

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 ‘super-organism’ — 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 objects¹. 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 colleagues² propose a possible solution, by showing that these different sorts of

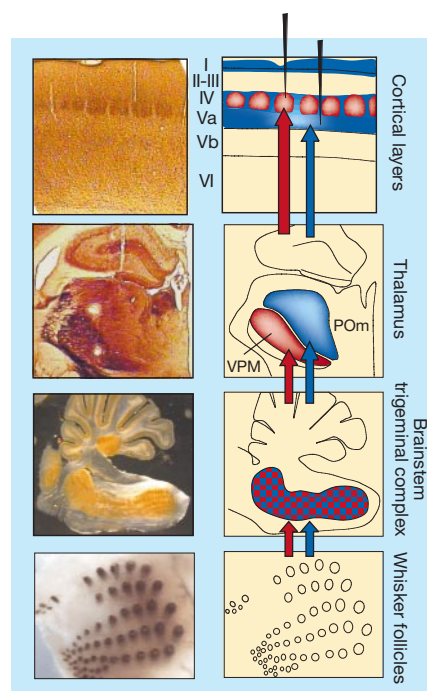


Figure 1 Parallel pathways for touch. Left, histological tissue from various levels of the rat's whisker sensory system. Right, the lemniscal (red) and paralemniscal (blue) sensory pathways, from receptors (bottom) to cortex (top). Bottom, the skin of the snout, where the follicle of each whisker is 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.

information are segregated into two sensory channels.

Neuroscience students learn that, in touch, vision and hearing, signals evoked by external events are quickly and reliably channelled to their respective sensory areas in the cortex of the brain through 'relay' neurons in the thalamus (Fig. 1). These channels have been termed 'lemniscal' pathways. But neuroanatomists have long recognized that the lemniscal groups of cells ('nuclei') occupy less than half the volume of the thalamus associated with each type of sensation. The remainder belongs to 'paralemniscal' sensory pathways. The physiological properties of paralemniscal neurons in the thalamus are difficult to classify using typical sensory stimulation protocols. So it has been difficult to assign any specific function to these pathways. But now, Ahissar *et al.*² suggest that the paralemniscal pathway associated with touch information picked up by a rat's whiskers can relay to the cortex information about the position of touched objects.

Each full forwards-backwards sweep of a rat's whiskers is called a whisking cycle. For the brain to obtain any useful information about the location of objects touched during this cycle, it needs to reconstruct the trajectory of the whiskers. Conceivably, the sensory cortex could receive data about the cycle directly from the motor systems that generate the whisker movements. But this does not appear to be the case. Motor cortex, although a major source of input to sensory cortex, does not carry a strong signal about whisker position³. By default, then, information about the whisking cycle must arise through a signal transmitted from the whiskers.

To identify the signal that reveals whisker position, Ahissar *et al.*² induced whisker movement in anaesthetized rats by directing air-puffs along the nose. The whisker deflections, in the range of 2–8 Hz, were taken as experimentally controlled whisking cycles.

The flow of information from whiskers to cortex is shown in Fig. 1. Lemniscal signals are transmitted from receptors at the base of the whiskers, via the brainstem trigeminal complex, to the medial portion of the ventral posterior nucleus of the thalamus (VPM), ending up in the tactile region of cortex. Paralemniscal signals are transmitted along a similar pathway, but through the medial portion of the posterior nucleus (POm) in the thalamus. Ahissar *et al.* looked at the neuronal responses to whisker movement in each of these brain regions. For each frequency of whisker deflection, the authors aligned the neuronal responses across cycles to yield an average response per cycle. They then measured the response latency (the time between the start of whisker movement and the beginning of neuronal activity) and response magnitude (the number of 'spikes' of neuronal activity per whisker movement).

They found that neurons in the trigemi-

nal complex — where the lemniscal and paralemniscal pathways are not yet distinct — fired with an identical response latency and magnitude regardless of whisking frequency. In both VPM and POm, by contrast, the response magnitude decreased as the frequency increased. But in VPM, response latency was constant regardless of frequency, whereas in POm response latency increased as whisking frequency increased. Neurons at the cortical targets of the two pathways (cortical layer IV for VPM, and layer Va for POm) behaved similarly to their thalamic inputs.

Ahissar *et al.* propose that a feedback circuit between sensory cortex and POm is responsible for the latency shifts with increasing whisking frequency. Cortical neurons in layer V have intrinsic oscillatory mechanisms⁴ and a powerful influence on POm⁵. Ahissar *et al.* suggest that POm neurons activate cortical inhibitory neurons; these then inhibit the cortical oscillators, which in turn drive cortex-to-thalamus feedback. The properties of this loop could account for the changing response latency seen in POm.

There is no direct proof that such feedback loops can decode whisker position. But Ahissar *et al.* have shown that this varying response to whisking frequency endows the paralemniscal system with the ability to process temporal information — such as object location — that varies on timescales as slow as single whisking cycles. By comparing the timing of feedback descending from the cortex with the timing of information ascending from the whiskers, POm neurons could signal where along the whisking sweep an object is located. The lemniscal pathway, by contrast, responds with a fixed latency, so it is better suited to representing object features — such as surface texture — that do not vary along the whisking cycle.

Can these ideas be generalized to other

sensations? What must be represented by the brain is unique to each kind of sensation, so one cannot expect the nature of sensory coding to be identical. The tactile sensory pathways form neural representations of objects that contact receptors in the skin; the visual and auditory systems form representations of objects at a distance.

But the observations made by Ahissar *et al.* raise some interesting ideas about how non-tactile stimuli may be represented. For example, neuroscientists debate whether the transmission of information is based on neuronal firing counts over relatively long time windows ('spike-count' coding) or on variations in neuronal firing within brief time windows ('spike-time' coding). Ahissar *et al.* have shown that it may be efficient for these codes to coexist. POm neurons transmit information about the frequency of whisker movements by shifts in response latency — a clear spike-time code. But the response latency determines the time window available for firing, so these timing shifts lead to spike-count differences, too. So frequency information is present in both the total spike count and the spike timing.

Time will tell whether or not these results can be applied to other sensory systems. But it seems that, at least for touch, the parallel pathways long recognized by neuroanatomists are beginning to acquire functional significance. ■

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Atmospheric physics

Enlightening water vapour

Brian J. Soden

The extent to which the Earth's climate will warm as a result of increasing carbon dioxide in the atmosphere depends largely on the response of water vapour in the upper levels of the troposphere (roughly 5–10 km above the surface). But our ability to monitor changes in water vapour there is limited by the scarcity of observing systems with sufficient accuracy and longevity to document its global variation and to detect trends.

On page 290 of this issue¹, Price demonstrates a remarkably robust relationship between upper tropospheric water vapour

and global lightning activity. This observation not only supports the idea that atmospheric convection moistens the upper troposphere, a characteristic of climate models that has been the subject of spirited debate², but may also provide a unique tool for monitoring purposes.

The importance of water vapour in regulating climate is without question. It is the dominant greenhouse gas, trapping more of the Earth's heat than any other gaseous constituent of the atmosphere. If water vapour concentrations increase in a warmer world, as is widely believed, the added absorption