

theories rigorously. Here are some of my reservations.

One generic problem is that Lynch's evidence comes from broad brush comparisons of extremely disparate types of organism. It is true that, on average, bacteria have much larger  $N_e$  values than most eukaryotes for which we currently have data, but they differ in numerous other respects as well, for example lack of regular sexual reproduction. As all good comparative biologists know, it is very difficult to disentangle cause and correlation from wide comparisons. Alternatives to many of Lynch's explanations of the patterns can be envisaged, and his arguments do not seem to rule these out. For example, as he himself describes in Chapter 7, the spread of transposable elements through the genomes of a host population is dependent on some degree of sexual exchange between members of the populations, and the correlations described by Lynch could thus at least partly be explained by lack of such exchange. Furthermore, his insistence on the importance of  $N_e$  is undermined by the fact that models of the maintenance of transposable elements in intergenic regions (where insertions have little direct effects on fitness) show that there is no difficulty in their establishment in very large populations. In accordance with this, maize and its relatives are chock-a-block full of transposable elements, yet have levels of DNA sequence variability as large or larger than *Drosophila* species, with their relatively low levels of transposable elements.

In relation to the evolution of introns, Lynch's model of their origin looks rather strained in relation to the evidence that introns seem to have been fairly prevalent in ancestral eukaryotes, so that their rarity and small size in many unicellular eukaryotes is a result of secondary loss. It is also undermined by evidence for high levels of DNA sequence diversity in some species of multicellular organisms with introns. Could it be that the invention of regular sexual reproduction made it easier for mobile, initially self-splicing introns to invade the genome in large numbers? This possibility is not explored by Lynch, who resorts (p. 261) to the untestable hypothesis that there was a long period of reduced  $N_e$  among ancestral eukaryotes. This is getting

dangerously close to the adaptationist just-so stories that he ridicules in the final chapter.

There are other difficulties worth mentioning. One is that, despite his advocacy of the importance of population genetics, use is made of only a limited set of the tools available in modern population genetics. For instance, recent work using comparisons of between-species divergence and within-species variability to detect departures from neutrality increasingly suggests that much non-coding sequence is under selection, yet this is not mentioned. Of course, this is not fatal to Lynch's general thesis, as it can always be argued that non-selective forces established the non-coding sequences in the first place, but it does make one wonder.

Despite these criticisms, Lynch's book is essential reading for anyone interested in this hugely important subject. It has provided us with a uniquely valuable overview of genome evolution, albeit heavily biased towards Lynch's own interpretations. I am especially in sympathy with the strong statements in the final "Genomfart" chapter (the joke is explained on p. 364) that "nothing in evolution makes sense except in the light of population genetics", and with the criticisms of dubious but fashionable concepts such as 'evolvability'.

It is too early to tell how well Lynch's own ideas will fare in the face of the evidence, although the concept of 'sub-functionalization' (by mutational loss of different sequence components in different members of a set of duplicate genes) seems to be receiving significant empirical support. There are reasons to expect that rigorous comparative tests of hypotheses about genome evolution will come to be based on careful contrasts of related taxa, differing in far fewer features than those used by Lynch. At present, there are too few genome sequences of independent pairs of related species to make this feasible on a large enough scale for there to be much statistical power in such independent contrasts, but the advent of rapid sequencing methods will probably remedy this fairly soon.

Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Edinburgh EH9 3JT, UK.  
E-mail: [brian.charlesworth@ed.ac.uk](mailto:brian.charlesworth@ed.ac.uk)

## Q & A

### Alan Cowey

*Alan Cowey graduated in Natural Sciences from Cambridge in 1957 followed by a PhD under Larry Weiskrantz. After a post-doc with Bob Doty at the Center for Brain Research in Rochester, New York, he returned to Cambridge as Demonstrator in Experimental Psychology and fellow of Emmanuel College. After a sabbatical year as a Fulbright Fellow at Harvard with Charlie Gross, he moved to Oxford as the Henry Head Research Fellow of the Royal Society and a Fellow of Lincoln College. He remains in Oxford as Professor, Emeritus, of Physiological Psychology. He was elected to the Royal Society in 1988, to the Academy of Medical Sciences in 1998, and a member of the Academia Europaea in 1989. He was President of the European Brain and Behaviour Society from 1986–88 and of the UK Experimental Psychology Society from 1990–92. From 1991–1996, directed the MRC interdisciplinary research centre in Oxford. If asked what he is, he replies "a behavioural neuroscientist with a special interest in vision and ignorance".*

#### **What attracted you to biology in the first place?**

The wrong things. I attended the local grammar school in Sunderland and had a master who was not a particularly good biologist, but to an impressionable schoolboy seemed like a renaissance man: interested in sport, poetry, music, drama, art, architecture, politics and travel. He taught me how to pole vault. If biology was good enough for him, it must be fine for me. Once hooked I never regretted it. He suggested that I should apply for Cambridge because it was "the best for science" and I obtained a place in 1954, before discovering I needed school certificate (now O-level) Latin, which I obtained by the educationally dubious process of acquiring what could be described as tourist's Italian and learning Virgil's Aeneid Book III by heart. I particularly liked the fact that biology was so diverse and such a complex system (a term not in use then) that even a student could do an experiment and discover something interesting. It's still true.

