
The Croonian Lecture, 1990: The Interdependence of the Behavioural Sciences

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The Croonian Lecture, 1990

The interdependence of the behavioural sciences

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INTRODUCTION

It is true to say that we live in a time of rapid social change. But it is easy to forget that we also live in, or one could say have lived through, a time of rapid change in the nature of science. The exponential growth of science, and its magnificent achievements, have been accompanied by its disintegration into a multiplicity of subspecies. It is no longer possible for an individual to be an all-rounder, and that makes it the more important that collectively we should not lose sight of the essential unity of the scientific enterprise. My aim here is to provide a framework to illustrate essential interrelations between the various subspecies that deal with behaviour and its underlying mechanisms, and to emphasize that the research worker must cross and recross the boundaries between them.

LEVELS OF COMPLEXITY

Introduction

Although the ultimate aim is integration, it is necessary to start with some distinctions between levels of complexity. Consider first the behaviour of individuals. Attempts to understand the behaviour of individuals can take two routes, which we can roughly characterize as the psychological and the physiological. The former attempts to describe regularities at the behavioural level, to spell out laws of learning, for instance. The physiological approach, by contrast, proceeds to a different level, attempting to account for behaviour in terms of muscles, neurons, hormones, etc., and itself involves several different levels of analysis, each with its own methodology and conceptual apparatus. The important issue here is that concepts useful at the behavioural level, such as the descriptive concepts of walking, swallowing or orientation reflex, and explanatory concepts, such as reinforcement or habituation, must be translated into quite different languages at the successive physiological levels, and could not easily be reconstituted from the physiological data if the behavioural level were not first understood.

Now let us move in the other direction. Social behaviour involves interaction between two or more individuals such that what each does is continuously influenced by what the other does or is expected to do. Concepts useful for describing behaviour at the interaction level, such as how far the behaviour of each

individual meshes or fits with that of the other, may be irrelevant when applied to the behaviour of individuals in isolation.

Interactions are often set within inter-individual relationships, such that each interaction is affected by past interactions with the same individual or by expectations of future ones. Relationships are of course multidimensional, and their properties depend on the strengths and relative strengths of different types of interaction. But the point to be emphasized here is that they may have properties that are simply irrelevant to particular interactions. For instance the partners in some relationships do many different things together, whereas in others they do only a few or one, such as drinking beer or playing squash: 'multiplex', vs. 'uniplex' is a property of relationships, but not of interactions.

And relationships are set within groups that may have properties irrelevant to the dyadic relationships within them: for instance the relationships may be arranged hierarchically, centripetally, and so on.

As we move up these levels of complexity from intra-individual mechanisms through interactions and relationships to groups, we move from one subspecies to another: from molecular biology through physiology, psychology to social psychology. And this is proper, for superficially similar phenomena at different levels of complexity may require different principles of explanation (Hinde 1987).

The case of aggressive behaviour

For the moment let me give but one example, the cause of aggression. For the physiologist this lies in brain mechanisms and hormone levels. Stereotaxic placement of stimulating or recording electrodes allows the identification of particular brain mechanisms responsible for the integration and motivation of aggressive behaviour in animals. Hormone studies show that testosterone often plays a crucial role. (We shall see shortly, however, that the physiologist who neglects analysis of the social situation may be led into over-simple generalizations.)

The psychologist is content at first to ascribe aggression to an aggressive propensity and to seek for causes in two directions—for factors in the individual's development that enhance this propensity, such as a harsh upbringing (see, for example, Sears *et al.* 1957;

McCord *et al.* 1961), and for contemporaneous factors that lead to its expression, such as current frustrations or the proximity of a weapon (Dollard *et al.* 1939; Berkowitz & La Page 1967). Soon, however, the psychologist is forced to acknowledge that even apparently simple aggressive acts are more complex than appears at first sight, and involve diverse motivational factors. For instance, developmental psychologists usually classify children's aggression into four types (Feshbach 1964, 1970; Manning *et al.* 1978):

- (a) specific aggression, used to gain or maintain objects or situations;
- (b) teasing aggression, without any such apparent object;
- (c) defensive aggression, given in response to an attack;
- (d) games aggression, escalating out of rough-and-tumble play.

However, these categories really represent a continuum, and aggressive acts must be seen as resulting from multiple motivations, such as 'aggressiveness', 'acquisitiveness' and/or 'assertiveness', the above categories representing extreme conditions (see figure 1). In other words there is a continuity of aggressive acts, the categories mentioned having very shady edges. The physiologist can rightly claim that an analysis in terms of propensities is only a first descriptive step in the understanding of mechanism, whereas the psychologist can point out that a physiological understanding of specific aggressive acts must include not only the mechanisms underlying the particular movements used to harm others, but other motivational mechanisms, such as those illustrated in figure 1, as well.

Of course, aggression usually involves an interaction between at least two individuals, and the stimuli that each provides to the other may be essential eliciting factors.

But, moving up another level, in our own species a large proportion of individual acts of aggression occur within the family and only a small proportion between individuals who were previously unacquainted (see Wolfgang 1958; Goldstein 1986). Such aggression is not merely an interaction between two individuals, and it requires an understanding of the dynamics of the relationship as well.

At the group level, further issues become even more important. Mob violence, for instance, is enhanced not only by the frustrations of individuals and by the availability of weapons, but by other factors specific to the group situation. Membership of the group produces a sense of group superiority and group loyalty, and of the inferiority of outsiders (Tajfel 1978). Group values may place a premium on violence, so that individuals behave aggressively to outsiders in order to rise in status among their peers. Charismatic leaders may manipulate group violence for their own ends (see Rabbie 1989).

