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Meeting February 11 1969

Ethology and Behaviour [Abridged]

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The Ritualization of Agonistic Behaviour as a Determinant of Variation along the Neuroticism/Stability Dimension of Personality

When two individuals have had a serious fight over some prize, the loser is likely to be dead, or unconscious, or physically incapacitated or suffering such physical pain that the winner is able to take the prize without further interference. But serious fighting is rare in nature. Comparative ethologists have shown that, in most vertebrate species, disputes between individuals are settled by ritual fighting in which neither of the contestants is seriously harmed. If there is no physical incapacity or physical pain, what induces the loser in a ritual combat to yield the prize to the winner? One possibility is that ritual yielding is subserved by mental incapacity and mental pain.

If so, it would appear that ethologists have provided at least one important biological function for that puzzling phenomenon, the human neurotic reaction. Human neurotic reactions, characterized by depression, anxiety and lack of self-confidence, are both painful and incapacitating. The hypothesis that these reactions have evolved as the yielding component of ritual agonistic behaviour is attractive on two counts. First, the hypothesis predicts that behaviour analogous to the human neurotic reaction occurs in all species in which agonistic behaviour is ritualized, and thus indicates a wealth of animal models for the study of human neurosis. Secondly, it provides some suggestions for prophylaxis and treatment.

The hypothesis is consistent with, and complementary to, many clinical observations about human states of depression and anxiety, observations which relate these morbid states to competition between individuals. Freud stressed the competition between father and son over the

mother, and neo-Freudians such as Sullivan have 'desexualized the Oedipus complex' (Birnbach 1962) by leaving out the mother and shifting the arena of competition from the family to the social group. Adler emphasized the influence of social inferiority and striving, and later workers such as Bibring (1953) have related the neurotic response to alterations in self-esteem. Joffe & Sandler (1965) point out that Freud considered mental pain to be parallel to physical pain, and they themselves define mental pain as a discrepancy between 'the actual state of the self on the one hand and an ideal state of well-being on the other'; one reaction to such a discrepancy is a depressive response, which is 'accompanied by an attitude which is essentially one of capitulation and retreat'. To relate the neurotic reaction to the yielding component of ritual agonistic behaviour is virtually to restate the hypotheses described above in ethological terms, and the only excuse for doing so is the hope that it will provide some additional heuristic advantage.

'Agonistic behaviour' is a convenient term which covers all aspects of conflict between members of the same species, including threat, fighting, domination, submission and retreat. 'Ritualization' refers to the evolutionary process whereby certain movements, vocalizations or structures have developed a signalling function. Ritual agonistic behaviour thus achieves the settlement of disputes by an exchange of signals rather than by an exchange of blows. The analysis of these agonistic signals in a wide variety of species has been one of the major achievements of comparative ethology (Hinde 1966). Some of the signals are 'intention movements' like raising the clenched fist, and in these cases it appears that the preparations for fighting have developed into a signalling system which has replaced the actual fighting. Even in those species which possess lethal weapons and could readily kill each other, serious wounding has been found to be rare.

In man, ritualized fighting occurs mainly between members of the same group, because the biological advantages of ritualization only occur when the fighting is between fellow group members or between blood relatives (however remote). In conflicts between human groups which do not intermarry, the situation is entirely different: therefore the fact that human beings are only too willing to kill strangers or members of other groups is not relevant to the present discussion. During the last few million years it seems likely that hominid groups were fairly small and that all the members knew each other personally. Two distinct types of agonistic behaviour appear to have arisen: ritual fighting within the group, and non-ritual fighting between groups. Human society is of course too complex for these simple divisions to apply, but our hypothesis relates the

development of neurotic reactions to agonistic encounters between an individual and those other persons whom he perceives to be members of one of the groups of which he himself is a member. It would be over-inclusive to attribute the evolution of the neurotic response entirely to competition between individuals, or even to the general field of interpersonal relations; for instance, it seems likely that some variation in neurotic response to predators and natural disasters would also be advantageous. Various hypotheses about the biological function of neurotic and depressive reactions have been discussed by Lewis (1934), Frank (1954), Price (1968*b, c*) and Hill (1968).

