Fish vision

. . . all the better for catching *Daphnia* with

from J. N. Lythgoe

THE most important factor that limits the fineness of detail that a fish can see is the size and packing of the cones in its retina. A new study that has recently appeared in *Science* (**218**, 1240; 1983) shows the practical effect of this for the bluegill sunfish — the larger it grows the smaller the prey it can see and catch.

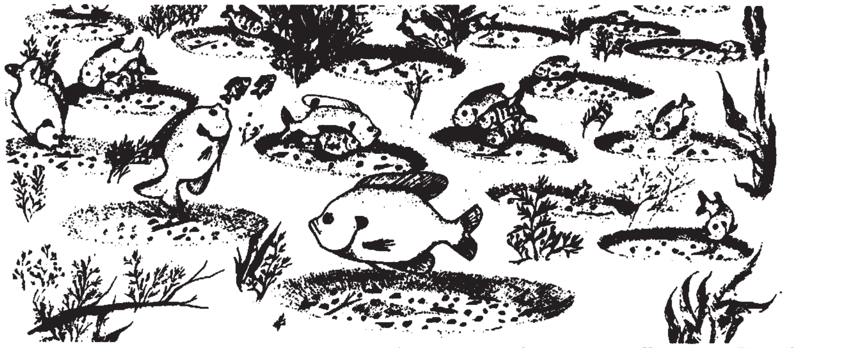
The techniques used by Nelson Hairston, Kao Li and Stephen Easter in their study of the bluegill sunfish (*Lepomis macrochirus*) were quite simple. Water fleas (*Daphnia*) of known size were introduced into a shallow tank containing several fish whose feeding manoeuvres could be monitored with a vertically mounted video camera. On sighting a *Daphnia* a fish would turn, swim towards it and snap it up. The distance between the point of turning and the snap was taken as the reaction distance. It was then possible to calculate the visual angle subtended by the *Daphnia* at about the time that the bluegill recognized it was good to eat.

It was found that the visual angle subtended by the *Daphnia* at the time of recognition varied from a mean of 27.8 minutes of arc for fish 3.7 cm long to 14.2 minutes of arc for larger fish 5.8 cm long.

The observation tank was brightly lit and it is unlikely that vision was limited by insufficient light, or indeed that the rods, which are the receptors for dim light vision, were involved at all. In these conditions the detail that an eye can resolve is limited by two fundamental factors. The first is interference to light as it passes through the pupil aperture, causing blurring of the image on the retina in a mathematically definable way. The second factor is the spacing between the centres of the retinal receptors (in this case the cones) which limits the detail with which the image of the visual scene on the retina can be sampled.

For the bluegill sunfish it is the spacing of the cones rather than interference at the pupil aperture that limits the ability to resolve detail. The twofold improvement in visual acuity as the fish grows is due to an increase in the number of cones that sample the image. The spacing of the cones themselves remains quite constant, but the area of retina, and hence the number of cones available to sample the larger image, increases as the eye grows larger.

The study reinforces the belief that big eyes are best. This is not because small eyes are less sensitive, as the brightness of the retinal image from an ordinary visual scene depends on the ratio of pupil aperture to focal length (the *f* number used by photographers). Provided this ratio remains constant, as it probably does in these eyes, the brightness of the retinal image is the same whatever the size of eye. Where there does seem to be a limit is in the cross-sectional area and packing density of the cones themselves. Thus the retinal 'grain' cannot be reduced beyond a certain point and a small retinal image cannot yield so much information as a large one.



A bluegill sunfish colony: bigger fish have bigger eyes and can see smaller prey. (Drawing from Dominey, W. J. *Nature* **290**, 586; 1981.)

