

of uncertainty: reducible and irreducible. The former is uncertainty about the external world, and can be reduced through exploration and learning. Only limited resources prevent this type of uncertainty from being completely eliminated.

Irreducible uncertainty, on the other hand, is more interesting, especially for its effect on behaviour. As Glimcher points out, Werner Heisenberg's uncertainty principle makes clear that the physical world has a quantifiable level of irreducible uncertainty that no amount of measurement or knowledge can eliminate. Glimcher extends this claim to the behavioural realm using game theory. The basic idea is that organisms will express irreducible uncertainty in their behaviour. The driving constraint that selected for such irreducible uncertainty is the need for interacting organisms to outperform others with whom they compete or on whom they prey. If organisms had only very complicated strategies for behaviour, it is conceivable that over millions of years a competitor could adapt to those strategies. Irreducible uncertainty, as a component of a behavioural strategy, cannot be learned and exploited by an opponent. Glimcher offers several concrete examples of these ideas. One take-home message is that most complex creatures should have internal processes that are roughly equivalent to a random-number generator.

Glimcher's central programme outlined in the book is laudable: determine exactly what a particular behaviour is 'for', quantify it in formal economic terms, and design experiments around the formal model. As he freely admits, this formula, although beguiling, is easy to state but hard to carry out. It reminds me of the maxim of novelist W. Somerset Maugham: "There are three rules for writing the novel. Unfortunately, no one knows what they are." Although it's not quite that bad in neuroscience, some features such as conscious awareness are difficult to understand from a computational perspective.

On balance, the book is provocative, encouraging a serious reconsideration of the utility of most neurophysiological work in alert animals. Is it really true that all such efforts are hamstrung by the implicit bogeyman of reflex theory? In what sense do present-day neurophysiologists make implicit assumptions consistent with such a limited view? Glimcher's claim in this area will certainly raise the hackles of more than a few, but what good is a book if it does not provoke? This book will surely ignite discussion and soul searching among serious neuroscientists, and Glimcher has bravely offered us a clear model to talk about. ■

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Beauty and the bees

Form and Function in the Honey Bee

by Lesley Goodman
International Bee Research Association
 (www.ibra.org.uk): 2003. 220 pp. £25 (pbk),
 £55 (hbk)

Thomas D. Seeley

The best-studied of all the millions of insect species in the world is the honeybee, *Apis mellifera*, particularly with regard to its sensory physiology and functional morphology. Since the pioneering studies of Karl von Frisch and Robert E. Snodgrass in the early part of the twentieth century, several generations of biologists have carefully measured the powers of discrimination of worker bees in every known sensory modality, analysed the mechanisms underlying these abilities with behavioural and electrophysiological techniques, and used light and electron microscopy to explain the anatomical bases of the bee's behaviour. As a result, the honeybee provides a solid baseline for comparative studies of most aspects of insect behaviour, physiology and morphology.

The composite picture assembled from all this work is one of highly developed sensory capacities and motor performances. Honeybees see the world in colour, perceive shapes and patterns, and can resolve rapid movement. Their olfactory sense is almost identical to ours, and their sense of taste is similar but generally less sensitive. Mechanosensory perception — including touch and sensitivity to airborne and substrate-borne vibrations — is also extremely rich as the bees have thousands of sensory hairs all over the body (even on the compound eyes) and stretch receptors inside the body, giving information on position, movement and orientation relative to gravity. Honeybees even have at least a limited responsiveness to Earth's magnetic field.

These impressive sensory abilities are used for sophisticated manipulatory behaviours such as building beeswax combs and negotiating complicated flowers, flying over distances of several kilometres to reach flower patches rich with nectar and pollen, and communicating with hive mates by means of diverse shakings, tappings and buzzings, and puffings of chemicals.

Form and Function in Honeybees by the late Lesley Goodman is a modern synthesis of honeybee sensory physiology and functional morphology. The last attempt at a comprehensive treatment of the sensory basis of this insect's behaviour was von Frisch's classic *The Dance Language and Orientation of Bees*, published in 1967. Not only has the literature on the subject increased enormously since then, but there is now a greater sophistication in understanding the ecological significance



Touchy-feely: the antennae and hairs of honeybees are equivalent to human fingertips.

of each sensory ability. For example, it is now known how the bee's colour vision system, which renders bees maximally sensitive to differences in light at wavelengths of about 400 nm (violet) and 500 nm (blue), has fostered the evolution of flowers with pigment combinations that have sharp rises and falls in reflectance in these two regions; such combinations are most easily discriminated and recognized by the bees. There can be no doubt that this book addresses an important need — and meets it beautifully.

Goodman started planning this book in 1996 with the ambitious goal of producing a volume on how bees function that would be both scientifically rigorous and yet readable (and also affordable) to a broad audience of beekeepers, undergraduate biologists and research scientists. She was unable to finish this project before her death from lung cancer in 1998, but did set up the L. J. Goodman Insect Physiology Research Trust to ensure that the book was completed posthumously. Thanks to the dedicated work of Richard J. Cooter, one of her first PhD students, and Pamela Munn, deputy director of the International Bee Research Association, this final wish was fulfilled magnificently.

The book is utterly gorgeous: each page is lavishly illustrated with beautiful coloured diagrams, specially commissioned paintings

and superb micrographs. Such a beautifully crafted book is rarely seen in science. Given its large format (24 cm × 34 cm) and its opulent contents, it can be valued as much as a work of visual art as an informative work of biological science. But I wish to emphasize that this is a rigorous scientific monograph. The contents are well referenced to the scientific literature (up to the mid-1990s), and the writing is clear and crisp.