The characteristics of yielding behaviour vary somewhat with the social structure of the species. Thus in territorial species the yielding takes the form of withdrawal; an excellent example has been provided by Wynne-Edwards' observations of the Scottish red grouse (Wynne-Edwards 1968): each year, after a series of ritual agonistic encounters, one-third of the population occupies the available territories, while the remaining two-thirds withdraw to areas which are unable to support red grouse and die from starvation or predation. In group-living species, most of which adopt a hierarchical social structure, yielding takes the form of submission, so that the individuals remain in the same group, the loser adopting a rank inferior to that of the winner. Whatever the type of social structure, agonistic encounters fall roughly into two types. Some encounters are between equals, such as when two individuals are fighting for a territory which belongs to neither, or in a group when the relative status of the two contestants is not already known (as might occur when a senior member falls ill or an ally dies). Other encounters are less crucial, such as border disputes between holders of adjacent territories, or an attempt by a non-territory owner to obtain an occupied territory; and in the group setting, when a senior animal disciplines a junior or when a junior attempts to rise in the hierarchy. A decision between equals requires a rather more severe and prolonged sequence of yielding behaviour on the part of the loser than is required when no change of status occurs, and it has been suggested that these considerations might be useful in the distinction between endogenous (or psychotic) and reactive (or neurotic) depressive states in man (Price 1968*a*).

We have postulated that the neurotic reaction evolved as a form of yielding behaviour, but why should there be individual variation in yielding behaviour? The answer to this question would appear to depend on two rather different features of the ritual agonistic encounter: for each contestant, it is advantageous for a decision to be reached quickly, and for that decision to be in his favour. Rituals by definition consist of signals,

and signals tend to be conspicuous, and therefore during an encounter each contestant must forsake the principle of camouflage and make himself more liable to attack by predators; therefore, provided that his chances of winning are kept constant, it is of advantage to each contestant that the encounter should be short. In group-living primates, whose agonistic signals tend to be less conspicuous than in territorial species, a brief encounter also lessens the chances of other members taking sides and thus favours the cohesion of the group. An agonistic encounter tends to be short if the contestants are unevenly matched, whether the loser succumbs to his adversary's blows or yields on receipt of his ritual signals. The greater the variation of yielding tendency in the population, the greater will be the chances that any two contestants are unevenly matched, and therefore the shorter will be the duration of the ritual agonistic encounters.

It is easy to see the advantage of yielding behaviour to the species as a whole, but what is the advantage to the individual who yields? Assuming the distribution of yielding behaviour in the population to be continuous, then it is likely that at one end of the distribution we will find individuals who do not yield at all. These non-yielders will win all their ritual agonistic encounters with yielders, and since there is clear biological advantage in being the victor in a ritual agonistic encounter, we must explain why it is that yielding behaviour has not been bred out of the population, even if it managed to get established in the first place. This is not likely to be a simple problem, but some of the reasons may be briefly summarized as follows:

(1) The disadvantage of being a yielder is counter-balanced by the likely mortality when two non-yielders meet each other. Thus it is advantageous to be a yielder when everyone else is a non-yielder, and to be a non-yielder when everyone else is a yielder. This dependence of the advantage of one's phenotype on the phenotypes of the rest of the population is analogous to the situation with mimetic butterflies and tends towards the maintenance of variation in the population.

(2) Yielding may be a disadvantage in encounters between same-sexed individuals but it may be an advantage in encounters between members of the opposite sex. In many species, as in our own, yielding behaviour is similar in many respects to female courtship behaviour. The female who is well-endowed with the ability to yield is able to turn an agonistic encounter with a male into a sexual encounter, with subsequent biological advantage to both parties.

(3) Because sexual maturity is reached before physical maturity it is advantageous for young males to yield to older males, who might other-

wise destroy them or 'psychologically castrate' them. This has been discussed in detail by Chance & Mead (1953).

(4) If selection between groups has been an important influence in human evolution, then groups which contain a proportion of yielders will have an advantage over groups which do not, and therefore the genetic substrate of yielding behaviour will be maintained.

