varied between 16.67 ms and 133.33 ms in 33.33 ms steps for the series of four experimental sessions, and in 16.67 ms steps for the series of seven experimental sessions.

Subjects were asked to eye-track the red dot, to pay attention to the white disc, and to indicate the direction in which the white disc appeared to move using computer keyboard keys. Each participant completed about 10 practice trials before beginning the experimental sessions. Two subjects (FG5 and SFS5) did an additional experimental session with a SPEM speed of 19.50 deg/s and with an ISI of 133.33 ms, identical to the one described earlier, except that all white discs' positions were shifted 1 deg leftward.

Results

For every trials of a subject, gaze location traces were filtered with a second order low-pass Butterworth filter with a cutoff at 50 Hz (Lindner, Schwarz, & llg, 2001). Then instantaneous eye velocities were computed by deriving the filtered gaze locations, and instantaneous accelerations were computed by deriving these velocities. Saccades were defined as accelerations greater than 700 deg/s^2. Intervals of 60 ms centered on saccades were removed from the velocity traces and replaced by linearly interpolated velocities. Mean velocity traces after saccade removal for every subjects and SPEM speeds are shown in Figure 1. Finally, closed-loop SPEM gain was obtained by dividing the mean, across trials, of these velocities between 500 ms (which corresponds to the appearance of the first

