

A critical experiment that could now be done is to exploit the 'down with novelty' phenomenon, to explore the putative relationship between LTP and memory. Such a study would examine whether exposure to novelty accelerates the rate at which recently acquired information is forgotten, and what types of novelty are effective in doing this^{10,11}. Any one-trial, hippocampus-dependent memory task would be suitable. However, the difficulty with any simple relationship between novelty and hippocampal memory function is that certain natural behaviours, such as food caching in scatter hoarding mammals, involve many items of new information, all of which have to be remembered for a time¹². A memory system that could recall only the last item cached, wiping out memory of earlier items, would be unhelpful.

Because humans and animals can readily recognize and remember many novel items in laboratory situations, event novelty and context novelty may have different effects. Perhaps many new items can be successfully encoded and recalled within a single familiar environment, whereas exposure to a novel environment shortly thereafter will threaten successful recall of items recently stored in the familiar environment. Even so, novelty is unlikely to be the sole determinant

of hippocampus-mediated encoding or forgetting — returning to the example of food caching, cache retrieval resets memories. Animals do not waste time returning to places from which caches have already been retrieved.

For the present, the electrophysiological data indicate that the new can drive out the new, but not necessarily the old. Xu and colleagues' findings are another novel twist on the yellow-brick trail of the engram. □

Richard G. M. Morris is in the Department of Neuroscience, University of Edinburgh, Crichton Street, Edinburgh EH8 9LE, UK.
e-mail: r.g.m.morris@ed.ac.uk

- Xu, L., Anwyl, R. & Rowan, M. J. *Nature* **394**, 891–894 (1998).
- Bliss, T. V. P. & Collingridge, G. L. *Nature* **361**, 31–39 (1993).
- Morris, R. G. M. & Frey, U. *Phil. Trans. R. Soc.* **352**, 1489–1503 (1997).
- Dudek, S. M. & Bear, M. F. *Proc. Natl Acad. Sci. USA* **89**, 4363–4367 (1992).
- Thiels, E., Barrionuevo, G. & Berger, T. J. *J. Neurophysiol.* **72**, 3009–3116 (1994).
- Heynen, A. J., Abraham, W. C. & Bear, M. F. *Nature* **381**, 163–166 (1998).
- Errington, M. L. et al. *J. Neurophysiol.* **74**, 1793–1799 (1995).
- Doyere, V. et al. *Hippocampus* **6**, 52–57 (1996).
- Staubli, U., Chun, D. & Lynch, G. J. *Neurosci.* **18**, 3460–3469 (1998).
- Knight, R. T. *Nature* **383**, 256–259 (1996).
- Honey, R. C., Watt, A. & Good, M. J. *Neurosci.* **18**, 2226–2230 (1998).
- Jacobs, L. F. in *Behavioural Brain Research in Naturalistic and Semi-Naturalistic Settings*, (ed. Alleva, E.) 301–322 (Kluwer Academic, Amsterdam, 1995).

Evolutionary ecology

Bedazzled by flowers

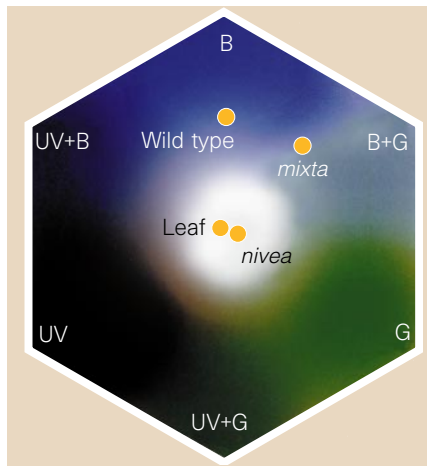
Nick Waser and Lars Chittka

Human eyes are dazzled by the diversity of flower colours, and early biologists naturally interpreted colour as a signal for other eyes — those of pollinating insects. A close look at flowers reveals surprising additional detail. Petals of the snapdragon *Antirrhinum majus*, for example, have a remarkable sparkling sheen caused by epidermal cells with a conical surface. In a recent issue of *Heredity*, Glover and Martin¹ argue that this sparkle adds to background flower colour in bedazzling and attracting bees, and their study is a welcome addition to a surprisingly small number of experiments that have explored the great diversity of floral features in higher plants.

Glover and Martin studied individual and compound effects of petal sparkle and overall colour. They used mutants at the *mixta* gene locus, which cause epidermal cells to develop a flat surface, and the *nivea* locus, which confer white rather than the normal magenta petals. The authors planted wild type, single mutant and double mutant snapdragons in a garden exposed to bees, and discovered that both *mixta* mutants (with dull petals) and *nivea* mutants (with white petals) suffer lower reproductive fitness, measured as the pro-

portion of flowers that produce fruit.

Glover and Martin conclude that bees prefer to visit sparkling, magenta flowers, thus increasing the fruit set. An alternative that would be useful to explore is that *mixta* or *nivea* genes have pleiotropic effects on characteristics other than colour, so that natural selection favours sparkle and bright colour indirectly, through the fitness value of these correlated characteristics. For example, the biochemical pathways leading to the production of flower pigments also generate



other end products that may affect survival, growth and defence^{2,3}. Reports of such correlated selection are increasingly common, and include examples of flower colour^{2,3} and other floral features⁴.

