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Human ethology: concepts and implications for the sciences of man

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Abstract: Human ethology is defined as the biology of human behavior. The methods it employs and the questions it poses are elaborations of those generally used in the various fields of biology, but especially adapted to the study of man. Observation and experimentation in the natural and seminatural setting as well as the comparative method derived from morphology play important roles in human ethology, and the exploration of phylogenetic adaptations constitutes one of its focal interests. On the basis of observations on experientially deprived and nondeprived children, comparative primate and animal behavior studies, and cross-cultural investigations, certain universal phylogenetic adaptations (in terms of fixed action patterns, innate releasing mechanisms, releasers, innate motivating mechanisms, and innate learning dispositions) have been found to occur. However, human ethology does not restrict itself to the investigation of phylogenetic adaptations. The question as to how a behavior pattern contributes to survival can be posed with respect to cultural patterns as well. Similar selection pressures have shaped both culturally and phylogenetically evolved patterns. Through cross-cultural studies a number of universal social interaction strategies have been discovered. Some of their apparent variation can be accounted for by the fact that innate and culturally evolved patterns of behavior can often substitute as functional equivalents for one another within a given context. Some social interactions can even become completely verbalized. Nevertheless, underlying structural rules remain the same. The discovery that nonverbal and verbal behaviors can substitute for one another bridges the gap between these seemingly distinct categories of behavior, and opens the way for the study of a grammar of human social behavior encompassing both the verbal and nonverbal.

Keywords: communication; cross-cultural studies; cultural evolution; environment; ethology; evolution; heredity; human ethology; nature/nurture controversy; nonverbal behavior; ritualization; sociobiology; verbal behavior

> Comparative studies based on the quasi-scientific theories of the inheritance of behavior and the predominance of genetic processes as causal in evolution and development of all species, including people – Lorenzian ethology, Wilsonian sociobiology – overlook significant differences among species and reduce quantitiative and qualitative differences in behavior to a unitary causal mechanism which is not sufficient to explain complex behavior.
>
> Tobach, 1976, p. 14

> Far from underestimating the differences which exist between the [above described] behavior patterns of higher animals and those accomplishments of man based upon reason and responsible morality, I assert: No one is more in a position to see the uniqueness of those specific human capacities than he who perceives them against the background of those far more primitive actions and norms of reaction that we still share with the higher animals.
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> Lorenz, 1971, p. 509; translated from the German original

When Darwin (1859) published his revolutionary ideas, many of his contemporaries felt insulted by the mere suggestion that they might have evolved from animal ancestry. Since then, the fact of our phylogenetic history has been accepted, but it is obvious that many people recognize this fact only as far as their morphology and basic physiology are concerned. Whether the concepts of phylogeny, selection, and inheritance are applicable to human behavior, however, is still a matter of considerable controversy.

Holzkamp-Osterkamp (1975), for example, expresses the view that man has withdrawn from the biological laws of selection; they shaped his evolution only until he began to live in a society based upon cultural convention. One also reads the opinion, expressed in many versions, that there exists no such thing as "human nature," man being the rawest of all raw materials, shaped by his environment according to the standards set by culture. Certainly, the *tabula rasa* concept of the British empiricists, which holds that man is born as a blank slate for experience to write upon, is nowadays espoused only by a few, but genetic contributions are still largely conceived as merely providing very general boundary conditions for behavior, such as in determining the bodily structures. Thus, sex is recognized to be genetically determined, but gender roles are attributed to cultural factors. And if, in referring to gender roles, one ventures to suggest that certain aspects of their associated behaviors may be "innate" too, one risks being called sexist (Tobach et al., 1974). Apparently, a basic fear of any sort of "biological determinism" prevails, something to the effect that anything recognized as innate to man must then be accepted as an inevitable fate.

The ethological point of view in particular is often represented in a distorted way in secondary sources. We need only examine Montagu's most recent book (1976, p. 55), in which he writes: "Konrad Lorenz and other ethologists of his persuasion hold that almost all animal behavior – and they include human behavior in this sweeping generalization – is instinctive." Since Lorenz, as well as the present author, has so often emphasized that man is a cultural being by nature, selected for adaptive modifiability of his behavior, Montagu's statement seems odd indeed. In the same book, the ethological concept of instinct is crudely depicted as an explanatory principle of the uncritical ethologist:

> " 'Instinct' undoubtedly constitutes the most popular of such explanations. Spiders spin webs by instinct, cats nurse their young by instinct, beavers build dams by instinct, and so on. Hence, when women nurse their young, and men 'defend their country' by killing other men, they do so by instinct. Are we to suppose that when women make beds and men build dams, such activities too are

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referable to some appropriate instinct? The absurdities of thought that have been committed in the name of 'instinct' constitute an object lesson in the systematics of confusion" (Montagu, 1976, pp. 63 – 64).

Having thus exposed the simplistic ways of ethological thinking and the obsoleteness of the concept of the innate (see the chapter "The Innate and the Acquired or Learned – a False Dichotomy"), Montagu emphasizes man's lack of instincts. Tobach et al. (1974) attack ethologists in a similar vein, accusing them, amongst others, of biological determinism.

It seems timely, therefore, to present our point of view for discussion in this multidisciplinary forum. In particular, I shall examine the concept of the "innate" and its relevance to an understanding of human behavior. A discussion of the comparative approach and the subject of functions and adaptations will introduce our theme. I wish to express the hope that this discussion will serve to bridge the gulf between ethologists and opposing groups of behavioral scientists. We share, after all, the basic objective of attempting to understand why we behave as we do, and even though some of what will be said concerning our approach is still tentative, I hope to demonstrate that even these speculations derive from observations worthy of consideration.

1. What is human ethology?

Human ethology can be defined as the biology of human behavior. Its special interests are distributed along lines largely congruent with its parent discipline, biology, namely morphology, ecology, genetics, phylogenetics, developmental biology, sociobiology, and physiology. The questions posed, and the methods employed in the efforts to answer them, are elaborations of the approach of these parent fields, but specially adapted to the study of man. Human ethology is based upon the theory of selection and inquires, for example, as to what selective pressures have operated to bring an observed structure into being, on the assumption that the structure somehow contributes to the inclusive fitness of its possessors.

Students of animal behavior have developed refined observational techniques, employed primarily in the natural setting. These allow for the discovery of regularities in the flow of events, from which conclusions as to function as well as underlying causal factors can be derived. The studies of Baerends and Drent (1970) exemplify the approach. This method of passive observation in the natural context is the basis for any study in human ethology, which begins with documentation and description and then proceeds to experimental analysis. Of particular importance is the comparative approach, arising from an interest in the phylogenetic aspects of behavior.

