

molecular parasites^{4,5}. Good parasites might wish to be gentle with hosts. (This is, for instance, the textbook explanation for the rapid loss of effectiveness of the myxomatosis virus introduced to control Australian rabbit populations in the 1950s — an attenuated parasite spreads more slowly but more surely through a larger and healthier host population⁶.)

The eukaryotic transposable element P, an inhabitant of the *Drosophila* genome, provides another intriguing example of self-restraint at the molecular level⁷. Some 30–50 partial or complete copies are borne by *Drosophila* strains designated P. The mating of P males with females from element-free M strains produces sickly and nearly infertile ('dysgenic') hybrids as a direct result of unrestrained P replication. Hybrids which do survive produce, over several generations, flies of increasing vigour with increasing tolerance to mating with P males. The hybrid stock has itself become P, and is said to have acquired P cytotype.

There are many ways this could be explained but the recent model of O'Hare and Rubin⁸ has particular appeal. P encodes, they suppose, a transposase and a regulator of transposition. The latter not only affects transposase activity (or synthesis) negatively, but its own activity (or synthesis) positively. Thus "in a dysgenic cross, P factor DNA is introduced into a background where there is neither transposase nor regulator, and expression of both functions leads (at least initially) to transposition. With time, positive feedback by the regulator of its own level of activity produces enough regulator to shut off transposition and the P cytotype is established".

The evolutionary value of self-restraint in transposable elements seems obvious intuitively, but it is always reassuring to have intuition confirmed by theory. The mathematics can be made fairly simple⁹. If χ is the average copy number of the element per cell, the net rate of multiplication for each cell in a (potentially) exponentially growing host population can be written as an expression in three terms, $\rho(\chi) = \phi(\chi) - \gamma \frac{d\chi}{dt} - \omega$. $\phi(\chi)$ is the rate of cell division, which may be diminished as the element load increases; γ is the probability that each new transposition causes lethal mutation; and ω is the basal level of cell mortality independent of the element load. For an element without any form of restraint, both χ and $d\chi/dt$ will increase exponentially with time and in due course $\rho(\chi)$ becomes negative. This may be due partly to declining $\phi(\chi)$, but mainly to rapidly increasing $\gamma d\chi/dt$. Once $\rho(\chi)$ is negative, host cells are dying faster than they are born so the host cell population is driven to extinction and with it the element itself. On the other hand, if the element acquires the trick of restraining its transposition so that its copy number is limited to n , then (provided $\phi(n) > \omega$) the cell multiplication rate remains positive as $d\chi/dt$ goes to zero. The upshot is

that, although the element may impose some small loss of fitness on its host, measurable as $\phi(0) - \phi(n)$, both of them continue to exist.

It takes little insight to deduce that, given these two alternatives, the better strategy for the transposon in the long run is to exercise self-restraint. The selection mechanism by which this outcome is reached is not entirely straightforward, however, since the force at work is the comparatively weak evolutionary process of group selection¹⁰; that is, it is through competition between groups, or clones, of cells containing both types of element that the unrestrained ones are eliminated and the restrained ones arise. Should competition arise within a clone, as would happen if a *Tn10* pIN mutated to become unresponsive to the inhibitory effect of pOUT, the unrestrained mutant would enjoy a temporary but strong selective advantage until the clone

was extinguished. Theory predicts that this type of behaviour should from time to time be observed, and it will be interesting to see if this is the case. □

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Waves and particles: the diffraction of electrons

LOUIS DE BROGLIE sparked one of the most productive controversies in twentieth-century physics when he suggested that a frequency could be associated with a fundamental particle of matter as though it consisted of a group of waves. Could wave-particle duality be experimentally demonstrated?

Two independent experiments performed in 1927 implied that it could: the first, a study by Clinton Davisson and Lester Germer, of the scattering of a narrow beam of electrons off a nickel crystal; the second, by George Paget Thomson, of the diffraction of electrons transmitted through thin films. Their respective detectors were a galvanometer and a photographic plate. In Thomson's first experiment, electrons from a cathode-ray tube traversed an extremely thin film of celluloid 10 cm in front of the photographic emulsion, the whole apparatus being evacuated to avoid attenuation of the electron beam by air molecules. A pattern of concentric rings certainly appeared, but the argument for electron diffraction was not

quite watertight since the atomic structure of cellulose was not yet accurately known.

Gold foil was substituted to provide a crystalline lattice of known structure, and shown here are the photographs which Thomson initially obtained (October 1927 at the University of Aberdeen). Larger rings (right) are associated with lower energies, as measured by the spark gap of the induction coil. The patterns, wrote Thomson later, "at once gave rings which agreed quantitatively with the theoretical expectation for a face-centred cubic lattice of side 4.06 Å". He concluded that the detailed agreement between his studies of electron diffraction and the de Broglie theory "must, I think, be regarded as strong evidence in its favour".

The photograph is reproduced by courtesy of the Science Museum (Natural History), where Sir George Thomson's original apparatus is also displayed. □

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