Diffraction and Visual Acuity of Insects

Abstract. *Burtt and Catton suggested that insects can resolve striped patterns finer than the theoretical limit set by the small diameter (30 microns) of the ommatidial lenslets. Events at the edges of the window behind which the patterns are moved explain these experiments without transgressing diffraction limitations. This interpretation leads to successful quantitative predictions of the effects of changing the boundary conditions.*

Insect visual acuity is known to be limited by at least two important factors, the diffractive properties of the dioptric apparatus, and the spatial sensitivity distribution of the primary receptor units. But evidence has been presented by Burtt and Catton (*1*) that the limits set by both of these factors are in fact surpassed, and that therefore a reinterpretation of the optics of the compound eye is necessary. The results reported here demonstrate a flaw in their analysis, and reconcile their data with the remainder of the literature on insect visual acuity.

In recent years, evidence from retinula cell penetrations (*2, 3*), optomotor experiments (*3–6*), and optical measurements (*7*) has permitted a description of the basic receptor units of the compound eye as sensors having a Gaussian-like spatial sensitivity distribution, whose peak lies along the optic axis of the ommatidium and whose width at half-response ($\Delta\rho$) is in the range 2° to 8°. As calculated by Götz (*6*), the dominant effect of this form of sensitivity distribution on resolution is an extremely rapid attenuation of contrast as the spatial wavelength (λ) of test objects, most commonly stripes, is made smaller than $\Delta\rho$. This attenuation is so drastic that for the experimentally determined range of $\Delta\rho$'s it imposes a more severe limitation on resolution than that which results purely from the diffractive properties of the very small (about 30 μ) ommatidial lenslets. For example, the contrast [defined as the Michelson visibility, $(I_{\max} - I_{\min})/(I_{\max} + I_{\min}) = \frac{1}{2}\Delta I/I_{\text{av}}$, where I is intensity measured in appropriate units] of a 3.0° pattern is very little affected by diffraction (assuming an aberration-free optical system), but is reduced to 0.1 percent by a Gaussian sensitivity function with a $\Delta\rho$ of 5.0°.

Burtt and Catton obtained electrophysiological evidence, in the form of spike trains recorded from a giant fiber in the ventral nerve cord of locusts and several dipterans, that insects can detect the abrupt displacement of striped patterns with maximum spatial wavelengths as small as 0.3°. This is not only better resolution than is indicated by any other evidence but is, in fact, below the Rayleigh limit of resolution (approximately 1.25°) calculated for an aperture of 31.4 μ and with an assumed peak spectral sensitivity at 5600 Å. To account for these startling results, Burtt and Catton (*1*) and Rogers (*8*) have invoked complex diffractive effects that are produced by a regular, closely spaced array of small apertures.

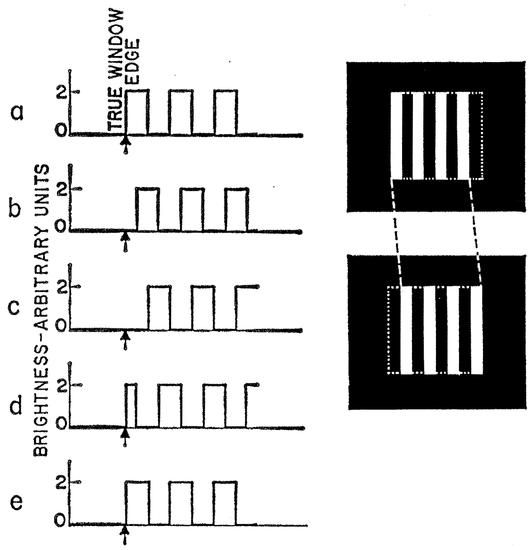
In order to investigate possible alternative explanations of the Burtt and Catton results, the following basic apparatus was constructed. Patterns consisting of enlargements of fine rulings made on large pieces of sheet film were viewed by a locust (*Schistocerca gregaria*) through a 15° or 20° square aperture in a black screen. The patterns were transilluminated by a diffuse, d-c powered, incandescent source of light so arranged that the stripes of the pattern could not cast shadows directly onto the eye; brightness of the white stripes was about 35 millilamberts, and the contrast about 90 percent. Reproducible movements of nearly constant velocity, starting from rest, were employed for stimulation. The preparation was mounted on a separate table with a heavy iron top resting on vibration mounts, and was protected from stray visual input; extensive control experiments gave no evidence of vibratory, auditory, or other spurious stimulation. The three ocelli and one compound eye of the locust were covered, and records were taken from the connective contralateral to the unobstructed eye. Tests were given in groups of five in scattered order, and each experimental point shown in Figs. 1 to 3 is the mean of ten tests. The total number of spikes occurring within 500 msec after the onset of each stimulus, typically 10 to 20 for a strong stimulus, was used as the measure of the response. Because of marked habituation effects, 30 seconds was used as the standard interval between tests.