The formal application of ethological methods to the study of man began about fifteen years ago. During the last ten years human ethological research has concentrated upon a number of focal points. These can be subsumed under the following headings: nonverbal and verbal communication, aggression, mechanisms of bonding, and aspects of social structure (rank order, incest taboo, gender roles, etc.). The themes listed under these headings overlap, of course. Moreover, the categories are broad. The ethology of aggression encompasses questions as to ontogeny and socialization, phylogeny, functional and physiological matters, territoriality, individual distance, conflict management, war, and so forth (Eibl-Eibesfeldt, 1975a). Names have been given to these subfields; "proxemics," for example, deals with certain aspects of man's distance keeping (Hall, 1966). And research on communication covers no less diverse fields. In terms of their objects and methods, certain focal areas of research could also be subsumed under the general rubric of "child ethology" (Blurton-Jones, 1972; McGrew, 1972). This wide category also impinges upon, amongst others, all four themes listed above.

Although not the sole concern of human ethology, one of its principal questions is whether biological heritage has determined human behavior to any significant degree. We will pursue this question below, and in order to do this, the comparative method, as well as adaptation, function, and some other basic concepts of ethology will be discussed.

Originally, human ethologists tended to issue from the ranks of biology and closely related disciplines (e.g., Tiger, 1969; Morris, 1968, 1977; Eibl-Eibesfeldt, 1966, 1972; Bowlby, 1969; Ainsworth, 1967). But scientists from more distant disciplines are now converging upon this field in increasing numbers, either by their emphasis on observation in the natural setting (Goffman, 1966, 1971; Marsh, Rosser, and Harré, 1978), or by a shared theoretical emphasis on the phylogenetic dimension.

2. The comparative approach

The comparative approach is a basic source of information, but it has been criticized for making too much of "similarities." Yet if we compare the structure or the behavior of animals and man, we do indeed encounter striking similarity. In greeting rituals, for example, weapons are turned away in a conspicuous fashion to indicate peaceful intent. Boobies sky-point with their beaks, the Masai thrusts his spear into the ground, and in our culture we salute state visitors with twenty-one averted guns. Similarities of this kind call for an explanation. They can be accidental, but most of the time they are not, being due rather to similar selective pressures that have shaped behavior during phylogenetic and cultural evolution alike, or else to a common heritage resulting from a shared ancestor.[1] In the latter case, we speak of homologies, in the former of analogies. Some comparisons between human and animal rituals will now be described in order to illustrate this principle.

Human and animal rituals. When a flightless cormorant *(Nannopterum harrisi)* returns to the nest to relieve his mate, he is allowed to stay only if he brings a twig. If he approaches without this present, he will be attacked. The ritual of proffering nesting material has an appeasing function. Analogous culturally evolved rituals of gift-passing are abundant in man.

Patterns of maternal care and infantile appeals are used for bonding in man as well as in birds. Mutual feeding is an example of a common courtship ritual in birds. Female herring gulls beg like nestlings, and thereby block the aggressiveness of the males, which results in their getting fed instead of being attacked. Mouth-to-mouth feeding is widespread as a feature of maternal behavior in man; it is also found to occur as "kiss-feeding," expressing affection (Figures 1 –3). Finally, the same movement patterns are often performed, without passing food, as a tender act, usually described as a "kiss" (Eibl-Eibesfeldt, 1972).

These similarities again are far from accidental. The patterns serve a similar function in birds as well as in man, and in both they are derived from parental behavior. Nonetheless, they cannot be traced to a common heritage. Parental behavior evolved independently in birds and mammals, and so did the rituals derived from them. The patterns must therefore be classified as analogies. If we turn, however, to the great apes, we find that kiss-feeding is part of the maternal behavior of chimpanzees, orangutans, and gorillas, and that chimpanzees kiss as an expression of friendly intent during greeting. We may with much greater confidence infer from these closely-related cases that kiss-feeding is homologous in the great apes and man (Rothmann and Teuber, 1915; Bilz, 1944; Lawick-Goodall, 1975; Eibl-Eibesfeldt, 1975b).

Patterns of aggressive behavior have become independently ritualized along similar lines in animals and man, developing into tournamentlike patterns of combat as well as occasionally into displays serving the function of bonding during greeting encounters. There even exist analogies between culturally evolved rituals and phylogenetically evolved patterns: indeed the processes of cultural and phylogenetic ritualization often follow a similar course, since many of the selection pressures and preadaptive starting points are, in principle, the same in both cases.

Signals – and ritualization concerns the evolution of signals – must

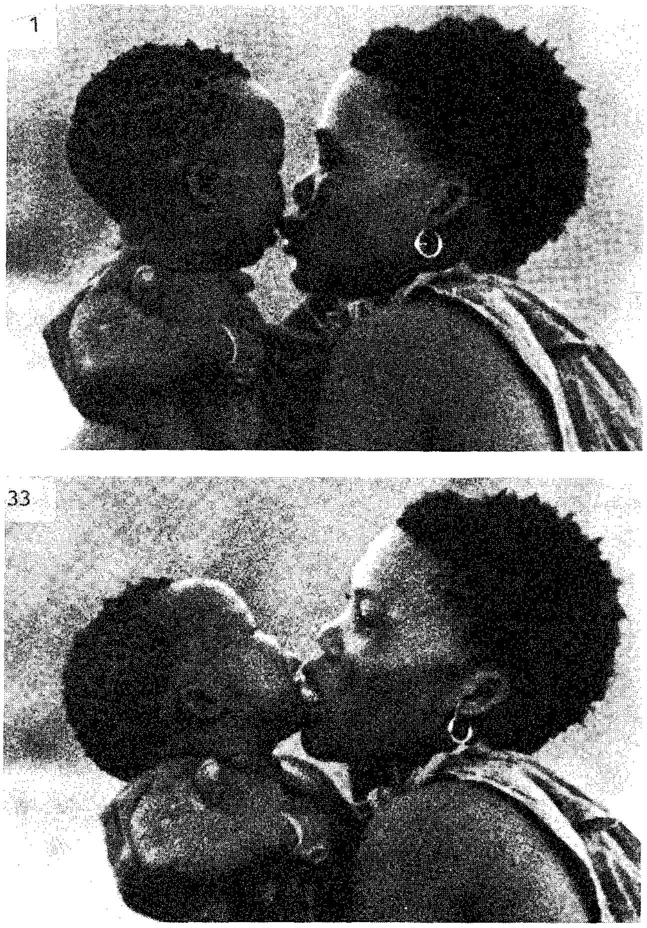

Figure 1. Kiss-feeding as a sign of affection. A !Ko bush girl feeding her little half-sister. At this age, !Ko babies are, in fact, not fed other than in this symbolic way. From a 16-mm film by the author (50 frames/second; the frame number appears on each photograph).

be conspicuous and easily recognizable, and they must unmistakably convey their meaning to their specific targets. The changes that movement patterns undergo during cultural as well as phylogenetic ritualization are therefore the same in principle. Movement patterns tend to become simplified and accentuated during the course of their evolution into signals, with their performance emphasized by rhythmic repetition. The courtship ritual "Tanim Hed," which we have filmed in New Guinea (Eibl-Eibesfeldt, 1974), provides a good example. During the courtship dance couples kneel side by side. Touching foreheads, they perform two sideward swaying movements with the head, which leads to nose-rubbing. This highly stereotyped sequence of movements is followed by two deep bows and then a return to synchronized head-turning. The entire ritual plays a role in mate selection and it is assumed that partners who easily achieve synchronization of their movements will find each other attractive (Pitcairn and Schleidt, 1976).

