

THE SEARCH FOR A GENERAL THEORY OF BEHAVIOR

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Failure of the behavioral sciences to develop an adequate general theory is seen as a result of the difficulty in deriving from evolutionary theory a subtheory, or set of subtheories, with satisfying applicability to the study of behavior. Efforts at general theories based on reflex concepts, or simple movements such as in orientation, have been unsuccessful in dealing with complex behaviors. Recent arguments that selection is focused at the level of the individual organism suggest the additional inadequacy that such theories fail to emphasize the selective compromises that exist at suborganismic levels. Evolutionary theories about behavior have tended to concentrate chiefly on patterns of historical change (phylogenies) without stressing adaptive (= reproductive) strategies, or have generally viewed adaptiveness erroneously as focused at group, population, or species levels. Human society is discussed briefly, in a context of selection focused at the individual level, considering six principal aspects: group-living, sexual competition, incest avoidance, nepotism, reciprocity, and parenthood. An effort is made to combine the approaches and data of biologists and social scientists in analyzing reciprocity in social interactions.



INTRODUCTION

THE STUDY of behavior encompasses all of the movements and sensations by which animals and men mediate their relationships with their external environments—physical, biotic, and social. No scientific field is more complex, and none is more central to human problems and aspirations. Nor has any field suffered more from the absence of a truly unifying theme or theory. Investigators of human behavior have been able to fall back upon the practical value of even slight predictability or manipulability, and upon the intrinsic attractiveness of insights into human history, either of individuals or of societies. Lacking even these crutches, the study of animal behavior has throughout its history repeatedly broken down into recitations of fascinating anecdotes, without logical main connections or satisfying generalizations and principles.

There has been no paucity of attempts to theorize. But all have failed, more often than not it seems in retrospect, for anthropomorphic reasons. In the 50 years following Darwin two efforts stand out—both inductive, both mechanistic, and both rejected for reasons that now seem irrelevant. In the late nineteenth century, with the pendulum swinging away from post-Darwinian anecdotalism and anthropomorphism, and with Morgan's law of parsimony ringing in their ears, the behavior-oriented biologists

were obliged to deal with Loeb's (1893, 1907, 1912, 1918) tropism theory. Its substance lay in beginning with the simplest orienting and locomotory movements, arranging, classifying, and combining these to build a structural science of behavior. Loeb's theory fell quickly into disrepute, and biologists still accept that Jennings' (1904) studies of ciliate protozoans were primarily responsible (Hargitt, 1906; Jensen, 1961; Marler and Hamilton, 1966), because they showed that "even such simple organisms as the ciliates" fail to behave according to Loeb's predictions. Somehow it has consistently been ignored that Loeb's original statements referred specifically to bilaterally symmetrical animals, while the ciliate protozoans have unusual and sometimes complex body symmetries and rotate during locomotion. No one seems to have considered seriously whether the supposedly random or trial and error turnings of Jennings' paramecium, butting repeatedly into the noxious region around a CO₂ bubble and backing off before advancing again, depend upon the body position when forward motion is resumed; whether this behavior is in fact the simplest response an animal with such unusual symmetry can give; or what such interpretations would mean in regard to Loeb's theory.

It is easy to suspect that it was actually Loeb's implication that animals respond

passively to external stimuli—or are forced by them—that made arguments against his theory more attractive than attempts to enlarge and modify it. Even Fraenkel and Gunn (1940) whose book on the orientation of animals was for decades a widely used and classic elaboration from Loeb's beginning, just as mechanistic and just as inductive, felt compelled to deny any similarity between their approach and Loeb's. Significantly, Fraenkel and Gunn and others cited as a principal reason for the downfall of Loeb's theory the disapproval of various authors of the automaticity and rigidity of his "mechanistic scheme of reaction." Right up to the present, the stance has been assumed by prominent writers on behavior that "No animal is a passive respondent to environmental commands" (Marler & Hamilton, 1966). Never has a reasonable explanation been given as to just what such a remark really means. One cannot but wonder how much the ancient dichotomies persist because man must keep his free will, his soul, or, to use the terms of Skinner (1971), his inner man and his freedom and dignity. Nowhere in all the criticisms of Loeb are the difficulties and inadequacies of building a science upon induction used to attack the practicality of a general theory of behavior based on simple movements.

In the early part of this century Pavlov (1927) discovered that simple reflexes, known since Descartes' time, could be conditioned, and Sherrington (1906) published his remarkable and timeless treatise on the integrative action of the nervous system. A new inductive science and theory of behavior was thus born, this one based on a functional, physiological unit rather than a structural, behavioral one. For a time the apparent dualism of conditioned and unconditioned reflexes must have kept some of the sting of mechanism out of this new approach.

But the connections between simple reflexes and complex behaviors were not to be easily drawn, and biologists and psychologists continued to be attracted to the study of function and performance at high levels. Some Russian behaviorists (see Razran, 1958; Mason & Riopelle, 1964) and others similarly inclined (Kennedy, 1954; Knoll, 1969) have clung steadfastly to the argu-

ment that Pavlov's ideas were in no way dualistic, that the reflex provides the only candidate for a basic unit in behavior, and that reflex theory still has no substitute. In most of the world, however, with a few special exceptions such as Skinner (1938) learning theorists seem hardly to have toyed with the notion that complicated behavior ought to be viewed as no more than collections of reflexes, conditioned or otherwise. The heart of their science became a high level abstraction, with neither a demonstrated physiological basis or unity, nor generality adequate to the assumptions. The study of learning nevertheless became the study of behavior in the eyes of most social scientists of the western world, and learning itself came to be used essentially as if it were synonymous with epigenesis, or all of the events of ontogeny in which environment and heredity interact.

In this interaction, environment was given the paramount role, almost to the exclusion of genetic variations as having any significance at all. There were doubts that even members of different species could behave differently, should their learning experiences somehow—a somehow whose difficulties were never specified—be made identical. Learning came to be viewed as some kind of return to randomness in the developing phenotype, the capacity to learn a simple loosening of genetic control during development. Significantly, some recent discussions have been concerned with constraints on learning (Hinde, 1970; Shettleworth, 1972; Garcia, McGowan, Green, 1972; Hinde and Stevenson-Hind, 1973). Despite the distinct implication that learning might be affected by evolution, or restricted by it, scarcely anyone yet speaks of the evolution of learning. Evolutionary progress has often been correlated with the addition of plasticity or learning capability. Man himself, at the most advanced level of this supposed progression, was and sometimes still is pictured as Locke saw him, a developmental blank slate upon which almost anything can be written with ease (Watson, 1914, 1930; Boulding, 1966; Montagu, 1968).

If learning theorists failed to relate their investigations either to existing physi-

logical knowledge or to evolutionary theory, so did they fail convincingly to embrace all behavior. In both humans and animals behavior patterns were being described for which no specific experiential antecedents were known, and in some assiduously examined cases none could be discovered (Alexander, 1968). In such circumstances the ancient dichotomies of instinctive and learned, stereotyped and modifiable, innate and acquired, could scarcely be expected to die out completely. Freud's efforts, beginning in the 1920s, to describe supposed instinctual aspects of human behavior and uncover their ontogenetic and hereditary bases, were paralleled remarkably closely a decade or two later by the Lorenzian ethologists. Both groups were attempting to understand high-level, complex behavior patterns, stereotyped in their makeups and with obscure ontogenetic antecedents; the similarities of their approaches and their conclusions were analyzed by Kennedy (1954; Kortmulder, 1968; Lindzey, 1967).

The efforts of Lorenz (1950, 1965, 1966) and other biologists sympathetic to his approach led to some far-reaching and curious effects upon the study of behavior, particularly in the realm of applying biological information to the understanding of human behavior. The European ethologists and their derivatives have been widely credited with having returned to behavioral study the evolutionary theme from which it had been so long divorced. In the sense that their approach was obviously comparative, and functional in terms of interest in survival or reproductive value, and also because they tended to concentrate on behavioral variations that seemed most clearly related to genetic variations, this view was appropriate. Furthermore, the notion was decidedly enhanced by the fact that the most vehement and bitter critics of Lorenzian ethology were sometimes learning psychologists and comparative psychologists whose views of the evolutionary process and its consequences for behavior were not always completely modern or understandable. This problem can be detected, and some of its history traced, in Razran (1971) and in the multiple reviews (Razran, Barnett, Fyodorov, Hinde, Kovach, Reynierse, Thiessen,

& Thompson, 1973). But in an important sense the Lorenzian ethologists never bridged the gap between evolutionary theory and behavioral analysis. Their efforts in some ways paralleled those of the old comparative anatomists. They were emphasizing patterns of change and phylogeny more than application of the principle of natural selection and the predictability of the effects of evolutionary process upon behavioral tendencies. When conflicts occurred, their searches for life functions seemed to focus either on survival and necessity rather than on differential reproduction, or on some supposed benefit to the population or species rather than benefits to the individual. Nowhere in behavioral studies, during the heyday of ethological theorizing, was there clear evidence of a modern understanding of Darwinian selection.