The basic results of Burtt and Catton proved to be entirely reproducible under stimulus conditions comparable to those which they used. Possible explanations were therefore considered under the following headings. The fine stripes might indeed be resolved, in which case either (i) the usual resolution criteria are not applicable to this case, or (ii) the criteria are applicable and some novel optical explanation, perhaps along the lines proposed by Burtt and Catton, is indeed necessary. Alternatively, in a class distinct from these, (iii) the response might be due to some edge effect associated with both the pattern and the window.

The fairly small size of the pattern has an important influence on the formulation of criteria for the limit of resolution, even in the absence of relative motion between the pattern and the window (*9*). However, the stimulus situation used in these experiments is dominated by a quite different and previously unrecognized complication.

Consider the purely geometrical interpretation of events occurring at the edges when a striped pattern perfectly aligned with the window is moved through a distance of one pattern wavelength (Fig. 1). There is an integral number of wavelengths within the window, the pattern contrast is 100 percent, and the immediate surround is black; all these conditions were realized in the original Burtt and Catton experiments. The half-cycle represented in rows *a* through *c* is clearly equivalent to moving the window itself through a distance of $\lambda/2$. Furthermore, the two opposite edges have moved in phase; if the window contained a nonintegral number of wavelengths, they would move out of phase. The description is more complex for the other half of the cycle, or when the brightness of the surround is not approximately equal to the minimum brightness of the pattern. But we can state the general assertion that the window itself constitutes a large perturbation in the visual field whose edges move in a complex manner as a striped pattern is moved behind it. If these edge phenomena can be detected by the eye, resolution of the pattern itself ceases to be a limiting factor.

That the locust can, in fact, perceive the movement of such a large dis-



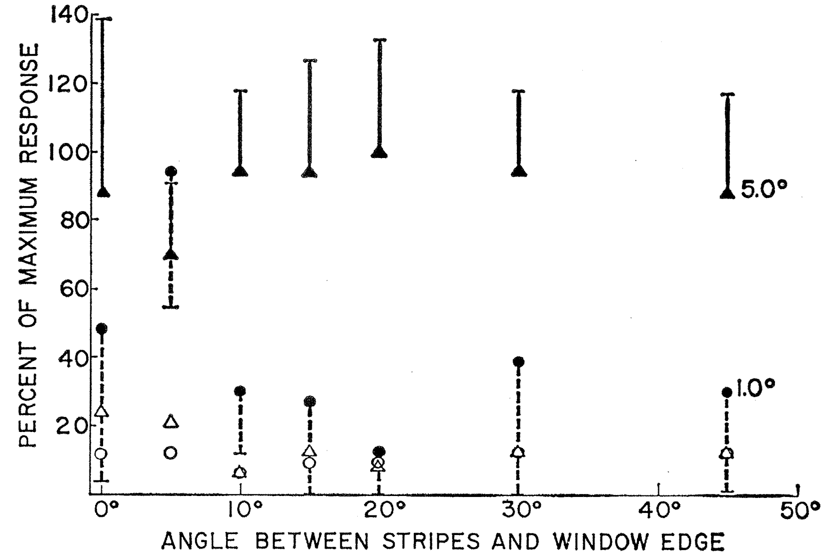


Fig. 1 (left). Origin of pattern-dependent window motion. Curves on left plot brightness against position, starting in the black surround and moving perpendicularly to the stripe orientation; from *a* to *e* the pattern has been shifted to the right in steps of $\lambda/4$. Drawings correspond to curves *a* and *c*; true windows are outlined by dotted white lines, and the two apparent window positions are connected by dashed lines. Fig. 2 (right). Effect of window rotation. Activity during testing with 1.0° stripes (solid circles) falls to the spontaneous level (that is, low frequency, sporadic firing in the absence of deliberate stimulation shown by open circles) when the window is rotated by 20° with respect to the stripes. The subsequent recovery represents one of several types of change in response with increased rotation, perhaps associated with changing degrees of spatial coherence of the residual edge effects. The response to 5.0° stripes (solid triangles) is not much affected. One standard deviation is plotted. Open triangles, spontaneous activity with 5.0° stripes.