Dialectical relations between levels of complexity

I shall return to the issue of aggressive behaviour later, but what I have said so far demonstrates not only

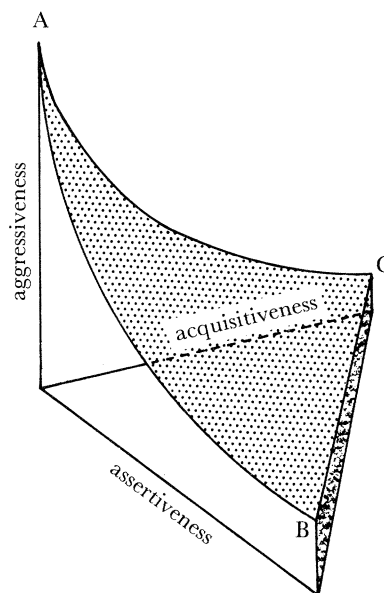


Figure 1. Simple model of relations between three behavioural propensities (aggressiveness, acquisitiveness and assertiveness) and aggressive behaviour. The latter would appear if the values of the three propensities produced a point above the dotted plane. A more complex model would allow for three-way interactions.

that different principles operate at different levels of complexity, but also that phenomena at any one level can seldom be fully understood without reference to others (see also Groebel & Hinde 1989). Students of many aspects of human behaviour have been led along fruitless paths because they failed to take account of other levels of social complexity. Thus developmental psychologists have found that what appeared to be characteristics of the child, such as whether or not the child is securely attached to its mother, or the nature of the child's temperamental traits, are influenced by the child's relationships (Grossmann *et al.* 1981; Main & Weston 1981; Stevenson-Hinde 1986). Tests of children's cognitive development may depend on the social context in which they are conducted (Donaldson 1978); cognitive development depends on interpersonal relationships (Vygotsky 1934; Doise & Mugny 1984; Perret-Clermont & Brossard 1985), and the cognitive operations an individual uses to solve a given problem may vary with the social situation (Carragher *et al.* 1985).

Such difficulties arise in part because the several levels are not independent but connected by mutual cause-effect relations (figure 2). Thus the course of an interaction depends on the nature of the individuals involved, and also on their expectations about future interactions or the course of the relationship, expectations based on experience in that or similar relationships, while the nature of a relationship depends (by definition) on the nature of the constituent interactions. And not only does the course of an interaction depend on the nature of the relationship in which it is embedded, but also, in the long run, the behaviour that individuals show depends on the interactions and relationships they have experienced in the past. Furthermore, the behaviour individuals show

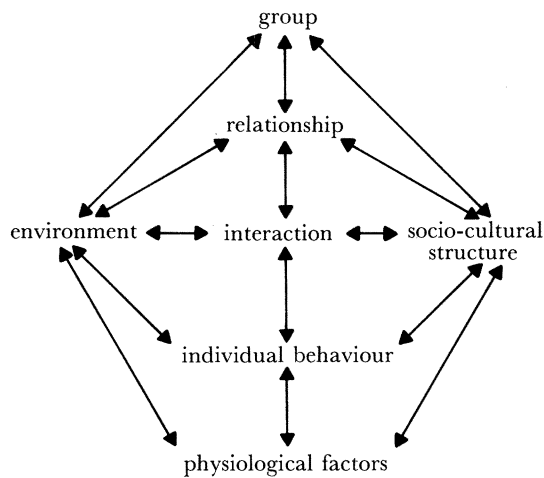


Figure 2. The dialectical relations between successive levels of (social) complexity.

is affected by endocrine and neural processes, and conversely those processes are affected by behaviour, past, present and anticipated. And at the more complex level, the course of every relationship is affected by the group in which it is placed: A's relationship with B is affected by B's relationship with C (figure 2) (Hinde 1987).

A full understanding of almost any aspect of human behaviour demands that we cross and recross between the several levels of social complexity. The behaviour of individuals depends both on their biological constitution, and on the social context in which they are situated.

It is my aim to exemplify this interplay involving dialectical relations between levels, showing how phenomena at any one level cannot be fully understood in isolation from other levels. Before proceeding, however, it is necessary to introduce two further levels, though here we use 'level' in a slightly different sense. One is the physical environment, which both affects and is affected by each of the levels of social complexity mentioned so far. Here, therefore, we require an understanding of ecological principles. The other is the socio-cultural structure, by which I mean the system of beliefs, myths, values, conventions, institutions and so on that are common to all or many of the individuals with whom we are concerned. This also, as I shall show, both affects and is affected by the successive levels of social complexity. And so our scheme now embraces not only physiology and social psychology, but also sociology and anthropology (Hinde 1987).

THE FOUR WHYS

In the remainder of this paper I argue that full understanding of any one aspect of behaviour requires us to be not merely interdisciplinary, but to move backwards and forwards between disciplines. But first let us further explore the understanding of behaviour at the individual level. The early ethologists, such as Niko Tinbergen and Konrad Lorenz, and before them Julian Huxley, all Fellows of the Royal Society, emphasized the importance of distinguishing four questions about behaviour, concerned respectively

with its causation, development, function and evolution (see, for example, Tinbergen 1963). To take an anatomical example, one of the digits on our hands, the thumb, has a set of movement possibilities quite different from the others. Why should that be so? The question can be answered in four ways: causally (the organization of the bones, muscles and nerves is different); developmentally (the finger and thumb rudiments took different courses in ontogeny); functionally (the thumb permits grasping, useful in picking up objects or climbing); and evolutionarily (our monkey-like ancestors also had opposable thumbs). In the same way a given behavioural character is susceptible to different explanations: a chaffinch's singing can be explained in causal terms (hormones, neural and vocal mechanisms, etc.), developmental (genetically influenced predispositions, learning, etc.), functional (its consequences for territoriality or the attraction of females) and in evolutionary terms (its relation to the simpler song of a related species, the blue chaffinch).

