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Illusory motion reversal is caused by rivalry, not by perceptual snapshots of the visual field

Keith Kline [a], Alex O. Holcombe [b], David M. Eagleman [a,c,d,*]

[a] Department of Neurobiology and Anatomy, Houston Medical School, University of Texas, 6431 Fannin St., Suite 7046, Houston, TX 77030, USA
[b] School of Psychology, Cardiff University, P.O. Box 901, Cardiff, UK
[c] Department of Psychology, University of Texas, Austin, USA
[d] Department of Biomedical Engineering, University of Texas, Austin, USA

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Abstract

In stroboscopic conditions—such as motion pictures—rotating objects may appear to rotate in the reverse direction due to under-sampling (aliasing). A seemingly similar phenomenon occurs in constant sunlight, which has been taken as evidence that the visual system processes discrete "snapshots" of the outside world. But if snapshots are indeed taken of the visual field, then when a rotating drum appears to transiently reverse direction, its mirror image should always appeared to reverse direction simultaneously. Contrary to this hypothesis, we found that when observers watched a rotating drum and its mirror image, almost all illusory motion reversals occurred for only one image at a time. This result indicates that the motion reversal illusion cannot be explained by snapshots of the visual field. The same result is found when the two images are presented within one visual hemifield, further ruling out the possibility that discrete sampling of the visual field occurs separately in each hemisphere. The frequency distribution of illusory reversal durations approximates a gamma distribution, suggesting perceptual rivalry as a better explanation for illusory motion reversal. After adaptation of motion detectors coding for the correct direction, the activity of motion-sensitive neurons coding for motion in the reverse direction may intermittently become dominant and drive the perception of motion.

Keywords: Perception; Illusion; Motion; Discrete processing; Snapshot hypothesis

1. Introduction

Does visual perception involve discrete or continuous analysis of the outside world? This question has old roots in the literature (Baer, 1864; James, 1890), and it enjoyed renewed popularity with the advent of cinematography—an obvious technological metaphor. To explain why asynchronous stimuli sometimes appear to be synchronous, a number of investigators in the 1900s proposed that conscious perception arises through the analysis of a series of "perceptual moments" (Allport, 1968; Efron, 1970; Stroud, 1948; VanRullen & Koch, 2003). More recently, the subject of discrete processing has fallen from favor, in part because a substantial fraction of the literature on this topic, although provocative, is not definitive.

One piece of evidence cited in support of discrete processing (Crick & Koch, 2003; Koch, 2004; McComas & Cupido, 1999; VanRullen & Koch, 2003) is a study by Purves, Paydarfar, and Andrews (1996) entitled 'The wagon wheel illusion in movies and reality', in which it was reported that under constant light, both a spinning wheel with spokes and a translating periodic pattern of dots occasionally appeared to reverse direction. An

* Corresponding author. Address: Department of Neurobiology and Anatomy, Houston Medical School, University of Texas, 6431 Fannin St., Suite 7046, Houston, TX 77030, USA. Tel.: +1 7135005709; fax: +1 7135000612.
E-mail address: david.eagleman@uth.tmc.edu (D.M. Eagleman).

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analogy was suggested to the wagon wheel effect in movies, in which—due to the discrete snapshots of the camera—the wheel can appear to be moving in the reverse direction. Purves et al.'s intriguing suggestion was that the continuous light demonstration supported a quantization of perception—for example, in 100 ms batches. They wrote, "The occurrence of this perception in the absence of intermittent illumination suggests that we normally see motion, as in movies, by processing a series of visual episodes." Crick and Koch concur, citing Purves et al.'s findings as an indication of "irregular batch-like effects in vision." However, we suggest that the relationship between the illusion reported by Purves et al. and the cinematographic wagon-wheel effect is only superficial, and the two effects represent vastly different aspects of visual perception. Therefore, in this manuscript we will refer to the reversal effect under continuous light simply as *illusory motion reversal* (IMR).