Homology versus analogy. It is often suggested that analogies can contribute little toward the understanding of human behavior, that only homologies are of interest, and that consequently one should concentrate predominantly upon the comparative study of primates. From this viewpoint, studies of greylag geese and cichlid fish could hardly contribute very much to our knowledge of ourselves.[2] I hope that the above examples succeed in suggesting that such restrictiveness may not be fully justified. It just depends on what one wants to know. Certainly the comparative ethology of primates has contributed enormously to the understanding of human nature. Indeed, the results of primate sociology make it appear probable that many of the universal features of human behavior (ranking, territoriality, incest avoidance) are rooted in our primate heritage. But if one wished to learn the laws, independent of phylogenetic relationship, underlying the construction of a ritual, one might be well advised to look at as many different forms of the ritual as possible: to proceed like a functional morphologist, who compares the wing of an insect with that of a bird, a bat, and even of an airplane. The functional laws governing the construction are in all cases the same, and can be derived from the study of analogy.

In a similar fashion one may ask under what ecological conditions a particular social structure evolves in different species. What are the selection pressures that give rise to ordering in terms of rank in various animal groups? What are the functional laws that underly monogamy, incest avoidance, or other features of social behavior? The study of analogies in fact reveals laws of much more general applicability than can be derived from the study of homologies (Wickler, 1967a). Thus, if we discover that ranking in groups as diverse as fish, reptiles, mammals, birds, and even insects obeys the same basic rules, the hypothesis that similar rules guide the analogous phenomenon in man is certainly not farfetched. Lorenz emphasized this point very clearly:

> "If I were the first scientist to see a dead octopus and, on dissecting it, discovered an eye built like ours, with a cornea, a lens, an iris, focusing muscles and a retina, I would be justified in assuming that this was a visual organ and in calling it an eye without further ado, even if I had no other proof of its function. 'Eye' denotes a functional concept; cephalopods and vertebrates have no common ancestors with eyes of this type: their eyes are functionally analogous, not phylogenetically homologous. An even better case can be made for the application of our functional concept of ritualization to both the biological and the cultural spheres, because we need not rely on detailed formal analogy alone. We know from observation and ample experimental verification that rituals, whether phylogetically or culturally evolved, do in fact perform the same functions of communication – those of canalizing aggression and of effecting the cohesion of pairs or groups" (Lorenz, 1966).

The value of this type of approach is clearly documented in Wilson's *Sociobiology* (1975). The study of analogies allows us to develop working hypotheses, which, of course, have to be tested as to their relevance to man by a detailed study of man.

3. Adaptation

Adaptation is another controversial issue. By definition, any structure that contributes to survival and fitness as reflected in reproductive success may be termed an adaptation.[3] Certainly, contribution to fitness as measured by reproductive success cannot always be derived from immediate observation, but rather by careful experimental analysis, as exemplified by the work of Tinbergen et al. (1962) on eggshell removal in the blackheaded gull. What can be inferred from observation, however, is the immediate beneficial effect of a behavior to its performer, which in turn permits a fairly good guess as to adaptive function in most cases.

We must also be aware that not every observed pattern fulfills an adaptive function. Sometimes, for example, structures lose their original adaptive value in a changed environment (including a changed social environment). They may be dragged along as historic burdens (like the appendix) and, if disadvantageous, they may be removed by subsequent selection. Thus, the Galapagos dove shows distraction displays, even though predators responsive to these behavior patterns fail to occur on the islands. The redheaded finch, a nest-parasite, still performs nonfunctional nestbuilding movements in a random fashion when sitting on a nest. And owing to his fear of strangers (see below), man is predisposed to live in individualized groups. Therefore, modern life in anonymous groups subjects him to a certain amount of stress. In this context fear of strangers is maladaptive.