(5) Yielding behaviour may not be genetically determined, but may be varied randomly, or instilled at some stage of development. In the case of baboons a rank order is established at adolescence before the lethal canines develop and while the adult males can control the fighting. This would seem particularly advantageous, as the fittest baboons would be likely to take the higher places in the adolescent hierarchy, and their subsequent greater reproductive advantages would ensure the maintenance of whatever characteristics make for fitness in the population. Two slight pieces of evidence cast doubt on this mechanism in the case of man. First, twin studies have shown that neuroticism is partly determined by genetic factors, although not so much as extraversion (Vandenberg 1967). Secondly, one would expect that adolescent factors such as games-playing ability in boys and good looks in girls, which are known to be associated with high social status in adolescence (Coleman 1961), would be negatively associated with neuroticism in adults; but in one study at least this relationship was not found (Price 1969).

All-important for the hypothesis are its heuristic implications. In the first place, the hypothesis predicts that behaviour analogous to human neurotic reactions should occur in all, or at least many, species in which agonistic behaviour is ritualized. This suggests a wealth of animal models for neurosis. Ethologists are aware of this (e.g. Welch 1967) and we can expect some interesting experimental work both to check the hypothesis and to provide clues to the pathogenesis and treatment of human neurosis. Angermeier & Phelps (1967) have compared certain biochemical variables in high- and low-ranking primates, with negative results, but this work is in its infancy; territorial species such as the red grouse would seem to be favourable subjects for this sort of work, as it may be possible to discover neurophysiological or biochemical differences between the grouse who obtain territories and those who withdraw in a suicidal manner to die in the grouse wilderness; the monogamous primate *Callicebus moloch* would also be a good subject, as these animals show marked depressive reactions in captivity (Mason 1968, personal communication), although whether these are induced by the loss of spouse, the loss of territory or

the conditions of captivity has not yet been determined. There would also appear to be scope for pharmacological studies on these lines, as any psychotropic agent which enabled a group member to rise in the hierarchy, or even to live happily at the bottom of the hierarchy, would make a promising drug for a trial in human neurosis. The natural, as opposed to experimental, occurrence of animal neurosis is usually viewed with some scepticism, in spite of descriptions of marked variations in behaviour between high- and low-ranking animals (Price 1967). But it is worth remembering that human neurosis is largely a subjective affair, and the behavioural accompaniments are more often confined to limitation of certain types of behaviour than to any positive deviations.

As far as the treatment and prophylaxis of human neurosis goes, the hypothesis offers suggestions along three main lines:

(1) Training in the social skill of conducting an agonistic encounter may reduce the incidence of real and apparent defeat. As in non-human primates, the direct gaze is an important component of ritual agonistic encounters, and it is an astonishing fact that few people can sustain a direct gaze for more than a fraction of a minute (Argyle & Dean 1965). Training in this skill might suit the methods of behaviour therapy. Moreover, it is important that the individual should know when he is in an agonistic encounter and when he is not. The direct gaze, although threatening in an agonistic situation, may be erotic in a sexual situation and strengthening in a context of trust and friendship. Not only is the context important, but subtle variations in facial expression such as the position of the eyebrows and mouth may provide clues as to the meaning of the gaze. Blurton Jones (1967) has pointed out that some children appear to send the wrong signals or to misinterpret those that they receive, and these children should benefit from training in social signalling. In small stable communities in which everyone knows his rank and who he is allowed to stare at and who he is not, misunderstandings are probably rare; but in our own fluid society, in which encounters with strangers are common, it may well be that we need more skill in these matters than our evolution has catered for.

(2) For those who are overly susceptible to the effects of agonistic encounters, it may be advisable to encourage the avoidance of such encounters, a technique adopted by some religious orders which forbid eye-contact.

(3) The agonistic encounter may be restructured in the mind of the participant so that the criterion of success is entirely changed. This technique is used by religions which emphasize the temporary nature of the earthly hierarchy as compared with the eternity of the heavenly hierarchy. 'Blessed are the meek: for they shall inherit the earth.' Thus the meaning of the agonistic encounter is entirely changed for the religious combatant; by yielding and turning the other cheek he turns a temporal defeat into a spiritual victory.

However, these speculations are of small importance compared with the need for a direct experimental approach to the human ritual agonistic encounter. It is here that the hypothesis may be refuted by the finding that there is no relation between neurotic behaviour and ritual defeat.

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The following paper was also read:

Mother/Infant Interaction in Rhesus Monkeys
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