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Ant and human farmers face similar problems

Ants of the tribe Attini discovered agriculture 50 million years before humans (Mueller *et al* 1998). Today, nearly 200 species in 12 genera of these ants cultivate fungus gardens in the Nearctic and Neotropical regions; in the Palaeotropics, this niche is occupied by fungus-growing termites. It is believed that the act of fungus cultivation evolved just once in the attines (Wilson 1971). The primitive attines cultivate fungus on insect frass and decaying vegetation while the advanced attines are the eponymous leaf-cutting ants. These ants carefully select leaves from species that are low in fungistatic compounds, such as phenolics, carry them to underground nests where they are masticated, and plant them in soil along with fungal mycelia and glandular secretions containing proteolytic enzymes. Obligate fungal symbionts break down structural carbohydrates in the leaves and produce nutritive protruberances called gongylidia from their hyphae. The ants consume these gongylidia and also feed them to their larvae. They also prevent the fungi from forming fruiting bodies or sporophores; consequently, the fungus is clonally propagated. In the advanced attines, the queen tucks a pellet of the mutualistic fungal mycelia into her infrabuccal pouch before her nuptial flight, and then uses this fungal innoculum to seed a new fungus garden in the new colony.

Until recently, it was believed that the ants were capable of maintaining axenic gardens; that is, they were able to weed out all non-mutualistic fungi and keep the garden free of microbial pathogens and parasites. Phenylacetic acid and *b*-hydroxydecenoic acid (myrmicacin) produced by the metapleural glands of the ants have antibiotic activity which possibly aids in this process. Recently, fungus gardens were found to contain antibiotic-producing bacteria of the genus *Streptomyces*, which like the mutualistic fungus innoculum, are also transmitted vertically from colony to colony (Currie *et al* 1999b). This may lead one to suppose that the ants have the problem of pathogens and parasites well under control. However, the highly virulent microfungus *Escovopsis* (Ascomycota) can devastate fungus gardens. In a study of this phenomenon in Costa Rica, Currie *et al* (1999a) found that *Escovopsis* is more prevalent in gardens of the derived ant lineages than in those of the primitive ones. Furthermore, the fungal symbionts of the derived ant lineages, such as of the ant genus *Atta* (the classical leaf-cutter), appear to be clones of ancient asexual fungal cultivars that have co-evolved with their partners, while those of the primitive attines appear to have been domesticated relatively recently from free-living sexual stocks (Chapela *et al* 1994). Cladistic analysis based on nuclear 28S ribosomal DNA has shown that, in contrast to the monophyletic origin of the attines, their symbiotic fungi are polyphyletic (Chapela *et al* 1994). Only in *Trachymyrmex*, *Acromyrmex* and *Atta* (all three higher attines) and in *Cyphomyrmex*, which is transitional between the higher and lower attines, does the queen carry a fungal innoculum to a new nest. Amplified fragment length polymorphism (AFLP) fingerprints have shown that some cultivars grown by different ant species are genetically identical and are asexual descendants of the same clone (Mueller *et al* 1998).

Clonal propagation of asexual cultivars apparently makes the fungus gardens of the derived attines vulnerable to the pathogenic *Escovopsis* while the fungus gardens of the basal attines are more resistant to such attacks. The Red Queen at work again (Currie *et al* 1999a; Wilkinson 2000)? The Red Queen hypothesis for the evolution of sex invokes the ‘arms race’ between host and parasite as an explanation for the prevalence of sex despite its two-fold cost relative to asexual reproduction (Jaenike 1978; Hamilton 1980). Villesen *et al* (1999) have brought in a new angle into the ant-fungus and Red Queen story. They note that queens of the higher attines exhibit the highest levels of multiple matings among ants (up to ten mates per queen) while those of the basal attines are usually singly mated. They claim that selection for multiple matings, which would increase the genetic heterogeneity of the nest mates, is critical in the social system of the leaf-cutters, which have large, long-lived colonies, and are under severe pressure from pathogens.

There is obviously still much to be learned about the interaction between sex, non-sex and pathogens in this mutualistic interaction between ant and fungus. Although ants were farmers much before us, their problems are the same as ours. Monocultures and a low genetic diversity of cultivars also leaves our agriculture vulnerable to attack. Even after 50 million years, ant farmers are not always ahead of the game.