Adaptations reflect particular features of the environment. The


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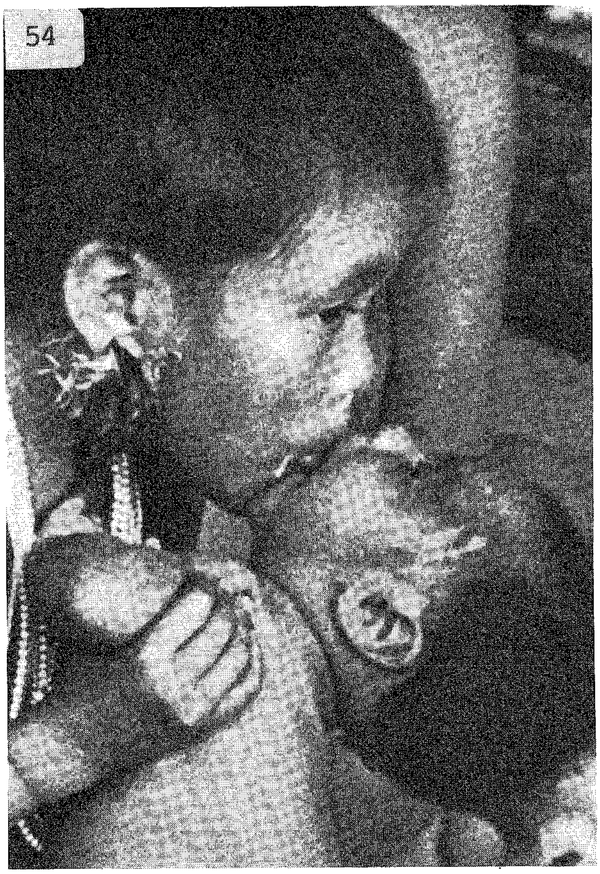
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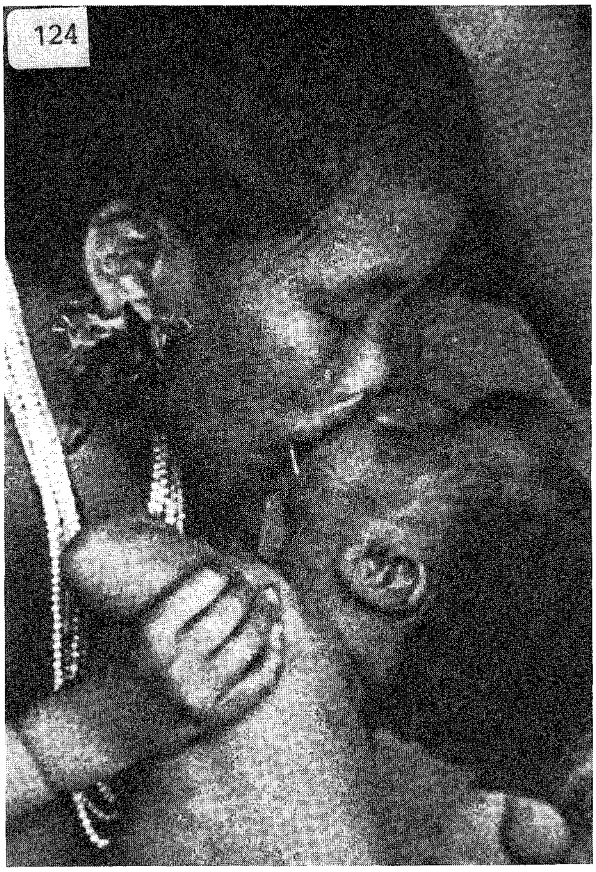
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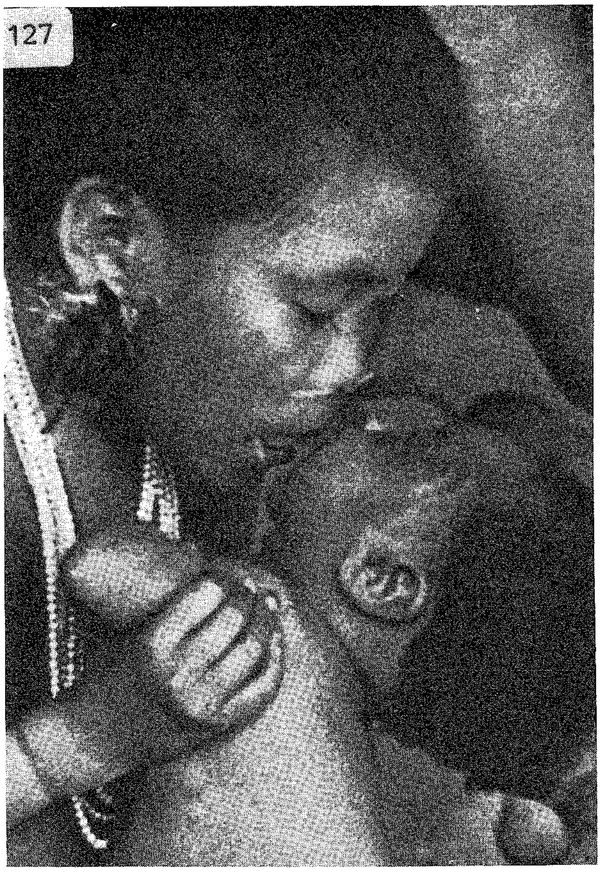
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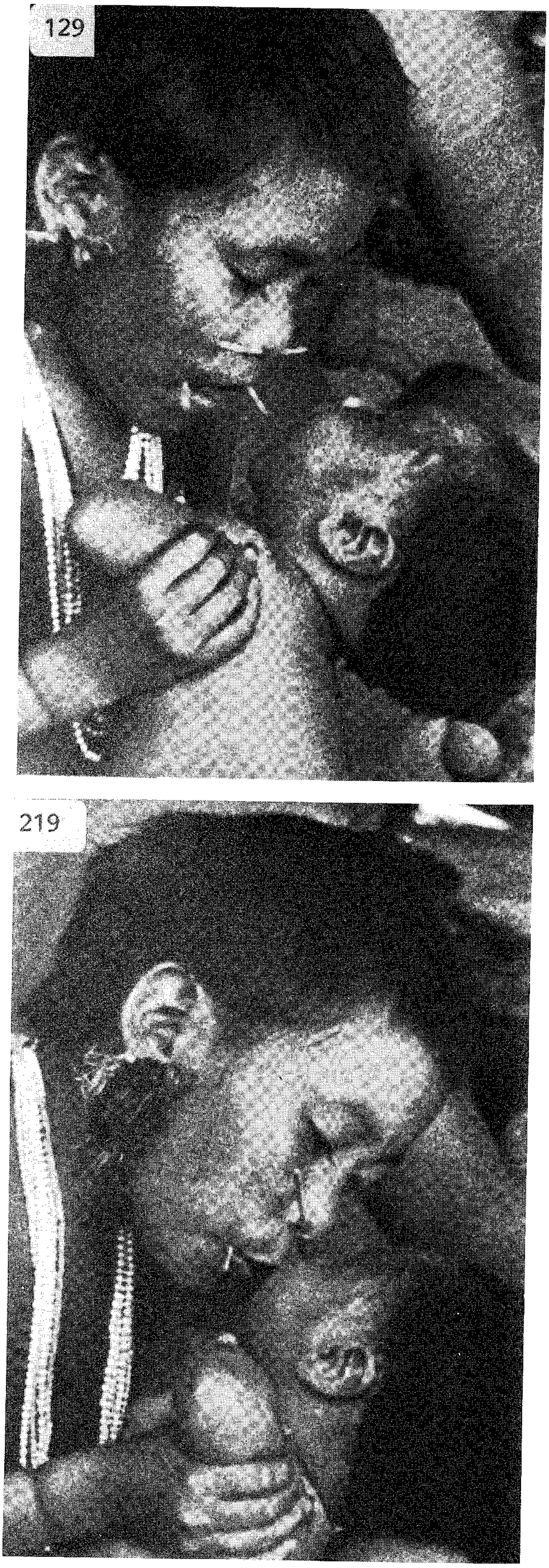

Figure 2. Kiss-feeding as a sign of affection. A Yanomami girl kiss-feeding her baby sister with saliva. From a 16-mm film by the author (25 frames/second).

hoof of the horse, as Lorenz (1965) once said, reflects the steppe, that is to say, it developed as a locomotor organ to fit this special type of ground. Every adaptation logically presupposes that by a prior process of interaction between the organism and its environment, information concerning certain environmental features was somehow acquired by the organism. This can either take place during phylogeny by the well-known processes of mutation, recombination and selection, or by cultural and individual adaptation. In the former case, the acquired information is stored in the genome of the species and decoded during ontogeny.

Experiential deprivation experiments. Whether an organism's behavioral adaptation is the result of phylogenetic, cultural, or individual adaptation can be tested by means of experiential deprivation experiments. For example, if birds of the same species sing an identical song, chance concurrence can be excluded and one can inquire as to what common source of information they may have tapped. If individuals of such a species are raised in complete social isolation in soundproof chambers and nonetheless produce their species-specific song, then we are forced to conclude that the information concerning the specific patterning must have been encoded in the genome (Sauer, 1954; Konishi, 1964, 1965a,b). The song pattern is then said to be phylogenetically adapted or "innate." The latter term is a shorthand description and means more precisely that the specific afferent, efferent, and interneuronal network responsible for this motor-coordination grows in a process of self-differentiation according to a developmental recipe ("blueprint") encoded in the genome. Of course, this is a process of individual development, and particular environmental stimuli may be influential at different developmental stages. The all-important point, however, is that in this special case no patterned information concerning the adaptation needs to be available to the growing organism for the adaptive pattern to occur.