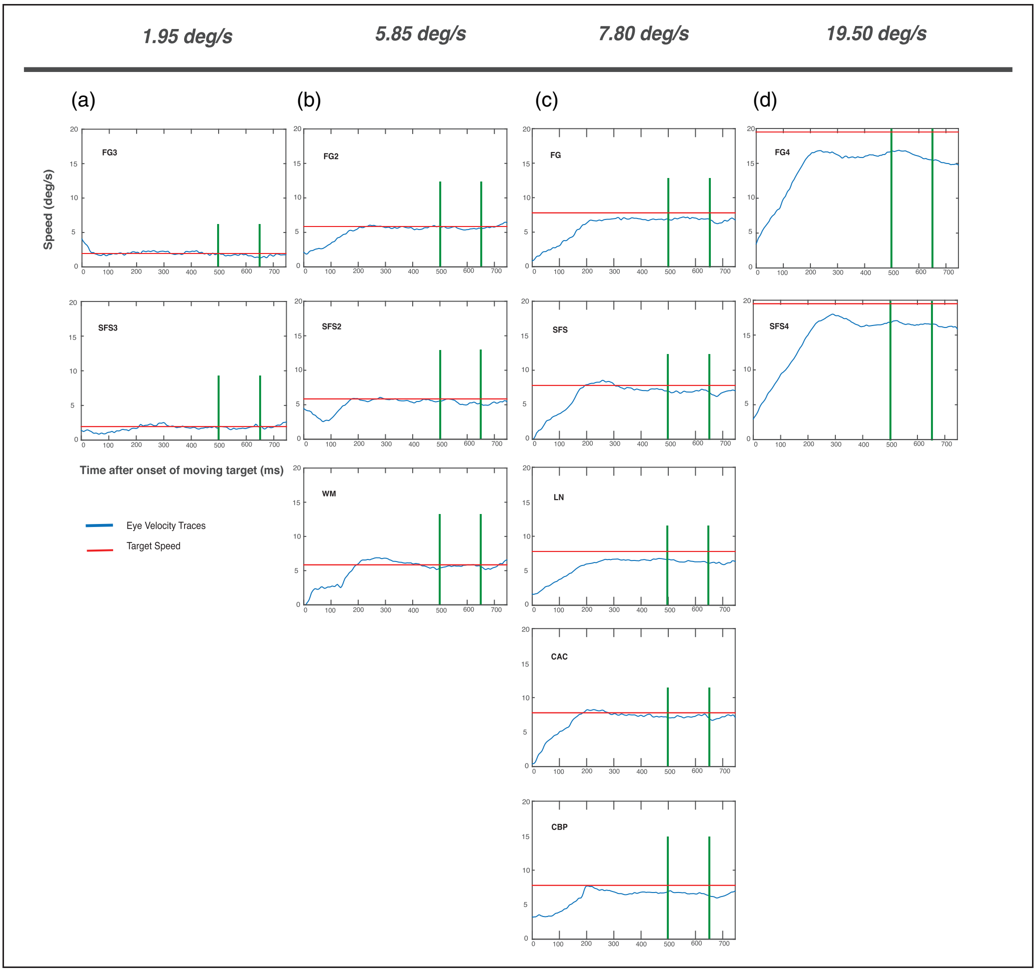

Figure 1. Blue curves represent the average individual filtered velocities as a function of time following onset of target motion after saccade removal. Red lines represent the speed of the moving targets. The green bars delimit the interval used to compute the gains (the first green bar coincides with the presentation of the first white disc).

white disc) and 650 ms after red dot motion onset by the red dot speed. Individual pursuit velocity gains are shown in Table 1.

The mean gain across subjects and SPEM speeds—0.89—indicates that pursuit quality was slightly under the ideal conditions. However, the most determinant factor for the hypothesis according to which subjects saw illusory motion from the first to the second retinal projections of the flashed disc during SPEM, with no extra-retinal signal compensation, is the mean horizontal displacement, including *saccades*, not pursuit velocity gain. We thus computed the mean horizontal eye displacement error relative to the red dot horizontal displacement between the two flashed white discs across trials for every subjects and SPEM speeds (Table 1). The mean of these errors was only 5.36%.

Table 1. Individual points of subjective stationarity (PSS) fitted parameters and other measures.

Subject	Red dot speed (deg/s)	Pursuit gain	Eye displacement error (%)	Linear fit slope (deg/s)	Linear fit y-intercept (deg)	R^2
SFS4	19.50	0.85	4.33	19.02	0.03	.99
FG4	–	0.83	3.22	19.19	0.02	.99
SFS5	–	0.80	0.49	–	–	–
FG5	–	0.78	6.48	–	–	–
CAC	7.80	0.89	6.79	7.31	0.05	.99
CBP	–	0.89	6.20	6.84	–0.02	.97
FG1	–	0.82	7.26	7.63	0.01	.99
LN	–	0.93	8.26	7.66	–0.03	.99
SFS1	–	0.86	8.94	7.73	–0.03	.99
FG2	5.85	0.96	6.27	5.64	0.01	.99
SFS2	–	0.92	3.45	5.82	–0.03	.99
WM	–	0.97	0.36	5.93	–0.02	.99
SFS3	1.95	0.86	0.72	2.04	–0.04	.99
FG3	–	0.93	6.00	1.75	0.00	.98

Then, for each subject, ISI, and horizontal offset, we computed the proportion of trials the subject responded that the white dot moved rightward. Next, we fitted cumulative Gaussian distributions to the six proportions—one for each of the horizontal offset—associated with each of the four or seven ISI (R^2 ranged from 0.87 to 1.00, with a mean of 0.99 and a standard deviation of 0.02), and extracted seven points of subjective stationarity (PSS). PSS are represented as black circles in Figure 2 (or as blue asterisks for the extra leftward-shifted sessions, Figure 2(d)).

Lines fitted very well to these PSS (Figure 2, black solid lines; Table 1, R^2), confirming the qualitative impression that the magnitude of MIAM is proportional to the ISI (or to the period in Video 1). Moreover, the slopes and y-intercepts of these linear fits were very close to those predicted by a SPEM analog of apparent motion, with no extra-retinal signal compensation whatsoever (Figure 2, solid red lines). The PSS of the two experimental sessions with a SPEM speed of 19.50 deg/s and an ISI of 133.33 ms—the one with the first white disc superimposed on the red dot and the other with the first white disc presented 1 deg to the left of the red dot (Figure 2(d))—are almost identical.

