Part XVI
Free Talk Session 9

ADAPTIVE FUNCTION OF COLOR VISION IN PRIMATES

Chihiro Hiramatsu
Department of Human Science, Faculty of Design, Kyushu University, 815-8540 Fukuoka, Japan

Trichromatic color vision in primates is unique among mammals whose color vision is normally dichromatic. The adaptive functions of color vision during the course of primate evolution have been debated for decades and are still under active discussion. The most popular hypothesis posits that detecting reddish fruits and/or young leaves from green foliage background is the primary function and driving force of the evolution of trichromacy. Another hypothesis argues that detecting social signals such as skin color changes is one of the important functions acquired by primates with trichromatic vision. Alternatively, some consider that functions of trichromacy might be more general and useful for various tasks. In this talk, I will review recent studies that investigated various functions of color vision in primates from the evolutionary viewpoint, with special emphasis on: 1) unique spectral tuning of primate trichromacy, and 2) polymorphic color vision in neotropical primates and humans.

PERCEPTUAL ORGANIZATION FROM VISUAL POSITIONS DISTORTED BY MOTION SIGNALS IN DRIFTING GABOR PATCHES

Hoko Nakada, Daisuke Hayashi, and Ikuya Murakami
Department of Psychology, The University of Tokyo, Tokyo, Japan

It is well known that visual motion processing has important roles in localizing objects, as demonstrated by robust illusions of positional distortion by visual motion. For example, De Valois & De Valois (1991) demonstrated that a stationary patch containing a drifting grating appears spatially shifted in the direction of motion. However, it is yet to be clarified how these local distortions in perceptual position might influence global perceptual organization. We arranged these drifting stimuli to form a shape with various configurations, and investigated whether the locally distorted positions influenced the global form solution. The experimental results indicated that spatially distorted perceptual interpretations of the local patches caused illusory formation of global shapes, perceptual grouping, and motion correspondence, and that the global perceptual organization was determined not only by local illusory positional shifts but also by the observer's perceptual set.

REDUCING BETWEEN-SUBJECT VARIATION IN MOTION-INDUCED BLINDNESS USING THE METHOD OF CONSTANT STIMULI

Amanda I. LeBel, Hanne K. Hansen, Nicholas C. Duggan, Alison Meurer, Emma G. DePierro, Stephen Z. Zhang, Andrew J. Kitt, & Wm Wren Stine*
Department of Psychology, University of New Hampshire, Durham, NH, USA
*<bill.stine@unh.edu>

Abstract

Motion-induced blindness (MIB) describes the disappearance of targets presented in the near periphery of the visual field when a moving mask is presented behind the targets. The targets typically vanish within ten seconds. Eye-movements refresh their appearance. Most studies of MIB have measured the total time of disappearance, asking subjects to press a button when the target is invisible and release the button when the target is visible. Empirically, very large individual differences in total disappearance time occur, which probably arise from differences in subjects' fixation abilities while targets transition from visible to invisible. We describe a procedure, akin to the method of constant stimuli, where subjects merely report at the end of a trial whether or not the targets vanished, with trial duration varying randomly across trials. The resulting psychometric functions show relatively little individual variation, and have proven sensitive to the manipulation of several independent variables.

Motion-induced blindness (MIB) describes the disappearance of static elements of a viewed stimulus, known as targets, in the presence of a moving array of elements, the mask. The phenomenon was noted by Breese (1899), where the target and the motion mask were presented to different eyes, and explored by Grindley and Townsend (1965; 1966), which they called movement masking. In the early 1990s, several authors explored perceptual filling-in (e.g., Anstis, 1989; Ramachandran and Gregory, 1991; Ramachandran, Gregory, and Aiken, 1993; and Spillmann and Kurtenbach, 1992, etc.), which seem to reflect the same mechanisms as MIB (Devyatko, Appelbaum, and Mitroff, 2017; Hsu, Yeh, and Kramer, 2004, 2006). Bonneh, Cooperman, and Sagi (2001) coined the term motion-induced blindness, presenting both the target and a coherently-moving mask binocularly.

