work, however, was in demonstrating that solitary waves retain their shape (this time in a crystal), even after colliding with each other. The authors invented the name soliton for these waves, just to emphasize that although a soliton is a solitary wave it retains its identity, even after a collision. The change of 'ary' to 'on' is not surprising, incidentally — physicists call things 'ons' at almost every opportunity (take electron, meson and photon, for instance) because the Greek word 'on' means solitary, and in each instance the suffix signals the principle that the entity concerned retains its characteristics.

We are well aware that a beam of light, even if it is emerging from the now familiar laser pointer used by lecturers, will spread out and change shape as it propagates. In air, this is all that will happen. But what about light propagation in other media, especially photorefractive materials — which, importantly, already have a mature fabrication technology to back them up? In this case light always heads for the region of highest refractive index (think of how a lens works), and a photorefractive material such as lithium niobate is special because the light grabs hold of the electrons and forces the index up, precisely and only where the beam is travelling. This is just what is needed to stop light rays from inside the beam from bending outwards and causing a change in beam shape. When beam spreading is stopped by the photorefractive material, a spatial soliton is formed and the beam can now be used as a stable optical guide, just like the familiar optical fibre.

The spatial soliton is, however, better than the fixed, 'hard' waveguide such a fibre constitutes. The reason is that it is a 'soft' guide that is easily tunable by changing the beam size. Furthermore, these soft guides can be set up at a millionth of a watt of power in most photorefractive materials. Having done this, the incredible thing is that tasks can be performed inside the guide. For example, another light beam can be sent down it at a million times this power, provided its colour forbids the grabbing of more electrons to change the guide, size or direction. Many more applications can be imagined for these novel waveguides, such as using them for optical wiring, to steer one beam with another in addressable arrays, and to act as switching devices and as logic units for a whole range of information processing and computing.

The reason why the new work of Mitchell and Segev is really compelling is because they have come up with a new soliton just when we have all become used to using coherent (laser) beams in which the phase at one point determines the phase at all points. Spatial solitons — self-trapped beams — which have randomly varying phase yet maintain a smooth, well-defined, constant profile in photorefractive materials, are a

truly significant outcome of modern soliton and materials science because of the ease with which they can be manipulated. Although there are still worries about how fast the photorefractive materials can react to light, or changes of beam direction, the discovery should herald an era of new, all-optical processing devices that are cheap and easy to implement. Russell's observation did

not change physics or technology in his own century nor most of our own. But with the real possibility of optical soliton communication systems and all-optical processors now on the horizon, it may well transform them next century. □

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Theoretical biology

A robust view of biochemical pathways

Leland Hartwell

Stanislaw Leibler, a physicist from Princeton University, and his student, Naama Barkai, have taken a fresh look at the design of a biochemical pathway. They have formulated a new concept, robustness, which has fundamental implications for the tolerance of genetic polymorphisms in outbred populations (page 913 of this issue: *Nature* 387, 913–917; 1997). Biochemical pathways are composed of groups of proteins that cooperate to transmit signals (as in the induction of gene expression by an extracellular hormone) or to function as machines (as in DNA replication).

Barkai and Leibler consider the chemotaxis pathway of bacteria, a set of 12 proteins that receives signals from the extracellular environment and transmits these signals to the molecular machinery that controls the motion of the bacterial flagella. This pathway allows bacterial cells to swim up gradients of attractants (such as food) or down gradients of repellents (such as poisons). Barkai and Leibler pose the following questions. Does the pathway work the way it does because evolution has fine-tuned the kinetic parameters and amounts of proteins to achieve the desired behaviour? Or is there something more fundamental at work in the construction of the pathway — something that is insensitive to fine-tuning, which they term 'robustness'.

To tackle these questions, they develop a computer simulation of the chemotaxis pathway and substitute altered kinetic constants and protein concentrations to see what effects these changes will have on the behaviour of the system. After thousands of simulated experiments they come to the conclusion that one aspect of the chemotactic response, the ability of the system to adapt to its basal state of response after perturbation, is robust. That is, gross changes in many parameters do not alter the ability of the system to adapt precisely (in this case for the frequency with which the bacterial flagella switch their direction of rotation to return to the frequency characteristic of no signal). More than 80 per cent of simulations in

Figure 1 *Escherichia coli* and its flagella in false-colour glory. Barkai and Leibler's concept of 'robustness' stems from their simulations of the bacterial chemotaxis signalling system ($\times 8,000$).

which every parameter had been changed randomly by a factor of two, or simulations in which any one parameter had been changed by several orders of magnitude, displayed nearly perfect adaptation. The robustness of adaptation is accounted for as a design principle of the pathway — one output of the signalling system (protein methylation) is a negative feedback circuit that reduces signal from the receptors.

