Available online at www.sciencedirect.com

SCIENCE DIRECT®

Neuroscience Letters 375 (2005) 23–27

Neuroscience Letters

www.elsevier.com/locate/neulet

Illusory percepts of moving patterns due to discrete temporal sampling

William A. Simpson[a,b,c,*], Uma Shahani[d], Velitchko Manahilov[d]

[a] Simulation and Modelling Section, DRDC Toronto, 1133 Sheppard Avenue West, P.O. Box 2000, Toronto, Ont., Canada M3M 3B9
[b] Centre for Vision Research, York University, 4700 Keele Street, Toronto, Ont., Canada M3J 1P3
[c] Department of Life Sciences, University of Toronto at Scarborough College, 1265 Military Trail, Toronto, Ont., Canada MIC 1A4
[d] Department of Vision Sciences, Glasgow Caledonian University, Cowcaddens Road, Glasgow G40BA, UK

Received 4 June 2004; received in revised form 10 September 2004; accepted 22 October 2004

Abstract

Continuously, moving objects under continuous illumination can be seen to move in a direction opposite to their actual motion. This illusory reversed motion can be explained as due to discrete temporal sampling of the moving stimulus by the visual system. If temporal sampling lies behind the illusory motion, then the probability of illusory motion should depend on the temporal frequency of the motion stimulus. By presenting contracting bull's-eye gratings of various spatial frequencies we were able to tease apart the drift speed and temporal frequency. The prevalence of illusory percepts depended on the temporal frequency, not the speed. The data suggest that the human visual system samples the incoming stimulation at a rate near 16 Hz.

Keywords: Visual motion perception; Motion illusions

Illusions are powerful tools for elucidating the neural mechanisms that underlie visual perception. The "wagon wheel illusion" [10] is the apparent backwards rotation of a wheel that is in fact rotating forwards. When this illusion is seen at the movies, it is due to temporal undersampling: the pictures in the movie sequence were taken too far apart in time and thus do not faithfully represent the actual wheel motion. However, this undersampling account does not explain why the wagon wheel illusion can occur outside the cinema when viewing continuously rotating objects such as fan blades and propellers under steady (DC) illumination.

Purves et al. [18] have suggested that illusory backwards motion with continuous stimuli is due to a form of temporal undersampling that occurs in the visual system. According to this idea the visual system processes information as a series of discrete episodes rather than as a continuous temporal flow [3,7,22,23]. We will label this the "strobe-in-head" theory. (The label is used for simplicity and is not meant to be taken too literally—for example, we do not assume an invariant strobe rate.) As is shown in the space–time diagram of Fig. 1a, if the internal strobe rate is adequate, the correct motion will be seen. If the strobe rate is too low, nonveridical percepts such as flicker (Fig. 1b) or reversed motion (Fig. 1b and c) will be seen.

Previous studies of illusory reversed motion have used moving dots as stimuli [18,25]. Such stimuli are not very suitable for assessing the strobe-in-head theory because their spectra contain energy at many temporal frequencies. Moreover, Purves's dots moved on the surface of a three-dimensional cylinder [18] and thus the speeds varied sinusoidally with horizontal position. The linear speeds of the visual elements on a rotating wheel [25] also vary with eccentricity. By using a contracting bull's-eye grating (Fig. 1d) we can present a moving stimulus that contains only one speed throughout. Spectrally, the contracting bull's-eye grating is very simple, which allows us to examine speed and temporal

---

[*] Corresponding author. Tel.: +1 416 635 2000x3142; fax: +1 416 635 2013.
E-mail address: william.simpson@drdc-rddc.gc.ca (W.A. Simpson).

0304-3940/$ – see front matter. Crown Copyright © 2004 Published by Elsevier Ireland Ltd. All rights reserved.
doi:10.1016/j.neulet.2004.10.059