If, as Purves et al. (1996) and other suggest, perception is based on discrete samples, like frames in a movie, then the perception of a spinning wheel under continuous light should match the basic properties that define the cinematographic wagon wheel effect. Yet Purves et al. observe significant differences between the cinematographic wagon wheel effect and the effect in continuous light. They acknowledge that under continuous illumination: (a) at a fixed speed of rotation, the perception of reversed motion does not occur stably, but instead occurs transiently and for only a small fraction of the viewing period, (b) the wheel never appears to come to a stop, (c) when the wheel appears to reverse, it appears to rotate at a faster speed than when moving in the forward direction, and (d) the illusory appearance of extra spokes occurs by the progressive addition of elements, in contrast to the multiplication of the actual number of spokes, as perceived in stroboscopic conditions. We have verified points (a)–(c) in our own experiments (below), although the perceived speed of reversed rotation was often slower than that of orthograde rotation. Observations (a)–(d) are sufficient to rule out discrete perception as the explanation for the effect. A proponent of the snapshot hypothesis might explain observations (a) and perhaps (b) by suggesting that the snapshot interval need not be constant, but observations (c) and (d) cannot be explained in this way. Further, observation (c)—the perceived increase in speed during illusory motion reversal—speaks against the snapshot hypothesis, which predicts that the reversed speed should always be slower. The perceived speed of reversed rotation during the wagon wheel effect in movies cannot exceed the wheel's actual speed of forward rotation. We will discuss other differences between IMR and the wagon wheel illusion below.

We now offer an alternative explanation for illusory motion reversal under constant sunlight. Most models of motion detection (Adelson & Bergen, 1985; van Santen & Sperling, 1985) appeal to the activity of motion detectors with properties similar to those of Reichardt detectors (Reichardt, 1961). Briefly, the detector responds to sequential changes in luminance at two points in the visual field (Fig. 1a). Such detectors are subject to error when presented with moving periodic patterns of the kind used by Purves et al. In particular, it is possible for the detector tuned to motion in one direction to be stimulated by motion in the opposite direction. Consider Fig. 1a, in which the two dots moving to the *left* stimulate the *rightward* motion detector. This spurious activation of the detector for the wrong direction of motion, sometimes called temporal aliasing, happens because S1 occupies the receptive field on the left and, soon after, S2 moves into the receptive field on the right. The detector has no way of knowing that S1 and S2 are different stimuli, and the pattern of excitation is identical to a single stimulus moving to the right. Thus, in the absence of any additional filtering mechanisms (such as those added by van Santen & Sperling (1985)), a detector signaling rightward motion may be excited by leftward motion of a periodic pattern.

Schouten (1967) had previously described instances of illusory motion reversal using a full radial grating stimulus instead of a horizontally rotating drum. Consistent with our interpretation, Schouten appealed to the fact that Reichardt detectors are vulnerable to temporal aliasing. Schouten, however, did not address the observation that the percept of reversed motion is sporadic, nor did he examine the durations of IMRs. The data presented below demonstrate similarities between perceptual rivalry and illusory motion reversal, and we therefore propose that the stimulated detectors for the reverse-direction are in a rivalrous relationship with the more highly stimulated forward-motion detectors, yielding the occasional experience of reversed motion. Motion opponency can be demonstrated by the motion aftereffect (Eagleman, 2001; Wade & Verstraten, 1998), in which a static pattern appears to slowly move in the opposite direction to the previously viewed moving stimulus. The motion aftereffect likely results from the adaptation of orthograde motion detectors; afterward, when viewing a static stimulus, the spontaneous activity of retrograde motion detectors exceeds that of the adapted motion detectors, thereby driving the percept.

In models of motion perception (e.g. van Santen & Sperling, 1985), the rightward Reichardt detector depicted in Fig. 1a is combined with a leftward detector, and the perceived direction of motion is determined by a subtraction stage in which the activity of the two detectors is compared. In our proposal, (1) prolonged viewing of leftward motion causes adaptation in the leftward-motion detector, and (2) the rightward-motion detector is spuriously stimulated by temporal aliasing. Due to rivalry between the opposite detectors—probably fueled by mutual inhibition—the rightward motion

