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DAVID YOUNG

Ethology and the Evolution of Human Behaviour: An Introductory Review¹

Behaviour patterns of animals vary so much from species to species that extrapolation to man is misleading: only the methods, not the results, of animal behaviour study are relevant to ourselves. Writing as a Christian and as an evolutionist (see Note 2) Dr. Young shows that a proper understanding of ethology destroys a number of popular notions, among them 'evolutionary ethics' and evolutionary 'explanations' of religion and theism. Dr. Young warns us also against what he calls 'biological intimidation'.

It is with some hesitation that I offer the following contribution on the evolution of human behaviour but the intrinsic fascination of the subject makes it worth discussing and recent biological research has provided fresh material for discussion. Few are likely to dissent from the view that the nature and origin of man is an important subject, especially in the context of Christian theology. It is not possible to tackle all the relevant considerations in so short a compass and so I shall keep as close as possible to my own subject, the biology of the nervous system and behaviour, and offer an introductory account of its scope and limits in contributing to the study of human evolution. In particular, I shall try to assess the contribution of ethology, the study of animal

behaviour, to our understanding of the transition from ape to man.²

It is just over a hundred years since the connection between animal and human behaviour was first systematically explored by Charles Darwin in two important books. In his well known *Descent of Man* (1871) Darwin presented the evidence for the evolution of man from lower animals and grappled with the difficulties which man's mind and morals presented for this thesis. This was followed by his *Expression of the Emotions in Man and Animals* (1872) which is less well known but no less important. In this book Darwin presented the first comparative study of particular behaviour patterns in man and other animals. Darwin had to contend with the view of the distinguished anatomist, Sir Charles Bell, that certain muscles in the human face had been specially created for the purpose of expressing the emotions. By contrast, Darwin showed that the muscles used in expressing emotion are also involved in other activities, that corresponding muscles exist in monkeys and apes, and that certain general principles regulate the expressions used by both man and animals in communicating emotion. Thus a sound basis was made for the comparative study of human and animal behaviour patterns.

The intervening years since Darwin wrote have not been as fruitful as might be expected. Darwin founded no school of behavioural study and it is difficult to find any work that was *directly* inspired by these two books. Recently a number of developments have brought a vigorous renewal of the subject, particularly the expansion of a zoological approach to behaviour study. This in turn has prompted popularisers to present their own versions for the benefit of the general public. Notable among these have been the biologists Desmond Morris (*The Naked Ape*) and Konrad Lorenz (*On Aggression*). Amateur biologists such as Robert Ardrey (*The Territorial Imperative* and *The Social Contract*) and Leonard Williams (*Man and Monkey* and *Challenge to Survival*) have also written similar books. All are assertative, dashing and brilliant in style and some have been justly successful as popular literature.

Now it will be as well to be clear about the significance of these popular books at the outset. On the one hand, it is good to see the biologists' contribution to an important topic receiving widespread attention and support. On the other hand, these popularisations are unfortunate in certain respects and suffer from a number of shortcomings. Firstly, they all present the subject in too cut and dried a fashion, as if most of the matters discussed were beyond dispute. Combined with the use of outmoded motivational concepts (discussed below) this leads to a misleading oversimplification of the whole topic. Secondly, none of these books offers a balanced survey of the field; rather each is essentially polemical, being designed to present a particular case without adequate regard for wider study or contrary evidence. Both Ardrey and Williams combine biology with a blatantly political bias (at opposite extremes of the spectrum, as it happens!). Thirdly, they present as knowledge many statements which are after all no more than likely guesses. Therefore none of these books should be taken too seriously but may be read for what they are: entertaining mixtures of fact and fancy. However, in some ways these books represent a ghastly caricature of what ethology is about, which is a pity because ethology does have an important contribution to make.