**What is the best advice you've been given?** I read it rather than received it, but it is from T.H. Huxley: "Those who refuse to go beyond the truth seldom get as far as the truth". That was when I realised everything should be questioned: God, the Zeitgeist, authority, the flavour of the month. It was liberating. It makes enemies, but no matter.

**What advice would you offer to someone starting a career in biology?** The same advice. But with respect to an area of research, I would say choose something that is emerging rather than retracting. Don't waste your time crossing the i's and t's of a supervisor who has worked on the same problem for years, unless that makes you happy. And if possible chose a supervisor who will allow you independence and even feed you his or her best ideas and let you run with them. As well, it is usually a good idea to change to another laboratory, a new set of techniques and a different scientific problem after a doctorate. Finally, very few people become wealthy as a result of their science; if it's wealth you want, do something else.

**If you were starting again knowing what you now know, would you follow the same career?** Definitely. Very few other careers allow and encourage such intellectual freedom.

**Do you have a favourite paper?** Yes, but may I crave indulgence and mention two in particular. The first is one of a pair in *Nature*, 1953, by Watson and Crick, in which they present their ideas about the structure of DNA. It was arguably the most influential biological discovery of the twentieth century. It is just over one page long and even its companion in the same volume is just over two pages. I have recommended it to students and post-docs for decades as an example of how to communicate ideas and findings succinctly and lightly. It contrasts sharply with the regrettable and increasing modern tendency to use phrases such as "...here we show for the first time..." and "...these important results demonstrate..." and even "...no other group has managed to...". Authors have lost sight of the fact that it is for readers to make these judgements.

The second is the brief paper in the *Lancet*, 1940, in which Heatley and colleagues reported that penicillin saved

the lives of four mice given a lethal injection of *Streptococcus*, whereas four other mice, injected but untreated, swiftly died. The result ushered in the era of antibiotics yet only eight mice, the minimum for a statistically significant difference between the two groups, were used. For many years I referred to the paper as an illustration of exemplary experimental design in connection with issues of the ethical use of animals in research. Heatley knew about refinement, reduction and replacement long before the 3Rs became fashionable.

**Do you have a scientific hero and if so who is he/she, and why?** Yes, Charles Darwin and I expect I share him with many colleagues. To my mind he was the greatest biologist of the nineteenth century. He was a colossus: totally independent, immensely perceptive and careful, in no rush to publish, staggeringly original, not afraid of opprobrium, and nearly always right. Alas, for a variety of reasons few students now read original works. All biologists know about Darwin but not many have ever read his books. It's a shame. It's like studying English Literature and not reading Jane Austen.

**What has been your biggest mistake in research?** In 1962, while working in Bob Doty's lab in Rochester New York, I plotted visual area 2 (V2) and its topographical relationship with, and dependency on, V1 in the squirrel monkey. I noticed that if the recording electrode was moved rostrally there was a prominent, short-latency, visually evoked response in the vicinity of the caudal superior temporal sulcus. My Fellowship was coming to an end and although it was extendable, I had a job to return to in England, so I did not explore it further. It was subsequently thoroughly investigated by Allman and Kaas (1971) in the Owl monkey, who called it area MT (for middle temporal). It is also known as the cortical motion area and it became, and remains, the most studied and the best understood of all extra-striate visual areas. I still have my lab books from Rochester and when I look at them I realise what an opportunity I overlooked. I should have stayed for another year.

**What is the next big question to be answered in your own area of research?** It is the nature of consciousness. As a graduate student

I was cautioned against discussing ideas such as conscious awareness, animal consciousness, covert attention, implicit knowledge, and the like. In my doctoral thesis and in one of my first papers (1963), I suggested that monkeys with visual field defects produced by removing small parts of V1 might not actually 'see' — in the sense of experiencing visual qualia — visual targets that they could discriminate and voluntarily respond to correctly. A referee thought that this line of argument was unsound because it was in principle untestable. But the editor allowed the speculation; what else is a discussion for? Over a decade later, the phenomenon was named 'blindsight' in neurological patients and, in 1995, Petra Stoerig and I demonstrated it in monkeys: we devised (oops, I nearly said 'for the first time') a way of asking monkeys whether a flash of light in a clinically blind field defect was perceptually like the same visual event in the normal visual field or whether it was a blank. It was the latter.

Technical advances made since then in recording and localising the activity of the brain (high density EEG, MEG, fMRI) and stimulating the brain (by TMS) while subjects perform various perceptual tasks mean that what is often called the neural correlate of consciousness can be pin-pointed. But correlates do not explain anything, which has to be the next big step. Even then the so-called hard problem of consciousness — why we have consciousness at all or the related issue of why the perceptual experience of something like long-wavelength light is red rather than something else — has no satisfactory solution at present.