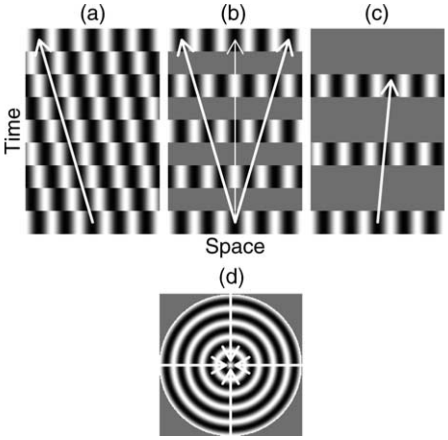

Fig. 1. Space–time diagrams of a drifting grating and a snapshot of the stimulus used: (a) if the visual system samples the moving stimulus at an adequate rate, the veridical motion shown by the arrow will be seen, (b and c) if the sampling rate is too low, flicker (thin vertical arrow) or reversed motion (arrow tilted right) will be seen, (d) in the experiments observers viewed a bull's-eye contracting sinewave grating that spontaneously altered its appearance between contraction, flicker, and expansion.

frequency as competing explanatory factors [21] in illusory reversed motion.

At the outset of these experiments we thought the strobe-in-head theory to be implausible. We thought it more likely that the reversed motion was due to a form of interference between the travelling waves set up by the stimulus on its retinotopic projection in V1 [9] and the complex, nonlinear travelling waves of activity that are also triggered by visual stimulation [12,16,17,20]. According to the "brain wave" theory, the interference between these two types of travelling waves will produce a net response that may have components that travel in the opposite direction to the stimulus, yielding illusory percepts such as reversed motion or flicker (counterphase flicker is mathematically the outcome when sinewaves moving in opposite directions are superimposed). If the brain wave theory is correct, the illusory percepts will occur at a fixed drift speed. The speed of the exogenous linear cortical travelling wave response depends on the speed of the stimulus; at some speed it will interfere maximally with the endogenous complex travelling wave, producing illusory percepts.

We measured the proportion of the time that observers saw illusory motion as we presented moving patterns whose spatial frequency and temporal frequency were independently varied [21]. When a set of fuzzy bars in a sine wave grating drifts past a given point on the screen, it produces flicker at a certain temporal frequency. The temporal frequency (Hz) is the product of the spatial frequency (c/degree) and the drift speed (degree/s). We measured the prevalence of illusory percepts as a function of drift speed. If the strobe-in-head theory is correct, illusory percepts should occur at a fixed temporal frequency and hence at a speed that varies according to the spatial frequency. When the stimulus temporal frequency is low enough, the strobe-in-head is fast enough to adequately sample the motion, and the veridical motion will be seen. At higher stimulus temporal frequencies, undersampling by the strobe-in-head will yield illusory percepts. On the other hand, if the prevalence of illusory percepts depends on the speed rather than the temporal frequency, we will have provided support for the brain wave theory.

The stimuli were generated using custom C software under MSDOS and displayed on an Iiyama VisionMaster monitor with short persistence phosphor. The stimulus was a contracting bull's-eye sinewave grating (Fig. 1d). Unlike a rotating pattern, the contracting bull's-eye has the same linear speed at all eccentricities. At the two viewing distances the display subtended visual angles of 15° and 7.5°. The refresh rate of the monitor was 120 Hz. The grey levels were linearized using an electronic RGB mixing method [15]. The mean luminance of the display was 30 cd/m^2; the grating contrast was 50%. The stimulus motion was presented as a computer animated movie sequence displayed at 120 Hz using a palette manipulation technique. This motion was not continuous; however, the displacement between successive frames was always less than 1/4 of the spatial period of the grating. The classical wagon wheel illusion occurs when the displacement of a spoke between frames is greater than 1/2 the spatial period.

The displays were viewed from a chin-and-forehead rest placed at 81 and 162 cm from the monitor. The subjects viewed the various stimulus spatial frequencies and temporal frequencies (drift speeds) in random order. The speeds used for each spatial frequency were selected on the basis of pilot experiments where the speed was increased in small increments from a level where the correct contracting motion was almost always seen to a speed where reversed motion frequently occurred. Each stimulus was viewed for 180 s while maintaining fixation on a small spot at the centre of the display. During a typical trial, the percept kept changing as the subjects viewed the display; the subjects pressed one of three mouse buttons to indicate whether they saw contraction, expansion, or flicker. The proportion of time that the subject saw each of the three percepts was computed. We report the mean values across five subjects since all subjects' data showed the same pattern.