Disappearance reflects both contrast adaptation (e.g., Troxler, 1804, fading) and neural inhibition (Bonneh, Donner, Cooperman, Heeger, and Sagi, 2014; Gorea and Caetta, 2009), with an upward shift in criterion (Caetta et al., 2007). Processing decreases in V4 while increasing in the intraparietal sulcus just prior to disappearance (Donner, Sagi, Bonneh, and Heeger, 2008), with the rate of disappearance related to V4 and the duration to V1 (Donner, Sagi, Bonneh, and Heeger, 2013). Single-pulse TMS of left posterior parietal cortex shortens disappearance time in phase with the disappearance cycle and lengthened duration out of phase, the right cortex yielding opposite effects (Funk and Pettigrew, 2003).

Random noise, motion, and then flickering masks are decreasingly effective (Spillmann and Kurtenbach, 1992; cf., Welchman and Harris, 2001). Disappearance increases with target and mask contrast, mask velocity, and mask density, and decreases with mask protection zone size, target size, and target rotational velocity, and aligned Gabor stimuli and close-proximity dot targets disappear together while orthogonal Gabor stimuli and

widely-separated dots disappear separately (Bonneh, et al., 2001). Decrement masks are more effective than increment masks with increment targets, and increment targets are easier to mask than decrement targets (Stine, Levesque, Lusignan, and Kitt, In press). Attention to the target increases disappearance (Grindley and Townsend, 1965, 1966; Schölvinck and Rees, 2009). The depth-plane of the mask and surface completion influence disappearance (Graf, Adams, and Lages, 2002). When a target in a grid disappears, the grid fills in the target's location (New and Scholl, 2008). Coherent motion is less effective than random motion masks during extended trials, perhaps due to motion adaptation (Wells, Sparrow, and Leber, 2011). Finally, color and texture may fade separately, and the direction of motion of a vanished target can be reported, implying separate mechanisms for color, texture, form, and motion (Ramachandran and Gregory, 1991). Clearly, both local and global processing are involved in MIB (e.g., Spillmann and Kurtenbach, 1992), as are early and late processing.

One issue that researchers confront while studying MIB are the large individual differences reflected in the dependent measures that are typically used (e.g., Graf et al., 2002; Figure 3; Spillmann & Kurtenbach, 1992, Figure 2 caption). Most often, experimenters ask subjects to indicate when a target is visible during a trial of constant duration by, for example, pressing a button when the target is not visible and releasing that button when the target becomes visible. From these data one often calculates total disappearance time (e.g., Bonneh et al., 2001; Bonneh Donner, Sagi, Fried, Cooperman, Heeger, and Arieli, 2010, Experiment 2; Bonneh et al., 2014; Devyatko, et al., 2017; Donner et al., 2008; Donner et al., 2013; Funk & Pettigrew, 2003; Gorea & Caetta, 2009; Graf et al., 2002; Grindley & Townsend, 1965; Hsu et al. 2006; New & Scholl, 2008; Schölvinck, & Rees, 2009, Experiment 2; Spillmann & Kurtenbach, 1992; Wells et al., 2011). Given that microsaccades modulate MIB (but do not account for MIB; Bonneh et al., 2010), vary with stimulus onsets (Valsecchi, Betta, and Turatto, 2007), and influence Troxler fading (Martinez-Conde, Macknik, and Troncoso, 2006), one might speculate that subjects vary in their ability to suppress eye movements when the target transitions. A few studies have asked subjects to simply indicate whether or not the stimulus vanishes (e.g., Grindley & Townsend, 1966; Ramachandran & Gregory, 1991; Ramachandran et al., 1993; Schölvinck, & Rees, 2009, Experiment 1; Welchman, & Harris, 2001). Building on this approach, we have used an adaptation of the method of constant stimuli (Hegelmaier, 1852; Laming and Laming, 1992; Stine et al., In press) in order to measure a psychometric function for target disappearance across trial duration. Briefly, the subject indicates whether or not one of the target stimuli disappears during an MIB stimulus interval randomly chosen from five possible values. Given the subject's task, eye movements after the first stimulus transition will have no influence on the subject's response.