ECOLOGY, POPULATION GENETICS, AND BEHAVIOR

By coincidence, long-standing difficulties of a parallel nature in the diverse fields of ecology, population genetics, and behavior were destined to cause a series of clashes in the thoughts and practices of biological theorists in the 1950s and 1960s, clashes whose reverberations are only now being fully felt in the social sciences. It is possible to believe that amidst the resulting rubble there is emerging for the first time a synthesis and an accuracy of focus that may yet yield a truly comprehensive and useful theory of behavior: an evolutionary theory yet a predictive theory; a philosophically significant theory, yet a practical and effective one; a theory valuable, acceptable, indeed indispensable, to biological and social scientists alike. In the perspective of this theoretical turmoil many of the old arguments are at once both understandable and easily dismissable.

For most of the first half of the twentieth century, biologists had floundered and failed in the business of developing, refining, and quantifying evolutionary theory. Then came Fisher (1929), Wright (1961), Dobzhansky (1937), Mayr (1942), Simpson (1950) and others in the next decades. With the advances of genetics, mathematics, and logic, there emerged an emphasis upon the

population as the principal unit of evolutionary change. Ecologists began to deal quantitatively and precisely with changes at population and community levels. Population geneticists built their formulations upon the concept of population fitness. This concept began as Fisher's average of the proportional fitnesses of the individual members of the population. But it came to be stated and understood as the mean population fitness, then the mean fitness of the population. As a result it erroneously became the focus of selective change on its own supposed merit (Fisher, 1958 p. 49). Behaviorists found justification for their tendencies to consider foremost what is good for the population or the species. Everyone in the biological and social sciences was exhorted to undertake a personal intellectual revolution that would lead him into something called population thinking and deliver him simultaneously from the typology of Plato and the oldtime taxonomists, and even from the evils of social Darwinism (Mayr, 1963; Hirsch, 1967).

Problems developed in the 1950s and 1960s when it became clear that to many or most biologists the population had become not merely the unit of evolutionary change but the principal unit of selection as well. In retrospect, the error seems inevitable, not only because of the biologists' emphasis upon populations but also because of the human tendency to think in terms of social groups. The consequences of this error were almost unbelievably important, and constitute a lesson of the largest magnitude in regard to the significance of theory in the proper guidance of investigation.

Ecologists, long impressed and puzzled by the apparent stability of natural populations, had concentrated during this period on explanations of population regulation involving built-in reproductive restraints supposedly evolved because of their value to the population or species as a whole. In population genetics, genetic load theory moved quickly from Muller's (1950) original concern with homozygous lethals and other seemingly unequivocally deleterious alleles in human populations to formulae that required genetic variability itself to entail increases in mortality (Haldane, 1957). This trend

reached extremes so patently ridiculous that populations with new beneficial alleles were seen as being in greater jeopardy than the old population with only the old allele, and in greater jeopardy than those with new deleterious alleles because of the larger number of genetic deaths entailed in the inevitable replacement in the first case (Brues, 1964, 1969; Wallace, 1968). Moreover, it becomes obvious that once these arguments are accepted, the more beneficial the new allele the greater the genetic load of the population because its presence makes the old allele even more deleterious! Among behaviorists, acceptance of the reality of species- or population- or group-preserving altruistic acts caused reproductive competition among individuals and families to be shunted aside as a focal point of explanation for social interactions. Social scientists, in particular, become fond of noting that we had finally escaped from the antiquated notions of Darwinian selection and the concept of nature "red in tooth and claw" (Montagu, 1968; Alland, 1970). Even some sophisticated evolutionary biologists have entered this trap with vague and puzzling demurrings on the topic of reproductive competition (Wilson, 1971).

Wynne-Edwards (1962) brought the ecological and behavioral aspects of these various views together. For the first time many of the problems were exposed, and as a result biologists chipped away at their solutions until Williams (1966). He argued that natural selection works chiefly at the level of the individual or the parents and their offspring and is generally impotent at the higher levels of group, population, or species. The effect was to throw the whole behaviorist-ecologist-evolutionist camp into a long series of controversies (Williams, 1971). From these a solid theoretical viewpoint is emerging that refutes much of the writing of earlier decades (Lewontin, 1970; Levins, 1970; Williams & Mitton, 1973).

Once it was realized that behavior assisting the population at the expense of its bearer could spread and be maintained only under peculiar and at least rare conditions of population structure, alternative hypotheses were generated. Population regulation began to be assumed once again to derive

from the effects of an updated version of Darwin's hostile forces of parasites, predators, diseases, food shortages, climate, and weather. Population cycles of puzzlingly predictable length, as in small mammals, were recognized under conditions modified by man's extermination or reduction of previously influential predators. Reproductive failures owing to physiological effects of stress during high densities were seen as more likely the results of new evolutionary situations than evolved mechanisms of population regulation. Reproductive slowdowns during high densities were viewed as conservation of reproductive potential by long-lived individuals until times when breeding was more likely to be successful. Facultative and evolutionary reductions in brood or clutch size with concomitant elaboration of parental behavior and apparent slowing of reproductive rates through lengthened juvenile life were viewed as adaptations increasing reproductive output rather than reductions in reproduction in the interests of the population or species. Mass emigrations from favorable habitat accompanied by high mortality during rapidly repeated population booms in migratory locusts, lemmings, and other organisms were seen not as suicide squads evolved to reduce population pressure in the home breeding area, but as the best means of reproduction in nomadic species evolving in temporary habitats.

The situation in population genetics has not clarified so quickly, but evidence of a new perspective is nevertheless emerging. When electrophoretic techniques uncovered what seemed to be enormous amounts of genetic variability, beyond the comprehension of the genetic load theorists, it was inevitable that they should seize first upon the notion of allelic neutrality. This explanation was made more palatable by the blindness of electrophoretic analysis to function, the support by molecular biologists of the existence of "nonsense codes," and the discovery of extremely similar isoenzymes and allozymes. Furthermore, population geneticists had never been able to incorporate satisfactorily the complex and entirely unavoidable problem of spatial and temporal variations or reversals in selection across

species' ranges. So they did not know, and do not yet know, what amounts of genetic variability and what allelic proportions to expect from selection alone (Gottlieb, 1971; Powell, 1971; Johnson, 1973).

Finally, allelic neutrality and genetic drift, as with mutationism at an earlier time, came all too easily as explanations to the anthropologists attempting to incorporate biological and evolutionary concepts into their field, yet striving to remain free of value judgments about human differences and the taint of social Darwinism. Many human oriented biologists seemed to believe they had to deal chiefly, on the one hand, with alleles evidently deleterious in all situations like those causing hemophilia or phenylketonuria, and on the other hand with phenotypic variations like eye and hair color without apparently different selective values and not known to be genetically linked to attributes of any greater importance.

For behavioral study the significance of all these events can scarcely be overestimated. To understand this we can begin with the rise of attention in the early 1960s to the concept of altruism (Williams & Williams, 1957; Hamilton, 1963, 1964; Maynard-Smith, 1965). Altruism is defined in most dictionaries as "unselfish concern for the well-being of others." But evolutionary theory, based on differential reproduction of genetic alternatives or survival of the fittest, seems to call for some kind of ultimate selfishness in reproductive competition.

Darwin, after all, had noted (1859, p. 201) that "If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced by natural selection." This remark seems to have gone unnoticed by generations of critics who argued that selective theory is circular and explains nothing because it explains everything. Neither Darwin nor any of his successors thought to emphasize the obvious conclusion that follows from his 1859 challenge, and is even more appropriate and startling. To find an adaptation in an individual that evolved because its sole or net effect is to assist a reproductive competitor

within the same species, would also annihilate Darwin's entire theory. For all of one's individual conspecifics are, in one sense or another, one's reproductive competitors unless they are genetically identical. Even individual offspring are included, in biparental organisms, for no parent's reproductive interests are identical with those of any of its individual offspring, but rather with its brood as a whole. When the paradox of altruism, in light of the seeming universality and enormous complexity of human social cooperation, is considered together with the indirectness of the relationship between the human genotype and its behavioral phenotype via learning and culture, it is small wonder that behaviorists and evolutionists failed to join their separate endeavors in a theoretically sound fashion.