It provides a wide audience with an astoundingly beautiful and admirably accurate account of how a worker honeybee smells and sees, tastes and touches, feeds and breathes, flies and stings, secretes wax and releases pheromones. Goodman has given all who are interested in the behaviour and physiology of bees an amazing gift. ■

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More on bees

Bumblebees: Behaviour and Ecology

by Dave Goulson

Oxford University Press, £55 (hbk), £27.50 (pbk)

Universal support

Echo of the Big Bang

by Michael Lemonick

Princeton University Press: 2003. 232 pp.
\$24.95, £17.95

Sean Carroll

The first pages of Michael Lemonick's new book grab the attention. Princeton University astrophysicist David Spergel is fretting over the implications of a new discovery, made from observations of the cosmic microwave background (CMB), which according to Lemonick implies that "much of the work in cosmology over the past two decades has been based on a faulty theoretical foundation". The observations are from NASA's Wilkinson Microwave Anisotropy Probe (WMAP), a satellite that measures, with unprecedented precision, temperature fluctuations in the relic radiation from the Big Bang.

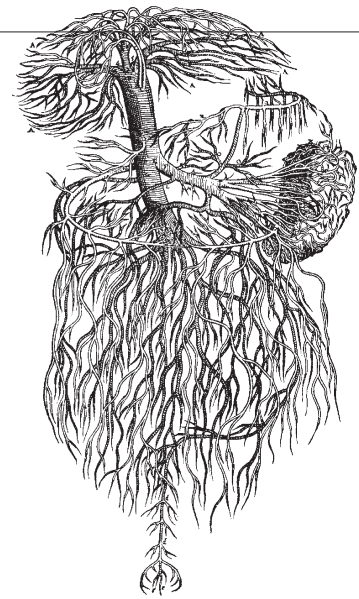
It is a gripping vignette, but puzzling: as we now know, the WMAP results didn't include any major surprises. If anything, WMAP provided a convincing capstone to a series of impressive advances in cosmology, demonstrating that our consensus picture of the Universe is fairly accurate. This picture can be hard to swallow, as it describes a Universe of which only 4% is made up of ordinary matter; the rest is a mixture of cold dark matter and an exotic 'dark energy', which remains nearly constant throughout space and time. When a purported consensus leans so heavily on the invocation of unseen substances, it is important to verify it from every

Vesalius's vessels

When Andreas Vesalius published his *De Humani Corporis Fabrica Libri Septem (On the Fabric of the Human Body)* in 1543, its accurate depiction of the human body from close observation of dissected bodies overturned centuries of medical dogma and led the way for the modern study of anatomy. William Richardson and John Carman have been translating this treatise; the third volume, containing Books III and IV from the original work, focusing on the veins, arteries and nerves, has now been published (Jeremy Norman, \$250). Although the accuracy of Vesalius' work on these soft tissues has not stood the test of time as well as the earlier skeletal work, the illustrations, like that of the portal vein shown here, are stunning. The vessels appear as if fixed in space, with the other internal organs simply invisible.

www.historyofscience.com

Mary Purton



angle; the WMAP results were justly hailed as an impressive example of such a verification.

Of course, the WMAP team did make fresh discoveries, as well as confirming existing views. The satellite measured the polarization of the CMB on large angular scales, which can be interpreted as evidence for re-ionization of the Universe by early star formation. In addition, a few tantalizing features of the WMAP data can be interpreted as evidence for something new, but these are hints rather than firm results; nobody has been moved to overthrow the theoretical foundations of cosmology.

The opening chapter does not explain the nature of the unsettling discovery to which it refers; it is a teaser, meant to draw the reader into the rest of the narrative. The mystery is only revealed near the end, where we learn that it refers to the possibility that the data indicate a finite spatial size to the Universe. But we also learn that this possibility is not taken very seriously; Spergel is quoted as saying: "We don't think it means anything." And Lemonick concludes the book by admitting that the WMAP team "wouldn't be saying anything shocking". A reader might feel somewhat cheated at this point.

This episode is emblematic of the frustrating nature of the book. Lemonick was given access to the inner workings of the WMAP team (as an embedded journalist, if you will), a collaboration whose deliberations were closely guarded from the rest of the scientific community. But Lemonick seems to want to tell a slightly different story to the one that actually happened — one in which a heroic band of plucky scientists raced against outside competition and fought valiantly against recalcitrant NASA bureaucracy, succeeding in the end in redrawing our picture of the Universe. In

reality, the talented and dedicated WMAP team worked within the context of numerous experiments, taking complementary approaches to understanding cosmology. The result was a triumph of the congratulatory rather than the revolutionary kind: we had it right all along.

The insider's view of how real scientists go about their everyday business is one of this book's strongest points. The human element is well illuminated, as in the account of the excitement and pressure accompanying the satellite launch itself. Indeed, human concerns are perhaps emphasized too much; the struggle over whether satellite components were to be assembled on Princeton's campus or at a NASA centre is likely to be less fascinating to the general reader than it was to the participants at the time.

A more important complaint is that the book takes too many shortcuts in explaining the science behind the CMB observations. It is hard to understand, for example, why the most visually striking product of the WMAP observations — a high-resolution map of the CMB fluctuations — is not included. For some reason, a simulation of the map is reproduced, but not the map itself.

WMAP (named after David Wilkinson, a team member and CMB pioneer who died in 2002) marks the end of a decade of upheaval and triumph in cosmology, which began with the original discovery in 1992 of CMB fluctuations by COBE, another NASA satellite. This book describes a small but important part of the achievements of the past 11 years. A comprehensive view of this most exciting time in the history of cosmology is a worthy story that remains to be told. ■

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