Method

Our methods have been described in detail previously (Stine et al., In press). Presented are data from two female unpaid volunteers (AKS and HKH) who were naïve with respect to our hypotheses, had normal or corrected to normal visual acuity, and signed informed consent with debriefing consistent with University of New Hampshire (UNH) Institutional Review Board policy. Several other subjects have run through our protocol with similar results.

All stimuli were achromatic and presented on a uniform background of 108 cd/m^2. Target dot luminance (increment—200 cd/m^2 vs decrement—15 cd/m^2), mask dot lumi-

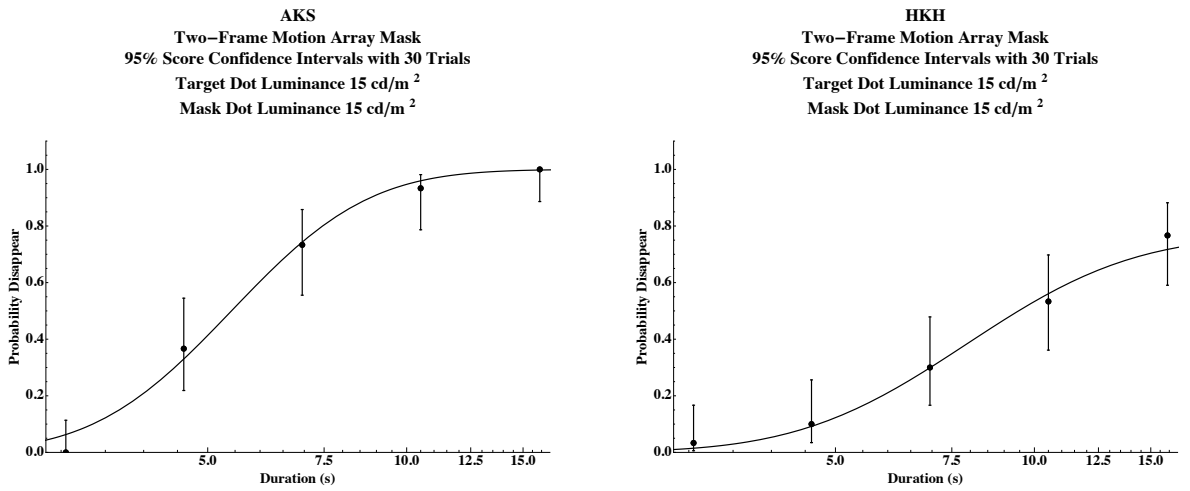

Fig. 1. Two psychometric functions with non-zero lapse rates (Klein, 2001) for decrement targets and masks and relative frequencies with 95% score confidence intervals (Agresti and Caffo, 2000; Agresti and Caffo, 1998; Wilson, 1927) as a function of trial duration on a log scale.

nance (increment—200 cd/m^2 vs decrement—15 cd/m^2), and trial duration (3.1 s, 4.6 s, 7.0 s, 11 s, or 16 s) were factorially combined, and a no-mask control condition (108 cd/m^2) for increment and decrement targets was added ($2 \times 2 \times 5 + 2 = 22$), to create 22 trial types presented in random order. Subjects indicated whether or not one of the target stimuli disappeared. Each session began with a 5 min adaptation to the uniform background and trials were separated by the background presentation for the previous trial's duration plus 2 s. Gaussian psychometric functions were fit as a function of trial duration on logarithmic coordinates (Klein, 2001). Relative frequencies were plotted with 95% score confidence intervals based on 30 trials (Agresti and Caffo, 2000; Agresti and Caffo, 1998; Wilson, 1927).