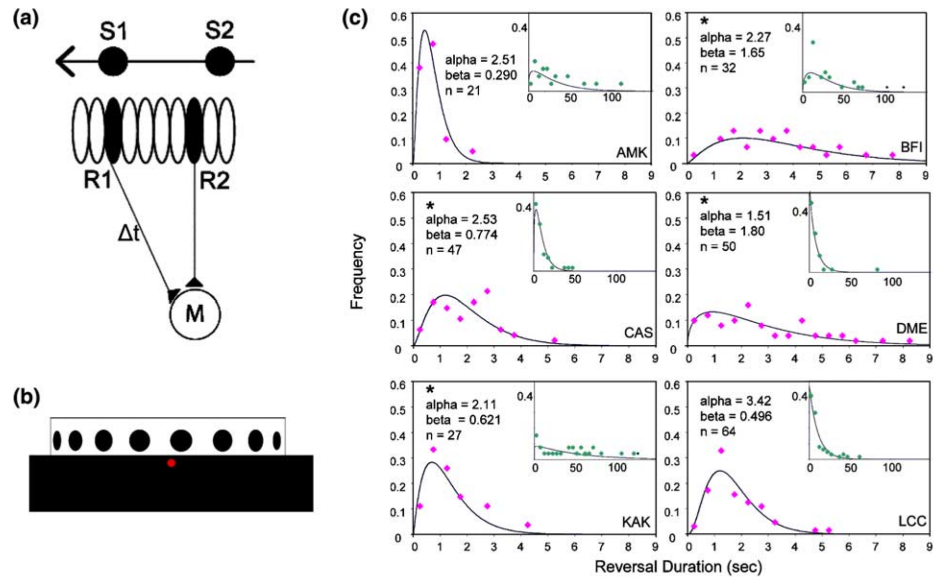

Fig. 1. The motion reversal illusion. (a) The Reichardt motion detector (M) receives input from photoreceptors R1 and R2, which respond to luminance change. Because there is a longer delay from R1 to M than from R2 to M, the detector will respond to an object moving to the right. However, a periodic stimulus moving to the left can spuriously excite the detector if S1 excites R1 shortly before S2 excites R2. This error is sometimes called temporal aliasing. (b) Schematic of stimulus. A rotating drum was presented under natural sunlight in a room next to large windows, with all artificial lights turned off. Sixteen dots were affixed to a drum of 148 mm diameter. Dots passed fixation at 8.5 Hz. Eye position was monitored with an Arrington research video-based eye tracker. (c) Observers held down a key for the duration that they perceived movement in the retrograde direction. Data from most subjects were consistent with a gamma distribution (asterisks indicate significant fit; Kolmogorov–Smirnov $p > 0.05$), typical for phenomena of perceptual ambiguity. Best fit parameters for the gamma distribution are shown. Bin width=500 ms. Distributions of the durations of orthograde perceptions are inset for each subject.

detector will intermittently be able to drive perception. We will refer to this model as the *rivalry hypothesis* of IMR. Note that we view this phenomenon as a relative of the motion aftereffect: here the effect of the adaptation is to influence the perception not of a static pattern, but rather the original moving pattern itself.

2. Experiment 1: Illusory reversal of a rotating drum

To distinguish our rivalry hypothesis from the snapshot hypothesis of Purves et al., we had six observers fixate a small laser light positioned 1° below a rotating white drum viewed from the side under sunlight. Evenly spaced around the side of the drum were 16 black dots (Fig. 1b, each dot subtended 0.82° visual angle, the drum was 14.8 cm in diameter and subtended 13° from the viewing distance of 63 cm). The drum rotated at 0.53 rps, and dots passed the point of fixation at 8.5 Hz. Observers pressed a key each time they observed illusory motion reversal, and held it down for the duration of the perception of reversed motion. Head movements were minimized by the use of a chin rest, and eye position was tracked.