Having said this, it must also be said that the reaction to this popularisation has often been needlessly violent. The anthropologist, Ashley Montague, wrote an almost hysterical attack on the views of Ardrey and Lorenz on aggression entitled "The new litany of innate depravity or original sin revisited", which contains statements quite as fundamentally absurd as any of the popularisers, e.g. that except for the reaction to sudden noise "the human being is entirely instinctless".³ Again the psychologist, Eisenberg, combines in one article some sensible points with a bitter personal attack on Lorenz, ostentatiously recalling Lorenz's sympathy with the right wing politics of Nazi Germany.⁴

Whenever scientific debate reaches this pitch we can be sure that clashes of personality and ideology are involved as well as scientific issues. I mention this only to set it aside: behavioural analysis is quite difficult enough without these extra burdens

involving the behaviour of the investigators ! But these examples offer a warning of the depths of feeling which may be evoked unexpectedly by discussion of this topic even in purely scientific terms.

Origins of Ethology

Ethology has now come to be used as a general term for the biological study of behaviour but it had its origin in a particular school of thought. This has very much a zoological tradition and orientation and its modern flowering, especially in application to man, represents a cashing of the cheque drawn by Darwin many years before. A number of zoologists had independently studied animal behaviour since Darwin but their efforts tended to be fragmentary and unco-ordinated. In the 1930's Konrad Lorenz gave impetus to the new work by criticising the earlier psychologists and welding a variety of concepts together to form a new overall theory of animal behaviour.⁵ Because of this, Lorenz is rightly considered "the father of modern ethology",⁶ even though some of his formulations are now outmoded (I suspect that Lorenz's name will be remembered after those of his critics).

In retrospect, two particular characteristics may be singled out as significant in the ethological approach. One of the main features of the work of Lorenz and Tinbergen was their emphasis on the description and analysis of the normal behaviour of animals in their natural surroundings. This led to the discernment of natural behaviour structures or episodes, which largely seemed unaffected by the environment and so might reflect genetic programming. This in turn rejuvenated the experimental study of behaviour, for as Medawar has succinctly put it, "it is not informative to study variations of behaviour unless we know beforehand the norm from which the variants depart".⁷ The other special characteristic of this ethological approach was an interest in the evolution of behaviour, which was studied by means of the comparative method. Just as the comparative anatomist may infer the course of evolution from the comparison of skeletal and other structures, so the ethologist could infer the course of evolution from the study of behavioural structures in related species.

Of course this new approach did not make its way unopposed. It met with strong criticism especially from comparative psychologists who expressed strong differences of theoretical standpoint, as well as differences of interest.⁸ Much of this criticism was soundly based and has led to the abandonment of any unified, grand theory of animal behaviour. Suffice it to say here that this period of mutual criticism has passed into a period of interaction and to some extent of co-operation and synthesis. There is often little difference in the actual work done by people with these different backgrounds.

Ethological Analysis of Behaviour

The modern biological analysis of behaviour resulting from these developments covers a wide range of problems which may be considered under four main categories. The following instances are intended only to illustrate the general approach and current concepts. By way of example, the much discussed case of aggression may be selected.

Firstly, observing animals in as natural surroundings as possible, the ethologist studies the normal behaviour to see when particular behaviour patterns occur and the extent to which different actions are correlated. In some cases it is possible to study this quantitatively and to group different actions objectively by means of statistical analysis. In the case of aggression (that is patterns of threat or attack between one animal and another) such study shows that these occur in definite contexts such as competition over food, defence of offspring, dominance disputes or territory. In these contexts aggressive patterns are almost invariably linked with other elements such as retreat because threatening attack also involves the risk of being attacked (the resulting compound behaviour is termed *agonistic*). Moreover, aggressive encounters are terminated by definite cues involving linked sequences of aggression, submission and sometimes reassurance. The details naturally vary very widely in different species and larger animal groups.