Results and Discussion

Using our analog to the method of constant stimuli, single psychometric functions from two subjects in the same condition show that the Gaussian cumulative distribution with a non-zero lapse rate approximates our data well (Figure 1). In particular, threshold trial durations for disappearance are well defined.

Across different combinations of increments and decrements, all of the functions fit the data well, with well-defined thresholds (Figure 2). Note that for two conditions, those without a mask (2 and 5 from top to bottom), there was little or no target disappearance. Decrement mask with an increment target yields the strongest effect (4), followed by a decrement mask with a decrement target and an increment mask with an increment target (1 & 6). An increment mask showed the weakest effect with a decrement target (3).

That decrements suppress increments maximally is consistent with the 'stronger' input of OFF cells relative to ON cells (Stine et al., In press). Evidence suggests that such increments and decrements are initially processed by ON and OFF ganglion cells (e.g., Dolan & Schiller, 1994; Schiller, 1992; Schiller, Sandell, and Maunsell, 1986), representing channels preserved through to cortex, and maintained as a distinction to higher levels of cortex (Dacey, 2004; Xing, Yeh, and Shapley, 2010). OFF processing provides faster

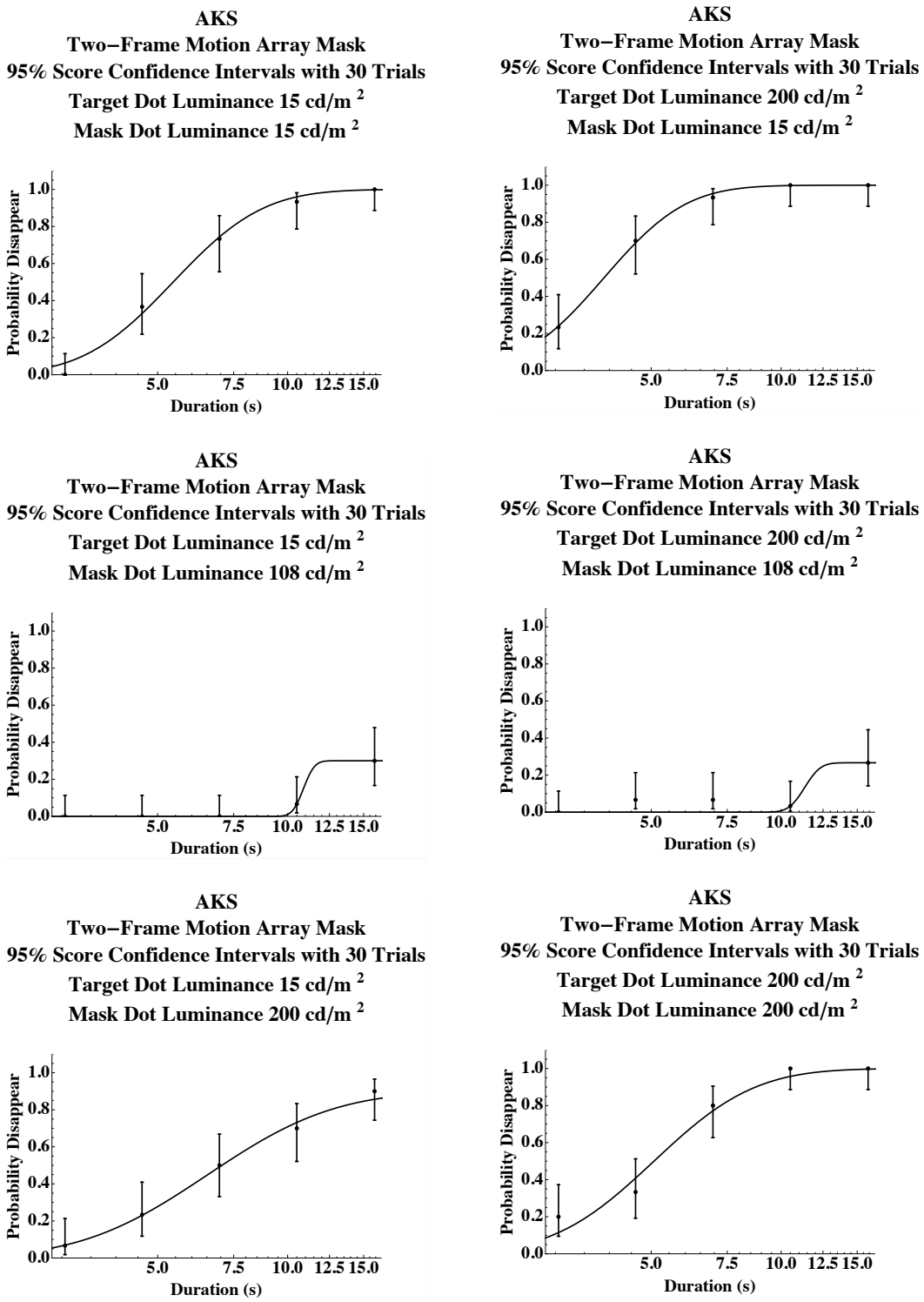

Fig. 2. From left-top to right-bottom are psychometric similar to those of Figure 1 for a single subject, AKS, across six conditions: 1—decrement target and mask, 2—decrement target and no mask, 3—decrement target and increment mask, 4—increment target and decrement mask, 5—increment target and no mask, 6—increment target and increment mask.

response times and lower thresholds than ON processing (e.g., Balasubramanian and Sterling, 2009; DeMarco, Hughes, and Purkiss, 2000; Jin, Wang, Lashgari, Swadlow, and Alonso, 2011; Komban, Alonso, and Zaidi, 2011; see Westheimer, 2007).