The ontogeny problem cannot yet be entirely solved. However, ontogenies are no more nor less than means to ends, the ends being adaptive functions leading to increased reproduction over alternatives that existed at some time during selective history. As Haldane put it, one can strike a match any of many different ways: it is only whether or not the flame is produced that counts. We can assume that whether a behavior is acquired by learning of one sort or another, whatever the stimuli, context or timing, the particular ontogenetic route followed was the most reliable available during selective history. It becomes clear that many ontogenetic questions are ultimate ones and will not be solved for a long time. This conclusion deserves careful consideration by the two branches of behavioral biology, psychology and ethology; both have assumed ontogenetic questions to be primary.

For two reasons it is not reasonable to put behavior aside—either behavior in general or any particular behavior—until we have worked out the problems of its ontogenetic and physiological backgrounds. First, behavior is such a centrally important phenomenon in understanding animals, and in humanity's understanding of itself, that any increase of predictability from whatever source can be immensely valuable. Second, the most useful methods of investigating developmental and physiological problems will become apparent only as a result of the

accumulation of direct knowledge about behavior itself.

REFLEX THEORY AND NATURAL SELECTION

Perhaps these problems can be clarified by considering the controversies about reflex theory. Essentially the same arguments have raged over the nature and theoretical significance of reflexes as over the nature and theoretical significance of complex behaviors, or even behavior as a whole.

Reflex and reflex arc are terms that connote to a physiologist the simplest stimulus-response chains, minimally involving a sensory or afferent neurone and a motor, effector, or efferent neurone. The number of neurones or series of neurones in both afferent and efferent parts of the circuit can be increased, and intervening interneurones can be added, without prejudicing use of the term reflex.

Several questions, however, have been raised about the reflex serving either as a basic or as the fundamental unit of behavior. First, Watsonian and Skinnerian behaviorists used the term reflex to refer to any stimulus-response chain (Skinner, 1938). They not only accepted the reflex as the fundamental unit of behavior, but they operated on the assumption that behavior patterns in general are elicited phenomena which ultimately involve physiological reflexes of the sort already demonstrated for a few responses. Skinner, after appropriating Sherrington's (1906) laws applying to physiological reflexes and their interactions for his stimulus-response reflex, felt it necessary to exempt from this consideration what he called operant behavior—behavior for which antecedent stimuli were unknown. He was explicit, despite his stated intention of being objective, that such operant behavior, as contrasted with respondent behavior, be dealt with separately.

Several kinds of complaints have been lodged against the attitude that all behavior may be composed of chains and combinations of reflexes. One argument is that the approach requires a more mystical view than its counterpart that learning, consciousness, voluntary or volitional acts, and other analyzed categories of complex behavior involve some other as yet undemonstrated

physiological phenomena. Two other arguments are perhaps most prominent, and most relevant here.

First Sherrington (1906) argued that pure or simple reflexes do not exist in normally functioning animals "because all parts of the nervous system are connected together and no part of it is probably ever capable of reaction without affecting and being affected by, various other parts and it is a system certainly never absolutely at rest." Hence, the response of any individual neurone would depend not only on the input from the particular afferent pathway stimulated but also on input from other parts of the nervous system. In other words, whether or not a particular stimulus effects a response depends upon what Sherrington called central excitatory and central inhibitory states.

The simple, pure, or individual reflex may be a purely abstract concept, physiologically a convenient, if not a probable, fiction and indefinable in the sense that in the living animal functioning in its natural environment its effects and concomitants cannot be wholly identified and do not transpire in isolation. To an evolutionary biologist it does not follow that the important conclusion from Sherrington's statement is that the reflex "is not a physiologically definite mechanism or an anatomically definable structure . . . [rather] is only definable by reference to the concept of voluntarily initiated action" (Efron, 1967). The fact that reflexes are not independent, like Dobzhansky's (1961) statement that "heredity is particulate but development is unitary," merely emphasizes that selection below the level of the whole organism, as well as above it, is relatively impotent.

Selection may sort alleles according to their effects on the attributes of organisms, but even in sexually recombining forms it is the organism as a whole that is chiefly favored or disfavored, not the isolated attributes. In completely asexual forms, selection below the level of the whole organism is essentially nonexistent. Reflexes, therefore, should be integrated as Sherrington thought they were, whether or not and to whatever extent any other basic units of behavior can be discovered. In the sense that Efron

argues the point, there should be no basic units at all in behavior as a whole, only the stream of behavior that comprises the organism's life performance, which Pavlov (1927) called the life reflex.

These facts deserve more reflection, for they are as important to those who study organisms only at the population level as to those who study them at suborganismic levels. We cannot expect to interpret function satisfactorily at either level except in light of the reproductive strategy of the individual organism. Effects at population levels are not expected to be maximized or optimized, for they are incidental to the reproduction of the individual organism. In the same sense, the function of each somatic cell in a metazoan is to commit suicide according to a particular evolved pattern which enhances the survival potential of the gametes.

One effect of a reductionist approach to any biological problem is that it tends to lead the investigator to conclude that he has discovered factors that are limiting not only in some immediate or relative sense, but in an evolutionary and absolute sense as well. This kind of conclusion seems to generate partly because an all-too-close correlation exists between the finer and finer analysis of a mechanism or structure and the failure to continually relate the results back to larger questions. To concentrate on one attribute, or one concordance of processes or patterns, makes it easy to forget that no attribute is selected alone. Because an organism is a bundle of selective compromises, no single one of its attributes is likely to be maximized or optimized.

When the physiologist investigating water balance in a desert rodent discovers the limits of desiccation tolerance, he may decide that this limit has some special or broad significance. In fact it is more likely to be the result of the particular selective compromises that have occurred in the evolutionary environment of that organism. It is almost always possible to build a better system of water balance, a better locomotory mechanism, a better extruder of toxic products, or a better temperature control device. What stops the evolutionary process at any particular point is the difficulty in building

a better organism. Any study of function which fails to take into account the reproductive strategy of the whole organism—no matter how clear the actions and effects of chemicals, organelles, or organs may seem to be—necessarily must lack focus. The seriousness of this effect will depend upon many factors; the important point is that it is a useless and wasteful shortcoming in any case.

The term voluntarily initiated action in Efron's argument brings us to a second important and difficult problem. The anatomical basis for conditioning of a reflex has never been demonstrated, nor has a clear understanding been developed of the relationship between conditioning of simple reflexes and the nature of complex learning. The nature of consciousness, voluntary or purposeful acts, and the movement of responses into and out of these categories in conjunction with conditioning, is still totally outside physiological knowledge. In physiological terms, we do not know what happens when pupillary dilation is "elaborated to occur at a bell signal preceding darkening of the room" or when, still later, even "the words 'the bell rings' will cause pupillary dilation." Or when "the subject can himself bring about pupillary dilation by saying the words 'the bell rings,' or even by thinking of these words" (Astrop, 1967, p. 418). Neither do we know what happens when acts at first conscious and deliberate, such as the movements involved in playing a musical instrument, become possible without conscious and specific thought or intent.

Perhaps more instructive is the problem presented by unconditioned reflexes. From where do they come? If conditioned responses, like learned behavior, are acquired, then it is not surprising that biologists should exercise the prerogative of terming all the rest innate, inborn, or inherited. The same adjectives have been used, of course, for units of behavior of all sizes and complexities. But, in fact, we do not know that reflexes or behavior in the second category are indeed unconditioned or unlearned in any specific sense of these terms. Like Skinner's operant behavior, they are responses whose antecedents are unknown.

Except for the argument about conscious

or voluntary acts somehow necessarily being different from physiological reflexes, or chains and combinations of them, to my knowledge the only evidence brought forward to deny the reflex as the fundamental unit of behavior comes from those biologists who have studied the firing patterns of pacemaker neurones or groups of neurones. Such processes have been studied not only in mammalian hearts but also in the lobster cardiac ganglion (Maynard, 1955), and in patterns of grasshopper flight (Wilson, 1968) and cricket stridulation (Huber, 1965; Horridge, 1961). In the last case genetic variations have been correlated directly with pacemaker rate variations. In one case pacemakers acting in series to produce complex song patterning have been shown to occur in different ganglia of the cricket central nervous system. The genes affecting their respective firing rates have been shown to be located on separate chromosomes (Bentley & Hoy, 1973). Concerning such patterns, often termed as well endogenous, Bullock (1961) says "it seems at present likely that for many relatively complex behavioral actions, the nervous system contains not only genetically determined circuits but also genetically determined physiological properties of their components so that the complete act is represented in coded form and awaits only an adequate trigger, either internal or external."