Discussion

We discovered that two identical white disc flashed at the same location appears to move during the closed-loop stage of SPEM in the direction opposite to that of the eye movement. We called this novel phenomenon *MIAM*. Using the method of constant stimuli, we measured the required displacement of the second disc in the pursuit direction to null the effect. We observed a strong linear relationship between the PSS and the ISI for a given SPEM speed in six subjects. The slopes and y-intercepts of these linear fits were well predicted by the hypothesis according to which subjects saw illusory motion from the first and second discs' retinal projections during SPEM, without extra-retinal signal compensation. This was the case for SPEM speeds between 1.95 and 19.50 deg/s, which indicates that MIAM is invariant to SPEM and apparent motion speed. This also suggests that SPEM and apparent motion share mechanisms in both slow and fast motion processes (see also Matsumiya & Shioiri, 2015). Finally, the PSS of the two experimental

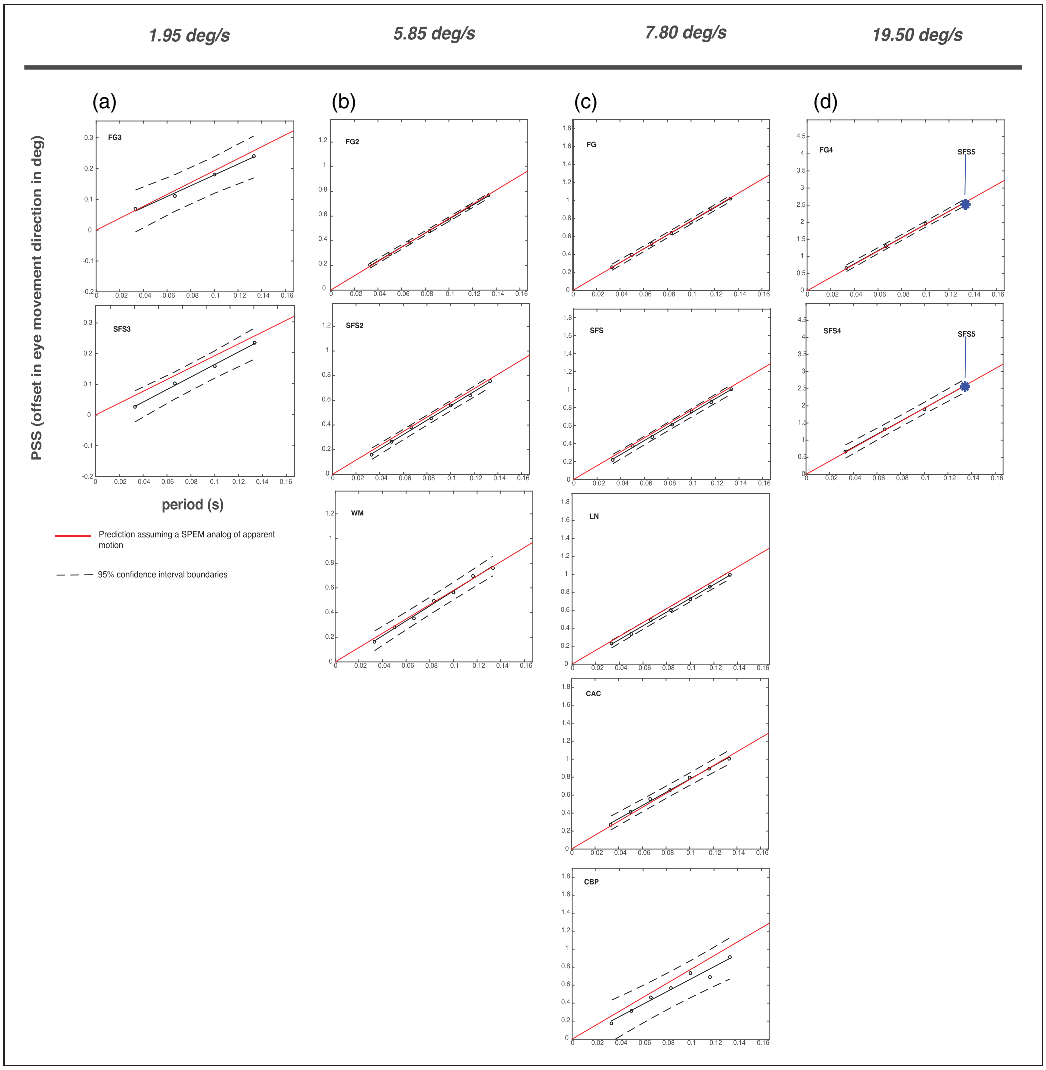

Figure 2. The magnitude of MIAM for every subject as a function of ISI and SPEM speed. Black circles represent points of subjective stationarity or PSS (i.e., the offsets of the second flashed white disc required to null MIAM); solid black lines are the best linear fit to these data points; dashed black lines indicate the boundaries of the 95% interval of confidence of the fitted lines; and the solid red lines is the prediction assuming a SPEM analog of apparent motion, with no extra-retinal signal compensation whatsoever. Blue asterisks in the scatterplots are the PSS for the sessions during which SPEM speed was 19.50 deg/s, ISI was 133.33 ms, and the first white disc was presented 1 deg to the left of the red dot.

sessions with a SPEM speed of 19.50 deg/s and an ISI of 133.33 ms—the one with the first white disc superimposed on the red dot and the other with the first white disc presented 1 deg to the left of the red dot (Figure 2(d))—are almost identical, suggesting that MIAM is invariant to retinal location at least within the fovea.

Several studies converged to show that the middle temporal area in the macaque and other primates and its human homolog, the human MT complex, respond to stimulus conditions that induce apparent motion (Goebel, Khorram-Sefat, Muckli, Hacker, & Singer, 1998; Liu, Slotnick, & Yantis, 2004; Mikami, 1991; Muckli et al., 2002). The brain locus of the compensation for the retinal slip resulting from SPEM seems to be distributed along the visual pathway. Neuroimaging studies in humans have