The result also highlights, probably at a relative high level of processing, the interdependence of OFF and ON cell inputs to higher cortex (e.g., toward V4 and the intraparietal sulcus). That decrements suppressing decrements and increments suppressing increments are roughly equivalent, and less effective than decrements suppressing increments, might suggest a relatively even balance between the role of target and mask with respect to increments and decrements. Finally, as one might expect, increments are least effective in masking decrements.

Our analogue to the method of constant stimuli would seem to provide an approach that yields robust results. Of course, it is well-known that such an approach is laborious. The degree to which the technique of presenting varying trial durations with the subject indicating simply whether or not a component of the stimulus disappeared during the trial could be applied to efficient non-parametric or parametric procedures (e.g., stochastic approximation, Robins and Monroe, 1951, or QUEST, Watson and Pelli, 1983) is an open, though interesting, question.

Using our constant-stimuli approach to measuring MIB enhances one's ability to observe the influence of subtle factors.

Acknowledgements

We gratefully acknowledged the UNH Undergraduate Research Office, Honors Program, and College of Liberal Arts.

References

Agresti, A., & Caffo, B. (2000). Simple and effective confidence intervals for proportions and differences of proportions result from adding two successes and two failures. *The American Statistician,* 54, 280-288.

Agresti, A., & Coull, B. A. (1998). Approximate is better than "exact" for interval estimation of binomial proportions. *The American Statistician,* 52, 119-126.

Anstis, S. (1989). Kinetic edges become displaced, segregated and invisible. In D. Man-Kit Lam, & C. D. Gilbert (ed.), *Neural mechanisms of visual perception* (pp. 247–260). Houston, TX: Gulf Publishing.

Balasubramanian, V., & Sterling, P. (2009). Receptive fields and functional architecture of the retina. *Journal of Physiology,* 12, 2753-2767.

Bonneh, Y. S., Cooperman, A., & Sagi, D. (2001). Motion-induced blindness in normal observers. *Nature,* 411, 797-801.