Still, what do we know of the manner in which such firing rates generate? We know nothing except that they are remarkably constant and have not been altered despite considerable effort and imagination, in some cases, by a variety of investigators. Their ontogeny is unknown. If, however, we continue to view the organism and all its attributes as a product of the interaction of the zygote and its environment, then, if the firing pattern did not occur in the zygote itself, a properly parsimonious attitude would suggest that some interaction of the embryo with a peculiarly stable and predictable aspect of its environment yields the observed firing rates. The evolutionary biologist notes, for example, that in crickets only the eggs overwinter in many species, and that no sounds heard in the spring would be the right ones from which to learn. He is not,

therefore, surprised that for the ontogeny of cricket acoustical signals and responses, acoustical stimuli, the logical and expected category of learning stimuli in other animals such as man, have been excluded as influences by selection. Recognizing the significance of precision in signalling between male and female at mating time, he is not astonished that whatever stimuli may be involved in appearance of the pacemaker rates, they are immune to most environmental perturbations, inside or outside the laboratory.

From whence comes the neural pathway that makes up an unconditioned reflex, or provides the inputs that cause some to deny the existence of reflexes? It is as naive to call them inherited as it is to describe as innate any behavior pattern with a cryptic ontogeny. If the learning theorist assumes that somehow, sometime, the learning (or at least the ontogenetic) sequence will be unravelled for every behavior, so may the reflex theorist assume that someday the antecedents of unconditioned reflexes will be well enough known that environmental deletions or alterations will change the unconditioned reflex.

BEHAVIORAL THEORY AND EVOLUTIONARY THEORY

Since Darwin initially provided the means of testing for the existence of an evolutionary process and for its significance in accounting for the attributes of living organisms, biologists have accepted with increasing decisiveness the hypothesis that all attributes of life are outcomes of that simple process. Evolution has become the central theme and theory in their science, the general principle that they are constantly testing and expanding or modifying if necessary. It is the concept by which they develop their hypotheses, and from which they determine to a large degree which observations or comparisons to make, which experiments to do and which ones to do first.

The social sciences, which also deal with attributes of life, present a dramatic contrast. If anthropology has struggled to incorporate evolutionary theory, psychology and sociology scarcely mentioned it. Biologists must take part of the blame. Psycholo-

gists and sociologists study behavior. Through most of the twentieth century biologists have largely failed in understanding how behavior relates to evolution. For decades behaviorists in biology were considered anecdotalists and second-rate natural historians. There was no cumulative growth of understanding about animal behavior. Why should social scientists be expected to find evolution important in their studies of human behavior if the biologists could not apply it to the behavior of nonhuman animals?

In spite of their own failures to correlate behavior and evolution, most biologists are convinced that social scientists have no satisfactory theoretical base for their science. Social scientists generally have failed to realize the strength of this conviction among evolutionary biologists. Many biologists dismiss sound psychological and sociological investigations because in their own view such experimentation is poorly focused or irrelevant. As Kroeber, the cultural anthropologist commented, "[among] biologists and often psychologists and men in other sciences . . . the sense always crops up in their minds that we are doing something vain and unscientific, and that if only they could have our jobs they could do our work for us much better" (Stocking, 1968, p. 289). Asimov (1962, pp. xi-xii) supported an implication all too prevalent in science when he suggested that only the methods of the physical scientists can solve behavioral problems "None of the social sciences is what a chemist, physicist, or physiologist steeped in quantitative measurements would call 'science'; with the best will and effort in the world the social scientists have still not discovered 'what makes Sammy run!'. . . [only when] the central problem of life . . . was exposed to the scalpel of the physical sciences . . . was . . . the foot of man . . . for the first time placed upon the highway of true life science, a highway that may (and should) end finally in as detailed an understanding of life and mind as now exists in connection with atoms and molecules." I believe that many of the ill-fated excursions of biologists into human behavior during the past two decades may have generated partly because such views made it seem too

easy to correct erroneous approaches prevalent in the social sciences.

It will not be easy, however, to build a sound theoretical view of behavior in general, and of human behavior in particular. I believe we must realize that: (1) whatever we hypothesize must accord with our knowledge of evolution and (2) a useful, predictive, general theory of behavior is unlikely to be constructed by building upward toward greater complexity from the engram, the reflex, or some simple unit of activity. The question of how, then, we are to proceed leads to some basic questions about how problems are solved in different disciplines, particularly those that deal with the phenomena of life.

A METHODOLOGICAL ARGUMENT

The history of biology suggests that any problem, like the analysis of behavior, can be approached from two entirely different directions. One is to search first, or most vigorously, for a basic unit. Subsequently, one hopes to construct an explanatory framework by discovering how the basic units are put together, i.e., how they are organized and how they operate in combination. In behavioral studies we can identify with this approach Loeb's effort. He sought to construct a science of behavior beginning with the simple orienting movements and moving toward the complex. The approach is exemplified by parallel efforts using the reflex concept, both by physiologists and by behaviorists who modified the reflex for their purposes into a stimulus-response unit without necessarily a known physiological basis. When learning theorists search for the engram, they are to one degree or another adopting this approach to understanding learned behavior.

A basic unit, in this sense, is a component that most likely represents a repeated structure or function, perhaps with variations, throughout the whole phenomenon being investigated. Presumably, it is a unit relatively low in the structural or functional organizational hierarchy, but not the lowest conceivable.

Presumably, basic units are also those units, low in the hierarchy and repeated with possible variations, that have most

meaning in the context of understanding the whole phenomenon. This may mean that a basic unit is the smallest structural or functional unit both unique and common to the phenomenon being investigated. The reflex is obviously a more attractive basic unit of behavior than is the atom or some fundamental particle of physics. The last two units carry little meaning for behavior. Likewise a stimulus-response unit is more attractive than, say, trial and error learning or CNS triggering of neuronal firing patterns, which are evidently not common to all behavior.

The expectation that identification and description of a basic unit or component is an appropriate route, or the best route, toward clarification of a phenomenon implies that the investigator is assuming a particular model of the phenomenon. This fact may be overlooked. The particular model being assumed, of course, involves a criterion that the components of the phenomenon are not all unique, and that a fruitful approach is to seek first those patterns that are most extensively represented, or recognizable even with variations, and therefore will yield the greatest generalizing power. Another way to view this approach is that it attempts to predict repeated or generalizable components and then tests for their presence.

The dangers in this procedure appear twofold. First is the possibility that the model is wrong; that the phenomenon being analyzed includes no basic unit that is meaningful in the sense of being frequently represented or involving a pattern that is generalized; even that the phenomenon is not singular but a deceptive convergence of separate phenomena lacking overlap in any meaningful sense other than that causing the confusion. Presumably such a relationship ultimately will become apparent, but this may happen only after delay, particularly if the level at which a basic unit is sought is far removed from the level at which definition of the phenomenon has been focused. Thus, should there be no basic unit of learning at the chemical or molecular level, discovery of that fact might be an almost impossible task, and a search for such a unit, once initiated for whatever

reason, might continue fruitlessly for an indefinite period.

Second, it may be difficult to understand that a unit low in the hierarchy of organization, and discovered to be basic in the sense that it represents a frequent pattern, in fact carries little meaning for the phenomenon of interest. Again, there is the paradox that truly basic units will be far removed from the level at which the phenomenon is defined, but such units may also be decreasingly likely to carry meaning at the level from which they are far removed. DNA may be the secret of life insofar as it represents the mechanism of inheritance; but the additional information necessary to predict anything at all about the parental behavior of a shorebird or the extent of inbreeding among Australian aborigines may be so extensive and particular as to give any aspect of molecular structure and function little meaning for such problems.

These dangers represent shortcomings not of the method, but in its application. They are identifiable as special hazards because of attributes of the humans who must employ the method.

It is commonly believed that the approach of evolutionary biologists is more or less diametrically opposed to that described above. Evolutionists do not seem to be generalizing from a basic unit when they assume that natural selection, or survival of the fittest, is their chief guiding principle. We can understand this if we realize (1) that the phrase has come to be accepted as a universal in biology; (2) that parallel or related generalizations are always more particular and in some sense subsidiary to it. Thus ". . . the sex ratio will so adjust itself, under the influence of natural selection, that the total parental expenditure incurred in respect of children of each sex, shall be equal. . . ." (Fisher, 1958). Or: ". . . the reproductive rate (in particular, clutch size) has been evolved through natural selection to correspond with that number which, on average, gives rise to the greatest number of surviving offspring" (Lack, 1954). Or: "The social behavior of a species evolves in such a way that in each distinct behaviour-evoking situation the individual will seem to value his neighbor's fitness against his own

according to the coefficients of [genetic] relationship peculiar to that situation" (Hamilton, 1964).