Secondly, the ethologist attempts to probe the causation of such behavioural sequences. Thus in the case of aggression, this is usually triggered by the proximity of another individual in one of the above contexts and sometimes only by certain features of another individual. The threshold and degree of response are evidently determined by a great variety of factors such as hormone level, feedback effects from previous activities, arousal of the central nervous system, etc. The upshot of a great deal of work during recent years in this area of animal behaviour is that the unitary drive concepts of behaviour, originally formulated by Lorenz and others, have been abandoned and it is recognised that the causation of any one type of behaviour is multifactorial. Drive concepts have proved useful at a preliminary stage of analysis for relating dependent variables in behaviour, but as physiological analysis proceeds, drive constructs cease to be relevant. Nowadays therefore it is positively misleading to talk about an aggressive drive, sex drive, etc. particularly where it is implied that these are internal forces that must find expression.⁹

Thirdly, analysis proceeds to the study of the development of behaviour in the individual. Here again, considerable changes have occurred in our concepts over the last few years, not without a certain amount of confusion. The concept of instinct has gone the way of drive and in particular the dichotomy of instinct versus learning is no longer useful. Individual behavioural characteristics result from a continuous interaction between organism and environment at all stages of development ; genes produce their effect only by virtue of the environment in which they act and the environment affects behaviour only by virtue of the genetically determined susceptibility of the organism. Hence modern studies on the development of behaviour try to unravel the influence of the internal and external sources of programming in the actual developmental sequence. One of the most fully studied examples is the development of bird songs which has turned out to be far from simple and illustrates the complexity of processes underlying apparently straightforward behaviour patterns.¹⁰

Fourthly, it is also possible to study the functions, that is to say the survival value, of behaviour. This has been done especially

by Tinbergen and his co-workers. The animal's behaviour is viewed as an integral part of its equipment for survival. The function of particular behaviour patterns can be studied both by the comparative method and by experimental analysis. One can elucidate the adaptive features of the behaviour patterns and begin to suggest the selective forces which may have shaped their evolution.¹¹

Application of Ethology to Man

In considering the application of this biological study of behaviour to man, one must begin by noting that the popularisers have often provided good examples of how *not* to do this. Thus their liberal sprinkling of phrases like "innate spontaneous action" or "territorial imperative" reveals the hasty use of concepts of instinct and drive, which are no longer adequate for dealing with animal behaviour, much less the more complex behaviour of man. Tinbergen has pointed out the central weaknesses: "Most writers who have tried to apply ethology to man have done this in the wrong way. They have made the mistake, to which I objected before, of uncritically extrapolating the results of animal studies to man. They try to explain man's behaviour by using facts that are valid only of some of the animals we studied. And, as ethologists keep stressing, no two species behave alike. Therefore, instead of taking the easy way out, we ought to study man in his own right. And I repeat that the message of the ethologist is that the methods, rather than the results, of ethology should be used for such study".¹²

As a result of the hasty popularisation, the ethological study of man currently finds itself in a false position, overacclaimed by some, shrugged off by others.¹³ On the one hand, the popularisations have led to an uncritical acceptance in some quarters of their bold but unsubstantiated extrapolations to man. On the other hand, some professional students of human behaviour have, in rejecting the claims of popular ethology, unwisely rejected the ethological approach as a whole.

The constructive application of ethology to man may be

undertaken along two main lines and one of these is the proper use of the comparative method. For this one should study man's closest relatives, the anthropoid apes and some monkeys, for resemblances and differences in behaviour patterns, rather than extrapolate from widely different animals such as birds and fishes in spite of their elaborate social behaviour. In fact one of the major recent developments is the detailed study of several primate species under natural conditions and this has yielded much data relevant to such a comparison. It is difficult to select from the many interesting findings that have emerged but the work on chimpanzees is particularly relevant.¹⁴ Wild chimpanzees are able to make simple tools, that is they not only use an object for a purpose but can modify it to suit that purpose. Further, the younger individuals can acquire this and other habits through observational learning in a social context. And again they can collaborate to achieve a common purpose, such as a group of adult males combining to hunt a monkey for food. Thus studying chimpanzees in their natural habitat has revealed previously unsuspected capabilities and ones which have at times been thought unique to man. Altogether, chimpanzees and other primates have an elaborate social life based on an extensive system of communicative sounds and gestures, having elements in common with man. This then is the sort of data on which a proper comparative study can be made.