The explanations, it will be noted, belong to different disciplines or sub-disciplines (endocrinology and physiology; ethology and comparative psychology; behavioural ecology; and evolutionary biology), yet are in no way incompatible with each other. Indeed they may overlap: to return to an earlier example, although the causes of mob aggression may be sought in current frustrations, the preceding long hot summer, or the conditions of upbringing of the participants, questions of immediate causation and development merge (figure 3). Functional issues concern a different sort of causation: that acting through natural selection on development. And functional changes may be related to evolutionary ones.

Indeed the different questions are often interfertile. For example, aspects of behaviour with related functional consequences may have related causal bases: in many species a variety of reproduction-related activities depend on similar endocrine states. And evolutionary changes may be traced to changes in developmental processes: 'allometric' growth involves a change in proportions consequent upon a change in

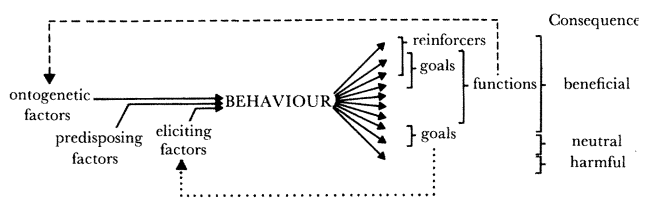


Figure 3. Relations between ontogenetic and causal factors and consequences. The distinctions between ontogenetic and predisposing and between predisposing and eliciting factors are often somewhat arbitrary. Among the consequences, the categories of reinforcers, goals and functions only partly overlap. Although a goal is normally achieved as a consequence of behaviour, an internal representation (anticipation) may contribute to causation (dotted line). Consequences may be beneficial, yet not provide material for the action of natural selection (i.e. not be functions in a strong sense). Exceptionally, harmful consequences can be goals. The discontinuous line indicates evolutionary consequences on the next generation.

overall growth so that a difference in size between species is accompanied by gross changes in proportions and metabolic demands, resulting in changes in behaviour. In addition, evolutionary changes may be associated with functional ones: the learned elaboration of the chaffinch's song over that of the blue chaffinch can be ascribed to evolutionary pressure to maintain specific distinctiveness, unnecessary in the island-dwelling blue chaffinch (Thorpe 1961).

CROSSING THE LEVELS OF COMPLEXITY

Thus in gaining a full understanding of the behaviour of individuals we are already at the meeting point of several subspecies. But in analysing even the causation of behaviour we are often forced to move backwards and forwards between physiological and behavioural levels of analysis. I now consider some examples that exemplify the issues.

Canary nest building

Figure 4 illustrates the interrelations between the physical environment, behaviour and endocrine state in the nest-building of female canaries. Continuous lines represent experimentally established positive effects, the discontinuous lines negative effects, and the dotted lines probable effects not yet established with certainty.

Environmental factors, including lengthening days, acting via the hypothalamo-pituitary-gonad system, result in gonadal development and the release of oestrogen into the blood stream (Follett *et al.* 1973). This sequence of physiological events makes the female responsive to the male's courtship. Interaction with, and the formation of a relationship with, a conspecific male result in further development of the reproductive system. The oestrogen produced causes the female to start building a nest. However, the effectiveness of oestrogen in inducing nest building is influenced by external factors, such as the length of the circadian light period or exposure to male song. For example, oestrogen-treated gonadectomized females build more if exposed to male songs or longer days.

Nest building results in the construction of a nest, and thus in a change in the stimuli the female receives from the physical environment. Stimuli from the nest are received through the ventral areas of the skin. Their sensitivity to stimuli from the nest is increased by the development of a brood patch, involving loss of feathers, increased vascularity and heightened tactile sensitivity. These stimuli from the nest result in a change in the selection of nest material (from grass for the outside to feathers for the lining), a decrease in nest-building behaviour, and further reproductive development. It will be apparent that the reproductive cycle involves a continuous interplay between environmental factors, hormonal factors and behaviour, (the latter including individual behaviour, such as nest-building, and also interaction and relationship formation with the male) (Hinde & Steel 1966, 1978). The behaviour cannot be fully investigated in the absence of some physiological analysis, nor can the

