

underlying simple cells in cat cortex. Inhibitory synapses, employing the transmitter γ -amino butyric acid (GABA), are plentiful in the cortex, especially in layer 4, and much effort has been expended in trying to understand their function. One of the most popular notions, advanced by Blakemore and Tobin⁵, was that a cell's orientation selectivity might be sharpened if it were to receive inhibitory inputs from other cortical cells with different orientations. This process would be analogous to events in the geniculate, where the power of the receptive field's surround to countermand the influence of the centre is enhanced, and seemed to be confirmed by Sillito⁶ — he observed a loss of orientation selectivity of simple cells when the drug bicuculline, a GABA antagonist, was applied to the cortex.

On the other hand, evidence for the original idea of direct excitation came from Chapman, Zahs and Stryker⁷. They first determined the orientation selectivity of cells in a single orientation column in cat cortex. Then, by applying kainic acid or muscimol to the cortical surface, they eliminated all impulse responses in cortical cells but preserved the impulse activity of the geniculate afferent fibres. When they recorded receptive fields of a number of these fibres, all in the same orientation column, they found that they occupied a long narrow strip that paralleled the orientation of the cells they had previously recorded. Further support came from Tanaka⁸, and from Reid and Alonso⁹, in experiments in which impulses simultaneously recorded from a simple cortical cell and a geniculate cell were cross-correlated. Both studies found that in the two cells, receptive-field regions of the same sign — excitatory or inhibitory — were almost always superimposed.

Finally, two studies from Ferster's laboratory, one published in 1986 and the other in this issue, also point towards excitation from geniculate inputs as the cause of orientation selectivity. Both made use of intracellular recordings of cortical cells, and any reader must surely have wondered why no one had used these methods sooner: intracellular recording allows one to define the properties of a cell in terms of its impulse responses, and then to examine separately the summed excitatory and inhibitory inputs. The answer, of course, is that making such recordings requires consummate skill plus the patience and determination of Job. But if the recordings are successful they can give simple, decisive answers.

In the earlier paper¹⁰, Ferster showed that, in response to visual stimulation, the summed inhibitory inputs to a simple cell, in the form of inhibitory postsynaptic potentials, showed the same orientation preference as the cell itself, with the same peak orientation and identical sharpness of tuning. If the function of the inhibition

were that of sharpening the tuning, the orientation preference of the inhibition should have been different or at least broader.

In the second set of experiments¹, Ferster and his colleagues recorded intracellularly using the whole-cell patch technique, which is roughly equivalent to intracellular recording but more powerful — and still more difficult. They first determined the orientation selectivity of the cell and then suppressed the local impulse activity in that part of the cortex by surface cooling. This should abolish all visually evoked synaptic potentials except those arising from direct geniculate inputs — and indeed it did abolish all the inhibitory input and a fair proportion of excitatory inputs. The receptive fields of the remaining excitation had exactly the same orientation preference and sharpness of tuning as the cell itself before cooling. I find this compelling evidence that the orientation selectivity depends not on inhibitory inputs from neighbouring cortical cells (themselves activated by geniculate inputs, directly or over several stages), or indeed on excitatory polysynaptic inputs that might also serve to sharpen selectivity (by a previously proposed process that others have termed 'selective amplification'). As Ferster *et al.* point out, however, it is still possible that some excitatory input of cortical origin may have survived the cooling; layer 6, the furthest

from the cooling element, is known to send excitatory input to layer 4.

Thirty-five years ago Wiesel and I would have been incredulous had anyone suggested that only now would our scheme for explaining simple cells be vindicated or disproved. At this rate we may expect to have a verdict on a similar proposal we made for complex cells by 2031. Extracellular recordings can tell us about the transformations the cortex makes in the information coming into it, but it is far harder to learn exactly how these transformations come about, in terms of the wiring and the excitatory and inhibitory connections. Ferster and his colleagues have shown that it is possible. □

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EVOLUTION

The games lizards play

John Maynard Smith

IN evolutionary theory, an evolutionarily stable strategy (ESS) is a strategy, or phenotype, that is stable in the sense that, if most members of a population adopt that strategy, or have that phenotype, no alternative mutant strategy can invade the population. In simple models, there is usually either a 'pure' ESS (always do the same thing), or a 'mixed' ESS (sometimes do A, sometimes do B, with fixed probabilities). In the latter case, it may also be stable for some individuals always to do A, and others always to do B: that is, there may be a stable genetic polymorphism, instead of individuals adopting a mixed strategy. For some models, however, there is no ESS: the frequencies of different strategies in the population cycle indefinitely. It seems that Sinervo and Lively (page 240 of this issue¹) have now found a real example of that phenomenon.

The logic of the case they describe is that of the 'rock-scissors-paper' game: rock beats scissors, scissors beat paper, and paper beats rock. In the side-blotched lizard, *Uta stansburiana*, males have one of three throat colours, each associated

with a different behaviour. The difference between colour morphs is highly heritable. Orange-throated males establish large territories, within which live several females. A population of such males can be invaded by males with yellow-striped throats: these 'sneaker' males do not defend a territory, but steal copulations. The orange males cannot successfully defend all their females. However, a population of yellow-striped males can be invaded by blue-throated males, which defend territories large enough to hold one female, which they can defend against sneakers. Once sneakers become rare, it pays to defend a large territory with several females. Orange males invade, and we are back where we started from.