I want to emphasize that we are fully aware that there is nothing like a song or any other behavior *per se* contained in the zygote: this disclaimer is necessary because certain writers have implied that ethologists believe in such simplistic preformationism. Eisenberg (1971), for example, clearly expressed this opinion:

> "I would argue that there is no behavior, certainly nothing like intelligence, or mating behavior or display patterns . . . in the zygote. Such notions are utterly absurd carry-overs from preformationism. What the DNA specifies are chemical constituents. These constituent enzymes and substrates interact with one another and with the internal and external environment of the developing organism to produce successive stages of ever greater complexity, with the sequential emergence of new properties at each succeeding stage of development. It is the nature of interactions that must concern us, not so that we can disregard the genetic code, but so that we can understand it and its environmental dependence" (p. 522).

Ethologists certainly agree, and so one wonders who the intended target of this passage might be! Certainly biologists are aware that developmental processes involve interactions between the organism and its internal and external environment. Spemann's classic experiments (Spemann, 1938) as well as those of Sperry (1945a,b, 1965, 1971), have provided basic insight into these processes of self-differentiation.

Sperry demonstrated that growing neuronal fibers selectively seek their receptor and effector organs and thus prefunctionally establish proper connection. If the eye of a newt larva is rotated 180 degrees, inverted vision results. With further cutting and scrambling of the optic fibers, the subsequent neural regeneration does not restore normal vision, but continues to produce inverted vision so long as the eye remains in the rotated position. If a piece of skin from the back of a frog embryo is transplanted to the belly region, the frog will scratch its back when tickled on this graft. This indicates that the graft is innervated by the same fibers that would have innervated it in its original location.

"Each fiber in the brain pathways has its own preferential affinity

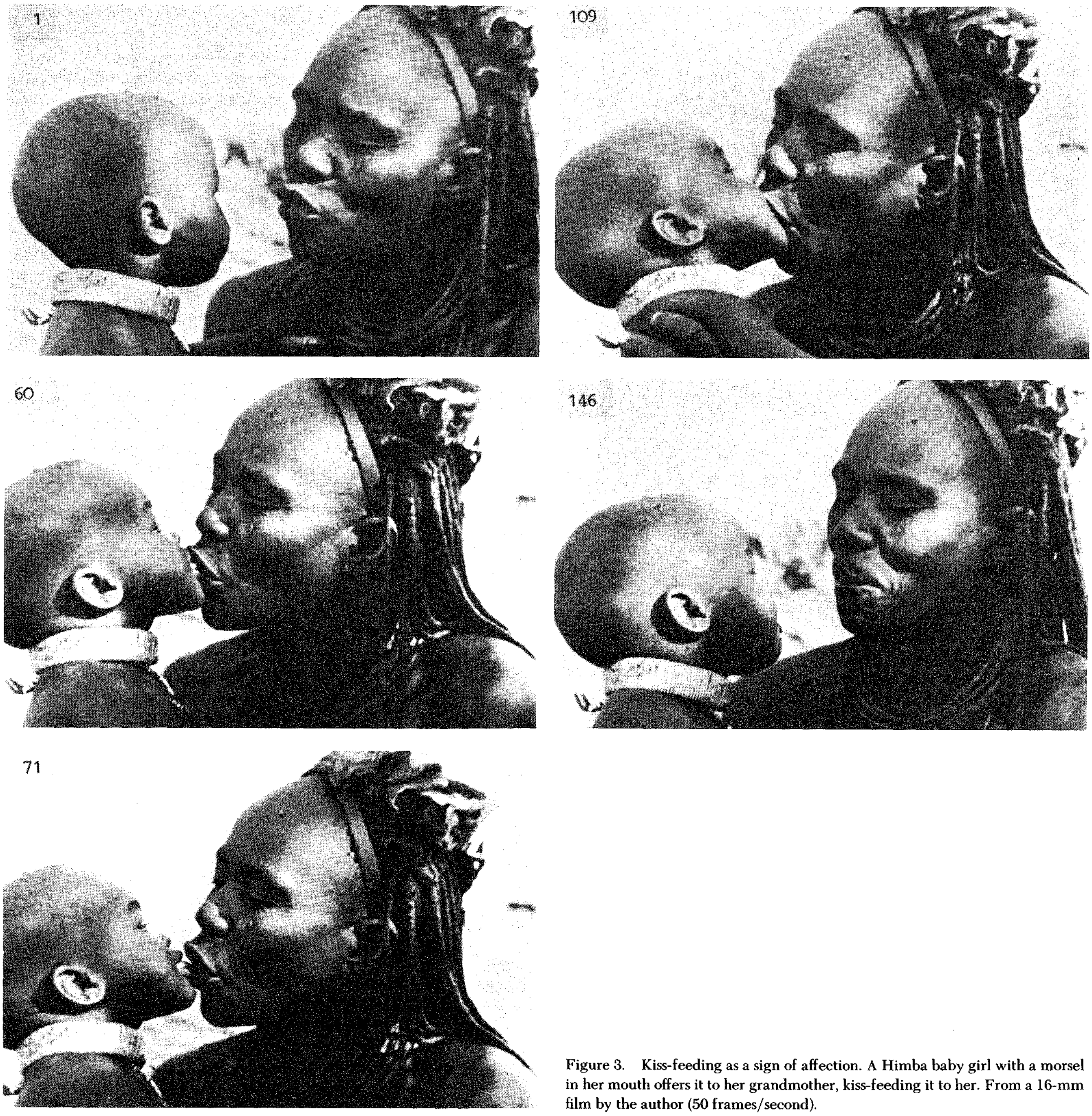

Figure 3. Kiss-feeding as a sign of affection. A Himba baby girl with a morsel in her mouth offers it to her grandmother, kiss-feeding it to her. From a 16-mm film by the author (50 frames/second).

> for particular prescribed trails in the differentiating surround. Both pushed and pulled along these trails, the probing fiber tip eventually locates and connects with certain other neurons, often far distant, that have the appropriate molecular labels. The potential pathways and terminal connection zones have their own individual biochemical constitution by which each is recognized and distinguished from all others in the same half of the brain and cord. Indications are that right and left halves are chemical mirror maps. . . . In general outline at least, one could now see how it would be entirely possible for behavioral nerve circuits of extreme intricacy and precision to be inherited and organized prefunctionally solely by the mechanism of embryonic growth and differentiation. . . .
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> "As yet the meaning and impact of these changes has only begun to permeate into areas outside biology and ethology. In the more human areas of behavioral science like clinical psychology, psychiatry, anthropology, education, and the social sciences generally, the prevailing conceptual approach on this subject remains today essentially unchanged or very little changed from where it stood thirty years ago" (Sperry, 1971, pp. 31 – 32).