The second main way in which ethology may be applied to man lies simply in employing ethological methods to study particular examples of human behaviour. Eibl-Eibesfeldt has employed the technique of high speed filming, without the subjects' awareness, to make a comparative study of human facial expressions. He has been able to show that many basic gestures, such as greeting with the eyes, agree in the smallest details in people from widely separated cultures, including isolated primitive tribes. This is an important demonstration since the existence of culture-independent expressions has often been denied.¹⁵ Ethological methods are also being applied to the study of non-verbal communication among children. In a study of autistic children, the Tinbergens have been able to provide strong evidence for the hypothesis that many cases of autism are social reactions caused

by a hostile social environment and are not due to brain damage or to genetic factors.¹⁶ Again on the subject of children, a series of controlled experiments, involving direct observation of behaviour in the experimental situation, is providing strong evidence that children of pre-school age can learn aggressive patterns of behaviour by watching film or television (even cartoons) and enact these in their later play.¹⁷

It is still very early in the ethological study of human behaviour but the examples given look promising. One can see that a serious biological account of human behaviour patterns, such as aggression, should be possible. The comparative primate studies can indicate how far man's primate heritage predisposes him toward certain types of behaviour, as well as highlighting significant differences in behaviour. The experimental studies can indicate how the biological predispositions to particular behaviour may interact with specific social learning situations to produce great individual differences.¹⁸ It seems legitimate to conclude that ethological methods may be applied successfully to the problems of the evolution and causation of human behaviour patterns, including some of medical and practical importance.

Ethology and the Evolution of Distinctively Human Behaviour

The applicability of ethological study to human behaviour naturally leads to the question of how far such a biological approach might be able to throw light on those forms of social behaviour which are uniquely human and whose origins are at present something of a mystery. Human behaviour is distinguished from that of other primates chiefly by man's culture — the ability to learn and transmit information from one generation to another through the medium of tradition in the widest sense. However, culture is still a biological phenomenon which is not unique to man, and cultural changes occur in the behaviour of primates and other species. Man is distinguished by the very much greater development of culture and the greatly accelerated pace of cultural change compared with genetical change in human evolution.¹⁹

Consider, for example, the origin of human moral behaviour. In his useful book, *The Ethical Animal*, C. H. Waddington advanced the thesis that evolution has endowed man with a certain innate capacity to acquire ethical beliefs, but without any specific beliefs in particular, and that during the early life of the individual processes go on by which these potentialities become realised. Recent studies enable us to make some suggestions about how such a course of events could have come about. We can begin to see that, especially in the primates, a species' cultural inheritance and genetical inheritance must interact in a complex way in the process of biological evolution. For an animal living in the kind of social environment now known to exist in primates would be exposed to the selective effects of the surrounding environment in a less direct way than would a member of a nonsocial species. Natural selection will affect the individual through a social filter. And so during evolution it may be expected that the genetic programming of the behaviour of the species will tend increasingly to be influenced by the social behaviour of that species.

Now field studies of the higher primates show that individual animals are capable of highly independent actions involving individual initiative. This capability is employed in the maintenance of dominance hierarchies, in co-operative hunting and other important social activities. It is also occasionally employed in what it is tempting to call antisocial activities, where one individual gains some immediate advantage at the expense of another. But in a complex society, a consistently antisocial individual would be likely to reduce its success in leaving offspring through its failure to follow the normal patterns of social behaviour. And so a genetically programmed predisposition to accept norms of conduct and to be receptive to instruction in such matters could be of selective advantage to the individual animal in a social context. Thus it is conceivable that the earliest development of primitive ethical capacity could have been originated through natural selection.²⁰

Waddington and some other biologists have proposed that the course of this behavioural evolution as determined by natural selection might itself be used as a criterion for judging modern

ethical systems. Such 'evolutionary ethics' represents a philosophical position, which is open to damaging, and in my view fatal, criticisms. For one thing there is the general difficulty of how any matter of fact, such as the course of evolution, can be translated into an ethical imperative. This has been made clear by several philosophers²¹ and the biologists have not succeeded in overcoming their criticisms. Secondly, evolutionary ethics blurs the distinction between genetical and cultural inheritance. It will be generally agreed that the particular ethical beliefs which we hold are the product of our human culture, and the course of cultural evolution, by which these concepts have changed and developed, is evidently determined by factors other than reproductive success. Hence in so far as the modern flowering of ethical beliefs is a cultural phenomenon, it cannot be fully judged, or explained, by the process of natural selection that may have led to its inception.

