way round this problem is to use a gain doublet[8] — that is, two closely spaced regions of gain where the zone between has steep anomalous dispersion but without strong pulse distortion (Fig. 1b). This is what Wang *et al.*[5] have now achieved.

The experiment by Wang and co-workers creates this type of gain doublet in a six-centimetre cell containing caesium gas by using two laser fields closely spaced in frequency (see Fig. 1a on page 277). They first measured the refractive index of the caesium using a third 'probe' laser, and produced a dispersion curve similar to Fig. 1b, with a steep gradient in the anomalous dispersion region corresponding to an expected $v_g = -c/330$. When they sent a 3.7-microsecond light pulse through the medium, it appeared at the exit of the cell before it arrived at the entrance. Although the pulse itself is only shifted forward in time by a modest fraction (1.7%) of its width, this corresponds to the wavepacket leaving the cell 62 nanoseconds before it arrives — in other words, travelling nearly 20 metres away from the cell before the incoming pulse enters it. Compared with the time to travel six centimetres in a vacuum (about 0.2 nanoseconds), the 62-nanosecond lead means that the group velocity of the pulse inside the medium is $-c/310$, close to the predicted value.

In this experiment, each of the different frequency components making up the pulse experiences a slightly different dispersion in the medium. The relative phases between them are therefore changed and the pulse shape is shifted to bring the pulse wavepacket (or group velocity) forward in time. So the anomalous dispersion leads to interference between different frequency components of the pulse that produce the superluminal effect. Although amazing, this type of superluminal pulse propagation does not violate the principle of causality.

There remains, however, some debate about what is the true speed at which information is carried by a light pulse. Traditionally the signal velocity of a light pulse is defined as the speed at which the half peak-intensity point on the rising edge of the waveform travels; in this experiment, this is clearly superluminal. In contrast, some researchers argue that the true speed at which information is carried by a light pulse is not the group velocity of a smooth pulse, but rather the speed at which a sudden step-like feature in the waveform travels, which so far has not been shown to exceed *c*. Superluminal effects are especially interesting in the case of light pulses consisting of only a few photons, in which it could be argued that the group velocity is the same as the velocity of the individual photons. The type of superluminal behaviour discussed here is also predicted to apply to single photons[8], which might have implications for the transmission of quantum information. ■

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Biophysics

Science in motion

Philip Ball

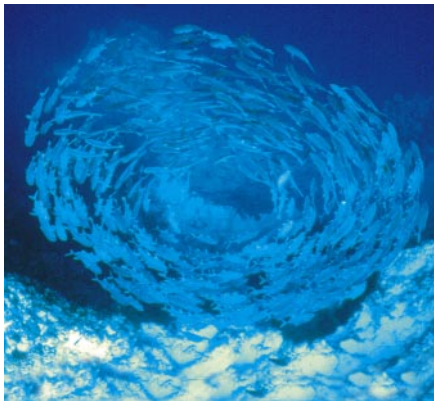
'If it moves, it's biology', goes the saying, but the moment one asks how it moves, physics intervenes. Between the release of chemical energy and the buzz of a fly's wing there is a host of minor mechanical miracles. At the other end of the scale, co-operative motions of groups of organisms ranging from bacteria to fish and humans can influence the movements of individuals. Can it be a coincidence that both fish and slime mould cells swarm in the same patterns (Fig. 1)? A workshop* in Budapest last month showed how physical and biological sciences can collaborate to explain these miracles of motion.

Motion in biology is a cascade of mechanical transduction processes, from the molecular scales of time and length upwards. At every level in this hierarchy, biological motion provides perhaps the ideal testing ground for the current migration of physicists towards biological problems. At the molecular level, the two have long been blended in conventional biophysics, which has been revitalized by single-molecule probe techniques. It is hard to imagine how, without these, one could unravel the secrets of muscle proteins such as titin — the spring that gives relaxed muscle its elasticity. For example, the inequivalence of stretching and contracting in individual titin molecules can be attributed to rapid unfolding and slow refolding of repetitive protein domains (M. Kellermayer, Pécs Univ., Hungary).