These and other experiments (see Grobstein and Chow, 1975, for a discussion of the more recent findings) have in fact demonstrated that modifiability by external influences is often quite limited, particularly as far as the central nervous system is concerned. Ikeda and Kaplan (1970) have gone on to show the existence of genetically programmed behavior by providing evidence that the patterned neural activity underlying particular movement of a *Drosophila* mutant is coded by a single gene. For further evidence, see Bentley (1971) and Bentley and Hoy (1972).

Gene-environment interaction. In this case of bird song mentioned above, one may still argue that at a lower level of integration, learning, say, breathing coordination, may have contributed to developing prerequisites for singing. This could well be the case. However, if the bird is able to perform its specific song even when reared in complete social isolation, this proves that at a higher level of integration the information underlying the specific patterning was indeed encoded in the genome. The environment simply did not provide that specific information. Numerous agents like oxygen, temperature, nutrition, and a variety of sensory stimuli have exerted their influence on the growing bird, but there is no indication as to how these could have provided the patterned information characteristic of its song.

The often repeated argument that a distinction between innate and acquired components of behavior cannot be made since both inextricably and diffusely intermingle at every stage of development can no longer be upheld in the face of these facts. Deprivation experiments clearly reveal the source of the information underlying such an adaptation, although questions must of course be addressed to the appropriate level of integration and only to the specific adaptations under investigation (Eibl-Eibesfeldt, 1975b; Lorenz, 1965). Then, if the information underlying the behavioral pattern in question proves to be phylogenetically acquired, we can use the expression "phylogenetic adaptation," with the terms "innate" or "instinctive" as synonyms.

I wish to emphasize that the whole nature/nurture issue should not be considered as a matter of either/or, nor can the contribution of each be measured quantitatively, in terms of percentages. It is a matter of *how* both contribute to the development of certain characteristics, "nature" providing a range of modifiability. What is inherited is a "prospective potential." Ethologists seek the source of the information underlying an adaptation, a decisive step in the analysis of behavioral development.

4. Phylogenetic adaptations in animal behavior

Fixed action patterns, innate releasing mechanisms, and releasers. Ethological studies of the past three decades have demonstrated that phylogenetic adaptations determine behavior in various ways. Animals are provided with functional motor patterns at birth or at hatching: each newly hatched duckling teaches us this fact. The duckling can walk, swim, or preen its feathers; and it makes no difference whether it is brooded by a hen or a duck: its behavior will be ducklike. Some of its specific patterns, however, are not present at birth. Stereotyped courtship patterns, such as the grunt-whistle, head- and tail-bobbing, and the like, mature during ontogeny (Lorenz, 1935). As soon as a newly hatched chaffinch emerges from its egg, it shows the very characteristic food-begging response of gaping. Other behavioral patterns mature during ontogeny without need of further patterned information concerning their specific adaptive function. A mallard develops all the highly specific courtship postures of its species even if reared in complete social isolation. These motor patterns are called fixed action patterns or *Erbkoordinationen*.[4] Animals are thus equipped with innate motor patterns. In addition, they are *capable of responding adaptively to certain stimuli upon first encounter*, manifesting a kind of *a priori* "knowledge."

A frog that has just undergone metamorphosis and climbs out of the water does not need to learn how to catch flies with a flick of the tongue. Until then it has been a tadpole, scraping algae from the substrate by means of specialized scraping jaws. Yet all at once it knows how to catch small prey with a steady tongue-flick movement. Experiments with dummies have shown that the newly metamorphosed frog will snap at anything that moves, including small leaves and pebbles (Eibl-Eibesfeldt, 1951), but it quickly learns to avoid noxious prey. The originally unselective response serves its purpose, since normally the only moving objects in the frog's environment are prey. The innate ability to respond to simple stimuli – in this case moving objects – presupposes a filtering mechanism which "selects" certain specific stimuli, releasing the relevant behavioral sequences only in response to them. This has been termed the "innate releasing mechanism" – IRM – (Tinbergen, 1951) or "innate template" – *angeborenes Schema* – (Lorenz, 1935). The neuroethological investigations of Ewert (1974) have illuminated the processes by which the visual stimuli of prey and predator are analyzed within the central nervous system of the toad. Numerous social responses in animals are initiated by such innate releasing mechanisms, for example, courtship behavior, fighting, following responses, and submission (Tinbergen, 1955; Eibl-Eibesfeldt, 1975b). In these cases, in which communication is advantageous to both participants in an interaction, mutual adaptation between the sender and the receiver of a signal takes place. The sender develops signaling devices like conspicuous colored spots, feathers, expressive movements, pheromones, vocalizations, and so on. These signals are called releasers and evolve by a process called ritualization (Huxley, 1923). They are matched to IRMs in the receiver.

During its reproductive period the male stickleback establishes a territory and develops a red belly; it drives rivals away, but courts females sporting a silver swollen belly. If the male is exposed to an exact model of a stickleback with neither a red nor a swollen belly, it will show no interest; but a sausage-shaped wax dummy with a red underside is attacked immediately, while a silver swollen-bellied one is courted. This behavior is displayed even by male sticklebacks raised in isolation (Cullen, 1960; Tinbergen, 1951).

Behavioral sequences can often be elicited by several different key stimuli of this sort, each being individually effective. Male sticklebacks threaten each other at the border of their territories by adopting a head-down, threatening posture. If a horizontally positioned dummy without a red belly is presented to a male, no attack is released, but when the same dummy is presented in a vertical position, attack results. If the two attack-releasing signals occur in one presentation, they combine additively, eliciting a stronger response. This law of heterogenous summation was discovered by Seitz (1940) and has since been confirmed in a number of studies.

The same releasing structure can act differentially on the two sexes. The red belly of the male stickleback releases aggression only in other males; females exhibit attraction toward and preference for red-bellied males. An interesting variant is exhibited by a subspecies of the three-spined stickleback living in the Cephalis river of western North America, where it is preyed upon by the fish *Novumbra hubbsi*. In this case, predation counteracts selection for red coloration and all males in the area are black. Females in the area, however, are still attracted toward red-bellied males, which in experiments are preferred by a ratio of 5:1. The receptor mechanism in the female underlying responsiveness to the original stimulus has apparently failed to adapt to the change that took place some 8,000 years ago, but has instead remained conservative (McPhail, 1969). Some behavioral traits in man can be similarly interpreted (see Eibl-Eibesfeldt, 1975b).

The strength of a response to a stimulus is partially a function of the releasing quality of the stimulus. From an evolutionary point of view, it is interesting that releasing stimuli are to a certain extent susceptible to exaggeration. It is possible to create an experimental situation in which an exaggerated stimulus leads to a grotesque response. Such is the case when an oyster-catcher prefers an egg four times the length of its own, although it cannot even settle down on it (Koehler and Zagarus, 1937).

Both external and internal factors determine the magnitude of a response. Baerends et al. (1955) have shown that in *Lebistes* both the strength of the fish's motivation and the releasing quality of external stimuli determine the resultant observable behavior.

