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Genes and Memes

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The Extended Phenotype by Richard Dawkins
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The Extended Phenotype is a sequel to *The Selfish Gene*. Although Dawkins has aimed his second book primarily at professional biologists, he writes so clearly that it could be understood by anyone prepared to make a serious effort. *The Selfish Gene* was unusual in that, although written as a popular account, it made an original contribution to biology. Further, the contribution itself was of an unusual kind. Unlike David Lack's classic *Life of the Robin* – also an original contribution in popular form – *The Selfish Gene* reports no new facts. Nor does it contain any new mathematical models – indeed it contains no mathematics at all. What it does offer is a new world view.

Although the book has been widely read and enjoyed, it has also aroused strong hostility. Much of this hostility arises, I believe, from misunderstanding, or rather, from several misunderstandings. Of these, the most fundamental is a failure to understand what the book is about. It is a book about the evolutionary process – it is *not* about morals, or about politics, or about the human sciences. If you are not interested in how evolution came about, and cannot conceive how anyone could be seriously concerned about anything other than human affairs, then do not read it: it will only make you needlessly angry.

Assuming, however, that you are interested in evolution, a good way to understand what Dawkins is up to is to grasp the nature of the debates which were going on between evolutionary biologists during the 1960s and 1970s. These concerned two related topics, 'group selection' and 'kin selection'. The 'group selection' debate was sparked off by Wynne-Edwards's book, *Animal Dispersion in relation to Social Behaviour*. Its thesis is that animals regulate their own numbers behaviourally, rather than being passively regulated by food. Wynne-Edwards further suggested that animals have evolved special displays, usually involving social aggregations (black-cock leks, shearwater rafts, the mass aerial dances of mosquitoes), which inform them of their numbers, so that they can respond by breeding if numbers are low and by refraining if numbers are high. He noted that the entity which would benefit was the whole population, which would not outrun its food supply, and not the individual, which would leave more progeny if it continued to breed regardless of numbers. He therefore suggested that the necessary behavioural adaptations had evolved by 'group selection' – i.e. through the survival of some groups and the extinction of others. Most biologists have doubted whether such a process could actually be effective, and have argued that natural selection typically acts by favouring some individuals rather than others, and not some populations rather than others. However, Wynne-Edwards did raise in a particularly clear way the question of the level at which selection acts – individual, population, species or ecosystem.

At almost the same time, W.D. Hamilton raised another question about how natural selection acts. He pointed out that if a gene were to cause its possessor to sacrifice its life in order to save the lives of several relatives, there might be more copies of the gene present afterwards than if the sacrifice had not been made, because relatives might carry copies of the gene inherited from a common ancestor. The suggestion has obvious relevance for the evolution of social behaviour. To model the process quantitatively, Hamilton introduced the concept of 'inclusive fitness'. To understand this, you must first appreciate that scientists use the word 'fitness', as they do 'force', in a technical sense only loosely related to its colloquial meaning. 'Fitness' is a property of a 'genotype' – that is, of individuals of a particular genetic constitution. Crudely, it is the expected number of offspring produced by individuals of a given genotype in a given environment. Hamilton saw that to use fitness in this sense could lead to wrong predictions about how the frequencies of genes in populations would change – i.e. about evolution. He therefore replaced this classical fitness by 'inclusive fitness', which includes, not only an individual's own offspring, but any additional offspring raised by relatives with the help of that individual, appropriately scaled by the degree of relationship: for example, if I (or more precisely, people with a genotype like mine) help my sister to raise a child she would not otherwise have, that raises my inclusive fitness by one half. It has since become a rule of thumb among students of social behaviour to say that animals will behave so as to maximise their inclusive fitness.

Dawkins, while acknowledging the debt we owe to Hamilton, suggests that he erred in making a last-ditch attempt to retain the concept of fitness, and that he would have been wiser to adopt a full-blooded 'gene's eye' view of evolution. He urges us to recognise the fundamental distinction between 'replicators' – entities whose precise structure is replicated in the process of reproduction – and 'vehicles': entities which are mortal and which are not replicated, but whose properties are influenced by replicators. The main replicators with which we are familiar are nucleic acid molecules – typically DNA molecules – of which genes and chromosomes are composed. Typical vehicles are the bodies of dogs, fruitflies and people. Suppose, then, that we observe a structure such as the eye, which is manifestly adapted for seeing. We might reasonably ask for whose benefit the eye has evolved. The only reasonable answer, Dawkins suggests, is that it has evolved for the benefit of the replicators responsible for its development. It is, he says, foolish to argue about whether some behaviour pattern has evolved for the benefit of the individual or of the group, since both individual and the group are vehicles. Although, like me, he greatly prefers individual advantage to group advantage as an explanation, he would prefer to think only of replicator advantage.