If selection does act directly through pollination, this could take several forms. Mutants might attract a different mixture of bee species than wild-type flowers. Or, they might elicit fewer visits or other behavioural changes in the same species of bee. Although direct observations of snapdragon pollination remain to be done, advances in cognitive neurobiology provide some fascinating suggestions as to how bees might respond to the different genotypes.

A preference against the white *nivea* mutants, which reflect ultraviolet light¹, is easily predicted — such flowers resemble green foliage to a bee's eye (both are 'bee-uncoloured'; see Fig. 1). A distinction that our eyes make easily is difficult for bees, whose colour perception does not code brightness⁵. A preference against *mixta* mutants could be predicted on different grounds. These mutants appear pink compared with the magenta ('bee-blue') wild-type petals, and they also lack sparkle. The angular resolution of a bee's eye is far too coarse for it to see sparkle⁶, but bees easily learn to distinguish petals of different textures with their antennae or feet⁷. The bees lack any innate bias in this tactile sensory modality, but they learn to associate texture with superior nectar or pollen reward in flowers.

Bees can also distinguish pink ('bee-bluegreen') *mixta* mutant flowers from wild-type flowers by means of their colour vision (Fig. 2, overleaf). Should *mixta* flowers offer a poor reward as a pleiotropic effect of the mutation, bees would learn to discriminate against them. Also, there is some evidence for an initial bias by naive bees against bee-bluegreen flowers, and this might have evolved because plants with such flowers often provide an inferior floral reward⁸. But this bias is easily overcome by learning⁷.

These possibilities contrast with a classical assumption that different flower colours

Figure 1 How bees perceive colour. The point generated by a coloured object in the colour hexagon informs us how bees will perceive the object through their ultraviolet (UV), blue (B) and green (G) receptors, and through further processing of receptor signals in the central nervous system. Wild-type *A. majus* flowers are 'bee-blue', whereas *nivea* mutants are perceived as 'bee-uncoloured'. These mutants are hard to detect against green leaves, which fall into the same colour category for bees. 'Bee-bluegreen' flowers, such as the *mixta* mutants, are discriminated against, either because of an innate bias or because they offer less reward.

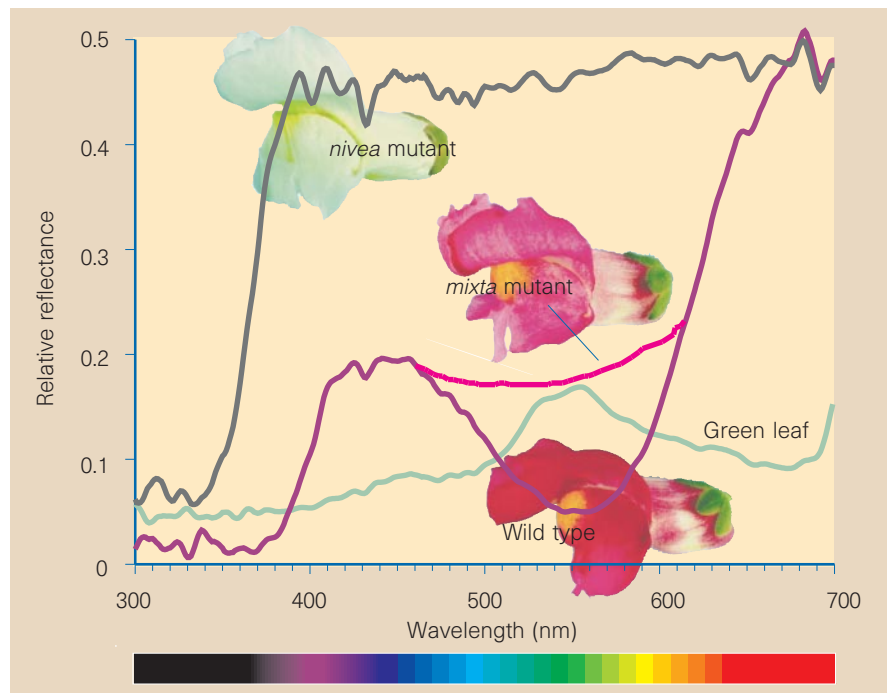


Figure 2 Reflectance spectra of *Antirrhinum majus*. A colour shift from purple to pink (as in *mixta* mutants) is generally mediated by an increase in green reflectance⁵ (pink curve). Ultraviolet-reflecting white flowers (such as the *nivea* mutants) usually reflect all light above 360 nm (grey line), whereas ultraviolet-absorbing white flowers cut off at 420 nm. Mutant spectra are inferred from flowers of over 1,000 other plant species⁵.

and shapes attract different pollinators and, indeed, that they often represent adaptations of plant species to specialize on different pollinators. This is the idea of ‘pollination syndromes’, which Glover and Martin refer to throughout, and which underlies other studies of floral evolution.