failed to find any trace of a compensation for SPEM in area V1 up to area MT; the response in these visual areas seem to correlate with retinal motion signal, not with perceived motion (Haarmeier & their, 1998; Lindner, Haarmeier, Erb, Grodd, & Thier, 2006; Tikhonov, Haarmeier, Thier, Braun, & Lutzenberger, 2004; Trenner et al. 2008). However, there is evidence for SPEM compensation before area MT in the primate brain. Neurons encoding visual motion independently of SPEM—so-called real-motion cells—represent about 10% to 15% of the cells in areas V1 and V2 and about 40% of the cells in area V3A (Galletti & Fattori, 2003). Moreover, it was shown that about 8% of cells in area V1 exhibited percept related activity in the awake behaving monkey (Dicke, Chakraborty, & Thier, 2008). With this in mind, one parsimonious neural explanation for the failure to compensate for the SPEM analog of apparent motion under MIAM conditions is that the critical compensation occurs either before the computation of apparent motion in the visual processing stream (in area V1, V2, or V3), or in a parallel pathway. In other words, the small retinal slip resulting from the brief presentation of the first disc would be cancelled along striate and early extra-striate visual areas and so would the equally small retinal slip resulting from the brief presentation of the second disc but, most importantly, the much larger retinal slip resulting from the Gestalt grouping of the two discs in MT would not.

Haarmeier et al. (1997) described the unique case of a patient with relatively large bilateral extrastriate cortex lesions, which experiences false perception of motion due to a complete inability to take eye movements into account when faced with self-induced retinal image slip. Probably as a result of the conflict, this condition creates between the visual, vestibular, and somatosensory senses (Reason & Brand, 1975), this patient suffered from dizziness and nausea. What we have shown here is that for stroboscopically illuminated stationary objects such a complete incapacity of cancelling retinal displacement resulting from SPEM is the norm. We believe, therefore, that MIAM might play a role in *flicker sickness* in which observers report nausea and feeling dizzy when, for example, in a helicopter (Cushman & Floccare, 2007) or working with intermittently flashing lights (Ulett, 1953).

Declaration of Conflicting Interests

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Supplemental Material

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References

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436.