References

Chapela I H, Rehner S A, Schultz T R and Mueller U G 1994 Evolutionary history of the symbiosis between fungus-growing ants and their fungi; *Science* **266** 1691–1694

Currie C R, Mueller U G and Malloch D 1999a The agricultural pathology of ant fungus gardens; *Proc. Natl. Acad. Sci. USA* **96** 7998–8002

Currie C R, Scott J A, Summerbell R C and Malloch D 1999b Fungus-growing ants use antibiotic-producing bacteria to control parasites; *Nature* (*London*) **398** 701–704

Hamilton W D 1980 Sex versus non-sex versus parasite; *Oikos* **35** 282–290

Jaenike J 1978 An hypothesis to account for the maintenance of sex within populations; *Evol. Theor.* **3** 191–194

Mueller U G, Rehner S A and Schultz T R 1998 The evolution of agriculture in ants; *Science* **281** 2034–2038

Villesen P, Gertsch P J, Frydenberg J, Mueller U G and Boomsma J J 1999 Evolutionary transition from single to multiple mating in fungus-growing ants; *Mol. Ecol*. **8** 1819–1825

Wilkinson D M 2000 Running with the Red Queen: reflections on ‘Sex versus non-sex versus parasite’; *Oikos* **91** 589–596

Wilson E O 1971 *The insect societies* (Cambridge, Massachusetts: Belknap Press of Harvard University Press)

RENEE M BORGES
Centre for Ecological Sciences,
Indian Institute of Science,
Bangalore 560 012, India
(Email, renee@ces.iisc.ernet.in)

Of fragrant shapes and colourful sounds: The world of a synaesthete

"I wanted the taste of this chicken to be pointed, but it came out all round…well, I mean it's nearly spherical; I can't serve this if it doesn't have points."

"Moscow? It's darkish grey, with spinach-green and pale blue in places."

"The smell of wintergreen has ragged edges, and peanut butter smells like things falling down and backward."

Synaesthesia is an unusual perceptual phenomenon, exemplified in the above quotations, in which a person apparently – some might say literally – 'tastes' a shape, 'sees' colour in a sound, or 'feels' a sound (Cytowic 1989, 1993; Baron-Cohen and Harrison 1997; Harrison 2001). Derived from the Greek words *syn*, meaning together, and *aesthesis*, perception, synaesthesia is an involuntary physical experience in which the stimulation of one sensory modality reliably leads to vivid sensations in one or more different senses. Although first described over a century ago, the physiological and mental mechanisms underlying this peculiar union of the senses largely remains uncharted even today. Its clear and self-consistent phenomenology clearly distinguishes it from ordinary metaphor or sound symbolism – a sharp taste, bitter memory or a dull sound, deliberate artistic contrivances that all of us use so commonly in our lives and that have sometimes been referred to as "synaesthesia" to describe their multisensory nature.

The overall population prevalence of synaesthesia seems to be rather high – about 1 in 2,000 (Harrison 2001) surprisingly, about 85% of these are women. Most of the eminent personalities who we know were definitely synaesthetic are, however, men – the novelist Vladimir Nabokov, the Russian composer Alexander Scriabin and the British artist David Hockney are examples. Interestingly, all were known for their art and creativity. In general, each synaesthete's list of associations is idiosyncratic and may even differ between identical twins. However, the associations for a particular individual tend to be stable over time; most synaesthetes report that they have had the condition for as long as they can remember. Synaesthesia often runs in families in a pattern consistent with either autosomal or X-linked dominant transmission (Cytowic 1993). Parents of either sex can thus pass the trait to their children of either sex, affected individuals appear in more than one generation of a pedigree, and multiple affected sibs can occur in the same generation. Male-to-male transmission has not been encountered yet.

Most synaesthetes appear to be highly intelligent and possess excellent memory, but demonstrate uneven cognitive skills. Mathematical abilities and spatial navigation skills, for example, often tend to be compromised. In general, synaesthesia appears to be a left-hemisphere brain function and the hippocampus seems to be critical for its experience (Cytowic and Wood 1982). Harrison (2001) explains synaesthetic phenomena in terms of the numerous interconnections between different sensory pathways in the brain that humans are born with. These usually die off within the first six months of life, but if the normal input into a pathway is cut off – as, for example, during congenital blindness – some of these pathways may retain their connections. Harrison (2001) suggests that in synaesthetes, many of these connections normally persist into adulthood and consequently give rise to cross-modal perceptions on receiving stimuli from any one of the interlinked sensory pathways.

