

Conclusions

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THIS WAS AN UNUSUAL MEETING between biologists and human scientists. In these concluding remarks, I will concentrate on two topics which were looked at from both sides of the divide. First, rather briefly, the use of optimization theory to analyse behaviour, and second, at greater length, the nature of mind, and in particular the difference between human and primate minds.

Optimization theory, and game theory, which is simply the extension of optimization to cases in which different participants have conflicting interests, has been widely used both in biology and economics, but rather little used in the rest of the human sciences. The use of optimization is easier to justify in biology than in economics, because natural selection provides a dynamics which will, subject to constraints, cause a population to evolve towards an optimum, and specifies the quantity—Darwinian fitness, or, crudely, expected number of offspring—that will be optimized. In economics, the dynamics of natural selection is replaced by an assumption of rationality, which often does not hold, and the quantity maximized—‘utility’—is hard to define or measure. For these reasons, optimization and game theory have, I think, proved to have greater explanatory power in biology.

One feature of optimization models in biology that can give rise to misunderstandings is that, often, little is said about the perceptual and cognitive processes determining the behaviour of individual animals. Indeed, optimization models are often a guide to understanding cognitive processes, rather than based on a prior knowledge of them. The point is important in understanding the use of optimization in several of the papers in the symposium, so I will say a few words about it. One of the earliest applications of game theory to animals (Brockmann & Dawkins 1979)

analysed the behaviour of digger wasps. The first model formulated by the authors predicted behaviour rather badly. It turned out that this was because they had assumed, reasonably enough, that a wasp knows whether another wasp is using the same burrow. Further observations showed that wasps do not know: when this was allowed for, the model gave good predictions. This story illustrates two points: optimal behaviour does indeed depend on the perceptual and cognitive abilities of the participants, and optimization models can be a good starting point for a study of behavioural mechanisms.

These points are likely to be relevant to the papers by Dunbar, Borgerhoff Mulder, and van Schaik at the symposium. Dunbar uses an optimization approach to predict group size in several genera of primates as a function of three variables—climate, predation pressure and cognitive ability. Von Schaik discusses the importance of infanticide by males in determining group size and structure. Neither author has attempted to explain how the behaviour of individual animals generates the optimal group size. But this is not intended as a criticism: optimization models are a stimulus to mechanistic studies of behaviour, not an alternative.

> The absence of behavioural mechanisms may seem even odder when the object of study is the human animal. Borgerhoff Mulder describes changes in marriage strategies in changing circumstances in rural Kenya. She does so by asking whether male behaviour is optimal in the new circumstances, although, as she makes clear, she is not able to show that it is Darwinian fitness that is being optimized, but only traits that may well be correlated with fitness. It is not the case that men are consciously trying to maximize their fitness, or even that they are conscious of the criteria that they are using in choosing marriage partners. Yet her approach is very much in the spirit of behavioural ecology as applied to other animals: first find out what is being maximized, and only then ask how it is being done. I must confess that, when I first met this approach to human behaviour, I was unsympathetic. Surely we have reasons for what we do. But I have been impressed by at least some of the earlier work along these lines, notably by Irons (1979) and Dickemann (1979). The great virtue of the approach is that it makes very specific predictions, and so is testable. Borgerhoff Mulder's data on marriage strategies are promising: if optimization methods are inappropriate, the data surely ought to show it.

There is, however, a possible criticism of Borgerhoff Mulder, other than the simple objection that is strange to imagine that people are maximizing their fitness without being aware of it. This is that the adaptation she observes is to a social environment that has existed for a time that is far too short to permit the evolution of a genetic adaptation to that environment. Maximization of fitness, therefore, requires that humans possess a

behavioural repertoire that will maximize fitness even in a new and unfamiliar environment.

Cosmides & Tooby take a different view of the relation between evolution by natural selection and human nature. The theory of evolution, they argue, predicts that universal features of human nature should be such as to maximize fitness in the 'environment of evolutionary adaptedness': that is, the environment in which most of our behavioural evolution occurred. There is, therefore, no reason to expect our behaviour to be adaptive in the modern world. Since evolutionary change is slow, the argument is persuasive. But I also see some force in Borgerhoff Mulder's argument that the question is an empirical one, best investigated by applying straightforward optimization methods to existing populations in existing environments. If, as her own work on marriage strategies and earlier on food-gathering suggests, human behaviour can be explained as optimal in the current environment, there is no need to invoke adaptation to an 'environment of evolutionary adaptation'. In contrast, Tooby & Cosmides prefer to rely on the theoretical prediction that genetic adaptation is possible only to an environment that lasts for many generations. Fortunately, perhaps, it is not my job to decide between these alternative research strategies.