The empirical support for these conclusions is as follows. The frequencies of the three morphs were followed for a complete cycle, lasting six years. The fitness of individual males was estimated from the number of females they monopolized, or shared with neighbours. The regression of fitness on the type of neighbour was also estimated. These fitness values were of

precisely the kind to drive the cycle. In particular, no morph was fitter than all others when it was common, so no pure ESS exists.

There is a special pleasure when a curious piece of natural history fits a theoretical prediction. The observation of three distinct male strategies is not new. Gross and Charnov² described three kinds of males in bluegill sunfish: territorial males,

sneakers and female mimics. But it turned out that there are only two lifetime strategies: grow big, and hold a mating territory, or sneak when young, and then, when too big to hide, pretend to be a female and enter the mating territory that way. This is an example of a two-strategy mixed ESS, or, more probably, a genetic polymorphism. In stoats³, there are also three male strategies: territory holders, sneakers

and 'roamers'. However, the strategies again turn out to be in part dependent on age. Young males either hold territories, or sneak copulations. Older males are dominant in interactions, even with territory holders, and roam around acquiring copulations. In neither of these cases is there any reason, in theory or observation, to suspect cycling.

The mere fact that, in the lizard case, no morph is uninvadable is not sufficient to ensure a frequency cycle: there might be a stable polymorphism. Analysis of the rock-scissors-paper game suggests that the cause of cycling, as opposed to polymorphism, may be subtle and hard to measure. However, a simulation incorporating the measured fitnesses of the three lizard morphs did in fact cycle.

Are there other games that cycle? If only two pure strategies are available, cycles will not happen for plausible pay-off values. But if there is a single variable, size for example, that can vary continuously, there may be no ESS. Instead, there can be a sawtooth oscillation: for example, size may increase gradually until a threshold is reached, when the population can be invaded by very much smaller individuals. Myself and Brown⁴ tentatively suggested that such a game might account for the apparently anomalous observation that 90 per cent of mammalian lineages get larger with time, yet the size distribution across species does not increase. We proposed that lineages get larger because of male-male competition, but large size lowers fitness in contexts other than competition, so that large individuals can be replaced by smaller mutants, or, more plausibly, by a smaller species. This would result in a sawtooth oscillation, with gradual increases and sudden decreases in size. Roughgarden⁵ observed that a reverse type of cycle has occurred in Caribbean lizards. On islands, lizards get smaller as an ecological adaptation, but are then replaced by a larger species through interference competition. Both of these cases involve species replacement: an intraspecific cycle would require invasion by a mutant of implausibly large effect.

It seems, then, that Sinervo and Lively have reported the first example of a population cycle caused by frequency-dependent changes in fitness arising from intraspecific interactions. I suspect that it will not be the last. □

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EXTRASOLAR PLANETS

Silhouettes of future worlds

A HOPEFUL assumption among many astronomers, science-fiction readers and those who are pessimistic about the human race is that planetary systems are commonplace. Unfortunately there has been little evidence for extrasolar planets until the past few years, with tentative detections of a few massive planets (*Nature* 378, 355-359; 1995 and 379, 397-398; 1996) and increasingly strong indications of the existence of protoplanetary systems, in the form of disks of gas and dust around young stars. But now six disks have been imaged directly by the Hubble Space Telescope, and an analysis of their properties by Mark J. McCaughrean and C. Robert O'Dell (to appear in the *Astronomical Journal* in May) hints that more than half of all stars may form planetary systems.

Four of the six are shown here, seen in silhouette against the bright background of the Orion nebula. Their appearances indicate a common disk-like shape seen at different angles, with the uppermost nearly edge-on, hiding its central star. The stars are between 0.8 and 3 million years old and similar to the Sun in size, from 0.3 to 1.5 solar masses.

Contrary to theorists' expectations, McCaughrean and O'Dell find that the disks have sharp edges. Encounters with other stars may be responsible for trimming the disks, in which case the implied rate of encounters is consistent with their being able to survive for about ten million years, which should be long enough to form planets.

The authors also note the significance of similarly dark components in many of the small ionized circumstellar clouds in Orion, and of an infrared 'excess' in the spectrum of 60 to 80 per cent of all the stars in the cluster. It seems that disks are indeed common. But is there enough material in them to make planets?

McCaughrean and O'Dell can only put lower limits on the mass of dust, because it is likely that the disks are opaque at optical wavelengths, and so the space telescope can't 'see inside' them. The lower-limit masses are not enough to form planetary systems like ours. A better estimate can be made using millimetre wavelengths, where the disks are almost transparent. Until those results come in — perhaps within the next few months — we can all be much more justifiably hopeful, if not yet quite convinced.

Stephen Battersby



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