turbance through a distance equal to $\lambda/2$ of the effective test patterns is shown in two ways. First, the giant fiber responds to the movement of the window itself, in the absence of any pattern, through a range of distances corresponding to the half-wavelengths of patterns whose movements elicit a response. Second, in optomotor experiments in which isometric neck torque is the measure of response the locust will follow the oscillation of a pair of windows, of the dimensions used in the giant-fiber experiments, when the peak-to-peak amplitudes correspond to the pattern-dependent window motion described here (*5*).

As already stated, information about changes in the visual environment during pattern motion is provided to the animal in at least two ways: the stripes of the pattern move, and the edges of the window-plus-pattern complex move. Utilization of the first alternative requires the presence of some contrast related to the high fundamental spatial frequency of the pattern in the image plane(s) of the optical system, and this is limited by diffraction. Utilization of the second alternative is not directly limited by diffraction, because no high frequencies are crucially involved. Two different experimental tests of the edge-effect hypothesis were performed.

The first type of experiment depends upon the spatio-temporal coherence of the disturbance at the edges being destroyed. If the viewing window is rotated while the orientation of the stripes remains unchanged, there results a severe limitation on the extent of continuous edge from behind which a given black stripe can appear. Figure 2 shows the results of this experiment for two patterns: 5.0°,

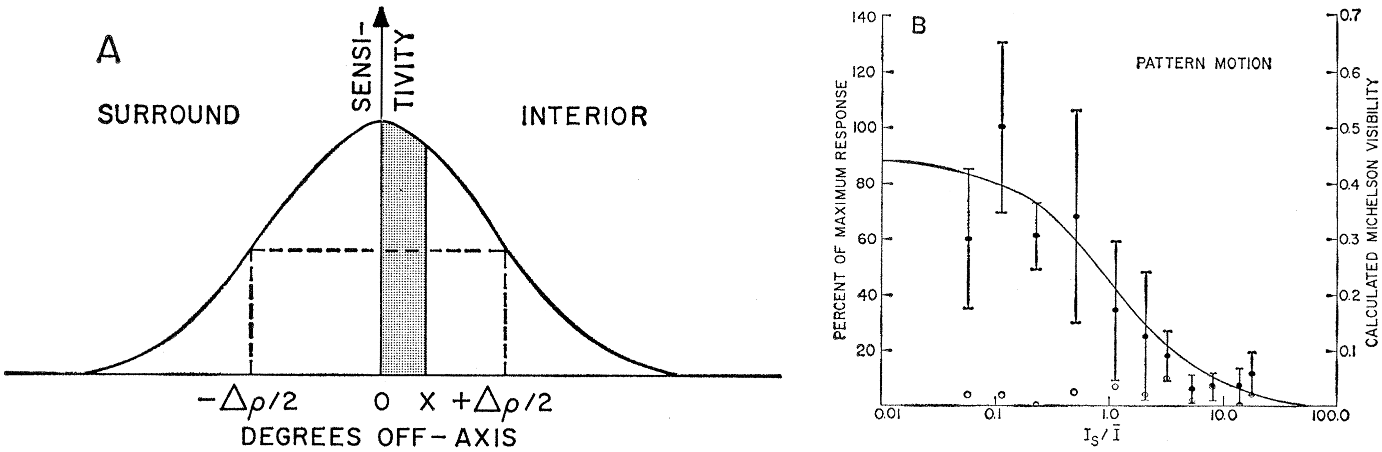


Fig. 3. Effect of changing the brightness of the surround. (*A*) Illustration of calculation of the effect of surround brightness on pattern-dependent window motion. (*B*) Sample experiment with a 1.5° pattern. Solid curve calculated as explained in text and plotted against right ordinate. Experimental values, shown with two standard deviations, plotted against left ordinate; spontaneous activity shown by open circles.

which will elicit modest optomotor responses, and 1.0°, which is at the Rayleigh limit and totally ineffective in optomotor experiments (*5*). The response to the fine pattern sinks to zero at about 20° misalignment, while the response to the 5.0° pattern is virtually unaffected. The response to fine patterns is always strongly depressed by window rotation, but the detailed shape of the response curve is variable and depends at least on the distance through which the pattern is moved and on the initial phase relationship of the pattern and the edge of the window.