Yet in what sense or to what extent can survival of the fittest, or some other phrase describing differential reproduction, be said to be a basic unit in the study of living organisms? Evidently it qualifies in two regards: apparently, it is both common to all life and, in the sense of a cumulative effect resulting from continuity of genetic lines, unique to living things. In what sort of hierarchy of complexity, though, can it be considered a basic unit in the sense that it is only a component, and somehow low in the hierarchy?

I believe there are two senses in which this may be true. First, even if differential reproduction is the principal guiding influence it is only one component in the evolutionary process in which chance events can lead to genetic elements being gained (mutation), lost (drift), or changed in relative frequencies. Second, in a temporal sense, differential reproduction can be seen as a phenomenon occurring at each stage or time in the evolutionary process that has given rise to all life; but since selection changes direction frequently and its effects are cumulative, effects at different times, places, or stages of evolution may be different.

In the sense that mutability is heritable and thus its rates, but evidently not its directions, are subject to selection, survival of the fittest thus refers to an overall process universal to life and unique to life. But it also refers to a series of events recurring throughout the cumulative process of evolutionary change spanning and apparently continuous across some four billion years. In this latter sense, any and all events of natural selection can be viewed as basic units in the temporo-spatial structure of life. To the extent that the other basic units in this structure, inheritance, mutation, drift, and isolation—which together with differential reproduction comprise the evolutionary process—are less important as guiding forces, survival of the fittest also becomes the most meaningful basic unit in the temporo-spatial structure of life.

If our assumptions thus far are reasonable,

then we should be able to do with natural selection what all scientists expect to do with a fundamental unit once it has been identified and characterized. We should be able to use it to predict meaningful things about the phenomenon of which it is a basic component. Furthermore, if the characterization of natural selection that I have given above is accurate, then it should be more valuable in this regard than any other single category of information about living things.

We do not, then, begin the analysis of behavior or any other biological phenomenon with the smallest identifiable units of structure or function, or with units identified in any sense by their size in relation to whole phenotypes or social structures. Instead, we focus on those units which, in terms of environments, represent concordances of selective forces, or units of function. They will be identifiable only because of the existence of opposing concordances of selective forces. Every aspect of life may be seen as the result of compromises between such opposing patterns of selection. If the pelvis of the human female is so narrow in relation to the skull size of infants at birth that mothers sometimes die during parturition, we do not assume that pelvises cannot widen further. We do assume that the selective advantages of larger skulls have outweighed the selective disadvantages of parturition mortality, but not those of wider pelvises. The latter may relate to abilities in other contexts, such as mobility.

We sometimes identify appropriate units of selection in a somewhat circular procedure by recognizing their integrity. Integrity of a unit in the structural-functional hierarchy of life indicates the existence of a concordance of selective forces. Thus, in a species with sexual recombination in its reproductive process, genes, supergenes, chromosomes, genotypes, individuals, families, clans, societies, cultures, and species suggest to us by their identifiability that they are, in some ways and to some extents, significant units of selection. In a secondarily asexual species many of the same units exist, but those below the level of genotype are no longer significant units of selection. The extent to which the status of a selective

unit is imposed by consistencies in the extrinsic environment can be illustrated by considering the local population in a demographic sense. Integrity of local populations can depend entirely upon physical boundaries. In sexual species, if boundaries are fickle, local populations fail to achieve separate identities as a result of geographic variations and reversals of selection because they interbreed. On the other hand, when physical boundaries persist, local populations differentiate and become, to a greater, if still relatively slight, extent, units of selection (Williams 1966, 1971; Lewontin, 1970; Levins, 1970; Boorman & Levitt, 1972, 1973; Wilson, 1973; Alexander, in preparation). Subpopulation units may be held together more or less by intrinsic phenomena relevant to selection, such as relatively great degrees of genetic overlap as with clans, or mutually profitable divisions of labor, as between mates or parents in sexual species.

HUMAN SOCIALITY AND NATURAL SELECTION

In this light, the social network of human behavior becomes a pattern of selective forces involving, I believe, a few principal components. The individual is at least a main focus. Within the pattern we can discern an interplay of selective forces, some relatively extrinsic, i.e., such as climate, food, and predators, and some relatively intrinsic, i.e., such as nepotism, reciprocity, and sexual competition. I will conclude this essay by identifying what I believe to be several principal threads in the fabric of human society. I will first list certain central questions about each, then enter upon an analysis, principally of reciprocity, which I believe illustrates particularly well how the largely uncorrelated approaches and data of biological and social scientists can be combined fruitfully.

I believe that six aspects of human behavior can be used profitably to describe and analyze the background of all human social interactions in terms of a history of differential reproduction.

1. *Group-living.* When individuals clump they inevitably increase the intensity and directness of competition for all resources,

including mates, and increase the likelihood of disease and parasite transmission. Usually they are, as well, more conspicuous to predators. Why, then, have humans and many other organisms apparently always lived in groups larger than the smallest reproductive units of a male, female(s) and offspring? What are the particular selective advantages that have caused, maintained, and shaped this aspect of human existence? How have the peculiarly human form of group-living and the appearance of culture, in turn, affected the relative potency of selection at levels above that of the individual? What are the backgrounds of the various rules of societies, and to what extent are they beneficial to groups and detrimental to individuals (Alexander, 1971, 1974)?

2. *Sexual competition.* Sex ratio selection is such (Fisher, 1958) that approximately equal numbers of adult males and females are produced in all human and primate societies, regardless of whether or not polygynous units exist, and regardless of the proportion of either sex that goes mateless. How have the resulting kinds of competition for mates, and for the best mates, been expressed in the kinds of social groups in which humanity has evolved, or lived, for so long? How has such competition affected degrees and kinds of sexual dimorphism, breeding systems, parental care, cooperation, and aggression (Trivers, 1972; Alexander, 1974)?

3. *Incest avoidance.* Avoidance of close inbreeding is one of the outstanding universals in human society. Indeed, it represents the core of Freudian psychology, as well as in analyses of so-called primitive societies by anthropologists. To some social scientists, incest has represented the central conflict of the ontogeny of human behavior (Lindzey, 1967). What are the disadvantages of close inbreeding, and how have they shaped societies? What have been the functions of incest avoidance across human history (Alexander, in preparation)?

4. *Nepotism.* In general, the reproductive interests of different individuals will overlap to the degree that their genetic makeup overlaps. If they are genetically identical, their reproductive interests are identical. If they are 50 percent alike genetically, their

reproductive interests are twice as similar as if they are only 25 percent alike, etc. To what extent and in what fashion have humans evolved to take advantage of variations in genetic overlap among members of social groups (Hamilton, 1964, 1972; West-Eberhard, 1975; Alexander, 1974)?

5. *Reciprocity.* How have humans traded benefits to mutual reproductive advantage? To what extents and in what fashions have they developed complex capabilities to cheat in such interactions? How has trading of benefits become intricately with nepotism (Trivers, 1971; West-Eberhard, 1975; Alexander, 1974)?

6. *Parenthood.* How have adult humans evolved so as to assist the reproduction of their offspring, and to use their individual offspring so as to maximize the parents' overall reproduction? How have male and female parents cooperated and competed in these regards? To what extent is the behavior of any individual human a result of selection that maximizes personal reproduction, and to what extent of selection that maximizes its parent's reproduction? When and how does parental influence wane and disappear? Which rules and conventions of societies are merely collective parental inclinations (Trivers, 1972, 1974; Alexander, 1974)?

Until very recently these questions essentially were unexplored from viewpoints compatible with and exploiting theories of human behavior that afford natural selection a central role. None of the more or less rudimentary excursions that have so far appeared has seriously undertaken to combine the approaches and data of biological and social scientists.

RECIPROCITY, NEPOTISM, AND GROUP-LIVING IN HUMANS

The passing of benefits between and among individuals and groups is so integral a part of human existence that to develop a useful and comprehensive scheme for classifying such behavior according to its functions and origins seems an almost impossibly large and diffuse task. An enormous amount of writing by anthropologists and sociologists exists on this topic which is at the heart of all social theory and analysis. Psychologists,

as well, have analyzed altruism extensively. Biologists, in contrast, only recently have attempted to understand the backgrounds of altruistic behavior (Hamilton, 1963, 1964, 1972; Trivers, 1971; West-Eberhard, 1975; Alexander, 1974, in prep.). Their analyses have scarcely involved humans or mentioned the prolific writings of the social scientists, and the latter have as yet paid scant attention to the biologists' efforts (Campbell, 1972; Cavalli-Sforza & Feldman, 1973; Ruyle, 1973).

In general, the differences between biologists' and sociologists' writings on altruism are that the biologists deal with simpler situations because their focus is to explain particular behaviors in light of a basic theory depending upon differential reproduction of alternatives. Recently, at least, they have tended to insist that their explanations be compatible with selection at the individual level.