Innate releasing mechanisms operate in monkeys as well. Sackett (1966) reared rhesus monkeys from birth under conditions of social deprivation: they could neither look out of their cages nor see their own mirror images. They were then shown slides representing conspecific monkeys, landscapes, geometric shapes, and so on. After a given slide had been presented once, the monkeys could voluntarily view it again by pressing a lever. With frequency of voluntary projection as an indicator of picture preference, it turned out that the monkeys enjoyed looking at pictures of conspecifics. Projection frequency for these slides increased rapidly; upon seeing them the young animals emitted contact calls, approached, and even tried to play with the image. Slides that did not depict monkeys evoked only brief periods of interest and the projection rate remained low.

Among the monkey pictures there was one which represented a threatening adult, and even this remained popular for a while. At the age of two and a half months, however, the monkeys' behavior changed. Suddenly the "threat" picture released withdrawal, self-clasping, and fear vocalizations, and projection rate dropped rapidly. As the animals had been deprived of any social experience until that time, this change must have resulted from maturation of an IRM for recognition of expressive patterns. It is certainly plausible that this should occur at two and a half months, for at that time juveniles normally make contact with others in the group and recognition of the threat expression assumes paramount importance.

Releasers are not only found in the visual modality. The varieties of frog calls, cricket chirps, and bird songs are also characteristics subserving the recognition of conspecifics. Distress calls are the only signal to a mother hen indicating that her young are in danger. If a glass bell is placed over a chick so that its mother can see but not hear it, all its struggling will fail to restrain the hen from departing with the rest of her brood. In contrast, a mother hen will respond quickly upon hearing one of her chicks call from the other side of a wooden fence. She runs to the barrier and stays there calling, although she cannot see the chick.

A female turkey will provide maternal care to any object that vocalizes like one of her brood. A stuffed polecat, which in no way resembles a turkey, elicits brooding behavior when fitted with a speaker emitting the appropriate calls. Such vocalizations are the only signals releasing brooding behavior; deaf female turkeys will kill their own young because they cannot hear their calls (Schleidt et al., 1960).

Drives, neurogenic motivation, and central motor generators. Animals are known to be motivated by built-in physiological machinery giving rise to "drives." This term is to be understood as generally descriptive of the fact that animals do not always wait passively for stimuli to impinge upon them before emitting a response: they actively seek certain stimuli. There is no unitary drive mechanism, however. A diversity of physiological systems must act to incite an animal to seek (through so-called *appetitive behavior*) stimulus situations that allow specific motor patterns to be performed (Lehrman, 1953; Hinde, 1966; von Holst, 1935). Sexual behavior, hunting, feeding, drinking, and, at least in some species, aggressive behavior, are in part based upon such internal motivating mechanisms.

Of particular interest is the neurogenic motivation, first described by von Holst (1935) as underlying the swimming movement of eels and other fishes. He found that completely deafferentiated spinal eels (i.e., with spinal transections cutting off sensory input) swam with perfect coordination and without any pause until death occurred, demonstrating that groups of motoneurons could spontaneously generate impulses that were centrally integrated sufficiently to produce coordinated muscle activity.

Neurogenic spontaneity and central coordination have since been demonstrated to occur for a number of other motor patterns. Lorenz, on learning about von Holst's findings, elaborated on the hypothesis that all innate motor patterns are more or less driven by spontaneous groups of neurons, and showed that the latter's constant discharge in motor action is blocked by inhibitory mechanisms. A long-lasting blockage without release causes action-specific energy to be dammed up, releasing appetitive behavior, which in turn causes the animal to search for the adequate stimulus stiuation in order to perform the action. During this phase the animal is so eager to perform that he responds to stimuli that would not normally release the action. Some hints as to the physiology of such storage are suggested by neuropharmacology: neurotransmitters stored in submicroscopic vesicles seem to play an important role in spontaneous neuronal acitivity.

Numerous studies on vertebrates as well as invertebrates have demonstrated the existence of central motor activity generators, and the notion of neurogenic motivation is thus well supported by neurophysiological evidence (Roeder, 1955; Bullock, 1961; Bullock and Horridge, 1965; Pearson, 1972; Elsner and Huber, 1973: Fentress, 1976).

Imprinting, early learning dispositions, and the preprogramming of behavior. Finally, learning is determined by phylogenetic adaptations such that animals learn what contributes to their survival and adaptively change their behavior through experience. For instance, it has been found that some animals learn during early sensitive periods to perform specific responses to certain objects, and once these responses are conditioned to them, the connection seems to be resistant to behavioral extinction, in some cases to the extent of irreversibility. If male zebra finches are raised for the first three months of their lives by society finch foster parents, they will at sexual maturity prefer female society finches as mates. This preference will show up at maturity even if the finches are returned to their conspecifics after the first three months, and even after being mated to females of their own kind: if given a choice after successfully mating and raising young of its own species, the finch will prefer the foster-parent species to its own. This phenomenon has been called imprinting (Lorenz, 1935; Hess, 1973; Immelmann, 1966).

A further learning disposition has manifested itself during these foster-parenting experiments: zebra finches exposed to the song of their foster parents for the first thirty-five days of their lives, at sexual maturity sang like their foster parents, even if after exposed exclusively to the song of their own species. They evidently memorize the song during a sensitive period and this has priority over any later experience.

"Learning disposition," like "drive," is a descriptive term and does not imply a unitary mechanism. The study of bird song, for example, has clearly demonstrated that identical outcomes – in this case that a bird learns the song of a conspecific – can be achieved in different ways (Konishi, 1964, 1965a,b; Marler, 1959; Thorpe, 1961); Chaffinches, for example, know what they have to imitate. From a variety of tapes presented to them they pick the preferred species song for imitation. By means of an innate schema – Konishi coined the term "template" – they know which is the right song to imitate. Male swamp sparrows learn their songs and fail to learn those of the song sparrow from the same region. Marler (1978) spliced syllables from tape recordings of both species into an array of swamp-sparrow-like and song-sparrow-like temporal patterns. Swamp sparrows learned only those songs composed of conspecific syllables, irrespective of whether the temporal pattern was swamp-sparrow-like or song-sparrow-like. This was also found to occur in birds reared in total isolation from adult conspecific sounds. We are therefore forced to assume that the birds are phylogenetically tuned to recognize their species-specific syllables and that they show an innate preference for imitating them.

In considering our own phylogenetic origins, would it not be reasonable to ask whether human behavior might be preprogrammed in similar ways? The mere suggestion, however, that man's behavior, and in particular his social conduct, might be in part preprogrammed by phylogenetic adaptations has evoked polemical replies from environmentalists. These have accused biologists of "biological determinism," of tending to support authoritarian, conservative principles, and thereby justifying the status quo and fostering fatalistic attitudes on the grounds that nothing can be done about innate traits. This, even though ethologists have repeatedly emphasized that man is able culturally to control all his behavior, including its innate components: that man has to be educated. Before we discuss the consequences of a strict environmentalism as opposed to the biologist's approach, let us examine the evidence for our hypothesis that human behavior is in part preprogrammed.