At the same time, I see no need to maintain that there is a conflict between natural selection and moral values (as persuasively argued by David Lack²²) so long as one can be clear about the distinction between genetical and cultural inheritance. Just as our genetical inheritance determines our ability to develop language but not which language we shall speak, so the particular ethical systems we accept come not from our genetical but from our cultural inheritance. And this cultural inheritance includes certain influential episodes such as that on Mount Sinai.

This is an area of discussion in which it is particularly easy to overlook the limitations of the biological approach. For instance, in *The Naked Ape*, Desmond Morris attempts to explain religious behaviour in man by the disappearance of the dominant male social structure, which he supposes was present in our immediate ancestors. This may have nurtured a certain psychological orientation in the individual, as well as giving advantage to the group and these features became maintained by the invention of a supernatural dominant male in the sky. Now what needs to be called in question about such an explanation is not its accuracy so much as its adequacy. It may be granted that some such account of the origin of religion is possible (even if this particular

one is not correct) but to the extent that developed religion, like ethics, is a product of cultural evolution, it cannot be fully explained as a phenomenon in terms of its distant origins in the social structure of early man and his primate ancestors. In general, it is meaningless to explain a behaviour pattern which is highly evolved within a species as nothing but a survival of the incipient stage of the behaviour in that species or its immediate ancestors.

Explanations of this general kind are often accompanied by the supposition that belief in the existence of God (philosophical theism) must be false because it is merely a survival from the primitive delusions and psychological needs of early man. But once again this extension of the discussion takes us out of biology and into philosophy with an argument which Bevan has aptly termed "the method of anthropological intimidation".²³ As Bevan points out, the fact that modern theism is connected by a process of gradually changing beliefs to primitive notions, is equally compatible with the view that belief in God is false, and with the view that belief in God is true and so does not provide evidence for either. Modern biological beliefs are also similarly connected back to man's primitive notions and needs with respect to animals and plants but no one on that account supposes that biology is nothing but a survival of primitive fancy! The important point here is that discussion about belief in God involves a genuine philosophical issue and one that is not to be foreclosed by the method of anthropological intimidation.

Ethology and the Nature of Man: Conclusions

We have seen that the modern study of animal behaviour has made fresh progress recently in the refinement of its methodology and in the actual results achieved. In particular these methods have been applied to our close relatives among the primates with results that are of special interest for human origins. If the gap between animal and human behaviour seems less large than it used to, this is because modern comparisons have upgraded our estimate of animal capabilities rather than downgraded man, as the Victorians feared.

The biological methods of ethology cannot provide all the answers concerning the causation and evolution of human behaviour. This is an area where the biologist needs to be specially careful of inadvertently slipping from biological into philosophical discussion. But bearing the limitations of the biological approach in mind, ethological methods do provide the tools to do the job and I consider that we can be cautiously optimistic about achieving a biological understanding of the origins of human social life. The rapid development of primate studies over the next 10 to 20 years may be expected to yield models of social evolution which are factually plausible. If this work is taken in conjunction with the increasingly satisfactory fossil record, it should become possible to outline the probable course of human behavioural evolution.

J. Z. Young has spoken of our new knowledge of the brain and behaviour effecting a revolution in our understanding of ourselves.²⁴ But it is rather confusing to describe our growing knowledge as revolutionary: while there is much that is new and important, there is little that is strictly revolutionary in the newer biological work. I rather take the view that the application of ethology and neurobiology within their area of competence can serve to render more definite and to clarify much that previously could only be the subject of speculative guesses, however philosophically expressed. The steadily increasing interest and importance of this approach is reflected in the fact that courses in human biology, including the sort of material reviewed here, are becoming commonplace in universities as interdisciplinary or bridge courses available to students from the arts and medicine as well as the sciences.