One limit to the size of the cones themselves relate to their properties as a light guide. The outer segments, which contain the light-sensitive visual pigment, have a lighter refractive index than the surrounding cytoplasm and hence act as tiny light guides. In the sunfish the outer segment of each cone is about 2,000 nm across. If their diameter were much smaller than this, the light-guiding property of the outer segments would probably be reduced, leading to light leaking across from one cone to its neighbours. Thus the capacity of small fishes, and indeed that of any small animal, to see fine detail is likely to be limited by the size of the eye itself and as the authors of the *Science* paper point out, this will provide a selective advantage for the continuous retinal growth noted in many fish. □

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Non-linear systems

Coherent excitation in biology

from F. Keilmann and D. B. Kell

SUPPLY of energy to a material system may lead to the excitation of a coherent mode in which the motion of many of the particles that compose the system becomes highly correlated. Such coherent excitation is seen in masers and lasers, for example, and involves a nonlinear change in certain properties of the material. Some fifteen years ago H. Fröhlich (*Int. J. Quantum Chem.* **2**, 641; 1968 and *Adv. Electronics Electron Phys.* **53**, 85; 1081) conjectured that coherent excitation of electrical oscillations might play an important part in biological as well as physical systems. Recently, physicists and biologists met in Germany to discuss progress in assessing the nature and existence of such coherent excitations in biological systems. The general conclusions of the meeting* were that coherent excitation had now been shown to be an intimate feature of biological activity; further progress would rely on detailed studies of well characterized material.

In his early work, Fröhlich carried out a theoretical study of the electrical oscillations of sections of biological membranes and showed that a supply of metabolic energy above a critical rate could lead to coherent electrical oscillations. Such excitations are not, however, restricted to membranes and it is possible for interactions to occur between systems of equal frequency at a distance at which ordinary chemical interaction is absent and electrostatic interaction is screened. The possibility of coordinated activity of large regions thus appears. Estimates of the frequency of coherent oscillations of membranes gave values in the 10^{11} Hz range — the same as that of electromagnetic millimetre waves. If biological systems do in fact make internal use of such excitations then great sensitivity to external radiation at the relevant frequencies should be expected. Work reported at the conference suggests such sensitivity exists.

A remarkable 44 per cent increase in the fertility of *Drosophila melanogaster* was reported (G. Nimtz, University of Köln) to occur in the first generation after irradiation of pupae for 5 days with microwaves (40 GHz) at an intensity of only 10 μW cm^{-2}. In a study of puffing patterns in the giant chromosomes of *Acricotopus lucidus* (F. Kremer, Max-Planck-Institut, Stuttgart), a fivefold increase in the number of condensations of Balbiani rings ($\alpha <$ 0.5 per cent) was observed after only 2 h of low-intensity irradiation at 64–69 GHz. Reproducible

*The international symposium on 'Coherent Excitations in Biological Systems', held at Bad Neuenahr on 29 November–1 December 1982, was sponsored by IBM Germany; chairman H. Fröhlich. The proceedings are to be published by Springer Verlag.

changes of about 10 per cent in the average growth rate of yeast cells *Saccharomyces cerevisiae* (W. Grundler, Gesellschaft für Strahlen- und Umweltforschung, Neuherberg), were observed at several frequencies near 42 GHz. Use of fine-scaled frequency tuning showed the response to be highly resonant, such that detuning by only 1 part in 10^4 obliterated the effect. The sharpness of frequency response together with a step-like dependence on the microwave intensity is in agreement with theoretical requirements.

When human red blood cells are dispersed in plasma they appear to carry out brownian movement until they attach to each other, forming rouleaux which, under the microscope, have the appearance of stacks of coins. In extensive microscopic investigations, S. Rowlands (University of Calgary) found that the erythrocytes appear to rush forwards towards each other once they have approached to within about 4 μm. Analysis of the movement in terms of the Smoluchowski theory permits a quantitative evaluation of the interaction. If the attraction arose from coherent membrane oscillation then the measured attraction satisfies the requirements of the theory; it disappears when the membrane potential is removed by a change of the plasma *p*H, or when they are depleted of their metabolic energy. The attraction reappears when both are restored.

What kind of biological structures might be responsible for these remarkable findings? Current ideas on the ultrastructure of various cells (J. Clegg, University of Miami) lay emphasis on the microtrabecular lattice and its attendant 'bound' water as a possible vehicle for cytoplasmic organization in general and for the transfer of coherent excitation in particular. Mouse fibroblasts (L cells) suspended in 0.3 M sorbitol contained only 0.5 g H_2O per g dry mass, and were virtually in the solid state, yet metabolized in a fashion indistinguishable from that of 'normal' fibroblasts. Evidently a cytoplasm exhibiting a bulk aqueous milieu is not a feature crucial to cellular function.