For most subjects, the distributions of IMR durations were well fit by a gamma distribution (Fig. 1c; see raw data in Table 1). A gamma distribution typifies the dynamics of multistable perception as reported in binocular rivalry (Lehky, 1988; Leopold & Logothetis, 1999; Levelt, 1965) and with ambiguous figures like the Necker cube or shapes defined by ambiguous shading (Taylor & Aldridge, 1974). We confirmed a good fit to the gamma distribution in 4 of 6 subjects ($p > 0.05$, Kolmogorov–Smirnov test), but 2 fits deviated

Table 1
Data from individual subjects for Experiment I. Median and mode of IMR durations, viewing time before first IMR was perceived, cumulative duration of IMR expressed as percentage of total viewing time, best fit gamma distribution parameters α and β

Observer	Median (s)	Mode (s)	Time to first reversal (s)	Cumulative reversal time (%)	α	β
AMK	0.620	0.750	67	2.4	2.51	0.290
BFI	3.220	1.250	104	11	2.27	1.65
CAS	2.012	0.250	16	17	2.53	0.774
DME	2.269	0.250	496	10	1.51	1.80
KAK	1.292	0.250	128	2.5	2.11	0.621
LCC	1.405	1.250	13	14	3.42	0.496

somewhat ($p < 0.05$; Fig. 1c). The distributions of durations of orthograde motion perception fit a gamma distribution in 3 of 6 subjects ($p > 0.05$; Kolmogorov–Smirnov test; Fig. 1c insets). The shape of the gamma distribution can be understood as expressing two tendencies of multistable percepts: first, the tendency to change states at random which yields an exponential distribution ($e^{-\lambda x}$) and second, the tendency to stay at the current state, perhaps due to inertia or a refractory period (x^{r-1}, ascending part of the curve). In the present case, the proposed rivalry is not equiprobable, as in the Necker cube, but is instead heavily biased toward perceiving motion in the orthograde direction. In the current study, we estimate an average $91 \pm 6\%$ probability of perceiving orthograde motion—in other words, IMR was seen an average of 9% of the total viewing time (see Table 1).

Interestingly, the amount of viewing time before the illusion was first seen was quite variable for the different observers (see Table 1). This highlights yet another difference between IMR and the wagon wheel illusion in movies: in the latter, there is no period of prior fixation required for the perception of reversed motion.

In summary, the temporal pattern of motion reversals is distributed in a way characteristic of rivalry. The snapshot hypothesis, in contrast, has no reason to predict a gamma distribution. Further, if the sampling rate were constant, the snapshot hypothesis should predict continuous perception of the reverse direction. The sporadic nature of the illusion would require a rapidly changing sampling rate.

For one subject, there seemed to be increased eye movements after the offset of IMR. Otherwise, we found little relationship between eye movements and the onset or offset of IMR (data not shown). Also, some observers reported supernumerary dots, although we did not explore the manner (multiplicative vs. additive) in which these extra dots appeared.

3. Experiment 2: Measuring illusory reversal of two (mirrored) drums

The distributions of reversal durations observed in experiment 1 support the possibility of rivalry as an explanation for IMR, but by themselves they do not rule out the snapshot hypothesis. To directly address the snapshot hypothesis, we introduced a mirror to create a second image of the rotating drum (Fig. 2a). The snapshot hypothesis predicts that *both drums will appear to reverse simultaneously*, since discrete sampling of the visual field should interact identically with the two drums.

Five observers fixated a laser dot situated halfway between the two rotating images (viewing distance 63 cm;