Observers were presented with animation sequences of a contracting bull's-eye grating (Fig. 1d). The animation was not continuous but, critically, the grating never jumped more than 1/4 of the spatial period in successive frames (as shown in Fig. 1a). Thus, such nonveridical percepts as reversed motion or flicker should have never been seen with our displays. Nonetheless, the contracting bull's-eye grating spontaneously changed its appearance at random times during a trial. The percentage of the viewing time that observers saw the contracting grating as expanding or flickering is plotted as a function of the grating drift speed in the top panel of Fig. 2. The nonveridical percepts occur more often as the drift speed increases. If the drift speed were the important parameter, the curves for the different spatial frequencies would coincide. However, the curves progressively shift to higher speeds as the spatial frequency declines. The bottom panel of Fig. 2

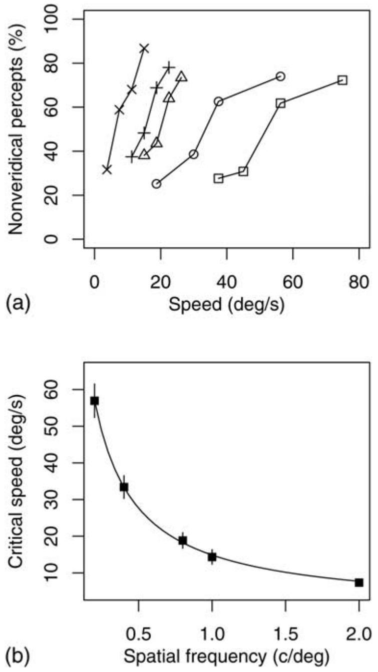

Fig. 2. The prevalence of nonveridical percepts (reversed motion or flicker) depends on the temporal frequency: (a) the percentage of the time that flicker or reversed motion was seen (averaged across five observers) as a function of the drift speed for spatial frequencies of 0.2 c/degree (square), 0.4 c/degree (circle), 0.8 c/degree (triangle), 1.0 c/degree (+), or 2.0 c/degree (×). The psychometric functions shift to the left as the spatial frequency increases. (b) The critical speed (50% point of the functions in (a)) declines as the spatial frequency increases. The averages and standard errors across five observers are shown. The fitted curve shows that nonveridical percepts occur at a fixed temporal frequency of 16 Hz.

shows the critical speed (50% point) of the curves plotted as a function of the spatial frequency. According to the strobe-in-head theory, the critical speed is actually a fixed temporal frequency. Fig. 2b shows the least squares fit of the curve

$$C = \frac{F_{\mathrm{t}}}{(F_{\mathrm{s}} + a)} \tag{1}$$

where C is the critical speed, F_{t} is the temporal frequency of the strobe-in-head, F_{s} is the spatial frequency of the stimulus, and a is a parameter that allows the internal representation of the spatial frequency to be different from the stimulus. This curve describes the data well with a fitted internal strobe frequency (with standard error across five subjects) of 16 ± 1.5 Hz. The pattern of results shown in Fig. 2 is consistent with the strobe-in-head theory.

Our results indicate that the sampling rate used in processing motion is about 16 Hz. This figure is in line with other evidence. Ansbacher [3] concluded that the internal strobe rate was 18 Hz, based on apparent shrinkage of a continuously rotating arc. Sunfish, when surrounded by a striped drum moving at a temporal frequency below 10 Hz, will spin like the hand on a clock to track the drum movement [26]. At around 15 Hz the swimming changes in a way consistent with their seeing ambiguous motion in the same region where humans see it. Above 20 Hz the fish begin rotating backwards, indicating that they see reversed motion. The fish results are very similar to those reported here and indicate an internal strobe rate of 15–20 Hz. Schouten [19] reports that percepts of the correct motion, flicker and reversed motion coexist at a speed of 10 Hz. Finally, we suggest that cinema films may achieve their realism by using a frame rate—24 Hz—close to the native sampling rate used by the visual system (note that cinema superimposes additional whole field flicker onto the display). Other evidence supporting the notion of discrete visual sampling is reviewed by Van Rullen and Koch [23]. The rate of visual sampling must be greater than 8 Hz because kittens raised under 8 Hz strobe lights have profound motion processing deficits [8]. Before leaving the topic of the internal strobe rate, it is important to note that the measure used here depends on the subject's criterion, and that not only the subject's criterion but also the underlying internal strobe rate may vary over time (just as do other discrete physiological processes such as spike rate, heart rate or blink rate).

Although the results are consistent with the strobe-in-head theory, other explanations are possible. Let us now consider in turn three control experiments that allowed us to rule out competing explanations.