For example, the mapping by Bradshaw *et al.*⁹ of quantitative ‘speciation genes’ in monkey flowers, genus *Mimulus*, assumes that differences in flower colour and shape erect reproductive barriers between lineages, transforming them into separate biological species. This requires that different colours and shapes automatically confer specialization on different pollinators, but the evidence¹⁰ suggests otherwise — different insects and other pollinating animals possess colour vision with broad spectral sensitivity, and colour is mainly an advertisement rather than an innate attractant for experienced pollinators. In the case of monkey flowers, Sutherland and Vickery¹¹ had earlier shown that, from direct observations of pollinators, bumble-bees and hummingbirds do not specialize on different colours and shapes. So, we may have to look beyond pollinators to explain reproductive isolation between plant species¹².

Whether a bee or other pollinator prefers one flower over another is a result of many factors: innate preference (if any); past experience of one flower as more rewarding than the other; familiarity with one or the other flower; ease of handling of one or the other; and sensory limitations that may make one

flower more detectable. These components have been dissected for honey bees and other bees, but we are just beginning to merge these advances with pollination ecology, and to explore the implications for plant fitness. This merger is an exciting prospect — it should allow us to transform the traditional framework of pollination syndromes into a more satisfying picture of the interactions between flowers and pollinators, and their evolutionary consequences. □

Nick Waser is in the Department of Biology, University of California, Riverside, California 92521, USA.

e-mail: waser@citrus.ucr.edu

Lars Chittka is at Zoologie II, Biozentrum, Am Hubland, D-97074 Würzburg, Germany.

e-mail: chittka@biozentrum.uni-wuerzburg.de

- Glover, B. J. & Martin, C. *Hereditas* **80**, 778–784 (1998).
- Levin, D. A. & Brack, E. T. *Evolution* **49**, 1017–1022 (1995).
- Fineblum, W. L. & Rausher, M. *Ecology* **78**, 1646–1654 (1997).
- Campbell, D. R., Waser, N. M. & Price, M. V. *Evolution* **48**, 55–68 (1994).
- Chittka, L., Shmida, A., Troje, N. & Menzel, R. *Vision Res.* **34**, 1489–1508 (1994).
- Dafni, A., Lehrer, M. & Kevan, P. G. *Biol. Rev.* **72**, 239–282 (1997).
- Menzel, R. in *Neurobiology of Comparative Cognition* (eds Kesner, R. P. & Olten, D. S.) 237–292 (Erlbaum Inc., Hillsdale, NJ, 1990).
- Giurfa, M., Núñez, J., Chittka, L. & Menzel, R. *J. Comp. Physiol. A* **177**, 247–259 (1995).
- Bradshaw, H. D. J., Willbert, S. M., Otto, K. G. & Schemske, D. W. *Nature* **376**, 762–765 (1995).
- Chittka, L. & Waser, N. M. *Israel J. Plant Sci.* **45**, 169–183 (1997).
- Sutherland, S. D. & Vickery, R. K. *Great Basin Natur.* **53**, 107–117 (1993).
- Waser, N. M. *Oikos* **82**, 198–201 (1998).

Daedalus

Total protection

Immunization, that brilliant medical invention, is a way of arming the body’s defences in advance of an attack. You inject a foreign protein characteristic of the disease organism; the immune system raises antibodies against it, and acquires expertise in detecting the protein and neutralizing its threat. Any pathogen bearing that protein is thereafter rapidly overwhelmed by primed and practised immunological defences.

Daedalus now wants to generalize this technique. The immune system seems to be able to produce antibodies to any protein, or any number of proteins. So DREADCO biologists are devising a universal immunization. At first they planned to exploit modern combinatorial chemistry to synthesize a mixture of all possible proteins, and inject it into test subjects. But the combinatorics defeated them. With 20 possible amino acids at each link in a protein chain, an immunization containing just one molecule of all possible 20-link chains would weigh well over a kilogram. And much longer chains are common.

However, life uses only a small subset of proteins, those with useful foldings; many of them are common to several species. So Daedalus’s team is now scouring farms, zoos, botanical gardens, and culture archives to acquire samples from, or a specimen of, every known living thing. They plan to mix and homogenize the specimens, and extract their proteins. The resulting mixture will still be wildly complicated, but should be a feasible immunization.

DREADCO’s ‘Noah’s Ark Vaccine’ will be powerful indeed. An injection of it will bring a horrific feverish reaction as the subject’s immune system is challenged simultaneously by millions of foreign proteins. A graded series of shots will be needed, starting with very tiny doses and only gradually building up to the full prophylactic dose. The subject will then be immune to absolutely everything.

Given to the whole population, Noah’s Ark Vaccine will transform medicine. Colds, ‘flu, infections, all the bacterial and viral diseases will vanish. Even if the baffled organisms mutate, they will simply hit another component of our fully primed immune systems. Even a pathogen protein not in the vaccine may still be close enough to one that is, to trigger its response. Medical costs will be cut right back. Only diseases of the immune system itself, such as AIDS, will remain to plague us.

David Jones