But whereas the movements of motor proteins like myosin and kinesin and springs like titin are being decoded residue by residue, it appears that something else may be needed to convert protein movements into the motion of whole cells. Migrating cells are central to embryo development and wound healing.

Myosin typically collects at the trailing edge of the cell to pull it in the direction of motion, whereas a polymerizing network of actin pushes the leading edge forward (G. Borisy, Univ. Wisconsin-Madison). How can actin, a relatively limp filamentary polymer, develop any force to push on the cell membrane? The answer, it seems, is that repeated branching of the polymers, at an angle close to 70°, ensures a constant supply of short filaments at the front edge of the network. These are stiff enough to generate the necessary force. The branching is initiated on the inside of the membrane itself by a membrane-bound protein called Wasp, which activates a second protein, Arp 2/3, to secure itself to actin and provide a junction for a branching filament.

But how do new actin monomers add to the advancing tip if it is pushing against the membrane? Here help is on hand from physics, specifically from George Oster's idea



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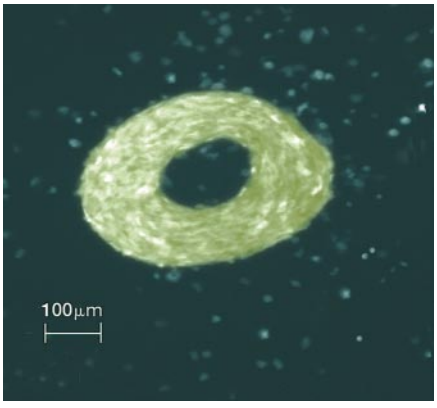

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Figure 1 **Swirling vortex motion is a mode of collective swarming behaviour exhibited by both fish (left) and slime mould cells (right).**

of a brownian ratchet. Thermal fluctuations of the flexible actin filaments expose the tip long enough for a new monomer to attach. Once the tip springs back, it ratchets the membrane forward by the length of one monomer. Brownian ratchets have found a life of their own in the physics literature; it is good to know this amounts to more than idle curiosity.

Granted that cells move, how do they know where to go? Under some circumstances — for example, during chick embryogenesis — tracking specific cells labelled with multicoloured fluorescent proteins seems to indicate a more or less random walk (R. Lansford, California Inst. Technol.). But *in vitro* studies of nerve cells known as astrocytes seem to show directional streaming motions into unpopulated areas (A. Czirók, Eötvös Univ., Budapest). M. Abercrombie suggested 50 years ago that mutual adhesion was enough to guarantee directional motion at the leading edge of a tissue. But there is directionality behind this edge too, which demands a more complex model.

Commonly, cell migration is guided by trails of attractant and repellent chemicals: the process of chemotaxis. Single-celled organisms apply this trick too, finding safety in numbers in times of stress. The best studied of these systems is the slime mould *Dictyostelium discoideum*, which aggregates into a multicellular 'slug' — a kind of 'superorganism' — when food is short. The slug cells differentiate into two types: one forms a long stalk, the other a 'fruiting body' containing spores, which will survive almost indefinitely until revived by favourable conditions. Virtually all stages of this process can now be modelled by making some simple assumptions about cell-to-cell interactions (H. Levine, Univ. California, San Diego).

Following migration, the spontaneous sorting of young cells into regions of different cell type can create coherent structures in tissues. This may be nothing more than a variation of the kind of phase separation observed between immiscible fluids (G. Forgács, Clarkson Univ., Potsdam; J. Glazier, Univ. Notre Dame). Differential adhesion between the various cell types, which is mediated by adhesion molecules at the cell surface, may create something analogous to surface tension for a cell cluster, and energy minimization would then take care of the rest. But, as ever in biology, one cannot take it for granted that variables such as surface tension will not change over time in an active cell.

At the ecosystem level, the 'why' of aggregation behaviour is not so obviously answered as for embryo cells or slime moulds. For animals that form groups, the benefits may depend on a delicate balance between such factors as foraging efficiency, distribution of the spoils and chances of attracting predators (J. Parrish, Univ. Washington). The diversity of spatial patterns arising from the tendency to aggregate offers rich grounds for physical modelling, and is as yet little understood.

