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Rods Cancel Cones in Flicker

THE retina of man is equipped with two separate receptor systems. Cones, operating best in relatively strong illumination, are the basis of daylight (photopic) vision. In dim illumination (scotopic vision) we rely on rod receptors alone, and the limitations of the rod receptor system are apparent in the character of our visual sensations: in scotopic conditions colour is absent, outlines are blurred and detail is lost. At intermediate (mesopic) levels of illumination, an interesting situation arises: the rod system and the cone system are simultaneously active, and the signals that they generate combine in the production of visual sensations. Unless these rod and cone signals interfere destructively with one another, a mesopic light stimulus must be visible if either rods alone or cones alone could signal its occurrence. Experiments on the visibility of flashes[1] have yielded results consistent with this rule; but in the following experiments with flickering light, the rule breaks down.

An observer directed his gaze at a feeble red spot. His attention was focused on the test patch, a flickering circular field which subtended 3° at his eye and was situated at 5° above his line of sight so that it produced an image on a retinal area well supplied with both rods and cones. The rest was dark except for a steadily illuminated circular background (diameter 8°) which extended over the test patch and was concentric with it. The background was blue-green (Ilford 603 filter) so that in mesopic conditions it stimulated chiefly rods. The test patch itself was yellow (Ilford 606 filter) so that rods and cones were equally sensitive to it at low intensities. The intensity of the test patch fluctuated sinusoidally with 100% modulation, that is, from twice its average intensity to completely dark. The observer had to adjust the average intensity of the test patch until he could just detect its flicker after prolonged exposure to it.

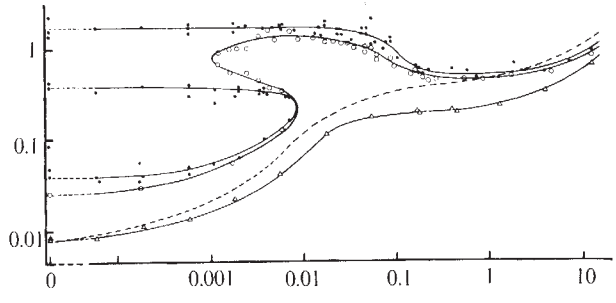

Fig. 1 Flicker detectability contours. The points show the test patch intensities at which three frequencies of flicker are just detectable against blue-green backgrounds of various intensities. At very low test patch intensities flicker is never seen. At high intensities it is visible at all three frequencies. The upper and lower sets of filled circles (7.5 Hz) are separated by a region in which flicker is not seen. The broken line indicates the intensities above which the outline of the 7.5 Hz test patch is visible. Points close together on the horizontal axis represent averages from different sessions. Intensities are in photopic trolands (logarithmic scales). Flicker frequencies: ●, 7.5 Hz; ○, 6.5 Hz; △, 3.5 Hz.

The results obtained for one observer are presented in Fig. 1. At a flicker frequency of 7.5 Hz (Fig. 1) the results differ considerably from the expected pattern. Instead of becoming more and more conspicuous as the test field intensity increased (vertical scale in Fig. 1), the flicker was visible at scotopic levels of intensity, and again at photopic levels, but not at mesopic levels. Mesopic test patches had clearly visible spatial outlines but looked steady. This mesopic null in flicker was less pronounced at 6.5 Hz (Fig. 1) and absent at 4.5 Hz.

Another unusual phenomenon is apparent in the way that sensitivity to flicker (at 6.5 or 7.5 Hz) varies with background intensity (horizontal scale in Fig. 1). In most visual tests the intensity required for detection of a stimulus against a background increases with increasing background intensity; and at scotopic intensities, the data of Fig. 1 show a typical upward trend. But at higher intensities of the flickering patch the opposite effect occurred: flicker that was not detectable in isolation could be seen when superimposed on a steady background. The dip in the upper set of filled circles in Fig. 1 shows that a background of 1 photopic troland could expose flicker in test patches of from 0.5 to 2 photopic trolands.