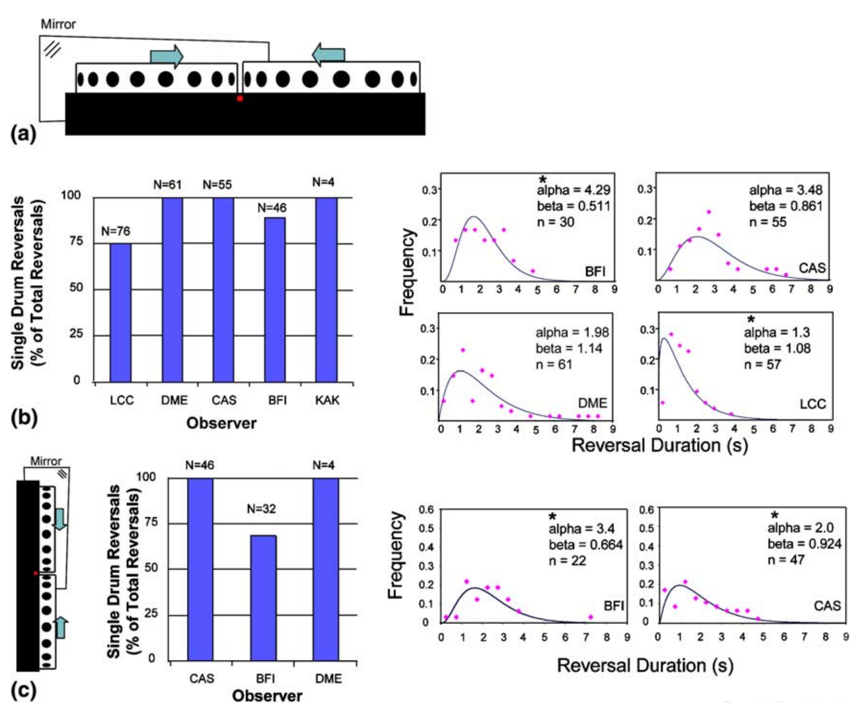

Fig. 2. The motion reversal illusion with two identical drums. (a) All stimulus parameters were identical to Fig. 1, with the addition of a mirror which provided the visual image of a second rotating drum. (b) Data from mirror experiment. Percentage of reversals in which observers reported one and only one drum reversing. Best fit parameters for the gamma distribution are inset. Distribution for 1 of the 5 subjects not shown due to insufficient number of data points. (c) Data from experiment in which the drum and its mirror image were positioned in same visual field. Percentage of reversals in which observers reported one and only one drum reversing. Distribution for 1 of the 3 subjects not shown due to insufficient number of data points.

the drum and its mirror image were separated by ~1° visual angle). Observers held down one of three keys for the duration of observed illusory reversal: one key for perceived reversal of the actual drum, another for reversal of the mirror image, and a third for when both stimuli were perceived to move in the reverse direction.

Durations of perceived motion reversal were well fit by a gamma distribution for 2 of 4 observers (Fig. 2a). For the fifth observer, an insufficient number of data points were collected for the goodness-of-fit analysis. Most importantly, observers almost never saw both drums in IMR simultaneously (Fig. 2b). Instead, one drum appeared to transiently reverse direction while the other continued to rotate in the orthograde direction.

For one participant, we computed the probability that reversals would have occurred in both images simultaneously by chance, assuming they were independent events, by multiplying (sum of reversal durations/total time) for one image by (sum of reversal durations/total time) for the other image. This yielded a probability of 0.003 for observer LCC. Since this number is smaller than the actual amount of simultaneous reversal reported by the subject (25% of all illusory episodes occurred in both images simultaneously), this could hint at cooperativity between the perceptions of the two drums; however, there is insufficient data to draw a firm conclusion. Observers BFI and KAK saw single-drum reversals in only the mirror image. Data representing the stimulus in which IMR was perceived was not recorded for observers DME and CAS, although they verbally reported having seen solitary reversals of each stimulus.

We note that the mirror image was slightly smaller because of the angle of the mirror (<2% difference); however, the frequency of stimulus presentation remained identical. Purves et al. report that the temporal frequency of the stimuli, rather than linear velocity or stimulus size, was the major determinant of perceived motion reversal. In the framework of the snapshot hypothesis, slight differences in stimulus size are irrelevant, and equal frequencies of stimulus presentations should cause illusory motion reversal in both images simultaneously.

4. Experiment 3: Two drums in the same visual hemifield

The above results challenge the hypothesis that the global visual scene is processed in discrete snapshots. However, since the two rotating drums appeared in different halves of the visual field, the independence of the two drums could be theoretically accommodated by the snapshot theory if the two hemispheres sampled the visual scene independently. To address this possibility, we replicated the experiment with both drums presented in the same visual field by orienting the stimulus vertically, 1° to the right of fixation (Fig. 2c). As in the previous experiment, illusory reversals of one drum were usually perceived independently of reversals of the other drum (Fig. 2c), indicating that hemisphere-specific clocking also cannot explain IMR. Assuming IMR occurs independently in the two images, for observers BFI and CAS there was a 6.4×10^{-4} and 1.0×10^{-4} probability, respectively, that IMR would have occurred in both images simultaneously by chance. The fact that observer BFI perceived reversals simultaneously 34% of the time indicates that for observer BFI, the reversals did not occur independently. However, even for observer BFI the incidence of simultaneous reversals fell far short of the 100% figure predicted by the snapshot hypothesis.