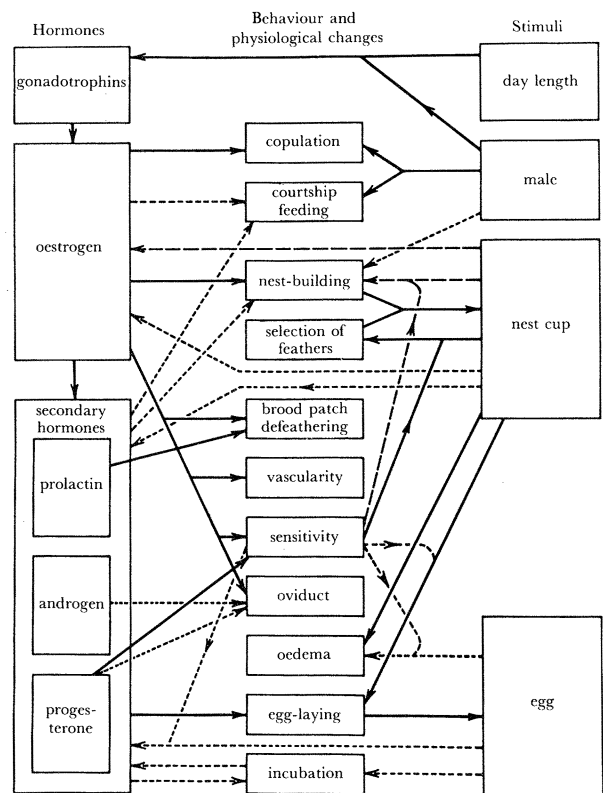


Figure 4. The relations between external stimuli, hormonal changes, and behaviour in the reproductive development of the female canary. The continuous lines represent positive effects, the discontinuous lines negative effects, and the short dashed lines probable relationships not yet established with certainty. Where the extent to which an effect may be indirect has not yet been established, only the direct effect is shown. The diagram includes reference to three aspects of brood patch development (defeathering, vascularization and sensitivity to tactile stimulation, such as that provided by the nest).

physiology be investigated properly in the absence of behavioural understanding.

Ring dove reproduction

A parallel analysis of the reproductive behaviour of the ring dove, carried out by the late D. S. Lehrman, and extended by Mei Cheng and their colleagues at Rutgers University, produced broadly similar general conclusions, though more detailed in many respects. J. B. Hutchison, working in Cambridge, has shown that the ring dove's behaviour has special properties which have made possible an important line of physiological analysis (Hutchison 1987; Hutchison & Steimer 1984, 1985). The courtship of this species consists of two phases, an initial 'aggressive courtship' followed by 'nest-oriented courtship'. Recently castrated males implanted with testosterone show both, but castrated males treated with oestrogens show only the latter.

That oestrogens should affect male courtship was at first somewhat surprising, because oestradiol cannot be found in the blood stream. However, it was known that an aromatase enzyme system in certain brain cells readily converts testosterone to oestradiol. Hutchison, working with Th. Steimer, showed that in the ring

dove this highly active aromatase system is precisely localized in the preoptic area, that is, in the brain region where oestrogen implants can induce nest-oriented courtship.

Hutchison noticed that the effectiveness of testosterone in inducing the second nest-oriented phase of courtship declined with time since castration, but that of oestrogen did not. This suggested that conversion of testosterone into oestrogen declines with time since castration. It was subsequently shown that testosterone treatment increases the rate of conversion of testosterone to oestrogen, preoptic aromatase activity being increased both by testosterone and autocatalytically by oestrogen as a metabolic product. By using crystalline implants positioned stereotaxically, it was possible to show that aromatase induction is a result of direct steroid action on cells in the preoptic area (Hutchison *et al.* 1986).

In the brain different enzymes compete for testosterone, which is converted also by a 5β -reductase system into inactive metabolites. These 5β -reduced metabolites increase in long-term castrates, the increase being correlated with the decreased behavioural effectiveness of testosterone (Hutchison & Steimer 1981). Androgen, however, suppresses the effect of 5β -reductase, probably by an indirect route. Thus the behavioural action of testosterone depends on a delicate balance between different enzyme systems: testosterone is probably not itself behaviourally active but is a pre-hormone, its behavioural effects depending on the way in which it is metabolized by enzymes in brain cells.

Of special interest is the finding that the direction of testosterone metabolism may depend on external stimuli. Testosterone is more effective in inducing nest-oriented courtship in (short-term) castrates if they are kept on long days or exposed to a female who 'nest solicits'. In parallel with that, male doves able to see interacting pairs of doves show higher levels of 17β oestradiol formation in the preoptic area than do visually isolated males.

Because of this effect of social stimuli on the brain mechanisms of courtship behaviour, it is necessary to test the decline of sexual behaviour after castration without exposing the subjects to another individual. Again, special characters of ring dove behaviour make this possible. 'Perch-cooing', an androgen-dependent behaviour, which is shown by the male in visual isolation, can be used instead. The effectiveness of testosterone in inducing this behaviour declines after castration in parallel with the increase in 5β -reduced metabolites in the brain. (It will, of course, be apparent that the particular mechanism whereby external stimuli modulate the behavioural effectiveness of testosterone in this species cannot apply to the effect of external stimuli on the behavioural effectiveness of oestrogen in the female canary.)

Of course, the studies I have mentioned form only a tiny fraction of research on hormone action in a wide variety of species. They do, however, show that an understanding either of how behaviour is controlled by hormones, or of the mechanisms of hormone action on behaviour, cannot be obtained unless the investigator is prepared to cross and recross the levels of complexity.

Dominance and sexual behaviour in talapoin monkeys

The need not only to integrate physiological and interaction levels, but also to consider dyadic and higher-order relationships, is exemplified by studies of dominance and sexual behaviour in monkeys. It has been shown, for several species, that sexual behaviour is related to dominance-subordination relationships between individuals (see, for example, Chapais 1983). For example, in captive groups of talapoin monkeys sexual behaviour is largely limited to the dominant males and females (see Keverne *et al.* 1985). The establishment and maintenance of rank, which used to be ascribed primarily to fighting ability, is much more subtle than that, and may depend on complex alliances between individuals, especially between kin (Datta 1983). Moreover, the immediate reason for the relation between dominance status and sexual behaviour may differ between the sexes. Although the high-ranking males of talapoin groups clearly boss the others, they are not the most frequently involved in aggressive behaviour. When a female solicits to a low-ranking male, he may be attacked by a male of intermediate rank. Apparently the control exerted by the dominant is 'indirect'. In the case of females, low-ranking females are prevented from mating by another mechanism: solicitations by a subordinate female to a male are usually rendered ineffective by competitive soliciting from a higher-ranking (and apparently therefore more attractive) female.

