Animal navigation

The bee's celestial compass

from R.C. Hardie

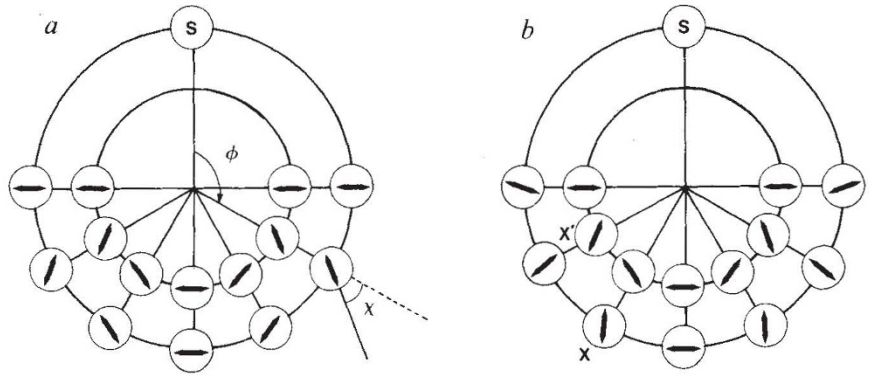
FORTY years ago, the famous experiments of Karl von Frisch showed that bees can navigate using polarized light patterns in the sky[1]. The mechanism by which they perform this feat remained unknown until a recent series of experiments led Rossel and colleagues to propose a simple, comprehensive solution to this classic problem[2-4]. On page 128 of this issue[4], Rossel and Wehner describe an ingenious and stringent experiment to test their hypothesis, which emerges unscathed.

The polarized light pattern in the sky derives from scattered sunlight, the direction of polarization (*e*-vector direction) always being at right angles to the plane defined by the observer, the Sun and the point in the sky being observed. A predictable but rather complex pattern is thus generated that changes as the Sun moves through the sky. The bee's problem is to deduce the Sun's bearing from the *e*-vector pattern even when only one small patch of blue sky is visible. The essence of the hypothesis of Rossel *et al.* is that, rather than performing celestial trigonometry or being informed of the patterns in all their detail, the bee possesses only a simplified map of the *e*-vector distribution in the sky.

In the bee's map (see figure) any given *e*-vector direction is assumed to have a fixed bearing with respect to the Sun irrespective of elevation in the sky or time of day. For example, a patch of sky with a horizontal *e*-vector lies exactly opposite the Sun (180°), a vertical *e*-vector at 90° to the Sun and so on. Ambiguities arising from the fact that any *e*-vector direction, in general, occurs at two positions in the sky are avoided by assuming that the *e*-vector lies in the half of the sky opposite to the Sun[5].

The map is embodied in an array of ultraviolet-sensitive photoreceptors in the dorsal rim of the eye[6]. Each photoreceptor is maximally sensitive to a particular *e*-vector direction, the direction rotating from the back to the front of the eye[7]. To use this map Rossel and Wehner suggest that the bee simply turns until the retinal map is in register with the *e*-vectors in the sky. When this is achieved, the photoreceptors generate a maximal signal that tells the bee that she is pointing directly away from the Sun. Because the bee's map is invariant, and corresponds only to the actual *e*-vector distribution at dawn and dusk, mistakes are bound to occur under certain conditions. It is these mistakes that led Rossel *et al.*[2] to deduce the bee's generalized map.

The mistakes, central to the hypothesis of Rossel *et al.*, distinguish it from the two other major hypotheses that seek to explain the bee's performance: (1) that the bee uses some abstract knowledge of the laws of scattering to reconstruct the Sun's position by celestial trigonometry[8]; or (2) she has a precise knowledge of the real *e*-vector distribution in the sky[9], either from a memorized 'snapshot' or from a hard-wired celestial almanac. There is still a discrepancy in the literature because previous studies[3,10] failed to detect mistakes like those made by the bees of Rossel and colleagues. Although no recent data contradict the extensive results of Rossel *et al.*, independent confirmation would be welcome.