Some experimenters have found reversed motion perception for drifting linear gratings placed in the visual periphery [1,11,6]. The direction reversal was explained as being due to spatial undersampling by the retinal receptor mosaic. In order to rule out this explanation, we repeated our experiment using a smaller visual field. In the first experiment the stimulus subtended the central 15° and thus intruded upon the peripheral retinal region where spatial undersampling is purported to occur (although see [4]). In the control experiment the stimulus subtended the central 7.5°; the outer edges were thus at an eccentricity of 3.25°.

As can be seen in Fig. 3, the pattern of results is the same as before. This time the estimated strobe-in-head rate is 18 ± 1.3 Hz. We conclude that retinal spatial aliasing is not the source of the nonveridical percepts observed for the contracting bull's-eye stimulus.

Purves et al. [18] used a motor to produce continuous motion that was viewed under continuous illumination. In order to show that illusory flicker and reversal percepts are not due to artifacts arising from our computer animation [14], we measured the critical speed using radial sine wave gratings (like spokes on a wheel) spun by a motor and viewed under daylight. The wheel initially rotated at a slow speed and the subject adjusted the speed gradually upwards until it reached the critical speed where reversed motion was first seen. The radial gratings were 6° in diameter, with a uniform grey region in the central 1.25°. The central grey region had a luminance equal to the mean luminance of 70 cd/m^2; the contrast of the gratings was 81%.

Fig. 4 shows the average results for three subjects. All subjects saw illusory reversed motion with the continuously rotating radial gratings viewed under diffuse daylight. As found with the computer animated displays, the critical speed declines as the spatial frequency increases. Eq. (1) again gives

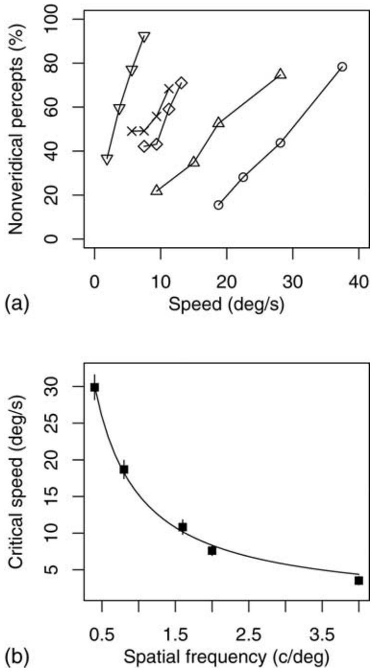

Fig. 3. Results from a control experiment using a small display show that nonveridical reversed motion and flicker percepts are not due to spatial sampling by the retinal mosaic. (a) The proportion of nonveridical percepts (averaged across five observers) as a function of the drift speed for spatial frequencies of 0.4 c/degree (circle), 0.8 c/degree (triangle), 1.6 c/degree (diamond), 2.0 c/degree (×), and 4.0 c/degree (inverted triangle). (b) The critical speed declines as the spatial frequency increases. The fitted curve shows that nonveridical percepts occur at a fixed temporal frequency of 18 Hz.

a good fit to the data, indicating that reversed motion is seen at a fixed temporal frequency. The estimated frequency of the strobe-in-head is 6.1 ± 0.6 Hz. It is difficult to compare this frequency to the frequencies measured in the previous experiments. In the previous experiments, the internal strobe frequency was estimated by fitting a curve to the critical speed defined as the 50% point of the psychometric functions measuring the total time that nonverdical percepts were seen during continuous viewing. In the present experiment, the critical speed was defined as the speed at which the subject first saw reversed motion. The difference in estimated internal strobe frequency can be explained by the differences in methods. It is very likely that the speed at which reversed motion was first seen corresponds to some point on the psychometric function that is lower than 50%. In any case, the important point is that the data are well described by Eq. (1). This supports the notion of discrete temporal sampling by the visual system.

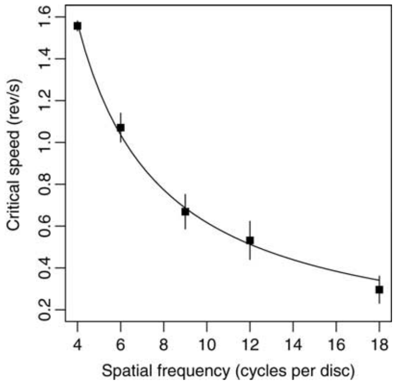

Fig. 4. The critical speed at which nonveridical percepts were first seen as a function of spatial frequency in an experiment using radial gratings spun by a motor and viewed under daylight. The averages and standard errors across three observers are shown. The curve is a least squares fit of Eq. (1).