**In what ways has the electronic revolution changed your life as a scientist?** In many ways, not all of them desirable. The ready access to information of all kinds is amazing, as is the rapid communication between scientists. And publishing will continue to change as open-access journals proliferate and original data can be provided for others to analyse and evaluate. Having said that, I doubt that many of us have the time or the need or the desire to rummage through the raw data from other labs. Scientists also need thinking time and there is progressively less of it. We are bombarded with electronic requests to review papers, assess grant applications, provide testimonials,

comment on essays from students in other countries, and — worst of all — provide information for incessant bureaucratic enquiries that should not be taking place at all. Non-compliance is rapidly followed by a further enquiry or a thinly veiled reprimand for being forgetful or hurtful or not attending to emails. It is madness.

**Is science organised effectively?**

Science can be pricey and the public pay for most of it. So scientists are accountable. Fortunately most of them appreciate this. Some areas of research can only be carried out in centres of excellence with shared expensive facilities, like high energy physics or high-field magnetic imaging. However, bureaucratic attempts to make diverse scientists from different laboratories and even nations collaborate in the name of efficiency and international development are often spectacular failures. Scientists usually know who best to collaborate with and usually manage to do so. And it is important that they should like each other. Friendship is the best catalyst.

**You study the behaviour of animals and humans: are there serious ethical issues in doing so?**

Yes. It is possible to exploit the good will of human subjects and even to harm them physically or mentally. Obtaining genuine informed consent from a patient is not trivially easy. Fortunately the scientific community is aware of this and local, national and international legislation at least means that research proposals are scrutinised and must be approved by knowledgeable and disinterested bodies. Investigators mutter about how long it can take to obtain permission to do certain things but I have not yet met any investigator who thinks that the legislation should be swept away. The ethical issues involving research on animals are much more controversial and depressing. Most of the 'debates' are little more than a heated ritualistic exchange of insults, slogans and physical threats. A proper discussion of what constitutes an animal's rights, or the nature of pain and suffering and how they can be detected and minimised, or whether the ends ever justify the means, rarely takes place except in esoteric books that are not widely read. The public debate is intellectually impoverished and lacks a genuine meeting of minds. In this respect little has changed in a century.

**Are you concerned about deliberate falsification of results in science?**

It is difficult to say no to this question for there are now several well-known examples in biology, some of them with a high profile especially in medicine. But malpractice exists in every professional group (the police, lawyers, politicians, the military, industry, even the priesthood) and all the evidence I have is that it is relatively rare in biology. A cynic would say that it is rare because it usually brings no financial or social gain in biology, and the cynic might be right. I am more concerned with a different kind of falsification, namely that many students now use electronic data bases to plagiarise for their essays, and even for their dissertations. Incredibly, when it is spotted by sharp-eyed readers or software programmes that can now detect it, students seem genuinely surprised to learn that there is anything undesirable about plagiarism.

**Was it difficult to combine a career in teaching and research?**

It was not difficult for me, but it might be were I starting out now. I liked teaching and found that whenever I encountered trouble in explaining something it was usually because I had not understood it properly. So I learnt a great deal by teaching. Probably all teachers are constantly reminded that there are students in the audience who are smarter than they are. That way I learned much from students and post-docs, including ideas for research. I might never have embarked on transcranial magnetic stimulation were it not for two imaginative post-docs. But so much of teaching now involves non-educational administrative duties (reports, student evaluations, committees, quality assessments, measures to increase transparency, up-dating the web site) that research has suffered without any clear evidence that the education has improved. In some respects it has worsened.

**What is your greatest remaining ambition in research?** To be the first rather than the last to recognize when mental ossification sets in and I can no longer do good research, and to stop at that point.

University of Oxford, Department of Experimental Psychology, South Parks Road, Oxford OX1 3UD, UK.  
E-mail: [alan.cowey@psy.ox.ac.uk](mailto:alan.cowey@psy.ox.ac.uk)

## Tail spins

Hummingbirds are not considered the most vocal of bird groups but many do make sounds; while some of these sounds are clearly vocal the source of some others has been less clear. Researchers have now found that the distinctive chirp of Anna's hummingbird males in the American south-west, during dives at speeds of 80 km/h, arises from the wind rushing through its splayed tail feathers. The feathers quiver in the same way as a reed in a clarinet vibrates when a musician plays the instrument to produce a musical note. In this way, the bird is able to produce a noise louder than anything it might try to make using its own tiny voicebox.

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### The feathers quiver in the same way as a reed in a clarinet

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The researchers said it is the first time that any bird has been shown to make a deliberate noise in this way, but they now believe that there are several other species of hummingbird that can sing through their feathers.

"This is a new mechanism for sound production in birds," said Christopher Clark at the University of California Berkeley, lead author of the study with Teresa J. Feo. "The Anna's hummingbird is the only hummingbird for which we know all the details, but there are a number of other species with similarly shaped tail feathers that may use their tail morphology in producing sounds," said Clark.

The researchers used high-speed cameras to record a male hummingbird's mating display as he dive-bombed a caged female or a stuffed dummy. The video showed how he unfurled his tail feathers for a split second at the bottom of his dive, which corresponded with a short 'chirp' lasting about 60 milliseconds.