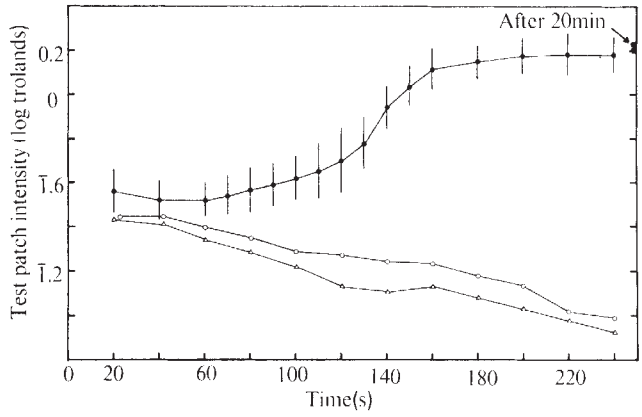

Fig. 2 "Recovery" curves for detection of three rates of flicker after exposure to a blue-green light of 130 trolands which is switched off at $t = 0$. The vertical lines show the range of ten curves for one observer. ●, 7.0 Hz; ○, 4.5 Hz; △, 3.5 Hz.

This unmasking of mesopic flicker by a background seems to depend on rod activity: it never occurred in foveal observation where rod involvement is slight. Some other evidence that indicates a dependence of unmasking on rod function is presented in Fig. 2. There the background was more intense than any used in the experiment of Fig. 1, but it was exposed before, and not during, the measurements. The curves represent the time course of flicker sensitivity after the light has been switched off. The observer continuously adjusted the intensity of the test patch, increasing it when flicker was not visible and decreasing it when flicker could be seen. The curve for 7 Hz shows a decrease in sensitivity in the dark. Like the recovery of sensitivity found at lower frequencies, this loss of sensitivity shows the slow time course that is characteristic of the return of sensitivity in rods. Therefore the abolition of flicker at 7 Hz is probably a consequence of rod intrusion; some kind of destructive interference between rods and cones is indicated.

Destructive interference might originate in either of two ways: by cancellation or by inhibition. Non-recurrent inhibitory

connexions linking the rod system to the cone system might, if they exist, allow each flicker signal to destroy the other. The cancellation explanation is simpler. Rod and cone signals might be conveyed without any interaction to a nerve centre that simply adds them together—destructive interference could occur as part of this summation process, if there were a phase difference between the signals. The likelihood of such a phase difference is high, since various experiments[2–5] have shown that the rod response occurs a little later than the cone response. If it is to account for the anomalies of mesopic flicker sensitivity, the phase difference must amount to about 180° at frequencies that show a mesopic null in flicker. Then peaks in the cone signal will coincide with minima in the rod signal and, if the two signals are approximately linear records (with equal amplitude) of the sinusoidal intensity fluctuation that elicited them, they will cancel when combined. A steady signal will result.

If this interpretation is correct it must be possible to eliminate the mesopic null by delivering stimuli asynchronously to rods and to cones. By compensating here for the difference between the phase lags of the two receptive systems, the signals generated by rods and by cones can be brought into phase with one another. Being in phase, they cannot cancel, and flicker should appear.

This revival of flicker by phase adjustments has been successfully achieved, using a blue-green light to stimulate rods (Ilford 603 filter, average intensity = 0.014 photopic trolands) and a deep red light (Ilford 609 filter, 1.5 photopic trolands) to stimulate cones. The two beams of light were both confined to the test patch. At 7 Hz and 100% modulation, either of these stimuli by itself flickered unmistakably, but if both together were admitted to the eye the flicker disappeared. Yet if a phase difference of 180° (a time interval of 72 ms) was introduced between the two, so that the green light was at its brightest when the red light was at its dimmest, the flicker became conspicuous. For one observer, the flicker became noticeable if the green beam was advanced in phase by more than 60°, or retarded by more than 40°.

Each beam formed a compact image in the plane of the pupil. Because cones, but not rods, are differentially sensitive to light incident on the retina from different directions[1], this allowed a direct test of the assumption that the red beam worked mainly through cones and the green beam through rods. The red beam intensity that gave least flicker (when in phase with the green beam) was determined in three conditions: first with both beams passing through the centre of the pupil, and then with either the green beam or the red beam displaced by 3.5 mm toward the temporal margin of the pupil. The cancelling intensity was not measurably different for the two points of entry of the green beam; the green beam therefore worked through rods. But when the red beam entered at the margin, its intensity had to be increased four times in order to abolish the flicker. So the red beam worked through cones.