Since all observers readily observed reversed motion with the continuously rotating radial gratings viewed under daylight, it is clear that artifacts arising from computer animation cannot be the cause of the nonveridical percepts measured in the main experiment.

It is possible that the illusory flicker and reversed motion are somehow due to eye movements. To test this idea, we ran a variation of the main experiment where the subject made saccades throughout a trial between two fixation marks separated by 3.2°. The subject made saccades back and forth at a comfortable rate (2 Hz) in time to a metronome.

When subjects fixated, nonveridical percepts occurred in random alternation with the correct percept of contracting motion. The mean number of nonveridical percepts in a run (based on four runs) was 33.25 and 22.5 for the two subjects, respectively. Making saccades abolished nonveridical percepts (mean 0.0 and 1.0, respectively, $p < 2\text{E}{-}16$ using Poisson generalized linear model).

It is clear that ordinary saccadic eye movements do not cause the nonveridical percepts measured in these experiments. It is possible, though, that microsaccades have a role to play. Retinal stabilization techniques would minimize the effects of these, and it would be interesting to see if illusory reversed motion is seen during retinally stabilized viewing. However, we think that eye movements of various sorts do not cause reversed motion for the following reasons. First, eye movements are minimal with a fixation mark (as we used). Second, the contracting rings stimulus does not induce optokinetic nystagmus (OKN), unlike linear movement displays, and that is why it has traditionally been used in the motion aftereffect literature to rule out eye movements as the cause of the motion aftereffect. Third, when linear motion is used, OKN is in the direction of the perceived motion [2], which implies that motion perception feeds eye movements rather than the other way around (according to all known physiology of OKN).

Continuously moving objects viewed in continuous light, as for example fan blades that are slowing down, can be seen as flickering or moving in the opposite direction to their true motion. As Purves et al. [18] have argued, humans behave as though they have a strobe light in their heads that undersamples the continuous motion. We independently manipulated the spatial frequency and the temporal frequency of the moving stimulus and found that, as predicted by the strobe-in-head theory, nonveridical percepts occurred when the stimulus temporal frequency became too high (exceeding the internal strobe rate). Control experiments show that these nonveridical percepts are not due to spatial undersampling by the retinal mosaic, to artifacts arising from computer animation, or to saccadic eye movements.

The random alternation of percepts that occurs when viewing the contracting bull's-eye suggests an attentional process is at work [13]. It has been proposed [5] that activity in the beta band (16–24 Hz) subserves visual attention.

There is more to it than attention, though: the attentional process will make alternative interpretations of an ambiguous stimulus such as a Necker cube only if the stimulus supports those interpretations. Thus, reversed motion should be seen only when the stimulus contains contrast energy components moving in the reverse direction. The spatiotemporal spectrum clearly shows that such components are absent when drifting gratings such as ours jump less than 1/4 cycle between frames. We suggest that the discrete temporal sampling process creates these spurious components.

There is no doubt that many of the properties of human temporal vision can be explained using continuous linear filters [24]. However, some lines of evidence, including illusory reversed motion, clearly point towards the existence of a discrete sampling mechanism. And it is clear that neurons produce spikes at discrete time instants, so discrete temporal sampling is intrinsic to neural signalling. Models of visual processing that are continuous in time are thus approximate, and, as we have argued, this approximation may break down under certain stimulus conditions.

Acknowledgements

We thank Sima Goheer and Abid Noor for their help in running these experiments. We thank Ian Howard for generously lending us a motor and controller.

References

[1] S.J. Anderson, R.F. Hess, Post-receptoral undersampling in normal human peripheral vision, Vis. Res. 30 (1990) 1507–1515.

[2] T.J. Andrews, A.N. McCoy, Can illusory motion disrupt tracking real motion? Perception 26 (1997) 269–275.

[3] H.L. Ansbacher, Distortion in the perception of real movement, J. Exp. Psychol. 34 (1944) 1–23.