Social scientists, on the other hand, are primarily concerned with analyzing and interpreting complex, existing systems of human interaction. They would prefer to develop their theories, one suspects, from such data rather than from the very general, and in terms of human complexities, seemingly vague, abstract, distant, and oversimplified generalizations of biological evolutionary theory. It is a long way from the differential reproduction of genes to an understanding of Wall Street or a Yanoamo feast.

Anthropologists have largely restricted their concern with evolutionary theory of biology to the terms of changes from pre-human to human behavior, and otherwise to morphological and physiological changes. Partly, this is a correlate of a rather general rejection of the notion that natural selection has any relationship to behavioral differences among existing, modern human groups, or, indeed, that such differences have any relationship to genetic differences at all. Unlike the modern evolutionary biologist, students of culture still see the benefits of systems of altruism or reciprocity as being chiefly applicable at the group level. Their concepts of function or adaptiveness usually involve the maintenance of the group as a

whole, with little emphasis upon variations in the reproductive success of individuals.

Psychologists have pursued their investigations of altruism as a part of learning theory with the implicit suggestion that tendencies to be altruistic or selfish result almost wholly from the accumulated effect of previous experiences in the same context.

How shall we reconcile these several approaches? From the evolutionist's point of view, two principles must be recognized. First, all organisms are assumed to be evolving continually to maximize their own inclusive fitnesses. Second, the giving of benefits of any kind to another organism always involves expense, however slight, to the beneficent individual. This expense includes a fitness reduction because of time and energy consumed, and risks taken. It also involves a relative fitness reduction resulting from the increase in fitness of the reproductively competitive recipient. Thus, all organisms should have evolved to avoid every instance of beneficence or altruism unlikely to bring returns greater than the expenditure it entails. With regard to group-living and culture, the important conclusion deriving from this observation is that the basic conflict in the conduct of a group-living organism is not "How can I help myself?" versus "How can I help the group as a whole?" It is "How can I help myself directly in the competition with others?" and "How can I help myself indirectly by helping my kin and cooperating in the social group in which I am forced to live if I am to reproduce at all—and upon the success and persistence of which my own persistence and reproductive success are therefore predicated?" There is no implication that in humans such questions are resolved through conscious reflection, always or to any particular degree. Nor is this argument, or any other advanced in this paper, social Darwinist in the sense that it is implied to say anything at all about how men ought to conduct themselves now or in the future. Instead, all of these arguments are hypotheses about history. Regardless of their ontogenetic or physiological backgrounds, however, the nature of genetic systems suggests that history has some relevance to the

problem of how modern men identify their problems and resolve their conflicts.

Returns, in an evolutionary sense, mean returns to one's genotype, or increased reproduction, either through one's own phenotype or through the phenotypes of his genetic relatives. From this beginning one ought to be able to calculate precisely the conditions under which particular acts of beneficence should cause the genetic backgrounds to spread which permit or facilitate them. Factors to be considered include (1) variations in cost-benefit ratios of particular acts owing to greater or lesser needs by potential recipients, (2) greater or lesser expense to potentially beneficent individuals owing to affluence, or extent of benefits available for dispensation at small cost, and (3) other asymmetries affecting returns, such as variations in the reproductive potentials of possible beneficiaries (Hamilton, 1963, 1964, 1973; Trivers, 1971, 1974; West-Eberhard, 1975; Alexander, 1974).

It is obvious that an organism helping a genetic relative may receive its reproductive or genetic return directly through the increased reproduction of the helped relative. It is also obvious that an organism helping a nonrelative can only gain through beneficence reciprocated directly to itself or to its genetic relatives. The question now is: To what extent do the transfers of benefits of any and all sorts between and among humans match the model these principles describe? To test this question we can begin by analyzing a remarkably detailed and appropriate review by Sahlins (1965).

Considering Sahlins' broadest generalizations first, we find him describing a "general model of the play of reciprocity" in primitive society by "superimposing the society's sectoral plan upon the reciprocity continuum" (Fig. 1). Sahlins divides reciprocity into three classes, which he terms generalized, balanced, and negative.

"Generalized reciprocity refers to transactions that are putatively altruistic. . . . The ideal type is Malinowski's 'pure gift' . . . 'sharing', 'hospitality', 'free gift', 'help', and 'generosity' . . . 'kinship dues', 'chiefly dues', and 'noblesse oblige' . . ." He mentions "the vagueness of the obligation to reciprocate" and uses as an example "for its logical

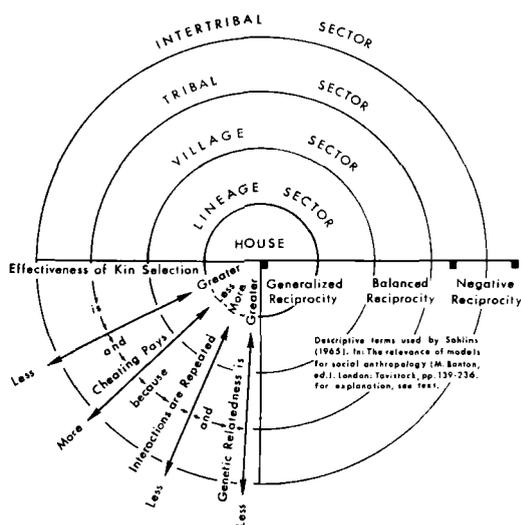


FIG. 1. This diagram from Sahlins (1965) illustrates types of reciprocity in primitive cultures. The information in the lower left quadrant has been added to suggest how kin selection and evolutionary principles accord with reciprocity as practiced by human groups.

value," the "suckling of children . . . the expectation of reciprocity is indefinite. . . . A good pragmatic indication of generalized reciprocity is a sustained one-way flow. Failure to reciprocate does not cause the giver of stuff to stop giving: the goods move one way, in favor of the have-not, for a very long period" (p. 147).

Sahlins' model concentrates generalized reciprocity in the household and implies its extension across the lineage sector of the village. He is in fact speaking largely of nepotism. Evolutionary biologists have dealt with such behavior under the rubrics of kin selection and inclusive fitness. They have come to expect that selection will mold organisms to assist their closer kin over their more distant kin, and kin over nonkin even when reciprocity in kind is unlikely, and at least to concentrate such one-way beneficence on genetic relatives, perhaps dispensing it to no one else. Sahlins is telling the evolutionists that their expectations are fulfilled to an astonishing degree in primitive human societies in which kinship is "the organizing principle or idiom of most groups and social relations."

The major difference between Sahlins'

generalized reciprocity and nepotism based on kin selection is that Sahlins has lumped together sustained one-way flows of benefits dependent upon returns in genetic currency, i.e., nepotism, and others which are really a form of balanced reciprocity. Chiefly dues and noblesse oblige are probably not best viewed as unreciprocated altruism, but as parts of exchange systems in which the returns are quite complex, or represent a promise or obligation dependent upon future contingencies with certain probabilities of occurrence. A reasonable analogue is an insurance policy. The returns on the investment may be realized only after great delay, and in particular cases never. Neither the insured nor the insurer considers or expects his part in the transaction to be altruistic.

Balanced reciprocity, to Sahlins, refers to direct exchange. "In precise balance, the reciprocation is the customary equivalent of the things received and is without delay. . . . 'Balanced reciprocity' may be more loosely applied to transactions which stipulate returns of commensurate worth or utility within a finite and narrow period. Much 'gift-exchange', many 'payments', much that goes under the ethnographic head of 'trade' and plenty that is called 'buying-selling' and involves 'primitive money' belong in the genre of balanced reciprocity.

"Balanced reciprocity is less 'personal' than generalized reciprocity . . . more 'economic' . . . the pragmatic test of balanced reciprocity becomes an inability to tolerate one-way flows; the relations between people are disrupted by a failure to reciprocate within limited time and equivalence leeways. It is notable of the main run of generalized reciprocities that the material flow is sustained by prevailing social relations; whereas, for the main run of balanced exchange, social relations hinge on the material flow" (p. 148).

Sahlins' description tells us two important things about this class of reciprocal transactions. First, it is clear that returns to benefit-givers cannot be measured via gains in the phenotypes or reproduction of the recipients. Reciprocation must, if the system is to be maintained, accrue to the benefit-giver. One expects, although Sahlins does not mention the possibility, that reciproca-

tion to one's close relatives might also satisfy such debts. In this category of reciprocation the actors are, in evolutionary terms, treating each other as if they were not genetic relatives. This means that the balance of genetic relatedness and reproductive competition among the participants is such that no gain is to be received by either treating the other like a relative. Diminishments of such competition between individuals generally correlate with geographic distance, but do does diminishing genetic overlap. Hamilton (1964, 1972) and others who have discussed kin selection have not clearly specified this condition. Its results are that, under certain conditions of gradual change in both relatedness and competitiveness with geographic distance from ego, nepotism cannot evolve; and that, in any case, nepotism will cease to be favored at distances beyond which genetic relatedness is continuing to diminish (Alexander, 1974).