However, the effects of dominance status on sexual behaviour are not just short term. Castration did not eliminate sexual behaviour in dominant talapoin monkeys, but did in subordinates: indeed, long-term subordinates could not be stimulated to sexual behaviour even by high levels of male sex hormone. Similarly, oestradiol reinstated the sexual behaviour only of those ovariectomized females that were high ranking.

That the absence of sexual behaviour in subordinate males is not due merely to the immediate presence of dominant animals was further shown by the finding that chronic subordinates failed to mate in the short-term, even when isolated with a female. This, incidentally, was not true of females. And the longer-term effect of dominance-subordination on males is probably not solely due to hormonal levels: although subordinate males have higher cortisol levels than males, this difference disappears in isolation, yet mating behaviour with a test female is not reinstated. Rather the absence of sexual behaviour in subordinates seems to be because of a sort of learned helplessness (Keverne *et al.* 1985).

Thus, to understand the incidence of sexual behaviour, it is necessary to take into account not only hormone levels, and the way in which the hormones are metabolized in brain cells, but also the sex of the individual concerned, individual learning and current and past relationships.

Endorphins in mammals

I am grateful to E. B. Keverne for pointing out to me that the increasing importance of an integration between neuroendocrine and behavioural data concerned with interactions and relationships is nowhere more clearly demonstrated than in current work on the opiate system in higher mammals. There is increasing evidence that β -endorphin is concerned with the neurophysiological consequences of reward vs. non-reward. Two closely related fragments of β -endorphin appear to have opposite effects on the extinction of a pole-jumping avoidance response, one delaying and the other facilitating extinction (Kóvacs *et al.* 1978). The distribution of the receptors of the β -endorphin system overlap with those areas of the limbic system known to support self-stimulation (Olds & Forbes 1981), and the receptor blocker naloxone depresses self-stimulation at various sites in the limbic brain. Moreover, in addition to being implicated in many other types of behaviour, β -endorphin is involved in many aspects of social behaviour. Thus it is associated with the early social bonding of mother and infant in a variety of mammals (Panksepp 1986). Both parturition in rodents and mother–infant bonding in sheep are associated with an increase in β -endorphin levels in the maternal brain (Wardlaw & Frantz 1983; Keverne *et al.* 1983; Mayer & Rosenblatt 1984; Keverne 1988). The distress calls given by infants on separation from mother are reduced by opiate agonists and intensified by opiate antagonists (Panksepp *et al.* 1978): this in turn is likely to have a long-term effect on the mother–offspring relationship. In monkeys, opiate receptor blockade has a negative effect on socio-sexual behaviour (Meller *et al.* 1980) but enhances the affiliative behaviours of huddling and grooming (Fabre-Nys *et al.* 1982). The affiliative patterns of behaviour shown by monkeys previously isolated for 24 h on reunion with peers is accompanied by an increase in endogenous CSF β -endorphin (Keverne *et al.* 1989), but such behaviours are diminished if the monkeys are pre-treated with morphine which, like β -endorphin, acts preferentially on the μ -receptor (Keverne *et al.* 1989). Such data can be integrated on the view that β -endorphin is released in the context of affiliative social interactions and ameliorates the symptoms of social deprivation.

Paradoxically, however, with long-term social subordination, monkeys show high levels of CSF β -endorphin, which are ineffective in ameliorating the depression of sexual behaviour, apparently because of a change in its metabolism or a ‘down regulation’ of the receptors or both.

These findings have an exciting implication for the study of human relationships. It has long been recognized, by psychoanalysts and others, that the nature of a child’s early relationships affect personality development (see, for example, Bowlby 1969): although others have emphasized also the importance of peer relationships (see Piaget 1929; Youniss 1989), there can be no doubt that what a child gets out of relationships with peers is affected by earlier intra-familial relationships (Hinde & Tamplin 1983). Be-

cause β -endorphin appears to be involved in both mother–infant relationships (in rodents and sheep), and in adult social relationships (in monkeys), it raises the possibility that relationships widely different in context but having a positive affiliative tone may share and influence mechanisms at the neuroendocrine level. It seems at least possible that the work on β -endorphin may hold the key to understanding not only some of the mechanisms involved in mother–infant bonding, but also perhaps some of those underlying its consequences on later human relationships.

Individual characteristics and relationships in institutionalized children

Some recent work on human relationships, although in no way suggesting that relationships of different types may not have common mechanisms, emphasizes also differences, and also highlights further complexities in the relations between individual characteristics, interactions and relationships. Tizard & Hodges (1978; Hodges & Tizard 1989) studied children who were admitted to a residential nursery in infancy. At around four years of age some of them were adopted and lived in circumstances generally advantageous in comparison with the general population, and some were subsequently returned to their biological families, mostly to live in socially disadvantaged and troubled situations. At eight years of age the previously institutionalized children showed some problem behaviour and poor peer relationships at school, especially those restored to their biological families. The adopted children tended to be affectionate and cuddly in their adoptive families, almost excessively so, whereas the restored group were somewhat less cuddly than matched control children. In adolescence more adoptees than controls showed signs of anxiety, but they appeared to be well attached to their adoptive mothers, whereas the restored children were more likely to have been in trouble with police or to have been referred for psychiatric treatment (or both), and had poor family relationships. However, the adopted and restored groups resembled each other, and differed from controls, in their peer relationships. They tended to be indiscriminately friendly to peers, but to lack a close friend, and they had difficulty in peer relationships. Three inter-related points may be made here. First, the nature of the child’s early relationships had long-term effects on personality functioning, and particularly on the ability to form relationships. Second, the long-term consequences depended on the subsequent rearing environment. Third, the consequences on social relationships were different from those on social behaviour.