I said earlier that Dawkins was interested in evolution, not in the human sciences. Yet, in *The Selfish Gene*, he introduced, perhaps unwisely, the concept of a 'meme'. A typical meme, as he then conceived it, is a limerick. He would now, I think rightly, prefer to use the word 'meme' only for the physical structure in the brain which represents the limerick. The spoken limerick is then the 'phenotypic expression' of the meme – to a geneticist, the appearance and characteristics of an organism are its 'phenotype' as opposed to its 'genotype', or genetic constitution. A meme can replicate, because if I, knowing a limerick, speak it aloud, the consequence is the appearance in your brain of a corresponding meme. Hence, by analogy with biological evolution, we can expect memes to 'evolve' phenotypic effects favourable to their own replication. However, it may make a crucial difference, as Dawkins acknowledges, that memes can replicate only by generating a phenotypic representation of themselves, whereas genes replicate by a direct template process.

Dawkins's meme concept has been criticised on the grounds that an 'atomic' theory of culture is necessarily wrong. This may well prove to be correct, although I am astonished at the confidence with which it is sometimes asserted. Animal bodies show a far higher degree of coherence and functional interrelationship than do human societies, and yet an essentially atomic theory of genetics has had a lot to say about the evolution of animal bodies. However, that is not the defence which, in *The Extended Phenotype*, Dawkins makes of memes. Instead, he defends himself by saying that he was trying to make a logical point – i.e. that whenever we meet entities capable of accurate replication, we can expect them to generate phenotypes ensuring their own survival. He is not making a takeover bid for the human sciences: he is trying to explain to us the mode of existence of replicators.

The Selfish Gene has already had one intriguing impact on mainstream biology: its influence is acknowledged by the authors of the concept of 'selfish DNA'. To explain this requires a brief digression. The classic picture of Menelian genetics is that each individual receives at conception one complete set of genes from each parent. This is true enough, but it has turned out that, in addition to these typical genes, there is a large amount of DNA in our chromosomes which has no obvious function. Much of it is present, not in two copies per cell, as we would expect for typical genes, but in very large numbers of copies. What is all this ‘repetitive’ DNA doing? No doubt much of it will turn out to perform some as yet unknown function useful to the organism. The novel suggestion is that much of it may be ‘selfish’, or ‘parasitic’. A cell is full of enzymic machinery for replicating DNA. Dawkins suggests that DNA molecules, which, unlike typical genes, contribute nothing to the life of the organism, might neverthless live inside cells, just as tapeworms live in intestines. As yet the matter is controversial, but it is very much in the spirit of Dawkins’s thinking that some DNA should be parasitic.

I know that Dawkins has been much puzzled by the hostility his first book aroused. In *The Extended Phenotype* he attempts to analyse and disarm this criticism. He ascribes it, in the main, to the fact that he is perceived as a ‘genetic determinist’. Is he a genetic determinist, and if so, is there any harm in it?

Dawkins is certainly a determinist as far as behaviour is concerned. That is, he thinks that an animal’s (or man’s) behaviour is the consequence of its (or his) genetic constitution, upbringing and immediate circumstances. He would not deny that an action may sometimes be a matter of chance. What he would deny is the existence of something called ‘free will’ as an additional cause of behaviour, over and above those already mentioned. It is only fair to say I agree with him, at least as a matter of assumption. One could only *prove* that actions could be fully accounted for by genes, upbringing and immediate circumstances by doing the full accounting, and that is too far off to be worth considering. But anyone who attempts a causal explanation of behaviour has to make the assumption that behaviour is caused – it is certainly made by Marxists, who have been Dawkins’s most outspoken critics.

I have found that if I make such an assertion to anyone but a professional biologist, I am likely to be met with the response: ‘But surely you believe in free will?’ To this, the answer is that, of course, I believe in free will. For example, I am writing this review of my own free will: no one made me do it. It is just that I do not see free will as an alternative to genetic and environmental causation. To say that I do something of my own free will says only that my mental disposition at the time was the deciding factor, and not physical constraint.

Dawkins, then, is a determinist, and so is every scientist who studies behaviour, even if they don’t know it. But Dawkins is not a *genetic* determinist – unless it be the late Cyril Darlington, no one ever was. J.B.S. Haldane started his lecture course on genetics with the words: ‘Genetics is that branch of science which studies the causes of the innate differences between fairly similar organisms.’ For our present purpose, the essential word in this definition is ‘differences’. If we see two people, one with dark hair and one with blond, we can ask: ‘Is the difference genetic or environmental?’ By ‘genetic’, we mean that the difference is caused by a difference between the fertilised eggs from which the two people developed. If one of them has dyed their hair, then the difference is environmental. Thus we can ask of a difference whether it is genetic or environmental, but not of a characteristic. To ask, ‘Is hair colour genetic?’ is, quite literally, meaningless. To have hair, of any colour, requires that you have both genes and an environment.