The second critical aspect of Sahlins' description is its emphasis upon the social relations of the participants. Repeatedly, he implies that participants in balanced reciprocity are associates and friends, i.e., individuals who expect to maintain good relations in the future and conduct their interactions accordingly. Cheating is minimal. It comes as no surprise that Sahlins sees balanced reciprocity as concentrated at the level of the tribal sector, and we may imply that it extends inwardly into the village sector, and probably into the lineage sector, but not, although Sahlins does not specify this point, beyond tribal limits except when coalitions, temporary or otherwise, cause tribal limits to be rather indefinite.

Again, Sahlins' model is an uncanny match for that of the evolutionary biologist. Indeed, these first two kinds of trading of beneficence are roughly what the biologists have called kin selection (Hamilton, 1963, 1964, 1972; Maynard-Smith, 1965) and reciprocal altruism (Trivers, 1971), respectively. Evolutionary theory not only recognizes the two categories almost precisely as Sahlins has distinguished them, with the exceptions noted, but it specifies the social levels at which generalized reciprocity gives way to balanced reciprocity (Fig. 1).

Sahlins' emphasis on the continuation of social relations among participants in balanced reciprocity raises the question of why this specification should be requisite. Why should bartering individuals maintain a balance in the face of certain opportunities to cheat, seemingly to their own advantages? But let us delay this question until we have considered Sahlins' third category.

"'Negative reciprocity' is the attempt to get something for nothing with impunity . . . 'haggling', 'barter', 'gambling', 'chicanery', 'theft', and other varieties of seizure . . . the aim . . . is the unearned increment. One of the most sociable forms, leaning toward balance, is haggling conducted in the spirit of 'what the traffic will bear.' From this, negative reciprocity ranges through various degrees of cunning, guile, stealth, and violence to the finesse of a well-conducted horse-raid. The 'reciprocity' is, of course, conditional again, a matter of defense of self-interest. So the flow may be one-way once more, reciprocation contingent upon mustering countervailing pressure or guile" (pp. 148-149).

Negative reciprocity, as one may predict, centers outside tribal and national boundaries. The more overt or blatant the cheating, the less likely one is to conduct it among relatives or groups of friendly persons, and the more likely he is to receive admiration or appreciation for success involving strangers or, better yet, mutual enemies.

We return to the question of why humans should cheat so much more explicitly or actively outside a certain circle than they do inside it. Sahlins describes these contexts of bartering as two of three major categories of potentially or superficially reciprocal interactions. The answer seems to be that it is least profitable to cheat those with whom, or with whose relatives and friends, ego or his relatives and friends must interact repeatedly.

In today's crowded world, try as we may, it is difficult to move away from other humans. There is scarcely any place left to go. In spite of this, it is still true that humans tend to live and behave in subgroups, even as they group when populations are at their lowest densities in the Central Deserts of Australia, the Kalahari Desert of Africa,

and the outreaches of the Arctic. The basic question, "Why group living?" is raised again. So long as one is uncritical about the levels at which natural selection is most potent, tendencies of individual organisms to live in social groups larger than the smallest reproductive unit of parent(s) and offspring do not seem to require explanation, particularly to an observer belonging to a species that apparently has always lived so. Having acknowledged that selection is most powerful at the individual level, however, we are returned to the fact that group-living involves the automatic disadvantages of increased competition for all resources and greater likelihood of parasite and disease transmission. We must, therefore, seek overcompensating benefits to the individuals involved. I have previously suggested (Alexander 1971, 1974) that only three selective contexts exist for such benefits.

(1) A safety in numbers effect, or lowered susceptibility to predation, either because of aggressive group defense, e.g., baboons, and perhaps musk ox, peccaries, and other species, or because of the opportunity of causing some other individuals to be more available to predators, of using the herd as cover, as with schooling fish and herds of small ungulates (Hamilton, 1971).

(2) The nature of food sources may make splintering off unprofitable, as with wolves dependent upon large game in certain regions, or with hypothetical groups dependent upon scattered large supplies of food that individuals locate too infrequently on their own.

(3) There may be an extreme localization of some resource, such as safe sleeping sites for hamadryas baboons or suitable breeding sites for some marine birds and mammals.

In the first two cases the grouped individuals gain because of the presence of other individuals; in the third they gain solely from the presence of some other resource in the immediate environment, i.e., other sources of mortality do not keep the population low enough to prevent extreme competition for the localized resource.

Along with Keith (1949), Alexander and Tinkle (1968), Bigelow (1969), Alexander (1971, 1974), and Wilson (1973), I reiterate here the argument that group-living in

humans, at least for a very long time, has been maintained and modified under the influence of the first of these three selective forces, and that the predators responsible have been other groups of humans. In other words, I suggest that human social organization has for a long time been guided by direct intergroup competition, and that this theory provides an adaptive background for increases in group sizes and complexity of social organization involving a built-in feedback effect of unparalleled explanatory value. As Wilson (1973) has put it, "A tribe might . . . dispose of an adjacent tribe, appropriate its territory, and increase its own genetic representation in the population as a whole relative to all others, retaining the tribal memory of this successful episode, repeating it, increasing the geographic range of its occurrence, and quickly spreading its influence still further through the population. . . . Once started, such a mutual reinforcement of cultural and genetic selection should be autocatalytic and irreversible. . . . In addition to being autocatalytic, such evolution has the interesting property of requiring a selection episode only very occasionally in order to proceed as swiftly as conventional genetic evolution by Mendelian selection."

This process, of course, does not require that one tribe actually wipe out another, either suddenly or completely, as Wilson implies, or gradually. Nor is genetic difference necessarily relevant to the overwhelming of one group by another, at least not in the manner usually considered. All that is implied is that ". . . men who were arranged in groups or teams, each dominated by a spirit of unity, would conquer or outlive men who were not thus grouped" (Keith, 1949, p. 43). We have observed, within recorded human history, the aggressive expansion of western Europeans into the New World and Australia, in particular, and their replacement through the decades of the populations that previously inhabited the continents involved. The genetic change that has occurred is not necessarily relevant to the success of the invaders; more relevant is the cultural background that provided the migrating Europeans with vastly superior weapons, agriculture, and technology. Also

relevant are those cultural and genetic differences between the invaders and the invaded which reduced the likelihood of amalgamation. Aborigines who resemble invaders physically are more likely to be assimilated genetically, just as those whose culture is such as to make them pliable in the face of alien domination are more likely to survive alongside and with the invaders.

Group-living, then, forms the warp of the fabric of human sociality, the directions of evolution of the other five factors listed above proceeding under its influence or significantly directed by its existence and nature. The question that is raised by the above comparison is: To what extent should cultural phenomena, the existence of which depend upon group functions that are in some fashion more or less independent of biological history and functions, correspond to a model based on the principles of natural selection and evolutionary biology? Sahlins' description clearly does correspond to that predicted on evolutionary grounds.

Among humans, group-living has a distinctive attribute, probably shared in rudimentary fashion by only a few other species with complex behavior, such as chimpanzees, baboons, some other primates, and canines. This distinctive attribute is the rapid formation, dissolution, and modification of coalitions within and between groups of various sorts. Such coalitions, as with any groups, could be formed against extrinsic forces such as weather or predators, against other groups of humans, or against single individuals. Anyone reading accounts of the lives of the Yanomamo Indians of South America (Chagnon, 1968, 1972) or especially the autobiographical account by Valero, the Venezuelan who lived with them for 20 years (Bioeca, 1970), cannot fail to be impressed with the way in which the threat of such coalitions represents the ultimate weapon to the Yanomamo. All of their actions are governed by the possibility that other tribes may combine to defend against or defeat them, or, for individuals, that groups within a tribe will either band against and ultimately kill the offender or, if he is powerful, leave his side because his aggression has led to such likelihood of coalition against him that he has become a

liability. One wonders if tendencies to be satisfied with single killings, or even threats, during tribal encounters or wars, in these as well as other peoples such as the Fore of New Guinea (Matthiessen, 1962), might not be evidence of the value of stopping short of actions that will lead to deleterious coalitions. Recently, the threat of coalitions probably served as the major deterrent to the United States from all-out war against the North Vietnamese.