Viewed in this way as an integral part of our overall study of man, there is no need to precipitate a sense of conflict between the biological study of man and other approaches such as the theological. But on account of the great differences in aims and methods, it is natural that a certain tension should exist between these diverse approaches. For this reason, it is difficult to envisage any unified study of man emerging in the foreseeable future. Nevertheless, it should be possible for these diverse approaches

to interact in a constructive and useful way and it is in this spirit that the present essay on the biological approach to man is offered.

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For ethological studies relating specifically to man and his primate relatives, see the very valuable review by A. Jolly *The Evolution of Primate Behaviour*, 1972, (Macmillan Series in Physical Anthropology) and the excellent first-hand account by J. van Lawick-Goodall *In the Shadow of Man*, 1971. N. Blurton-Jones has edited some preliminary studies on *Ethological Studies of Child Behaviour*, 1972.

A number of biologists have tried to set their work in a wider philosophical context. See especially

T. Dobzhansky *Mankind Evolving*, 1962, (New Haven, Yale U.P.), the essays by R. A. Hinde and G. A. Miller in Pringle, J.W.S., *Biology and the Human Sciences*, 1972, W. H. Thorpe *Science, Man and Morals*, 1965, and C. H. Waddington *The Ethical Animal*, 1960. For relevant philosophical interpretations of biology see M. A. Simon *The Matter of Life*, 1971, (New Haven, Yale U.P.) and A. G. N. Flew's valuable little book on *Evolutionary Ethics*, 1967.

There are very few books which try to set this work in a theological context but J. Hick *Biology and the Soul*, 1972, is a good example of what is needed. See also *Man: Fallen and Free*, ed. E. W. Kemp, 1969, (rather feeble except for the articles by David Jenkins), and for a spirited defence of theological concepts in relation to man (by a biologist!) J. Morton, *Man, Science and God*, 1971. K. Rahner, *Hominisation: The Evolutionary Origin of Man as a Theological Problem* is a good example of modern Catholic thought.

REFERENCES AND NOTES

An asterisk (*) indicates that the full reference is given in the bibliography above.

1. This essay is based on an earlier talk delivered to the Canberra Society for the Study of Religion and Theology.
2. Space does not permit a presentation of the evidence for human evolution or a discussion of the anti-evolutionary views held by some of my Christian colleagues. Since the evolution of man is taken for granted in this contribution it will be obvious that I disagree with the anti-evolutionary position but it is not possible here to discuss the nature of this disagreement. The anti-evolutionary position has recently been presented and discussed in **THIS JOURNAL**, 98 (2, 3), 5-60.
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8. Representative of such criticisms are the following: Lehrman, D. S., *Quart. Rev. Biol.* 1953, **28**, 337-363; Schneirla, R. C., *Psychol. Bull.* 1952, **49**, 559-597.
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10. For details see several articles in *Bird Vocalisations*, ed. R. A. Hinde, 1969, and Thorpe's article in *Non-verbal communication*, ed. R. A. Hinde, 1972.
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18. See Hamburg, D. A. (note 17) and for a good example of rigorous experimental studies on aggression, *The Physiology of aggression and Defeat*, ed. B. E. Eleftherion and J. P. Scott, 1971 (New York: Plenum). Excellent wider studies relevant to this whole section, are: Jolly, A., 1972 * and Tinbergen, N., Functional ethology and the human sciences, *Proc. Roy. Soc. B.* 1972, **182**, 385-410.
19. These points are brought out clearly in the following books: T. Dobzhansky, 1962 *; Medawar, P. B. *The Future of Man*, 1960; Smith, J. M., *The Theory of Evolution*, 1958 (Harmondsworth, Penguin).
20. Some psychologists might wish to express these developments in terms of the concepts of ego and super-ego but it is difficult to find any biologists working in the field of primate behaviour who take these concepts very seriously. Thorpe, 1965, * quotes Zangwill's acid comment that "the super-ego is that part of the ego which is soluble in alcohol".
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