The second type of experiment is based upon a consideration of the maximum net input available to ommatidia aimed precisely at the window edge during the half-cycle of pattern movement illustrated in Fig. 1, *a–c* or *c–e*. The input to one half the visual field is constant, and is equal to the surround brightness weighted by the idealized Gaussian off-axis sensitivity function; the input to most of the rest of the visual field is also constant, being equal to the average brightness of the pattern (= 1) again weighted by the sensitivity function; and a narrow block of width $x = \lambda/2$ to one side of the axis shifts between black (= 0) and white (= 2), as indicated in Fig. 3*A*. Thus the primary edge effect of moving an unresolved pattern is simulated, while the proper diffraction phenomena are lumped in the treatment of the remainder of the pattern as a homogeneous gray region of brightness $\bar{I} = 1$. The calculation (*10*) is formally equivalent to that done by Götz, except that numerical integration over the Gaussian weighting function replaces his analytical result.

Now, assume that the effective stimulus to a retinula cell is the temporal Michelson visibility or contrast (as already defined) available during pattern movement, considered for the entire visual field of that cell. Then clearly the signal will be maximal when the surround is black, and will be reduced when the surround brightness is increased. Michelson visibility for a half-wavelength of 0.75° and $\Delta\rho$ of 3.0° (*2, 3*) as a function of surround brightness is shown by the solid curve of Fig. 3*B*. The experimental values for a sample experiment fit the calculated curve sufficiently well that the edge-effect hypothesis must be accepted as one explanation of the Burtt and Catton experiments. The response to resolved stripes, for example 4.5°, is not diminished. In fact, when the inevitable edge effects are first minimized by window rotation, the response is enhanced by brightening the surround. This and other control experiments show that there is no general suppressive effect due simply to the brightness of the surround.

Detailed characterization of the stimulus features which are especially effective in activating this particular nerve cell is not necessary for the interpretation of the present experiments. For example, the difficulty of assessing the role of movement, as opposed to the stationary edge flicker described on the basis of similar psychophysical experiments with humans as performed by Barlow (*11*), has been skirted by describing the stimulus both as a pseudo movement of the window and as a change in brightness available to favorably oriented ommatidia. Some of the characteristics of the functional connections which this fiber makes with the receptor array have been investigated and will be reported elsewhere.

The general view of the insect dioptric apparatus presented by Burtt and Catton, and simulated in a simple physical situation by Rogers, has not been subjected to direct test by the present experiments and cannot, therefore, be ruled out. However, the results reported here on the one hand, are not predicted on the basis of the complex optical effects which they describe, and on the other, render their explanation of remarkable resolution unnecessary. Any explanation of their "anomalous" resolution based on a refinement of resolution criteria, taking account of the effects introduced by the small size of the grating, is similarly unnecessary though not directly excluded. There remains no evidence for resolving power in insect eyes incompatible with the simplest formulation of diffraction limitations applied to single ommatidial lenslets.

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Visual Resolution and the Diffraction Limit

Abstract. *Movement of a grating behind a fixed aperture can be detected by human subjects when the grating is well below the diffraction limit of the pupil and below acuity measured with stationary gratings. With movement one sees a flicker or ripple at the edges, and it is argued that these edge effects lead to spurious estimates of optical resolution in insects and man.*

According to the classical view of the compound eye, each ommatidium is an optical system that only accepts light falling on the eye from a particular small region of the visual field. However, recent results indicate that this view should be reconsidered. On the one hand, single ommatidia have been found to respond to light from a much larger region of the visual field than was expected, so that the pick-up areas of neighboring ommatidia apparently overlap extensively; on the other hand, it has been claimed that the whole eye resolves details below the limit calculated on the assumption that the angular acceptance of an individual ommatidium is limited by diffraction. Since resolution as high as this would be impossible according to the classical view, I shall first describe the following experiments.

Burtt and Catton (*1*) measured the visual resolution of locusts and flies by recording from the optic lobes or ventral nerve cord while moving a black-white grating behind a fixed aperture in the visual field. They usually obtained responses when the grat-