Human behaviour and the social context

That individual characteristics affect interactions in the human case hardly needs exemplifying, but the importance of the converse issue, that the nature of the interaction in which an individual is involved affects the characteristics he or she displays, has been recognized more recently. One may consider the extent

to which individual behaviour is affected by the context, and especially by the social context. Attempts to measure human individual characteristics in terms of personality traits have not been outstandingly successful, because the cross-situational consistency of such traits is seldom high, the usual correlation between measurements of the same trait in different situations being of the order of 0.30 to 0.40 in adults. Individuals differ in the extent to which their behaviour varies across situations and in the extent to which different types of behaviour are affected (see Mischel 1973; Endler & Magnusson 1976; Bem & Funder 1978; Kenrick & Stringfield 1980). It may be suggested that the most important situational factors are social or relationship issues, or, to put it in other words, the social behaviour of individuals is constantly affected by the interplay with other levels of social complexity.

Although the psychological data indicate that psychological traits seem to vary with the situation in which they are assessed, we are all aware of continuities in our own lives and those of others. There is a lawfulness, if it can be found. As an example, one may consider the relations between the behaviour of four-year-olds at home and preschool. First, there is very little consistency in behaviour between home and school. In comparisons between similar behavioural items (e.g. child friendly to mother with child friendly to teacher or child friendly to peers), very few correlations were significant (Hinde & Tamplin 1983). Characteristics of the child (as assessed from questionnaires addressed to mother, father, teacher and observer in school) show moderately high correlations within situations (i.e. mother vs. father at home, teacher vs. observer in school) but near zero correlations across the situations (Hinde & Tobin 1987). Thus children behave differently in home and school, and different children are affected by the transition in different ways. Because of this lack of cross-situational consistency, the only course is to look for home correlates of particular aspects of behaviour in school. Let us focus on the home correlates of hostility to peers in school. Baumrind (1971) in an earlier study had found that parent-child relationships fell into three groups on the basis of two dimensions of parent-child interaction which can approximately be described as follows: authoritarian (high on parental control, low on parental warmth), permissive (low on control) and authoritative (moderate control and moderate to high warmth). The most aggressive children tended to have 'authoritarian' or 'permissive' parents. When the number of children was plotted against these dimensions of the mother-child relationship (i.e. control and warmth assessed from mother-child interaction) it was found that two diagonal lines (rather than the orthogonal ones suggested by Baumrind's analysis) segregated most of the less aggressive from most of the more aggressive children. Although the position of these lines was originally fixed by eye, they replicated across samples (figure 5). Thus a particular type of interaction in school is related not (or at most weakly) to a similar type of interaction at home, but to a characteristic of the mother-child relationship involving the absolute and relative strengths of at least

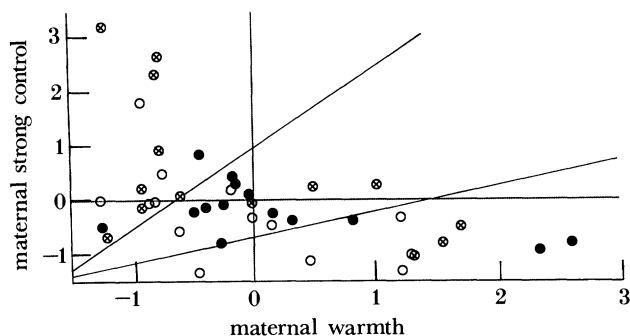


Figure 5. Relations between the maternal warmth and maternal control (assessed from observation data) and aggression by 4-year-olds to peers in school. Crosses indicate data for children in the upper third on aggression in school, open circles data for children in the middle third and filled circles for those in the bottom third.

two types of interaction. Understanding of cross-situational coherence requires us to cross the levels of social complexity.

Another example from the same study demonstrates the importance of the interplay between the characteristics of individuals, their relationships and the sociocultural structure. Four-year-old children were assessed for shyness on the basis of a maternal questionnaire. There was no significant difference between boys and girls in shyness, and virtually none in various aspects of parent-child interaction and relationship assessed from observation, questionnaire or interview. However, shy boys tended to have worse relationships with their parents, and to get on less well with siblings and peers, than non-shy boys, whereas for shy girls exactly the opposite was the case: shy girls got on better with parents, siblings and peers than non-shy girls (Hinde & Stevenson-Hinde 1986; Stevenson-Hinde & Hinde 1986). This finding has since been replicated by Radke-Yarrow *et al.* (1988) in a comparable community in the U.S.A. Interview data from our own study, and from one by E. E. Maccoby and H. Sants in California, indicate that the difference stems from parental values. Many parents like little girls to be shy (within limits), but regard shyness in boys as a failure. Thus parental values influence the nature of the parent-child relationship, and thus the development of the individual characteristics of the child.

Biological adaptation and human behaviour

1. Fears and phobias

At this point it is helpful again to bring in an evolutionary and functional perspective. Bowlby (1969), a London psychoanalyst with an unusually eclectic approach, pointed out that what had hitherto been regarded as the 'irrational fears of childhood - fears of falling, of darkness, of being left alone, of strangers - would have made very good sense in our environment of evolutionary adaptedness. Infant survival must then have depended on remaining attached to or close to the mother. This was one of the pivotal observations that led Bowlby to a new approach to child development ('attachment theory') that gave the relationship to the

mother a central place. But the point being made here is that an evolutionary perspective throws light on an aspect of individual behaviour that is concerned with the maintenance of the parent-child relationship.