Returning to primate societies, there is now a lot that can be said about the kinds of social systems found, and the reasons for them. Dunbar suggests that it should be possible to reconstruct the past history of human social systems, given knowledge of past climates and past dietary habits. Foley draws on our knowledge of present primate societies to make an ambitious reconstruction of the past 50 million years of human evolution. I was particularly attracted by his use of modern phylogenetic methods to deduce ancestral states. His paper is clear, and I see little point in trying to summarize it. But it is interesting that he identifies, not one crucial event in our ancestry, but a succession of such events.

I turn now to the nature of the human mind, and to the differences between the minds of men and apes. It is conventional, and probably correct, in the human sciences to assume that differences between cultures, in time or space, are not caused by genetic differences between peoples. I take it, however, that we agree that the differences between human and ape societies do depend, in large part, on genetic differences between us. But what is the nature of these differences, and when did they occur? A number of views, not necessarily mutually exclusive, were expressed on the nature of the differences.

I will start with the largely theoretical paper by Boyd. Although theoretical, his paper is based on a rather surprising observation. By and large, animals do not learn by copying one another. There are exceptions:

for example, birds learn the details of their songs by listening to adults, so that local song dialects arise. But in general, if two populations of a species behave differently, and if the difference can be shown to be culturally, not genetically, inherited, it is not because young individuals copy their elders, but because their elders create an environment in which individual learning is easy. If this is so, Boyd argues, continuous cultural change will not occur. But why is copying so rare in animals? Boyd suggests that it is because copying only pays an individual if it is already common in the population: in a population of non-copyers, copying is a bad strategy. Thus a genetic tendency to copy one's elders is difficult to establish, but, once present, likely to be maintained.

How far is it true that copying is rare in primates? Boesch argues that at least some of the behavioural differences between groups of chimpanzees in different places depend on imitation. The methods of using a stick to dip for ants are different in Taï and Gombe. Since the Gombe method is four times as efficient, it is hard to see how the Taï method could be explained solely by individual learning. A second example is the use of the same signal, leaf-clipping, in different contexts in different places. Although it is not strictly a matter of imitation, I cannot resist mentioning what was for me the most remarkable fact reported at the meeting. An individual chimpanzee, Brutus, can, by drumming on trees, send the message 'time for a rest', which is perhaps not too surprising, and 'time for a rest, and then move off in a specified new direction', which surely is. Lovers of social insects might claim that the latter is no more than a honeybee can do, but there is a difference: it is unlikely that Brutus was genetically programmed to signal a direction. It seems, then, that chimps do sometimes imitate. The same may be true of other primates. Discussing alarm calls, Cheney & Seyfarth remark, rather in passing, that 'infant vervets seem to learn appropriate usage simply by observing adults'. Thus vervet monkeys may inherit a tendency to respond to flying objects with a particular alarm call, but must learn by copying adults to make the call to eagles but not to pigeons. True, adult vervets do not correct mistaken signals by their offspring, but we rarely correct speech errors in our children either.

If it is strange that imitation should be so rare in animals, even stranger is the apparent absence of intentionality. Cheney & Seyfarth argue that, although both baboons and vervets make sounds that carry useful information, it would be a mistake to think that the signaller makes the call with the intention of altering the behaviour of the hearer. Indeed, there is no reason to think that the signaller conceives of the existence of a hearer. Thus vervets continue to give alarm calls after all other monkeys have taken cover, and baboons are more likely to answer their own barks than the barks of others. The point is important. In humans, co-operation depends in

part on 'social contracts': it is hard to form a contract with someone unless you can conceive of them as being an individual like yourself.

The ability to conceive of others as having a mind like one's own has sometimes been referred to as a 'theory of mind'. Tooby & Cosmides discuss the evolution of human altruism, co-operation and friendship in a way that implies such a theory of mind. They start by making the reasonable point that we need to regard altruistic behaviour as an adaptation only if, like the structure of the eye, it is too complex to have arisen as the unselected by-product of something else. Human altruism, they suggest, does possess the degree of complexity, and adaptedness for conferring benefit, that requires a selective explanation (the same is certainly true of altruistic behaviour in social insects, although the evolutionary mechanism is different). A simplified version of their argument goes as follows. Suppose that individual X repeatedly helps Y. This may be because Y has 'trained' X to help, by rewarding him when he did so. Such training would work only if X can classify his actions into those that help Y, and those that do not. If the helping actions performed are various, and sometimes novel, this requires that X has a theory of mind.