The bee's map (inner circle). A given *e*-vector direction, χ, is assumed to lie on a fixed bearing, ϕ, with respect to the sun (S). The bee rotates until her retinal map is in register with the *e*-vectors in the sky (outer circle) and then assumes she is facing directly away from the Sun. At dawn and dusk (*a*), the celestial *e*-vector distribution matches the bee's map perfectly; with the Sun 24° above the horizon (*b*), a different *e*-vector pattern arises. If the bee can see the whole sky she will still orient correctly because the errors in the left and right halves are in the opposite direction and will cancel each other out. If, however, she can see only one point, for example X, she would rotate until X′ coincides with X, thus making an error of 30°. (Adapted from ref. 3.)

In their early work, Rossel and colleagues showed that the single, invariant map of the bee is used under all conditions tested. In their new work they test the specific formulation of their hypothesis: namely that the bee rotates, scanning the sky with the map embodied in her retinal array and then interprets the direction which gives maximum output as pointing directly away from the Sun. With the real sky this occurs when the *e*-vectors in the sky are in register with the individual *e*-vector sensitivities of the photoreceptors. However, in the experiment the signal is generated by modulating the intensity of an ultraviolet light source using a feedback device to ensure that the intensity reaches a maximum when the bee reaches a predetermined position. The fact that this ingenious simulation does in fact result in the bee orienting just as she normally would do to the appropriate *e*-vector provides direct evidence for the scanning strategy proposed.

Rossel and Wehner's hypothesis has all the hallmarks of being correct. It is a classically simple solution to one of the more impressive intellectual feats in the animal world. It has successfully withstood a battery of experiments, the results of which would be perplexing, to say the least, on any other hypothesis.

The bee's strategy, although capable of generating blatant navigational mistakes in experimental situations, is likely to perform quite satisfactorily under natural conditions. In particular, errors induced in the left and right halves of the eye will be opposite in sign and will thus tend to cancel each other out. Further, as well as actually being correct at dawn and dusk, the bee's map of the celestial *e*-vector distribution also happens to represent the average values as they occur in the most polarized band of the sky[3]. In other words, with limited hardware the bee has developed the single map that is most likely to be correct at any time.

This is by no means the end of the story. Future developments are likely to occur on at least two fronts. First, it will be interesting to see how widespread this mechanism is. Many insects (including

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desert ants[11], crickets[12] and flies[13] have recently been shown to have similar arrays of polarization-sensitive photoreceptors in dorsal eye regions, and the desert ant, which also navigates by celestial polarization patterns, makes analogous navigational errors to the bee[14].

Second, progress may soon be made in unravelling the mechanisms of information processing. The work of Rossel and Wehner provides an indication of what sort of interneurones we might expect to find, and some elegant anatomical studies in the fly, which use the powerful technique of trans-synaptic cobalt migration, identify many of the interneurones in the polarization-sensitive pathways of this insect[15]. □

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Surface science

Helium atoms reveal phases

from J.A. Venables

HELIUM atom scattering is the ultimate surface tool, in that penetration into the bulk can be entirely neglected. The latest of several powerful tools for studies of surface structure and vibrations to reach maturity, the technique has in the hands of a group at Jülich, West Germany[1-4] revealed surface phonons on a platinum crystal and, in physisorbed xenon on platinum, two-dimensional phase changes and a series of discrete transitions towards bulk behaviour as the number of atomic layers is increased.