The fear of strangers that develops in the second half of the first year is of special interest in this context. There seems little doubt that this could once have been adaptive, and indeed it may be so now. Males in several primate species kill young not their own, and females behave punitively to strange young. Shyness has a genetic component in humans, implying that some individuals have a greater propensity to be shy than others (though not, of course, that some are predestined to be shy). But at the same time, social experience plays a crucial role. Shy parents may enhance shyness by being over-accepting of shy traits in their children, or by restricting their child's social experience, or they may attempt to compensate (Plomin & Daniels 1986). And, as we have seen, children brought up in restricted circumstances may be overly apprehensive of strangers, whereas children brought up in institutions may be overly effusive. Understanding shyness requires us to understand the role of genetic factors, individual behaviour, relationships and their interaction.

In a similar vein, it has been pointed out that human phobias are concerned with objects or situations that might primitively have posed a threat to survival (snakes, spiders, open spaces, crowds) but not to situations or objects that are real dangers nowadays, such as cars, aeroplanes or bombs (Marks 1987). Fear of snakes is an interesting case in point, illustrating the dialectic relations between individual behavioural propensities, relationships and the sociocultural structure. Children brought up in an institution, who have never seen a snake, show little fear if they first encounter one at ages one and a half or two and a half years, but avoid a snake crawling on the ground from about three years (Precht 1950). That such behaviour would have been adaptive in our environment of evolutionary adaptedness seems highly likely. However individuals vary greatly in the extent to which they fear snakes, and experience also plays a role. Young children (and monkeys (see Seyfarth *et al.* 1980)) faced with new and potentially frightening situations, monitor the behaviour of their caregiver, and guide their own behaviour accordingly. The extent of the fear shown to snakes may be closely related to the behaviour of the caregiver on earlier occasions when snakes were encountered.

Such observations are also in harmony with experimental data on rhesus monkeys which show that (a) wild-reared rhesus monkeys tested in the laboratory are almost always afraid of snakes; (b) laboratory-reared rhesus monkeys show little fear of snakes; (c) laboratory-reared rhesus monkeys shown a videotape of a wild-reared rhesus showing fear of a snake are likely to be afraid of snakes thereafter; but, (d) laboratory-reared rhesus monkeys shown the same videotape with the snake erased and a flower substituted do not become afraid of flowers (Mineka 1987).

These data point, in both monkeys and humans, to an initial (though individually variable) propensity to

fear snakes that is affected by the behaviour of conspecifics in the presence of snakes. However, in the human case that is not all. Snakes play a very important part in our mythology. In the myth of the Garden of Eden, in the Rubens paintings of snakes gnawing at the genitals of those cast down into hell, snakes nearly always symbolize evil. (There are some exceptions to this, but that is another story.) It is not good enough to regard the myths as given. Rather it seems that they are themselves a product of the interplay between basic human propensities, relationships and the socio-cultural structure. Thus an understanding of fears and phobias in humans brings in evolutionary issues, individual propensities, social relationships and the socio-cultural structure: we must cross and recross between these levels of complexity, and thus between the scientific disciplines whose province they are, to reach understanding.

2. Gender differences

As another example of the necessity to marry biological and psychological approaches, we may consider briefly the genesis of gender differences in human behaviour in close personal relationships. As argued elsewhere (Hinde 1987), the tendencies for human males and females to differ somewhat in behaviour in the context of close relationships, so beautifully documented by Peplau (1983), cannot be ascribed merely to social stereotypes in each society. Thus it is useful to consider separately several interrelated questions.

(a) How do the differences develop in the individual? Here the issues are partly in the realm of the physiologist, involving prenatal hormones, and partly in that of the developmental psychologist, concerned with such issues as modelling and differential reinforcement of behaviour deemed appropriate for boys and girls, guided in each case by the gender stereotypes prevalent in the culture.

(b) Why are the differences portrayed by the gender stereotypes in the direction in which they are? Why, for instances, are men portrayed as more assertive than women, why is male sexual jealousy almost invariably recognized and accepted but female sexual jealousy much less so? The answer here, in my view, must be an evolutionary one. The only theory that satisfactorily ties together the characteristics of human sexual anatomy and physiology and sex differences in behaviour is that of evolution by natural selection. Although the argument cannot be spelled out in detail here, it is briefly as follows.

(i) In mammals in general, the variance in male reproductive success is greater than that of females, and males compete for females. Hence their greater size, aggressiveness and assertiveness.

(ii) The size difference between men and women, by analogy with other mammals, suggests that there was a mild degree of polygyny in our environment of evolutionary adaptedness.

(iii) Males can be cuckolded and females cannot. Thus a male could expend parental care on an infant not his own, but this is less likely in females. Hence

female fidelity is more important to males than vice versa.

(iv) Males invest less in each offspring than do females. Thus infant survival is more important to females than to males. If paternal care is important for infant survival, the continuance of the male–female relationship is therefore more important to females than to males.

(v) Comparative study of the reproductive anatomy and physiology of the great apes reveals a correlation between anatomy, physiology and behaviour. For example in chimpanzees several males may mate with one female in succession, and competition for paternity includes sperm competition inside the female: in harmony with this, the chimpanzee male has exceptionally large testes and accessory glands. By contrast, the gorilla male, who had undisputed access to a group of females, has a small penis and testes. Applying the same sort of argument to humans, the small testes indicate that, in our environment of evolutionary adaptedness, the male had undisputed access to one or more females. In humans the exceptionally large penis, sexually attractive breasts, continuous female receptivity, etc., are in harmony with the view that copulation has a bond forming or maintaining function as well as a reproductive one (Short 1979).