Bonneh Y. S., Donner, T.H., Cooperman, A., Heeger, D. J., Sagi, D. (2014). Motion-induced blindness and Troxler fading: Common and different mechanisms. *PLoS ONE,* 9, e92894. doi:10.1371/journal.pone.0092894

Bonneh, Y. S., Donner, T. H., Sagi, D., Fried, M., Cooperman, A., Heeger, D. J., & Arieli, A. (2010). Motion-induced blindness and microsaccades: Cause and effect. *Journal of Vision,* 10, 1–15. doi:10.1167/10.14.22.

Breese, B. B. (1899). On inhibition. *The Psychological Review: Series of Monograph Supplements,* 3, 1-65.

Caetta, F., Gorea, A., & Bonneh, Y. S. (2007). Sensory and decisional factors in motion-induced blindness. *Journal of Vision,* 7, 1–12.

Dacey, D. M. (2004). Origins of perception: Retinal ganglion cell diversity and the creation of parallel visual pathways. In M. S. Gazzaniga, (Ed.). *The cognitive neurosciences,* 3rd Ed. Cambridge, MA: MIT Press.

DeMarco, P. J., Hughes, A., & Purkiss, T. J. (2000). Increment and decrement detection on temporally modulated fields. *Vision Research,* 40, 1907-1919.

Devyatko, D., Appelbaum, L. G., & Mitroff, S. R. (2017). A common mechanism for perceptual reversals in motion-induced blindness, the Troxler effect, and perceptual filling-in. *Perception,* 46, 50-77.

Dolan, R. P. & Schiller, P. H. (1994). Effects of ON channel blockade with 2-amino-4-phosphonobutyrate (APB) on brightness and contrast perception in monkeys. *Visual Neuroscience,* 11, 23–32.

Donner, T. H., Sagi, D., Bonneh, Y. S., & Heeger, D. J. (2008). Opposite neural signatures of motion-induced blindness in human dorsal and ventral visual cortex. *The Journal of Neuroscience,* 28, 10298 –10310. doi:10.1523/JNEUROSCI.2371-08.2008

Donner, T. H., Sagi, D., Bonneh, Y. S., & Heeger, D. J. (2013). Retinotopic patterns of correlated fluctuations in visual cortex reflect the dynamics of spontaneous perceptual suppression. *The Journal of Neuroscience,* 33, 2188–2198. doi:10.1523/JNEUROSCI.3388-12.2013

Funk, A. P., & Pettigrew, J. D. (2003). Does interhemispheric competition mediate motion-induced blindness? A transcranial magnetic stimulation study. *Perception,* 32, 1325–1338.

Gorea, A., & Caetta, F. (2009). Adaptation and prolonged inhibition as a main cause of motion-induced blindness. *Journal of Vision,* 9, 1–17. doi:10.1167/9.6.16.

Graf, E. W., Adams, W. J., & Lages, M. (2002). Modulating motion induced blindness with depth ordering and surface completion. *Vision Research,* 42, 2731–2735.

Grindley, G. C., & Townsend, V. (1965). Binocular masking induced by a moving object, *Quarterly Journal of Experimental Psychology,* 17, 97-109. doi:10.1080/17470216508416418

Grindley, G. C., & Townsend, V. (1966). Further experiments on movement masking, *Quarterly Journal of Experimental Psychology,* 18, 319-326. doi:10.1080/14640746608400049

Hegelmaier, F. (1852). Ueber das Gedächtniss für Linearanschauungen. [On memory for the length of a line.] *Archiv für physiologische Heilkunde,* 11, 844-853.

