

# Sex and sensibility

David L. Hull

**The Ant and the Peacock: Altruism and Sexual Selection from Darwin to Today.** By Helena Cronin. Cambridge University Press: 1992. Pp. 490. £27.50, \$39.50.

In his foreword to *The Ant and the Peacock*, John Maynard Smith applauds Helena Cronin for resisting the "recent fashion in the history of science . . . to ignore the science, but to describe in sordid detail the political tactics of the scientists". But Cronin's book itself is one more fusillade in the conflict between what Cronin calls modern darwinism and its pluralist opponents. Modern darwinians like Richard Dawkins, Mark Ridley and Maynard Smith emphasize the central role in evolution of genes, selection, adaptation and evolutionary stable strategies, whereas such pluralistic opponents as Richard Lewontin and Stephen Jay Gould argue that selection occurs at a variety of levels and ridicule what they take to be the panglossian adaptationism, panselctionism and genetic determinism of the so-called modern darwinians. Cronin compares her own reading of Dawkins' *The Selfish Gene* to crossing Wallace's line, the narrow but deep channel running between Bali and Lombok that marks the sharp separation between the fauna of Asia and Australia. "Here was a different world. Darwinism had entered a new era."

Cronin's book is a mixture of careful, perceptive history and enthusiastic advocacy, just the sort of history that present-day historians denounce as 'Whiggism', a term that is rivalled only by 'positivism' in the current lexicon of intellectual bad habits. According to historians, the relationship between knowledge of past and present science is not symmetrical. Present-day scientists can benefit from reading the history of their field, but the introduction of current knowledge into discussions of past episodes in the history of science is sure to distort our understanding. If Whiggism is the evil that so many historians claim it is, Cronin's book should be a disaster. It is anything but. On the contrary, she succeeds in keeping the past and present separate when she needs to and in illuminating past controversies by introducing current thoughts on the subject. In her exposition, the light of understanding shines in both directions.

Cronin investigates two issues in evolutionary biology — altruism as represented by the selfless sacrifice of neuter insects such as soldier ants, and sexual selection as represented by the male peacock's tail. She not only traces the

history of these two sets of interrelated problems from Charles Darwin and Alfred Russel Wallace to the present, but also argues for the virtues of certain solutions over others. It is difficult to think of two more fascinating topics than altruism and sexual selection. Goodness and sex are an unbeatable combination. These topics also serve to make clear the

that they did not possess. Although Wallace initially allowed that female choice might have some effect, he thought natural selection acting differently on males and females was the primary cause of sexual dimorphism. Eventually both Darwin and Wallace were forced to postulate nonadaptive mechanisms as well; hereditary tendencies for Darwin, physiological processes for Wallace.

The issue of female choice languished for over a century until proponents of modern darwinism resurrected it. As Cronin points out, when viewed from the gene-centred perspective of modern darwinism, the dispute between Darwin and Wallace over sexual selection becomes a tempest in a victorian teacup.



Not just a pretty tail: detail from the painting *Peacock and Peahen* by Tobias Stranover (1684–1731).

differences that divided Darwin and Wallace, and for a change Wallace gets his just due. Where can one find the most sophisticated and penetrating discussions of the evolutionary process prior to the rebirth of darwinism in this century? In the exchanges between Darwin and Wallace.

Darwin viewed sexual dimorphism as posing special problems for natural selection. How could extravagant secondary sexual characteristics such as the male peacock's tail be explained in terms of natural selection? Darwin suggested two mechanisms for such characteristics: the competition between members of the same sex (usually males) for mates, and mate choice (usually female choice). Darwin's contemporaries saw little problem with male combat. The formidable antlers possessed by males in the deer family, for example, are clearly used in battles for access to females. But female choice was quite another matter. It seemed to attribute abilities to organisms

The problems that Darwin and Wallace saw arise only when one concentrates on organisms instead of genes. From the gene-centred perspective of modern darwinism, sexual selection is merely a special form of natural selection.

"For Aesop, the social insects were a source of inspiration. For Darwinians, they were a source of aggravation", writes Cronin, but for the darwinians the aggravation did not stem, as it does today, from the altruistic behaviour of neuter insects, but from their remarkable adaptations. How could soldier ants develop such huge mandibles when they never reproduce themselves? Darwin insisted that no adaptation in one species can serve primarily to benefit organisms belonging to some other species, but he did not see intraspecific altruism as a serious problem. According to modern darwinians, it is. Any genes that lead an organism to behave in ways that decrease the likelihood that these genes will be passed on to later generations

should be rapidly eliminated.

According to Cronin, neither Darwin nor Wallace saw intraspecific altruism as a problem because they slid half-consciously from the good of organisms to the good of communities, colonies and even species, an elision that G. C. Williams finally brought forcefully to our attention. If treating organisms as units of selection is mistaken, then treating higher-level entities as units of selection is sure to lead to problems. Cronin agrees with Dawkins that genes can function as "replicators whereas organisms, groups and other levels in the hierarchy cannot. Natural selection is about the differential survival of replicators. So genes are the only serious candidates for units of selection." Here I think that Cronin reasons too quickly. Replication is necessary for selection but is not equivalent to it. Organisms are more than 'vehicles'.