5. Discussion

In summary, our results replicate previous findings of illusory motion reversal under constant illumination (Purves et al., 1996; Schouten, 1967), show that the illusion is compatible with patterns of perceptual rivalry (Fig. 1c), and rule out global or hemispheric snapshots of the visual field as an explanation for the effect (Fig. 2). Our data do not necessarily rule out object-based snapshots. However, the IMR observed in this study and others (Purves et al., 1996; Schouten, 1967) is considerably different from the wagon wheel illusion seen in movies in numerous ways (reviewed in the Introduction), which leaves discrete sampling theories dubious. Instead of perceptual snapshots, competition between opponent motion detectors—leading to perceptual rivalry—is perhaps the most parsimonious explanation for IMR. Consistent with a "winner-take-all" system of competing neural populations, prolonged viewing of a rotating drum yields alternating percepts of veridical motion or reverse motion. The approximate gamma distribution of reversal durations supports our hypothesis of rivaling opponent motion systems, since the durations of percepts fit the gamma distribution in studies of rivalry using stimuli that yield both equiprobable (e.g. face/vase, Necker cube) and non-equiprobable perceptual interpretations (Levelt, 1965; Murata, Matsui, Miyauchi, Kakita, & Yanagida, 2003).

A failure to see illusory motion reversals in continuous illumination was recently reported by Pakarian and Yasamy (2003), who asked observers to view a periodic rotating stimulus in both stroboscopic and continuous illumination. As emphasized above, the percepts elicited under these two conditions are quite different, and an expectation that the continuous illusion would be similar to the stroboscopic may have misled Pakarian and Yasamy into viewing the stimulus too briefly to experience the illusion. The stroboscopic wagon wheel effect is perceived immediately upon viewing an appropriate stimulus, whereas IMR requires variable periods of observation (between 13 s and 8 min for our subjects, see Table 1), during which adaptation is proposed to occur prior to the illusion's first occurrence. However, in accord with Pakarian and Yasamy, one of our observers failed to see any illusory motion reversals. Another subject who did see reversals in the single drum condition did not see reversals in the second experimental condition with two rotating images. The reason for some subjects' inability to see IMR, and the variability of the initial observation time required for those who do see it, is unknown.

Most recent arguments for quantized perception have relied on the findings of Purves et al. (1996) as well as Varela, Toro, John, and Schwartz (1981), who reported that the phase of cortical alpha rhythms determined whether subjects perceived two sequential dots as one or two separate stimuli (Varela et al., 1981). However, Varela later softened his claims about this finding (Gho & Varela, 1988), and more recent attempts to replicate the Varela et al. (1981) result have failed (Eagleman, unpublished data; VanRullen & Koch, 2003). Other psychological evidence (Arnold & Johnston, 2003; Burle & Bonnet, 1997; Geissler, Schebera, & Kompass, 1999; Treisman, Faulkner, Naish, & Brogan, 1990) is consistent with local temporal oscillations in visual processing, but does not at all imply that visual processing occurs in discrete snapshots. Thus, while quantized perception cannot be ruled out, there currently exists little meaningful evidence in support of it.

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References

Adelson, E. H., & Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. *Journal of Optical Society of America A, 2*(2), 284–299.

Allport, D. A. (1968). Phenomenal simultaneity and the perceptual moment hypothesis. *British Journal of Psychology, 59*, 395–406.

Arnold, D. H., & Johnston, A. (2003). Motion-induced spatial conflict. *Nature, 425*(6954), 181–184.

