

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. 3A. 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. 3B. 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 Burt and Catton experiments. The response to re-

solved 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 Burt 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.

JOHN PALKA

Department of Zoology,
University of California, Los Angeles

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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.

Burt 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-

ing had a period as small as 0.3° (occasionally as small as 0.15°), whereas the diffraction limit would be expected to prevent the resolution of gratings of period less than 0.95° , taking the ommatidial diameter (d) as 30μ , and the wavelength (λ) of the light used as 0.50μ . However, when I presented Burt and Catton's type of stimulus to human subjects I obtained the results shown in Table 1. An effect could be detected when a grating was moved behind a fixed aperture for angular periods of a half to a quarter of those required to "resolve" the grating, taking this to mean that the subject could tell whether the lines were vertical or horizontal. For the 3-mm pupil, the period of the just-resolvable stationary grating was considerably above the diffraction limit, and the period of the just-detectable moving grating was a little below it. However, when a 1-mm artificial pupil was employed the eye resolved stationary gratings down to the limit and could detect moving gratings a long way below it.

Thus, in the simple eyes of humans as in the compound eyes of insects, gratings below the diffraction limit can produce visible effects when moved behind a fixed aperture. Moreover, observing the appearance of these moving gratings gives a strong clue to what is happening. What one sees is a flicker, "ripple," or oscillation back and forth, at the edge of the fixed aperture: no movement is seen in the central part of the aperture, where the grating bars themselves are quite invisible, nor is it possible to tell the direction in which the grating is moving. For gratings only slightly below the ordinary resolution limit the edge effect is very prominent, and when the grating comes to rest one can often see, and can correctly name, the dark or light bar of the grating next to the edge.

At first it seems strange that these effects can be produced by a grating which looks like a uniform gray because it is below the limit of resolution. It might be argued that nothing that can be done in the image plane would enable the grating to be distinguished from uniform gray if the optical system had filtered out all the spatial frequencies which distinguish them in object space; and if the light distribution in the image is uniform, then it must be impossible to detect movement. However, it is misleading to consider how the optical system

Table 1. Results obtained with human subjects. Visual resolution was estimated by two criteria: (i) the ability to distinguish a vertical from a horizontal grating; (ii) the ability to detect movement of a grating behind a fixed aperture. Five subjects were used with pupil diameters of 3 mm and 1 mm. Luminance of test object was 150 cd/m^2 . Movement of a grating behind a fixed aperture can be detected when its period is well below the diffraction limit; hence this is a misleading test of resolving power.

Subject	Resolving power— period of grating (min)		
	Diffraction limit (λ/d)	Vertical from horizontal	Moving from stationary
<i>Pupil diameter, 3 mm</i>			
C.O.	0.64	1.13	0.32
E.T.	.64	1.16	.44
H.B.	.64	1.19	.43
G.W.	.64	1.26	.44
R.F.	.64	1.40	.50
<i>Pupil diameter, 1 mm</i>			
C.O.	1.93	1.98	.49
E.T.	1.93	2.02	.51
R.F.	1.93	2.05	.53
H.B.	1.93	2.15	.48
G.W.	1.93	2.26	.50

would handle the grating alone, because the stimulus object is not formed by the linear superposition of an aperture on a grating; hence one cannot consider separately the images of grating and aperture, then superpose these images to obtain the total effect.

A supplementary observation brought out another important feature of the stimulus situation. It was argued that if the abrupt cutting-off of the grating by the sharp edge of the aperture was important in producing the flicker, then blurring the edge of the aperture by defocusing would eliminate it. This proved to be the case: one edge of the aperture behind which the grating moved was placed 1 m from the observer's eye, the grating being 3 to 13 m away. All subjects agreed that no effects of movement could be seen at this blurred edge. Defocusing would seem to be a convenient way of eliminating edge effects in grating acuity tests.

Palka (2) goes further into the mechanism whereby these effects may be produced, and the following *reductio ad absurdum* is intended to show convincingly that it is not necessary to resolve a grating in order for it to produce marked effects on the appearance of an object interposed between it and the eye. Consider a fine, straight, black thread which can be seen against a uniform ground when it subtends

an angle of 1 second or less. A moment's thought will show that if the thread lies immediately in front of a black bar of a grating it must become invisible, yet a grating with black bars just wide enough to obscure the thread is much too fine to be seen as a grating; it requires a magnification of $\times 30$ to reach the limit of resolution. It is easy to demonstrate that a grating can conceal a thread in this way, and movement through a half period immediately restores it—in fact it becomes more easily visible than when it is in front of a uniform gray. Here one has a much more pronounced form of Burt and Catton's paradox: movement of a grating with a period an order of magnitude below the minimum resolvable produces easily discernible effects.

The conclusion must be drawn that the wavelength of the grating that just produces visible effects when moved behind a fixed aperture gives a misleading idea of the eye's resolution, and Burt and Catton's results are not impossible on the classical view of how the compound eye works. Optical interaction between the images produced by the lenslets of neighboring ommatidia (3) is interesting in its own right, but it is unnecessary to postulate that the insect makes use of the improved resolution that is theoretically attainable.

If gratings finer than the diffraction limit can produce visible effects, it may well be asked if this, or any other, so-called "limit" to resolution has any useful meaning. The purpose of specifying a value for angular resolving power is to give a guide to the number of separate cells into which the image can be divided; it tells one the number of dimensions, or degrees of freedom, in the optical image. To some people this may seem an abstract concept, but it has important practical consequences which are well illustrated by considering the angular separation of the ommatidia in an apposition eye.