Paradoxically then, flicker is invisible only when the light stimulus for rods is approximately in phase with the light stimulus for cones. This supports the cancellation hypothesis, for it is only when the stimuli are in phase that the postulated phase shift yields signals that can cancel. By creating that phase shift, the slowness of rods makes it possible to account for the mesopic null while retaining the assumption that the signal passing from eye to brain is simply the sum of the signals generated by rods and by cones.

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Piezoelectric Activity in Invertebrate Exoskeletons

PIEZOELECTRIC effects have been demonstrated in several biological structural materials, such as wood and bone[1–3], and in various organic polymers[4]. Additionally, piezoelectric activity has been detected in the otoliths of some species of bony fishes[5], where it is believed to be involved in sensory perception. On the basis of these findings it seemed worthwhile to assay the integuments of various invertebrates for piezoelectric activity, for they are related in structure, function, or composition to the materials listed above. Accordingly, a number of mollusc shells and carapaces of several arthropods were tested for evidence of piezoelectric properties.

Table 1 Impact Response of Mollusc Shells and Arthropod Carapaces to 5 g Weight dropped 10 cm

Organism	Electrical activity (peak-to-peak amplitude, mV)
(1) *Tellina angulosa*	50–65
(2) *Tellina alternata*	50–60
(3) *Arca zebra*	10–15
(4) *Anadara transversa*	20–30
(5) *Spisula solidissima*	35–40
(6) *Heterodonax bimaculatus*	4–6
(7) *Anomia aculatea*	12–15
(8) *Pecten gibbus*	8–12
(9) *Ensis directus*	50–80
(10) *Limulus polyphemus*	150–250
(11) *Callinectes sapidus*	30–40
(12) *Homarus americanus*	15–25

All readings into a 100 kohm load, ten readings per specimen.

Initial attempts to detect and measure piezoelectric activity by conventional sweep techniques, using thin, flat ground, polished specimens, produced ambiguous results; resonance and anti-resonance peaks of small amplitude were noted at many frequencies within a sweep range of 30 kHz to 2.5 MHz, reflecting the inhomogeneous structure of the material. To permit rapid, non-destructive, and unambiguous testing of the samples an impact technique was finally chosen and carried out as follows.

Samples were rinsed several times in distilled water and allowed to air-dry. Opposing electrodes were then painted on each surface with conductive silver paint (Dupont No. 4916). After the paint had dried overnight at room temperature, thin copper wire leads were attached to the electrodes with a small dab of low-melting point solder ('Cerroseal 35', melting point 110° C). The leads were then connected to the vertical amplifier input of a high-sensitivity oscilloscope, and recordings were made of the impact response to a 5 g lead weight dropped from a height of 10 cm onto the sample. Peak-to-peak amplitude of the initial electrical impulse was noted, and is presented in Table 1 for all samples tested. In all cases electrode area was $5\ cm^2 \pm 0.5$. Care was exercised when setting up the equipment to ensure that all connectors, cables, and measuring apparatus were non-microphonic. The oscilloscope and test area were acoustically isolated, and the connecting coaxial cable was wrapped in foam rubber. The leads from the sample under test were soldered directly to the ends of the coaxial cable.

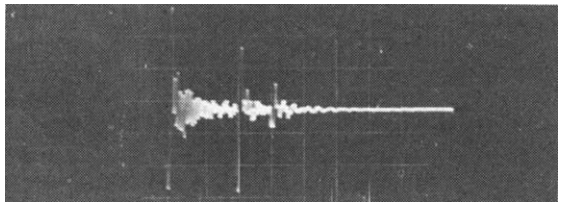

Fig. 1 Electrical response of *Tellina angulosa* shell to 5-g, 10-cm impact. Load resistance 100 kohm. Horizontal scale, 1 ms division^{-1}; vertical scale, 10 mV division^{-1}.