It is now widely recognized that the membranous systems of electron transport phosphorylation effect free-energy transfer by a bioelectrical mechanism, in that spatially separate protein complexes have been shown to act as more-or-less reversible proton pumps. Various studies, however, led to the conclusion (D. Kell, University College of Wales) that the free-energy transfer was effected between specific individual complexes, so that traditional stochastic ensemble models must be proscribed. A coherent excitation is thus a particularly attractive possibility for explaining the properties of this process. □

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Chandler wobble

Simulation shows wobble period neither multiple nor variable

from F.A. Dahlen

THE Chandler wobble, a 14-month free nutation of the Earth's principal axis of inertia about its rotation axis, has been continuously monitored for nearly a century. In spite of that, agreement about the fundamental nature of the observed motion is still lacking. Numerous workers, beginning with Chandler himself[1], have suggested that its period is either multiple or variable in time. The alternative view, which is preferred by most geophysicists and astronomers, is that the Chandler wobble is a single damped free oscillation of the Earth, maintained by some irregular excitation process. An article by Okubo in the December 1982 issue of *The Geophysical Journal* [2] should suffice to convince all but the most steadfast sceptics that the conventional view is correct.

Okubo has performed a straightforward numerical experiment. He generated an artificial Chandler wobble time series consisting of white noise passed through a single sharp resonance peak, and then subjected it to exactly the same analysis procedures used by those who have argued for a more complicated deterministic data structure. Colombo and Shapiro[3] and Gaposchkin[4], for example, have proposed that the Chandler wobble actually consists of two independent modes of oscillation separated in period by about 10 days. At first sight, such a conclusion seems strongly supported by the distinct 40–50-year beating visible in the twentieth century polar motion data after removal of the annual wobble; the beating leads in turn to a double Chandler peak in the polar motion periodogram. Okubo shows, however, that both these features are the expected consequences of passing a random input signal through a high-Q resonance peak. The beating is a result of interference between the two flanks of the peak, which gives rise to irregular amplitude variations on a time scale of order QT, where T is the resonant period. The beat period that emerges is consistent with the measured Chandler wobble with Q in the range 50–100. The double peak can be attributed to the well known statistical fluctuations inherent in periodogram spectral analyses of stochastic processes. The presence of a single damped mode is also corroborated by nineteenth century data collected and analysed by Yatskiv, Korsun and Rykhlova[5]. Their series from 1846 to the present shows irregular amplitude variations, which come to resemble regular harmonic beating during the twentieth century but not before.

Others, including Melchior[6], Sekiguchi[7] and Carter[8], have postulated that the Chandler period varies with time as a result of some underlying change in the properties or response of the Earth. These claims are generally based on a form of running spectral analysis, which shows evidence for a variation in instantaneous frequency, inversely correlated with amplitude, when applied to the Chandler data. Okubo examines several such methods and shows that in all cases virtually identical results are obtained when they are applied to his synthetic series. He concludes that "there is no positive evidence for the variable period model". The occurrence of instantaneous frequency variations of 1–2 per cent in the Chandler data is just another natural consequence of the random excitation of a damped harmonic oscillator with Q in the range 50–100.

Either a multiple or a variable period would be difficult to reconcile with existing theory, which predicts with some assurance that the Chandler wobble is a singe damped free oscillation of the Earth well isolated in the eigenfrequency spectrum. Smith and Dahlen[9] have recently shown that both its period and damping can be accounted for quantitatively by allowing for a slight frequency dependence of the shear dissipation in the mantle, of the form $Q_\mu \sim \omega^\alpha$ where ω is frequency and $\alpha = 0.1$–0.2. This substantiates a conclusion about the Earth's anelastic rheology first drawn by Jeffreys[10] in 1958.

The outstanding problem in the study of the Chandler wobble is, and has been for some time, the source of its excitation. Okubo's work confirms the generally accepted conclusion that the excitation has the statistical properties of quasi-stationary broadband noise. Earthquakes and atmospheric motions have both been discounted, as neither can account for the observed level of excitation. Hopefully, some clues will soon be forthcoming from the increasingly refined techniques of spatial geodesy, very large baseline interferometry and satellite ranging. □

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