To be a genetic determinist, then, would mean that one thought that all differences between the members of a species were genetic. Dawkins certainly does not think this: indeed, as far as I can tell he does not even have a bias in favour of emphasising genetic rather than environmental causes. Why, then, is he seen as a genetic determinist? The reason is quite simple. It is that, *when he is thinking about evolution*, he is only interested in differences that are genetic, and he is quite right. If two animals differ for environmental reasons, the difference may affect their chances of survival, but it will not affect the nature of their children, and hence will have no evolutionary consequences. Of course, if one were concerned, for example, with designing an educational system, environmentally-caused differences would be of profound importance. But Dawkins is not planning schools, he is talking about evolution.

Another reason why Dawkins angers people is that he thinks, and writes, in analogies. This is obvious in his very title, the ‘selfish’ gene. I have heard a distinguished biologist arguing passionately that, of course, genes are not selfish, because they are not self-aware beings, to which alone the term ‘selfish’ can properly be applied. I found it impossible to respond to his passion. I suppose that Dawkins referred to genes as selfish because he imagined that no one would take him literally. I do not regard genes as self-aware, but, when thinking about evolutionary problems, I sometimes say to myself: ‘Suppose I were a gene, would I cause my carrier to do A or B?’ I have every intention of going on doing so.

So far, I have discussed ideas already present in *The Selfish Gene*. What is new in *The Extended Phenotype*? In essence, having argued that we should think about the selection of replicators, and not of vehicles, Dawkins now suggests that we should dissolve the vehicle altogether. Consider, for example, a spider’s web. It is not part of the spider, but it is as much part of the phenotype coded for by the spider’s genes as is the spider itself. And if webs are seen as phenotypic expressions of spider genes, why should we not see the lakes resulting from the beaver’s dams as phenotypic expressions of beaver genes? The expression of genes does not end at the boundary of the body.

Applied to spider’s webs, this way of seeing things does not seem so strange. Dawkins goes on, however, to suggest that we should sometimes see the actions of one animal as part of the extended phenotype of the genes of another. He is able to make this plausible by quoting examples of the effects of parasites on their hosts. Larvae of the beetle *Tribolium*, infected by a protozoan parasite *Nosema*, fail to metamorphose, but instead continue to grow, reaching twice the size typical of their species, apparently because the parasite synthesises the appropriate insect hormone. Freshwater shrimps (*Gammarus*), infected with the immature stages of a parasitic worm, *Polymorphus paradoxus*, swim to the surface of the water instead of keeping to the bottom. If the worms are to develop further, their shrimp host must be eaten by a surface-feeding duck, typically a mallard, and it has been shown that mallards are more likely to swallow infected than uninfected shrimps.

In these and other cases, the behaviour of the host is such as to ensure the survival of the genes in the parasite. A more familiar example is a reed warbler feeding a baby cuckoo. Dawkins adds that colleagues with whom he has discussed the extended phenotype repeatedly came up with the same speculations. Do cold viruses cause us to sneeze so as to increase their chance of reaching another host? Does any venereal disease increase libido? These are speculations, but they are natural ones if we accept Dawkins's view.

To me, however, the most original chapter in the book is the last, on 'rediscovering the organism'. For most people, organisms are given, and the problem is to explain why they have genes. Once accept a gene's-eye view of evolution, however, and the question becomes: why do genes characteristically band together in organisms? I cannot here summarise Dawkins's answer: indeed, he does not claim to provide a final answer. I can, however, give some idea of his approach by mentioning some subsidiary questions he discusses. What are the limits of an organism? Obviously, a dog or a man or a pine tree is an organism. But is a stand of nettles, all derived by underground roots from one original seed, one organism or many? If we are going to count all the plants arising from a single seed as one organism, what of a clone of aphids, all descended by virgin birth from a single female, and all genetically identical? Does it matter that in the case of the aphids (or, to give a second example, in a clone of dandelions) each new individual is derived from a single cell, whereas in the stand of nettles this is not so? Does it matter whether the single cell is produced sexually or asexually?

In a sense, these questions are purely semantic: we can use the word 'organism' to mean what we like. However, since we think in words, our choices are important. What Dawkins is really asking is: what is the significance for evolution of these various patterns of growth and reproduction? His answer is that the crucial distinction is whether the new individual arises from a single cell, or from many. Essentially, this is because only in the former case is it possible for genes with interesting effects on development to be favoured by natural selection.

I have left till last what is to me the strangest feature of both books, because I suspect it will not seem strange to many others. It is that neither book contains a single line of mathematics, and yet I have no difficulty in following them, and as far as I can detect they contain no logical errors. Further, Dawkins has not first worked out his ideas mathematically and then converted them into prose: he apparently thinks in prose, although it may be significant that, while writing *The Selfish Gene*, he was recovering from a severe addiction to computer programming, an activity which obliges one to think clearly and to say exactly what one means. It is unfortunate that most people who write about the relation between genetics and evolution without the intellectual prop of mathematics are either incomprehensible or wrong, and not infrequently both. Dawkins is a happy exception to this rule.

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