Now, the types of changes that the chemotactic pathway is insensitive to are the types of changes that would occur naturally in an outbred population — natural polymorphisms that affect kinetic parameters or amounts of proteins. As a geneticist working with the yeast *Saccharomyces cerevisiae*, I am familiar with the curse of genetic polymorphisms. A particular mutation can be lethal in one background and have no apparent effects in another. The profound effects of genetic background lead one to wonder how outbred populations are able to tolerate all

the combinations of polymorphisms that exist in the population.

The concept of robustness suggests an answer. Biochemical pathways are constructed in such a way that their output is relatively insensitive to the types of variations that occur in natural polymorphisms. One might say that this result is inevitable, because any polymorphisms that frequently resulted in combinations that were lethal or caused infertility would be eliminated. However, Barkai and Leibler did not limit themselves to naturally occurring polymorphisms. If their simulations apply to the real world, their results imply that at least this particular pathway is insensitive to almost all polymorphisms.

How can we begin to think about the implications of genetic diversity on the biology of outbred organisms? Simple concepts that come to mind are those of complex traits and genetic modifiers, ideas that ultimately centre on one or a few genes. Rather than focusing attention on individual proteins, Barkai and Leibler suggest focusing attention on the collection of proteins that constitute a biochemical pathway. To generalize their concept, one could imagine that all pathways are constructed to be insensitive to fine-tuning. Although this hypothesis is certainly not justified by consideration of only one pathway, and that by simulation only, the idea leads to many interesting questions that are ultimately subject to experiment.

Obviously, the first question is what the consequences are if diversity is generated in a real cell. A second is the issue of what constitutes a pathway. The chemotaxis pathway considered by Barkai and Leibler is composed of 12 proteins sitting in a cytoplasmic sea of several thousand other proteins. Is the set that we consider a pathway the same as the set that evolution has considered a pathway? How could we tell? A result of Barkai and Leibler's suggests a test. They found that the ability to adapt to basal response was robust but that the time required to adapt was not. The set of proteins that constitute one pathway and affect one behaviour might be tested to see if they are part of or distinct from the set that constitute another pathway (and affect a second behaviour), in the following way. Introduce variation in one set of proteins that perturbs a non-robust parameter of behaviour 1; then determine whether this change affects a non-robust parameter of behaviour 2.

A further question is what the robust parameters of other pathways might be. An answer would identify the most important output of a pathway, the characteristic that was selected by evolution to be robust. Finally, do apparently redundant pathways exist because one has been selected to be robust for one output whereas another has been selected to be robust for a different output, thereby allowing the cell to be robust to both

outputs? It might be fruitful to consider genetic disease as due to those rare alleles that map outside the zone of robust variation.

Readers should turn to the paper itself on page 913 to find out in more detail about the authors' ideas. I am sure they will think of

many more questions that can now be formulated as a result of this powerful concept of robustness. □

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Biological oceanography

Sulphur, climate and the microbial maze

Gillian Malin

It might seem strange that marine algae and climate are linked, but there is a connection and it occurs through the production of a compound which breaks down to release volatile dimethyl sulphide — DMS, $(\text{CH}_3)_2\text{S}$ — and acrylic acid. Formation of the volatile trace gas has implications that go far beyond the level of an individual cell or microbial population, because DMS is a key compound in the global sulphur cycle and its oxidation products influence atmospheric acidity, as well as cloud formation and the Earth's temperature¹. The compound in question is dimethylsulphoniopropionate (DMSP), which algae synthesize to help maintain their

osmotic balance with sea water.

Papers on pages 891 and 894 of this issue advance our understanding of how DMS is produced in the marine environment. Gage *et al.*² reveal the biochemical pathway for DMSP synthesis in a diverse group of marine algae. Wolfe and co-workers³ provide fresh insight into the involvement of grazing microzooplankton in releasing DMSP from marine phytoplankton cells.

The main sources of DMSP in the natural environment are marine phytoplankton blooms, where high levels of primary production and biomass occur on a timescale of weeks (Fig. 1), and phytoplankton assem-

Figure 1 False-colour satellite image depicting the reflectance due to a large-scale bloom of *Emiliana huxleyi* in the northeast Atlantic, south of Iceland, in June 1991. Blooms such as this produce large amounts of dimethyl sulphide (DMS), the oxidation products of which influence atmospheric chemistry and climate. The rainbow colour scale represents high (red–orange) to low (blue–violet) levels of reflectivity of the upper layer of the sea. The reflectivity, which intensifies towards the end of a bloom, is due to the cells shedding coccoliths into the water column as they grow. (Image processed by S. Groom, Remote Sensing Data Analysis Service, Plymouth Marine Laboratory.)