Cronin also addresses two other differences between the views of Darwin and Wallace — the role of selection in speciation and the adequacy of a purely naturalistic theory to explain the moral and intellectual attainments of the human species. Wallace was fond of proclaiming that he was more of a darwinian than was Darwin. In the case of speciation he was right. Wallace thought that intersterility arose as an adaptation through natural selection, whereas Darwin thought that it was merely an incidental effect of selection acting on other characteristics. But with respect to the human species, Wallace was anything but a darwinian, because he appealed to supernatural causes. In fact, Darwin and Wallace disagreed with each other so profoundly on so many issues that it seems more than peculiar to claim that these two men were authors of the same theory. They agreed that species evolve but disagreed on just about every other particular of the theory, including the scope and efficacy of natural selection. Cronin points out these differences more dramatically than any previous writer, partly because she has not been afraid of using our current understanding to explain the past. □

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■ In June 1858, Darwin received Wallace's now famous letter, enclosing an essay in which Wallace described his own theory of evolution. "I never saw a more striking coincidence", Darwin wrote to Charles Lyell. "So all my originality, whatever it may amount to, will be smashed." The letters surrounding these events and the eventual publication of the abstract of Darwin's theory a year later appear in *The Correspondence of Charles Darwin: Vol. 7 1858-1859*, recently published by Cambridge University Press. Price £35, \$59.95.

## Nervous starts

J. Z. Young

**Foundations of the Neuron Doctrine.** By Gordon M. Shepherd. *Oxford University Press: 1992. Pp. 338. £35, \$39.95.*

**Cajal's Degeneration and Regeneration of the Nervous System.** Translated by R. M. May. Edited by Javier De Felipe and Edward G. Jones. *Oxford University Press: 1991. Pp. 769. £60, \$65.*

THOSE who probe the nervous system with electrodes probably seldom stop to consider the history of knowledge of the cells they are impaling. Yet it would help them to think about the problems that have arisen in the search for units of nervous activity. Since the days of Santiago Ramón y Cajal, most neuroscientists have depended on a rather simple



Cajal: proponent of "connection by contact".

picture of the neuron, with dendrites, cell body and axon as the essential unit. This has also been the model mostly used in artificial intelligence. Shepherd's book provides a survey of the history of the neuronal hypothesis. In his last chapter, he raises the question of whether we should now look for units both larger and smaller than the neuron.

The controversy at the end of the last century turned on the question of whether neurofibrils proceed from one cell to the next. It was conducted in fairly ferocious language. Cajal writes of his reticularist opponents, such as Golgi and A. Bethe, as "fanatics with haughty minds, inclined towards mysticism". Finally, in 1917, he is happy to write that "the unhorsed physiologist of Strasbourg [Bethe] decided to abandon the field. *Victis honos!*"

Cajal was, of course, correct in claiming that "connection is by contact", but his opponents were skilful light microscop-

ists and not so far wrong as he supposed. Now that electron microscopy has shown the correct relationships at synapses, we can see that their interpretations were in a sense correct. The finest branches of a nerve fibre may indeed appear to enter the end organ, for instance in the groove at the surface of a muscle fibre. There is no evidence that Cajal realized that it is the completeness of the two membranes that is important. If the finer branches run in a trough, the most honest light-microscope interpretation may be that there is continuity. Cajal's opinion was right, but his figures are almost all drawings.

The advocates of the neuron theory were themselves quite "haughty" and hasty in their rejection of all possibilities of "continuity". We know now that gap junctions may allow passage of ions and small molecules between neurons. Furthermore, there may be complete fusion of nerve cells if they always function together. For instance, the two giant cells of the squid initiate contraction of the muscle sac — and they are completely joined by a bridge: for jetting, both sides of the mantle must contract together. But where impulses are initiated there are synapses. This is a system of "Fused neurons and synaptic contacts", as the paper in which it was described was called in 1939. The fusion is the exception that proves the rule. Nerve fibres *can* fuse, but where decisions are to be made they are separated by synapses. I remember explaining all this to Sherrington (in about 1938). He looked up at me quizzically and said, "I hope that you are right Young, but I find it hard to believe." It is ironic that the squid's giant fibre synapse, more thoroughly investigated than any other, involves a syncytial postsynaptic fibre. I hope that Cajal would have enjoyed the joke (but I'm not sure that he would).

This history of old doubts and quarrels shows how hard it is to arrive at secure knowledge. As more has been discovered it becomes clear that the classical neuron doctrine needs to be extended. Almost from the start there were doubts as to what the term should include. The word 'neuron', originally suggested by Waldeyer in 1891, comes from the Greek, meaning, literally, tendon or sinew, and was applied through confusion to nerve trunks. Some authors therefore wished to keep the term neuron for the axon, whereas others (paradoxically) tried to use it only for the nerve cell body. Kölliker and others emphasized that the word should be spelled 'neurone'. This usage is still insisted on by some British physiologists and by Cambridge University Press. Shepherd nowhere mentions the history of this spelling. Many people must be puzzled to know which form to use and