Baer, K. V. V. (1864). Welche Auffassung der lebendigen Naturist die richtige? Und wie ist diese Auffassung auf die Entomologie anzuwenden? (Which view of living nature is correct? And how is this view to be applied to entomology?) In H. Schmitzdorf (Ed.), *St. Petersburg: Verlag der Kaiserlichen Hofbuchhandlung* (pp. 237–83).

Burle, B., & Bonnet, M. (1997). Further argument for the existence of a pacemaker in the human information processing system. *Acta Psychology (Amst), 97*(2), 129–143.

Crick, F. H. C., & Koch, C. (2003). A framework for consciousness. *Nature Neuroscience, 6*(2), 119–126.

Eagleman, D. M. (2001). Visual illusions and neurobiology. *Nature Reviews Neuroscience, 2*, 920–926.

Efron, R. (1970). The minimum duration of a perception. *Neurophysiologia, 8*, 57–63.

Geissler, H. G., Schebera, F. U., & Kompass, R. (1999). Ultra-precise quantal timing: evidence from simultaneity thresholds in long-range apparent movement. *Perception and Psychophysics, 61*(4), 707–726.

Gho, M., & Varela, F. J. (1988). A quantitative assessment of the dependency of the visual temporal frame upon the cortical rhythm. *Journal of Physiology (Paris), 83*(2), 95–101.

James, W. (1890). *The principles of psychology*. Dover.

Koch, C. (2004). *The quest for consciousness: a neurobiological approach*. Englewood, CO: Roberts and Co.

Lehky, S. R. (1988). An astable multivibrator model of binocular rivalry. *Perception, 17*(2), 215–228.

Leopold, D. A., & Logothetis, N. K. (1999). Multistable phenomena: changing views in perception. *Trends in Cognition Science, 3*(7), 254–264.

Levelt, W. J. M. (1965). *On binocular rivalry*. Assen, The Netherlands: Royal VanGorcum.

McComas, A. J., & Cupido, C. M. (1999). The RULER model. Is this how the somatosensory cortex works? *Clinical Neurophysiology, 110*(11), 1987–1994.

Murata, T., Matsui, N., Miyauchi, S., Kakita, Y., & Yanagida, T. (2003). Discrete stochastic process underlying perceptual rivalry. *Neuroreport, 14*(10), 1347–1352.

Pakarian, P., & Yasamy, M. T. (2003). Wagon-wheel illusion under steady illumination: real or illusory? *Perception, 32*(11), 1307–1310.

Purves, D., Paydarfar, J. A., & Andrews, T. J. (1996). The wagon wheel illusion in movies and reality. *Proceedings of National Academy of Sciences USA, 93*(8), 3693–3697.

Reichardt, W. (1961). On optical resolving ability of the facet eye of Limulus. *Kybernetik, 1*, 57–69.

Schouten, J. F. (1967). Subjective stroboscopy and a model of visual movement detectors. In I. Wathen-Dunn (Ed.), *Models for the perception of speech and visual form* (pp. 44–45). Cambridge Mass: MIT Press.

Stroud, J. M. (1948). The moment function hypothesis. MA. Thesis, Stanford University.

Taylor, M. M., & Aldridge, K. D. (1974). Stochastic processes in reversing figure perception. *Perception and Psychophysics, 16*, 9–27.

Treisman, M., Faulkner, A., Naish, P. L., & Brogan, D. (1990). The internal clock: evidence for a temporal oscillator underlying time perception with some estimates of its characteristic frequency. *Perception, 19*(6), 705–743.

van Santen, J., & Sperling, G. (1985). Elaborated Reichardt detectors. *Journal of the Optical Society of America A, 2*(2), 300–321.

VanRullen, R., & Koch, C. (2003). Is perception discrete or continuous? *Trends in Cognition Science, 7*(5), 207–213.

Varela, F. J., Toro, A., John, E. R., & Schwartz, E. L. (1981). Perceptual framing and cortical alpha rhythm. *Neuropsychologia, 19*(5), 675–686.

Wade, N. J., & Verstraten, F. A. J. (1998). The motion aftereffect: introduction and historical overview. In G. Mather, F. Verstraten, & S. Anstis (Eds.), *The motion aftereffect: a modern perspective* (pp. 1–23).