Human behaviour offers another layer of complication: the veneer of social conventions. In social sciences the tradition has been to assume that these dominate — that patterns of motion are dictated primarily by considerations such as courtesy. Hence the challenge posed by simulations in which people are represented by particles moving under little more compunction than that for a particular velocity and for collision avoidance (D. Helbing, Dresden Univ. Technol.). It is unnerving to watch these streams of disk-shaped pedestrians spontaneously arrange themselves into counter-flowing streams in a corridor, or passing in groups through a door before standing back and giving a chance to those coming in the other direction. And most chilling of all is to watch these automata converge on a narrow bottleneck under conditions of mass panic, and collectively block the exit in the crush to escape.

There are useful lessons for both parties from this kind of meeting between biology and physics. Even the most conscientious of physicists cannot expect to get all the necessary information from a textbook, nor to be confident without input from biologists that the neglected details are really dispensable or the resemblances between model and experiment more than skin deep. The biologists can learn that approximations are permissible even in the most complex of systems, and that complex behaviour can (even if that does not mean it must) arise from simple principles. As one speaker remarked, to make the interaction work, "we all have to be in the same room." ■

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Neurobiology

Parallel sensing

Mathew E. Diamond

Having a poorly developed visual system, rats use their whiskers to navigate, to explore, to detect objects, and to determine the size, shape and texture of those objects[1]. The 30 or so whiskers on each side of the snout sweep back and forth about four to ten times a second. This 'whisking' motion greatly expands the space that can be sampled, but it also complicates the calculations that the brain has to perform to identify the location of an object. The information carried by the nerves emanating from the whiskers is complex: what was touched, and where and when it was touched, must all be represented in the brain. This could easily overload the capacity of a single sensory pathway. On page 302 of this issue, Ahissar and colleagues[2] propose a possible solution, by showing that these different sorts of

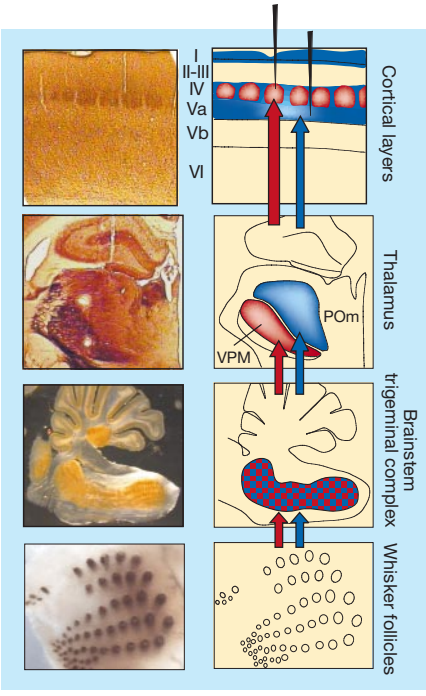

Figure 1 **Parallel pathways for touch. Left, histological tissue from various levels of the rat's whisker sensory system. Right, the lemniscal (red) and paralemniscal (blue) sensory pathways, from receptors (bottom) to cortex (top). Bottom, the skin of the snout, where the follicle of each whisker is visible. Sensory fibres lead from here to the brainstem trigeminal complex, where lemniscal and paralemniscal pathways are not yet distinct. Fibres then lead to the thalamus, where neurons in the ventral posterior medial nucleus (VPM) exhibit properties specific to the lemniscal pathway, and neurons in the posterior medial nucleus (POm) show properties specific to the paralemniscal pathway. The two pathways then lead to different cortical layers. Ahissar *et al.*[2] recorded the activity of neurons in all these brain regions (black lines show the positions of recording electrodes in the cortex). Their results show that the lemniscal pathway may convey information about what is touched by the whiskers. The paralemniscal pathway may encode information about the location of the touched object. Photographs supplied by S. Haidarliu and E. Ahissar.**