Hsu, L. C., Yeh, S. L., & Kramer, P. (2004). Linking motion-induced blindness to perceptual filling-in. *Vision Research,* 44, 2857–2866. doi:10.1016/j.visres.2003.10.029

Hsu, L. C., Yeh, S. L., & Kramer, P. (2006). A common mechanism for perceptual filling-in and motion-induced blindness. *Vision Research* 46, 1973–1981. doi:10.1016/j.visres.2005.11.004

Jin, J., Wang, Y., Lashgari, R., Swadlow, H. A., & Alonso, J.-M. (2011). Faster thalamocortical processing for dark than light visual targets. *The Journal of Neuroscience,* 31, 17471-17479.

Klein, S. A. (2001). Measuring, estimating, and understanding the psychometric function: A commentary. *Perception & Psychophysics,* 63, 1421-1455.

Komban, S. J., Alonso, J.-M., & Zaidi, Q. (2011). Darks are processed faster than lights.

The Journal of Neuroscience, 31, 8654-8658.

Laming, D., & Laming, J. (1992). F. Hegelmaier: On memory for the length of a line. *Psychological Research,* 54, 233-239. doi:10.1007/BF01358261

Martinez-Conde, S., Macknik, S. L., Troncoso, X. G., & Dyar, T. A. (2006). Microsaccades counteract visual fading during fixation. *Neuron,* 49, 297–305. doi:10.1016/j.neuron.2005.11.033

New, J. J., & Scholl, B. J. (2008). "Perceptual scotomas": A functional account of motion-induced blindness. *Psychological Science,* 19, 653–659.

Ramachandran, V. S., & Gregory, R. L. (1991). Perceptual filling in of artificial scotomas in human vision. *Nature,* 350, 699-702.

Ramachandran, V. S., Gregory, R. L., & Aiken, W. (1993). Perceptual fading of visual texture borders. *Vision Research,* 33, 717-721.

Robbins, H., & Monro, S., (1951). A stochastic approximation method. *Annals of Mathematical Statistics,* 22, 400-407.

Schiller, P. H. (1992). The ON and OFF channels of the visual system. *Trends in Neurosciences,* 15, 86-92.

Schiller, P. H., Sandell, J. H., & Maunsell, J. H. R. (1986). Functions of the ON and OFF channels of the visual system. *Nature,* 322, 824-825.

Schölvinck, M. L., & Rees, G. (2009). Attentional influences on the dynamics of motion-induced blindness. *Journal of Vision,* 9, 1–38. doi:10.1167/9.1.38.

Spillmann, L., & Kurtenbach, A. (1992). Dynamic noise backgrounds facilitate target fading. *Vision Research,* 32, 1941-1946.

Stine, W. W., Levesque, P. A., Lusignan, M. E., & Kitt, A. J. (In press). Motion induced blindness using increments and decrements of luminance. *Proceedings of the Latvian Academy of Sciences. Section B. Natural, Exact, and Applied Sciences.*

Troxler, D. (1804). Über das Verschwinden gegebener Gegenstände innerhalb unseres Gesichtskreises [On the disappearance of given objects from our visual field]. In Himly, K. & Schmidt, A. (Eds), *Ophthalmologic Bibliothek,* Vol. 2, (pp. 431-573). Jena: Springer.

Valsecchi, M., Betta, E., & Turatto, M. (2007). Visual oddballs induce prolonged microsaccadic inhibition. *Experimental Brain Research,* 177, 196–208.

Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception & Psychophysics,* 33, 113-120.

Welchman, A. E., & Harris, J. M. (2001). Filling-in the details on perceptual fading. *Vision Research,* 41, 2107–2117.

Wells, E. T., Leber, A. B., & Sparrow, J. E. (2011). The role of mask coherence in motion-induced blindness. *Perception,* 40, 1503-1518.

Wilson, E. B. (1927). Probable inference, the law of succession, and statistical inference. *Journal of the American Statistical Association,* 22, 209-212.

Xing, D., Yeh, C.-I. & Shapley, R. M. (2010). Generation of black-dominant responses in V1 cortex. *Journal of Neuroscience,* 30, 13504-13512.