Of course such arguments, which I repeat are merely sketched here, cannot prove anything about the causation of gender differences in human behaviour. But it would seem that the best available explanation of the direction of the differences between men and women in reproduction-related behaviour is that they arise from differences in propensities to learn which arose as adaptations through the agency of natural selection. The greater assertiveness of males, the greater importance of relationships to females, the institutionalization of male but not female sexual jealousy in nearly all societies, these and many other apparently unrelated facts about human behaviour can be integrated by the theory of evolution by natural selection. However, this evidence says nothing about the extent or patterning of gender differences in behaviour, or about how these develop.

(c) Why do the stereotypes in every culture so grossly exaggerate or distort the biological differences in the propensities between the sexes? Here the answer is partly in developmental psychology, partly in social psychology. The growing child's self concept involves seeing itself as a member of certain categories of which the most significant are the categories of male and female. And seeing itself as a member of a group, the principles involved in the differentiation between groups, so well documented by Tajfel (1978), apply: exaggeration of the differences between ingroup and outgroup, seeing the ingroup as superior, and so on. In addition other processes operate at the individual level to exaggerate the differences between the stereotypes of males and females.

(d) Why do the stereotypes differ between cultures? This, of course, is the province of social anthropology.

Thus an understanding of the genesis of gender differences requires us to come to terms with the

dialectical relations between successive levels of social complexity and the socio-cultural structure, and to use the resources of physiology, psychology, social psychology, anthropology and sociology and evolutionary biology.

International war

Finally, I mention two current world problems that demand a synthesis of natural and social sciences. The first is that of international war. As we have seen, different principles of explanation are required for aggression between individuals and groups. International war is different yet again. Modern war is concerned with access to resources or with matters of national prestige or power that are only distantly related to the life goals or immediate motivations of the individuals who do the fighting. War is an institution, with prescribed roles for soldiers, politicians, munitions workers and so on.

As an aside, I should explain that I am using the terms 'role' and 'institution' in a social-science sense, as follows. The language-based capacity of humans for culture permits the labelling of relationships and the classification of relationships into types. This permits the existence of a limited set of roles, involving specified rights and duties, within institutions within the society. Thus 'husband' and 'wife' are roles, each with its specified rights and duties (some obligatory and some merely expected, and differing between societies) within the institution of marriage. In the same way, I suggest, it is the rights and duties attendant on their roles in the institution of war that constitute the primary motivating forces for individuals in wartime. Elementary aggressiveness plays little part in the actions of combatants: they are guided by obedience, a propensity to cooperate, above all by duty consequent upon the role that they occupy. So one must ask what are the forces that keep alive the institution of war as a means for settling international disputes? In the short term, the propaganda of leaders plays upon basic propensities of individuals. An image of the enemy as evil, sub-human, selfish, pitiless, is created. This depends on two universal propensities: the fear of strangers, which develops in children in the second half of the first year and remains in some degree throughout life; and the tendency to see one's own group as more different from and superior to outgroups. In the medium term are the economic forces, the military–industrial–scientific complex, with vested interests in war machines. In the still longer term are religious, political, historical forces that bolster up the institutions of war. Thus in attempting to come to terms with the threat of nuclear war the natural scientist must first come to terms with the weapons and their capabilities, with verification procedures, with monitoring disarmament and so on. But the task is not then done. The natural scientist must ally himself with the social scientist who has expertise about the social forces at many levels of complexity that must be understood if the threat of war is to be removed (Hinde 1989).

Environmental issues

The second issue is that of pollution and the use of expendable resources. Again the physical scientist can monitor the ozone layer, model the build up of carbon dioxide and chlorofluorocarbons and find substitutes for scarce resources. But that is not the end of the matter. The forces that make for excessive consumption, the emphasis on consumerism and on competition must be countered. We need natural scientists who understand the social science issues and social scientists who understand the natural science ones.

The same issues arise over questions of development and conservation. Anderson & Grove (1987) emphasize how the development policies pursued in Africa by colonial and post-colonial governments have not only been economically unsuccessful but have been harmful to the natural environment and lacking in sociological insight into their potential impact on African populations. Equally, they stress, many conservationists and environmentalists fail because they seek to impose their own vision of society on local populations without considering the people's real needs. Anderson & Grove argue that the root of the difficulties lies in the way conservation and economic programmes have been put into the hands of specialists, biologists or economists, who have failed to take a broad perspective. Conservation must be incorporated within the planning and implementation of rural development, and development without conservation is ultimately futile.

CONCLUSION

We have seen that the various scientific disciplines concerned with behaviour tend each to be concerned with one level of complexity, and that at any one level different sub-disciplines are concerned with different questions. To reach even a partial understanding of behaviour, human or non-human, we must be prepared not merely to be interdisciplinary, but to cross and re-cross between the levels of social complexity. The understanding of human behaviour is only one part, albeit a crucially important part, of the scientific enterprise. A similar need to cross and re-cross the levels of complexity occurs in other life sciences and also in the physical sciences. This has more general implications. None of us can hope to be on terms with as many branches of knowledge as were da Vinci, Newton, Einstein or Darwin. But with the ever-increasing need for specialization we must not lose sight of the need to foster the relations between the branches of science. Collectively, we can promote the unity of the sciences. Although specialist societies, associations and academies are inevitable, liaison must be not only maintained, but fostered.

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