[4] P. Artal, A.M. Derrington, E. Colombo, Refraction, aliasing, and the absence of motion reversals in peripheral vision, Vis. Res. 35 (1990) 9397–9407.

[5] M. Bekisz, A. Wrobel, Attention-dependent coupling between beta activities recorded in the cat's thalamic and cortical representations of the central visual field, Eur. J. Neurosci. 17 (2003) 421–426.

[6] N.J. Coletta, D.R. Williams, C.L.M. Tiana, Consequences of spatial sampling for human motion perception, Vis. Res. 30 (1990) 1631–1648.

[7] F. Crick, C. Koch, A framework for consciousness, Nat. Neurosci. 6 (2003) 119–126.

[8] M. Cynader, G. Chernenko, Abolition of directional selectivity in the visual cortex of the cat, Science 193 (1976) 504–505.

[9] S.A. Engel, G.H. Glover, B.A. Wandell, Retinotopic organization in human visual cortex and the spatial precision of functional MRI, Cereb. Cortex 7 (1997) 181–192.

[10] D. Finlay, P. Dodwell, T. Caelli, The wagon wheel effect, Perception 13 (1984) 237–248.

[11] S.J. Galvin, D.R. Williams, N.J. Coletta, The spatial grain of motion perception in human peripheral vision, Vis. Res. 36 (1996) 2283–2295.

[12] J.R. Hughes, The phenomenon of travelling waves: a review, Clin. Electroencephalogr. 26 (1995) 1–6.

[13] K. Klein, A.O. Holcombe, D.M. Eagleman, Illusory motion reversal is caused by rivalry, not by perceptual snapshots of the visual field, Vis. Res. 44 (2004) 2653–2658.

[14] P. Pakarian, M.T. Yasamy, Wagon wheel illusion under steady illumination: real or illusory? Perception 32 (2003) 1307–1310.

[15] D.G. Pelli, L. Zhang, Accurate control of contrast on microcomputer displays, Vis. Res. 31 (1991) 1337–1350.

[16] J.C. Prechtl, T.H. Bulloch, D. Kleinfeld, Direct evidence for local oscillatory current sources and intracortical phase gradients in turtle visual cortex, Proc. Natl. Acad. Sci. U.S.A. 97 (2000) 877–882.

[17] J.C. Prechtl, L.B. Cohen, B. Pesaran, P.P. Mitra, D. Kleinfeld, Visual stimuli induce waves of electircal activity in turtle cortex, Proc. Natl. Acad. Sci. U.S.A. 94 (1997) 7621–7626.

[18] D. Purves, J.A. Paydarfar, T.J. Andrews, The wagon wheel illusion in movies and reality, Proc. Natl. Acad. Sci. U.S.A. 93 (1996) 3693–3697.

[19] J.F. Schouten, Subjective stroboscopy and a model of visual movement detectors, in: W. Wathen-Dunn (Ed.), Models for the Perception of Speech and Form, MIT Press, Cambridge, MA, 1967, pp. 45–55.

[20] I.A. Shevelev, V.M. Kamenkovich, E.D. Bark, V.M. Verkhutov, G.A. Sharaev, E.S. Mikhailova, Visual illusions and travelling alpha waves produced by flicker at alpha frequency, Int. J. Psychophysiol. 39 (2000) 9–20.

[21] E.P. Simoncelli, D.H. Heeger, Representing retinal image speed in visual cortex, Nat. Neurosci. 4 (2001) 461–462.

[22] J.M. Stroud, The fine structure of psychological time, in: H. Quastler (Ed.), Information Theory in Psychology, Free Press, Glencoe, Illinois, 1955, pp. 174–205.

[23] R. VanRullen, C. Koch, Is perception discrete or continuous? Trends Cogn. Sci. 7 (2003) 207–213.

[24] A.B. Watson, Temporal sensitivity, in: K.R. Boff, L. Kaufman, J.P. Thomas (Eds.), Handbook of Perception and Human Performance, vol. 1, Wiley, Toronto, 1986, pp. 6-1–6-43.

[25] P. Werkhoven, J.J. Koenderink, Reversed rotary motion perception, J. Opt. Soc. Am. 8 (1991) 1510–1516.

[26] E. Wolf, G. Zerrahn-Wolf, Threshold intensity of illumination and flicker frequency for the eye of the sun-fish, J. Gen. Physiol. 19 (1936) 495–502.