A fascinating aspect of synaesthesia that has rarely been explored is its relation to consciousness. Cytowic (1993) speculated that synaesthesia could be the conscious awareness of a normally holistic process of perception that is usually subconscious or unconscious in most of us but prematurely displayed in synaesthetes. If this is true, then each of us is unknowingly synaesthetic. Although intriguing, such a view may not necessarily be compatible with the above-mentioned mechanism proposed by Harrison (2001), which suggests that synaesthetes are clearly different in possessing unusual interconnections between different sensory pathways.

The direct involvement of conscious mental processes in synaesthetic experiences is explored in a recent paper on colour-graphemic synaesthesia (Mattingley *et al* 2001). This is a common variant of the syndrome in which individuals experience highly idiosyncratic, but consistent, sensations of colour on being presented with specific graphemes – either letters, words or digits. In one set of experiments, the authors displayed grey graphemes, which evoked particular colours, to 15 synaesthetes for a very short period of time and then asked them to name the colour of a rectangular patch subsequently presented to them. When the graphemes were presented for 500 milliseconds before the coloured patch was shown, all the tested individuals were able correctly to perceive the shape of the grapheme and this affected the speed with which they were able to correctly identify the colour of the patch. In comparison to normal controls, synaesthetes were quicker at naming the colour when it was the same as that evoked by the grapheme, but significantly slower when it was different. In contrast, when the grey grapheme was presented to the same individuals after the display of a visual mask, which is simply a pattern that reduces the visibility of the stimulus (here, the grapheme) so that it is not processed to the level of conscious awareness, the previous effect of the grapheme on colour naming completely disappeared. In other words, when the synaesthetes were not consciously aware of which grapheme they had seen, the colours normally associated with particular graphemes did not seem to be evoked at all.

An important question that arises here is that if letters and digits are being presented briefly and masked, is the visual system processing these stimuli at least to an early stage of representation? If, in fact, there was no such processing at all, the naming of the coloured patch in the second set of experiments must have proceeded without any effect of the earlier displayed grapheme.

In an elegant experiment to answer this crucial question, Mattingley and his co-workers conducted a virtually identical experiment on the same individuals. The only difference was that instead of the coloured patch, the test stimulus that required to be identified subsequently was the same or a different grapheme, but in a different case. Thus, if the first grapheme displayed was the letter 'A', the test grapheme could either be the letter 'a' or any other grapheme, say 'b'. Interestingly, both normal and synaesthetic individuals were able to identify the test stimulus more quickly if the same grapheme was presented in a different case than a different grapheme altogether. This clearly meant that although the test subjects were not aware of what they had seen, their brains had already processed the displayed visual information and had been able successfully to influence the subsequent task that was performed. Synaesthetic perception thus clearly requires conscious experience; mere cognitive processing of the stimulus by the brain to a level below that of awareness is not enough to evoke the characteristic multisensory images so typical of the syndrome.

An important implication of this particular study concerns the famous 'binding' problem in neurobiology. Are the separate features of any visually perceived object that are known to be processed separately in different cortical regions of the brain 'bound' together only when we become aware that we are observing them? Or, does our visual system store intact integrated images of such perceived objects? The work of Mattingley and his colleagues clearly supports the idea of modularity in the human cortex and suggests that consciousness is essential if we are to integrate unconsciously and separately stored features of visual information – colour and shape, in this case – into a comprehensive whole. Obviously, perceiving, and not merely seeing, is believing!

References

Baron-Cohen S and Harrison J E 1997 *Synaesthesia: Classic and contemporary readings* (Cambridge, Mass: Blackwell)

Cytowic R E 1989 *Synesthesia: A union of the senses* (New York: Springer Verlag)

Cytowic R E 1993 *The man who tasted shapes: A bizarre medical mystery offers revolutionary insights into reasoning, emotion, and consciousness* (New York: Putnam)

Cytowic R E and Wood F B 1982 Synesthesia I: A review of major theories and their brain basis; *Brain Cognition* **1** 23–35

Harrison J 2001 *Synaesthesia: The strangest thing* (Oxford: Oxford University Press)

Mattingley J B, Rich A N, Yelland G and Bradshaw J L 2001 Unconscious priming eliminates automatic binding of colour and alphanumeric form in synaesthesia; *Nature* (*London*) **410** 580–582

ANINDYA SINHA
National Institute of Advanced Studies,
Indian Institute of Science Campus,
Bangalore 560 012, India
(Email, asinha@nias.iisc.ernet.in)