Cornelissen, F. W., Peters, E., & Palmer, J. (2002). The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments & Computers*, *34*, 613–617.
Cushman, J. T., & Floccare, D. J. (2007). Flicker illness: An underrecognized but preventable complication of helicopter transport. *Prehospital Emergency Care*, *11*, 85–88.
Dicke, P. W., Chakraborty, S., & Thier, P. (2008). Neuronal correlates of perceptual stability during eye movements. *European Journal of Neuroscience*, *27*, 991–1002.
Filehne, W. (1922). Uber das optische wahrnehmen von bewegungen [On the optical perception of movement]. *Zeitschrift fur Sinnephysiologie*, *53*, 134–145.
Galletti, C., & Fattori, P. (2003). Neuronal mechanisms for detection of motion in the field of view. *Neuropsychologia*, *41*, 1717–1727.
Goebel, R., Khorram-Sefat, D., Muckli, L., Hacker, H., & Singer, W. (1998). The constructive nature of vision: Direct evidence from functional magnetic resonance imaging studies of apparent motion and motion imagery. *European Journal of Neuroscience*, *10*, 1563–1573.
Haarmeier, T., Thier, P., Repnow, M., & Petersen, D. (1997). False perception of motion in a patient who cannot compensate for eye movements. *Nature*, *389*, 849–852.
Haarmeier, T., & Thier, P. (1998). An electrophysiological correlate of visual motion awareness in man. *Journal of Cognitive Neuroscience*, *10*, 464–471.
Helmholtz, H. V. (1867/1925). *Handbuch der physiologischen Optik* [Handbook of physiological optics]. New York, NY: Optical Society of America.
Liu, T., Slotnick, S. D., & Yantis, S. (2004). Human MT mediates perceptual filling-in during apparent motion. *NeuroImage*, *21*, 1772–1780.
Lindner, A., Schwarz, U., & Ilg, U. J. (2001). Cancellation of self-induced retinal image motion during smooth pursuit eye movements. *Vision Research*, *41*, 1685–1694.
Lindner, A., Haarmeier, T., Erb, M., Grodd, W., & Thier, P. (2006). Cerebrocerebellar circuits for the perceptual cancellation of eye-movement-induced retinal image motion. *Journal of Cognitive Neuroscience*, *18*, 1899–1912.
Matsumiya, K., & Shioiri, S. (2015). Smooth pursuit eye movements and motion perception share motion signals in slow and fast motion mechanisms. *Journal of Vision*, *15*, 12.1–15. DOI:10.1167/15.11.12.
Mikami, A. (1991). Direction selective neurons respond to short-range and long-range apparent motion stimuli in macaque visual area MT. *International Journal of Neuroscience*, *61*, 101–112.
Miles, W. R. (1930). Ocular dominance in human adults. *The Journal of General Psychology*, *3*, 412–430.
Muckli, L., Kriegeskorte, N., Lanfermann, H., Zanella, F. E., Singer, W., & Goebel, R. (2002). Apparent motion: Event-related functional magnetic resonance imaging of perceptual switches and states. *Journal of Neuroscience*, *22*, RC219.
Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442.
Reason, J. T., & Brand, J. J. (1975). *Motion sickness*. New York, NY: Academic Press.
Sperry, R. W. (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. *Journal of Comparative and Physiological Psychology*, *43*, 482.
Tikhonov, A., Haarmeier, T., Thier, P., Braun, C., & Lutzenberger, W. (2004). Neuromagnetic activity in medial parietooccipital cortex reflects the perception of visual motion during eye movements. *Neuroimage*, *21*, 593–600.
Trenner, M. U., Fahle, M., Fasold, O., Heekeren, H. R., Villringer, A., & Wenzel, R. (2008). Human cortical areas involved in sustaining perceptual stability during smooth pursuit eye movements. *Human Brain Mapping*, *29*, 300–311.
Ulett, G. A. (1953). Flicker sickness. *AMA Archives of Ophthalmology*, *50*, 685–687.
von Holst, E., & Mittelstaedt, H. (1950). Das Reafferenzprinzip: Wechselwirkungen zwischen Zentralnervensystem und Peripherie [The reafference principle: Interaction between the central and peripheral nervous system]. *Naturwissenschaften*, *37*, 464–476.
Wertheimer, M. (1912/2012). *Experimentelle studien über das sehen von bewegung* [Experimental studies on seeing motion]. In L. Spillmann (Ed.), *On perceived motion and figural organization* (pp. 1–91). Cambridge, MA: MIT Press.