One difference between humans and other primates that arose frequently during the symposium is the competence for language. Chomsky (1957, and subsequently) has persuaded most of us that linguistic competence is peculiar, both in the sense of not being merely an aspect of general intelligence, and of being confined to humans. I accept this, but am less willing to go along with Chomsky's insistence that it is fruitless to speculate about the evolutionary origin of language. Perhaps our best hope of making progress on this topic is through the studies described by Gopnik on 'specific language impairment'. The existence of inherited defects in linguistic competence, not necessarily associated with any general cognitive disability, is a confirmation of Chomsky's claim that language is peculiar. But it also holds out hope that genetic analysis will help us to understand the nature and evolution of the 'language organ', just as it is now helping us to understand the nature and evolution of animal and plant development. Gopnik insists that she has not discovered 'the gene for grammar', but it seems that she has discovered at least one gene which, if mutated, causes a specific defect in grammar. There must be many such genes: after all, a 'language organ' could not be programmed by one gene. They may be hard to find, either because they are recessive (and so will not show up in parent and child), or because they have cognitive as well as linguistic effects. As an evolutionary biologist, I would be willing to place one bet. The language organ did not arise *de novo*. New organs usually arise as modifications of pre-existing organs with different functions: wings are modified legs, teeth are modified scales, jawbones are modified gill arches, and so on. It will be

interesting to learn what the part of our brain now dedicated to language was doing in our simian ancestors.

The idea of a special language organ has led to the suggestion that there may be other modules specific to other cognitive abilities, for example for social interaction, the manufacture of tools, or the classification of living organisms (see Sperber 1994 for a general discussion). It has been obvious for some time that there are different modules for analysing different kinds of sensory input—for example, visual, auditory, tactile. It has sometimes been argued that the cognitive part of the brain, unlike the preceptual, cannot be modular because its whole purpose is to combine different kinds of information. But this does not really follow. There are separate perceptual modules for visual and auditory inputs, but their outputs can be combined in deciding that an animal is a dog because it looks like a dog and barks like a dog. In the same way, the existence of separate cognitive modules, for example for social and technological functions, would not prevent the conceptual output from such modules being combined.

Mithen proposed an ingenious application of the modular theory of the mind to explain the cultural revolution which marked the transition between the extreme technical and social conservatism of the lower palaeolithic and the inventiveness, cultural diversity and rapid change of the upper palaeolithic. His idea is that the earlier period saw the separate evolution of modules for social interaction and for the manufacture of tools, and that the cause of the revolution was the development of communication between these modules. The result was a symbolic revolution, in which the products of technology were used to carry social information.

Aiello discusses the cognitive and linguistic evolution of modern *Homo* from ape ancestors, using primarily anatomical evidence as a guide. As a non-anatomist, I was impressed by how much can be deduced about behaviour from fossils. How, one might ask, could one possibly deduce anything about the linguistic ability of an individual by examining his thoracic vertebrae? If you read Aiello's article, you will find out.

Mellars discusses the same revolution from a different standpoint, emphasizing the dramatic nature of the transition in Europe, and reviewing its social and demographic consequences. As an outsider, I am left with some sense of puzzlement. It seems natural to seek for a biological underpinning for the cultural revolution that took place some 50,000 years ago. In the absence of biological change, it is hard to explain why almost nothing happened for the preceding half a million years, and why so much has happened since. Most biologists (and, I suspect, all sociologists) would accept that the causes of the later neolithic and industrial revolutions were cultural rather than genetic, but the change that Mithen and Mellars discuss looks different, if only because it was preceded by such a protracted period

of conservatism. But if the change was genetic, what was its nature? Which of the cognitive differences between apes and humans—in imitation, intentionality, social skills, linguistic competence, the integration of tool-making and social modules, or in some combination of several of these—underlay the transition between early and late palaeolithic? Equally puzzling is the fact that the transition is not associated in an obvious way with a change in physical type. It is true that, in Europe, the change is roughly contemporary with the replacement of Neanderthals by modern *Homo sapiens*. But modern *H. sapiens* appear first in Africa some 100,000 years ago, and their appearance is not associated with any obvious cultural change. In Europe, there is some evidence associating upper palaeolithic technology with men of Neanderthal type. We badly need to know more about what was going on outside Europe.

REFERENCES

- Brockmann, H.J. & Dawkins, R. 1979: Joint nesting in a digger wasp as an evolutionarily stable preadaptation to social life. *Behaviour* 71, 203–45.
- Chomsky, N. 1957: Syntactic Structures. Mouton, The Hague.
- Dickemann, M. 1979: Female infanticide, reproductive strategies and social stratification: a preliminary model. In *Evolutionary Biology and Human Social Behaviour: An Anthropological Perspective* (ed. N. Chagnon & W. Irons), pp.321–67. North Scituate, Mass. Duxbury.
- Irons, W. 1979: Natural selection, adaptation, and human social behaviour. In N. Chagnon & W. Irons ed. op.cit.
- Sperber, D. 1994: The modularity of thought and the epidemiology of representations. In *Mapping the Mind* (ed. L.A. Hirschfeld & S.A. Gelman), pp.39–67. Cambridge University Press.