First imagine a single ommatidium scanning along an arc through the visual field. The effective input for any one ommatidial position can be obtained by multiplying the intensity in the field at various angles to the axis of the ommatidium by the appropriate factor, and integrating the product. The polar acceptance curve of the ommatidium gives the appropriate factors, and the effective input as a function of scanning position is the convolution of

this curve with the actual intensity along the arc in the visual field. Now if the real and the effective inputs are considered as wave forms, it will be seen that the effective input will lack some of the higher frequency components of the real input. The extent of this high-frequency loss is related to the degree of smoothing caused by the ommatidium, and this in turn is roughly related to the breadth of its polar acceptance curve (4). The exact relations are best expressed in the Fourier domain: with Parseval's theorem, the Fourier transform of the effective input is the product of the transform of the real input with the transform of the polar acceptance curve. Thus it is the highest frequency in the transform of the polar acceptance curve that determines the highest frequency in the effective ommatidial input. It is true that the breadth of the curve gives a guide to this, but the detailed shape is important, and in this connection it is worth pointing out that the Gaussian shape commonly assumed for the polar acceptance is actually impossible: its transform includes all frequencies, whereas those beyond the diffraction limit must be wholly demodulated.

So far, it has not been mentioned that ommatidia occur only at certain fixed positions separated by the interommatidial angle. This is equivalent to the height of a waveform being measured at certain points and, according to Shannon's theorem (5), such sampling causes no loss of information if the sample interval is less than half the shortest wavelength contained in the wave form. Now the interesting point about diffraction is that it places an absolute upper limit to the frequencies contained in the effective input: there can be no frequencies whatever above λ/d (6). From this it follows that it would be uneconomical for insect eyes to have interommatidial angles much less than $\lambda/2d$, and I do not think this has ever been reported. What is remarkable is that this value does seem to be approached in the central zone of the bee's eye, and in those of the other diurnally adapted Hymenoptera of widely varying eye size and ommatidial number (7). It is difficult to see why the insect eye obeys the dictates of the diffraction limit and Shannon's sampling theorem unless, in these cases, spatial frequencies close to the diffraction limit are passed by the ommatidia. The well-designed eyes of these Hymenoptera provide an example

in which the anatomical arrangement of the ommatidia is well matched to the number of the degrees of freedom in the available input.

In other cases, especially where the eye has to work under low illumination, the polar acceptance of the ommatidia is doubtless broader than diffraction would necessitate. As Gotz (4) has shown, where this is so the interommatidial angle can also be greater without any information being lost. It is interesting to consider those instances where the interommatidial angle is greater than half the highest spatial frequency passed by the ommatidia, for then the high frequencies are not adequately sampled and can lead to the false appearance of spatial frequencies which were not present in the real input. These spurious components must be the ones responsible for the reversed optomotor responses in certain insects which Hassenstein (8) has described and others (9) have investigated intensively. Thus, these misdirected beetles illustrate one possible consequence of the number of ommatidia being improperly matched to the number of degrees of freedom in the effective input.

In spite of reports of broad acceptance curves and resolution beyond the diffraction limit there is no need to abandon Exner's classical description of the mode of function of the apposition compound eye, and diffraction at the ommatidial lenslet still appears to be the physical factor limiting the evolution of higher acuity in this type of eye. In some instances the number of ommatidia is well matched to the number of degrees of freedom in the effective optical input, but in others the number is too low and in these instances reversed optomotor responses to moving gratings can occur.

H. B. BARLOW

Neurosensory Laboratory, School of Optometry, University of California, Berkeley

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Sound Production by Cichlid Fishes

Abstract. *Adults of three cichlid species, Hemichromis bimaculatus Gill, Cichlasoma nigrofasciatum (Günther), and Pterophyllum sp., produce sounds of apparent biological significance. Both sexes of H. bimaculatus produce sounds, but whether both sexes in the other species produce sounds has not been established. The most intense tone frequencies in H. bimaculatus and C. nigrofasciatum lie generally between 300 and 500 cycles per second. The sound produced by Pterophyllum sp., however, has a broad maximum intensity around 3500 cycles per second and component frequencies over 10,000 cycles per second. Sound production appears to depend on the aggressiveness of the individual.*

Underwater sounds produced by fishes play an important role in the life of some species (1). Until now, however, over 95 percent of the species known to produce sound were members of either marine families or fresh-water cypriniform families. The only evidence that a fish of the fresh-water, noncypriniform family Cichlidae produced sounds was that of Bauer (2) who described a sound, heard outside the aquarium, made by a courting male of *Tilapia nilotica* (Linnaeus). We have now demonstrated that other species also produce underwater sounds, but the sounds are not of such intensities as to extend beyond the confines of the aquarium.

The sounds were recorded from three cichlid species, each representing a wide geographic area: *Hemichromis bimaculatus* Gill (Africa), *Cichlasoma nigrofasciatum* (Günther) (Central America), and *Pterophyllum* sp. (probably *P. scalare* C & V) (South America). Pairs and small groups of fishes were maintained and tested in 180-liter aquaria with water temperatures ranging between 25° and 27.5°C. The bottoms of the aquaria were covered with