The fluidity of coalitions plays a critical role in human sociality. Classifications of societies as ranked or egalitarian and concepts like social mobility refer principally to variations in the fluidity of coalitions. In turn fluidity depends upon or derives from two sources of power (1) variance in physical and mental prowess among individuals and (2) the nature and availability of wealth, weapons, or unusually good sources of other resources like food and shelter (Komorita & Chertkoff, 1973). Some sources of power differentials are more easily transmitted from generation to generation than others, e.g., in human societies, land and money may often be more heritable than the phenotype necessary to acquire them. In turn, fluidity of coalitions affects the nature of breeding or marriage systems: In a highly fluid mobile society, individuals are less likely to garner and hold disproportionate shares of any resources, including (for men) females: Hence, monogamy is more likely in fluid, egalitarian societies which, contrary to correlations suggested by some writers, may be structurally and technologically either simple or complex.

A further illustration of the potential significance of coalitions in human history and genetic change is afforded by Sahlins' (1967) analysis of what he termed the predatory expansion system of the Tiv people of Africa, who, by repeatedly forming coalitions between closely related groups against more distant relatives and groups, have managed to make themselves "the largest pagan tribal grouping in Northern Nigeria," numbering "over 800,000." Sahlins' and the Bohannans' (1953) descriptions of the group behavior of these people is an echo of phrases used by other authors such as Keith (1949), Alexander and Tinkle

(1968), Bigelow (1969), Alexander (1971), and Wilson (1973). Thus: "Success in this intrusive push for 'living-space' depends precisely and directly on ability to mobilize . . . to deploy the concerted pressure of many local groups in the tribal borders. *The Tiv-Nuer segmentary lineage system is a mechanism for large-scale political consolidation. . . . It has the decisive function of unifying 'within' for the purpose of standing 'against' The direction of expansion . . . is governed by tactical considerations; one moves against the bounding segment most distantly related to one's own, thus bringing the massing effect into maximal play*" (Sahlins, 1967, pp. 97, 110).

All of these behaviors by human groups hostile to one another support the hypothesis that much of human evolution has been guided by hostility between and among constantly changing social groups and coalitions of groups and individuals. It is within such a framework, I believe, that our understanding of the evolution of human behavior—by which I mean to include the tendencies and propensities of all modern men—must develop. It is from such beginnings, I believe, that we can most profitably build our efforts to adjust, control, and direct the behaviors of people and nations in directions compatible with the wishes of the greatest number of living humans in each era. In short, our theories of human behavior as well as our theories of animal behavior in general, must be evolutionary theories. And they must be evolutionary in the sense that modern biologists understand the process of natural selection, not in the terms of progress or movement from level to level characteristic of anthropological evolutionism (White, 1949; Sahlins & Service, 1960), not in the social Darwinist sense of natural laws that cannot or should not be violated, or instincts that cannot be thwarted; and not in the poorly focused and inadequate terms of the biology of the first two-thirds of the 20th century.

CONCLUDING REMARKS

That man has evolved his characteristics as a result of selection that never lost its potency at the individual level leads to the argument that civilization, and all of the

notions regarding social interactions that derive from it and from which it is derived, like justice, morality, and ethics, to some large extent comprise specifications of the limits to which the collective members of this or that society will permit individual members to go in the course of reproductive competition. That individual humans tolerate such restrictions must be because it has for millions of years been less profitable reproductively to go it alone. It is important that I do not say an outcome of the admission, tacit or otherwise, that it is less profitable reproductively to go it alone. In terms of evolutionary history, human behavior tends to maximize the bearer's reproduction. Selection has probably worked against the understanding of such selfish motivations becoming a part of human consciousness, or perhaps even being easily acceptable. We can recognize a triple paradox that the only organism capable of at least a feeble analysis of its own attributes must use the very attributes to be analyzed to carry out the analysis, when a central one of those attributes is a rather strong tendency to reject the results of all such analyses!

Consider the argument that group-living intensifies reproductive competition between individuals and requires continual pressure from some outside selective force such as predators to persist. It implies that human society is a network of lies and deception, persisting only because systems of conventions about permissible kinds and extents of lying have arisen. In terms of interpersonal relationships of individual humans there are few exceptions to this rule, and they are independent of the existence of society as such. Only one involves human social behavior. In any purely monogamous relationship between the sexes, the male and female involved share identical selective, i.e., reproductive, goals, hence cannot afford not to be honest with one another. This condition prevails when it is unprofitable for either partner to jeopardize the relationship and when nepotism does not extend outside the nuclear family. Monogamy in humans is of recent origin in most of the few cases in which it is enforced. It also persists in species that do not live in as intensely and

complexly social groups as humans. However, it may be difficult to argue that the potential for cooperativeness between mates was not involved in its appearance and spread in recent human societies. There are, of course, other forces that favor monogamy, i.e., collective power of males forced to be either monogamous or mateless in the polygynous system, pressure exerted by females to monopolize a male's parental behavior, etc. Perhaps there is significance as well in the numbers and unity of strength and purpose possible within groups of men who recognize beforehand that they are bound by societal rules to compete sexually only within limits that in effect give every individual a reasonable opportunity to participate. Socially imposed monogamy, in relatively affluent societies as opposed to ecologically imposed monogamy in marginal habitats, may represent a sort of ultimate example of the effectiveness of coalitions against the relatively few males who could, if it were permitted, succeed at polygyny. The few potentially polygynous males would be opposed as individuals, unlikely to form even a coalition with other potentially polygynous males. Monogamous societies may have spread because rigid limitations make divisive competitive striving a nonproductive enterprise and lead to a maximization of cooperativeness. It is not a triviality that humans so prominently compete in teams, team against team, both at play and at war. Few other animals do so, and perhaps no other species does so in play.

I can conceive of only one possible argument against the notion that society is based on lies. It is an intriguing argument and involves the definition of "lie." Consider the ten commandments: "Thou shalt love thy neighbor as thyself." But this admirable goal is clearly contrary to a tendency to behave in a reproductively selfish manner. "Thou shalt give the impression that thou lovest thy neighbor as thyself" might be closer to the truth. "Thou shalt not covet thy neighbor's wife." But should opportunity arise to impregnate any female without risk, particularly one whose offspring are likely to be tended by another male, differential reproduction will favor tenden-

cies to commit the act. Again, "Thou shalt make the coveting of thy neighbor's wife as inconspicuous as possible, preferably to the point of being quite negligible and unnoticed by thy neighbor or his friends and informants, and at least sufficiently so to convince him that thou wilt not take advantage during his absence (which, however, thou shalt do whenever risk is sufficiently low to make it on the average reproductively advantageous)." One might even add: "Whether thou knowest it or not!"

Consider two monogamous pairs cooperating or living in close proximity for some reason that represents reproductive advantage for both couples. If any resources are limited, any of the four individuals gains by securing for himself or his mate or both a disproportionate share. The profit in such behavior will depend on the likelihood and the significance of the risk to them of breaking up or reducing the effectiveness of the cooperation. When the relationship of individuals of the two sexes is considered, the same problem exists. Either male would gain reproductively by fathering as many of the total number of offspring as possible. Either female would gain, if she does not lose paternal behavior or her offspring in the process, by having her offspring fathered by the more fit of the two males. Any behavior of any of the four individuals short of full exhibition of whatever realization exists regarding such potential gains, and short of the behavior required to realize them, constitutes compromise, and constitutes lying to the extent that the motivation is in fact part of the involved individual's consciousness.

We encounter an intriguing complication. Selection must have kept such realizations out of the consciousness of individuals while simultaneously promoting the kinds of behavior that bring to completion gains such as those described above. Sincerity is easier when one lacks full realization of motivations reprehensible to fellows. Recourse to a higher authority for justification for actions of the sorts I have described above may be a predictable innovation in human society, given the reproductive significance of deception, trickery, and lying. It is not difficult to appear sincere if one is

sufficiently ignorant about his own motives to believe in fact that he is a just, moral, ethical person with mandates from Heaven for whatever particular actions he may feel are necessary or profitable to carry out. For an individual who must carry out all of his actions within a social group of one sort or another, sincerity is an invaluable asset.

The significance of these arguments for the problem of understanding how man goes about interpreting his universe is almost unimaginable. He will not see in himself what he does not wish to see, or what he does not wish his neighbors and fellows to see; and he is reluctant to see in other organisms what he will not see in himself. All of biology, all of science, all of human endeavors have been guided to some large extent by this circumstance.

Man is too complex to be understood by any attempt which fails to come to grips with questions like these, whether the approach is biological, philosophical, metaphysical, or employs any other or any combination of viewpoints and methods. I believe that serious consideration of such questions is one of the directions in which an evolutionary theory of behavior will take us. And I believe that it has become essentially impossible to defend any other theory with even a remotely comparable generality or usefulness.

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(Manuscript received May 16, 1974)