Such work clearly demonstrates that helium atom scattering is going to be important in unravelling the nature of 'two-dimensional physics' at surfaces and in adsorbed layers. But the technique has only recently become practicable through the development of high-pressure nozzle beam sources, effective differential pumping, high-energy resolution time-of-flight spectrometers and efficient single atom counting detectors. These non-trivial pieces of hardware, when attached to a large, but essentially standard, ultrahigh vacuum chamber, form the basis of the technique. The high-pressure nozzle gives a suitably monoenergetic incident beam with thermal energies of 0 to 30 meV, and the spectrometer can measure its energy width within 0.3 meV. The beams come into and leave the differentially pumped scattering chamber through small apertures with overall angular resolution of around 0.3°; thus very detailed angular scans are possible to analyse the diffraction patterns, either by rotating the sample or the detector.

Because the beam has such a low energy, it is an easy matter to distinguish elastic from inelastic scattering. Elastic scattering consists of diffraction and diffuse scattering from defects, whereas inelastic scattering results from atomic vibrations (phonons), which cause energy changes in the range 0–20 meV. In this respect, the technique is similar to neutron scattering from bulk solids, which is the main technique for determining the energies and momenta of phonons. However, in sharp contrast to thermal neutrons which travel several centimetres through solids, thermal helium beams interact so strongly that they only probe the tail of the electron distribution of the outermost atoms. Consequently the helium beam does not penetrate into the bulk. Thus with improved intensities and energy and momentum resolution, helium scattering has become increasingly competitive with low-energy electron scattering for studies of surface vibrations, and with higher energy electron and X-ray scattering for studies of surface crystallography. Of course, these latter techniques still retain advantages; in particular X-ray scattering has the highest angular resolution, whereas now electron techniques have the highest signal strengths.

These developments in helium atom techniques are well illustrated by the Jülich work on the surface phonons on a Pt(111) crystal[1], including the changes in phonon structure induced by oxygen chemisorption[2] and the structural and vibrational changes attendant on physisorbing xenon onto this same surface[3,4]. The time-of-flight spectrum on the bare (111) surface is now sufficient to show up crystallographic anisotropies in the surface acoustic (Rayleigh) wave[1]. The effect of chemisorbing oxygen in the p(2×2) structure is to halve the extent of the surface Brillouin zone, and to open up a gap at the zone boundary; this gap has now been observed very clearly for the first time[2]. Theoretical calculations invoke particular force constants which, by adjustment to agree with experiment, give information on the strength of both central and non-central forces between Pt and O atoms at the surface.

The elastic diffraction peaks studied in the case of physisorbed xenon[3] have been sufficiently sharp to study three separate phases: the commensurate (C) phase in which the Xe has the so-called $(\sqrt{3}\times\sqrt{3})R30°$ structure, in which the Xe surface mesh is $\sqrt{3}$ times the Pt mesh and is rotated by 30°; the incommensurate (I) phase compressed by around 6 per cent, and a further phase (R) compressed by around 10 per cent and rotated some 3°.

The corresponding C–I–R transitions have been seen previously for Xe adsorbed on graphite by both electron and X-ray diffraction; but this is the first time that helium atom diffraction has had sufficient angular resolution to see such transitions. Moreover strong scattering from the high atomic number bulk material would make Xe/Pt(111) difficult for either electron or X-ray diffraction. Because the helium beam sees only the outermost layer, the nature of the substrate is essentially irrelevant. In the latest work, the Jülich group have also shown that the time-of-flight spectra from these monolayer and multilayer structures are also very characteristic. Whereas the monolayer has an Einstein-like mode with essentially no dispersion, increasing layer thickness introduces dispersion, neatly revealing a discrete series of transitions towards the bulk phonon behaviour as the number of layers is increased[4]. □

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Meteoritic nitrogen

A slice through the Bencubbin meteorite found in Australia shows the shock-welded matrix surrounding metal with silicate and chondritic clasts. On page 138 of this issue, I.A. Franchi, I.P. Wright & C.T. Pillinger of The Planetary Science Unit at the Open University, UK show that virtually all the nitrogen in the meteorite is enriched with ^{15}N. The authors discuss the implications of these results for the origin of the components of the meteorite. The meteorite is about 65 cm wide.