5. Phylogenetic adaptations as determinants of human behavior

Man is certainly programmed to act in predictable ways, and much of his behavioral repertoire is clearly acquired during ontogeny. This remains undisputed. Less clear, however, is the magnitude and significance of the genetic contribution. Is human behavior to a certain extent preprogrammed by phylogenetic adaptations? Montagu (1968, p. 11) has written:

> "There is, in fact, not the slightest evidence or ground for assuming that the alleged 'phylogenetically adapted instinctive' behavior of other animals is in any way relevant to the discussion of the motive forces of human behavior. The fact is that, with the exception of the instinctoid reactions in infants to sudden withdrawals of support and to sudden loud noises, human behavior is entirely instinctless."

And he has not changed position since. In answering the question: Why should instincts not exist in humans?, he wrote (1976, p. 77):

> "For the best of all reasons: because they would be adaptively utterly useless to a creature that responds to the challenges of the environment by the use of intelligence and learning. Instinct may serve a useful purpose in other creatures, creatures that still live largely in a biological universe, but in the case of humanity, which has evolved as such in a largely human made environment, instinctive behavior not designed to meet the requirements of the human environment would have been thoroughly maladaptive, and would quickly have led to extinction of a population constitutionally so ill endowed. . . . If human beings ever had any remnants of instincts to begin with, they would have lost them."

Similar statements are not uncommon. I intend to show that they are basically incorrect, and that what is innate to man is not a negligible quantity but of fundamental importance, in particular with respect to social behavior.

Evidence is derived from four main sources: the study of babies and children; the study of the congenitally deaf and blind, and other experientially deprived individuals; cross-cultural investigations; and comparative studies of primates. It can be shown that a variety of motor patterns and unconditioned responses to certain stimuli determine not only certain innate motivating mechanisms but also many of man's basic social interaction strategies. Furthermore, there are strong indications that many complex cultural rituals are in fact elaborations of phylogenetically evolved interaction strategies.

The behavior of babies and children.

a. Motor and perceptual skills. The neonate already exhibits a number of functional motor patterns. It can suck and search for the breast with rhythmic head-turning movements; it has a highly differentiated repertoire of vocal utterances; it can smile, hold itself to objects by a grasping reflex, and so on. Of the five non-crying signals that Morath (1977) reports, one is produced during sleep and acts as a contact call. If a baby fails to emit this sound, mothers wake up and check, without being able to say why. Other sounds are emitted during drinking, signaling either comfort or discomfort. Sound spectrograms reveal similarities with nonhuman infant primate vocalizations. Babies are also capable of responding to stimuli in an adaptive way upon first encounter, prior to any particular relevant experience.

When human infants from two to eleven weeks old are restrained in chairs and exposed to symmetrical expanding silhouettes, they respond as if objects were approaching and about to collide with them. They avert their heads, lift their hands in self-protection, and exhibit higher pulse rates. They react similarly to large objects actually moving toward them. On the other hand, if the silhouettes are expanded asymmetrically, as if moving past, no such reactions on the part of the infants are observed (Ball and Tronick, 1971). Bower (1971, p. 32) comments as follows:

> "The precocity of this expectation is quite surprising from the traditional point of view. Indeed, it seems to me, that these findings are fatal to traditional theories of human development. In our culture it is unlikely that an infant less than two weeks old has been hit in the face by an approaching object, so that none of the infants in the study could have learned to fear an approaching object and expect it to have tactile qualities. We can only conclude that in man there is a primitive unity of sense, with visual variables specifying tactile consequences, and this primitive unity is built into the structure of the human nervous system."

At two months of age, infants are capable of recognizing form invariants under various transformations. It has been possible to train infants to manipulate with their heads electrical switches attached to a head rest; the reward was the appearance of a smiling person. The training signal was a cube measuring 30 cm at the edges presented to the subject at a distance of one meter. Infants rarely responded to a cube measuring 90 cm at the edges and presented at a distance of three meters, although the retinal image would be of the same size as that projected by the 30 cm cube one meter away (Bower, 1966).

Children also have an innate ability to integrate visual and tactile information. We know that an object that disappears behind a screen is still there. According to classical developmental theory, a child should acquire this constancy from experience in reaching behind the screen. Bower (1971) has measured the startle responses (rise in pulse rate) of infants being tested with various optical illusions. He projected apparent objects onto a screen, whereupon the infant would attempt to reach out for them. Failure to grasp the "objects" induced surprise, as measured by elevated pulse rate. In contrast, no change in pulse rate was recorded when the infant was allowed to actually grasp something. Thus an infant expects to be able to touch an object it sees. And since at the age of two weeks infants already respond to this experimental condition in the manner described, one can conclude that there is an innate expectation of tactile consequences following visual information.

A particular preadaptation to language learning is the phenomenon of categorical perception. If we present a continuum of syllables with all physical gradations from "ba" to "pa," for example, subjects do not perceive a continuum but hear either "ba" or "pa" in each case. The abrupt change in the perception from "ba" to "pa" occurs at approximately the same physical location in the continuum in all cultures. Categorical perception has also been shown to occur in the one-month-old baby, which suggests that it is an innate characteristic. IRMs seem tuned to syllables in a fashion similar to that found in the swamp sparrow and discussed above (Cutting and Rosner, 1974; Pastore, 1976; Liberman and Pisoni, 1977).

These and other auditory and visual experiments (see Bornstein, 1978) demonstrate the existence of specific innate information processing mechanisms in humans and are hence of considerable theoretical importance. They substantiate the viewpoint of Lorenz, who asserts that innate releasing mechanisms form the basis of many of our thought and attitude patterns. (For further information, see Bower, 1977.)

b. Imitative capacities of the baby. Meltzoff and Moore (1977) discovered that infants between twelve and twenty-one days of age can imitate facial movement patterns such as mouth opening, tongue protrusion, and lip protrusion, as well as some finger movements. They argue convincingly that learning was not involved and hypothesize that the imitative performance is accomplished through an active matching process mediated by an abstract representational system, which comes close to the assumption of an innate schema or template by which visual input and motor responses are matched. The authors seem to be unaware that this is the original concept of the innate releasing mechanisms. The hypothesis that early imitation might be based on an innate releasing mechanism is in fact discarded by the authors, since they feel that the motor patterns observed lack stereotypy in the baby. This, and the fact that four different gestures are imitated, renders the approach in their opinion unwieldy. But this argument is not convincing. We know that "fixed" action patterns show variability, in particular during their ontogenetic development. Even a simple smile can occur in a variety of intensities, and variability increases when other motor patterns are superimposed. Nonetheless, our detectors are tuned to recognize smiles and many other expressive patterns. Should it be found, however, that babies were able to imitate a great variety of observed motor patterns – and in a recent letter to the author Meltzoff indicates this to be the case – then we would be confronted with an interesting case of a phylogenetic adaptation tuned to recognize and

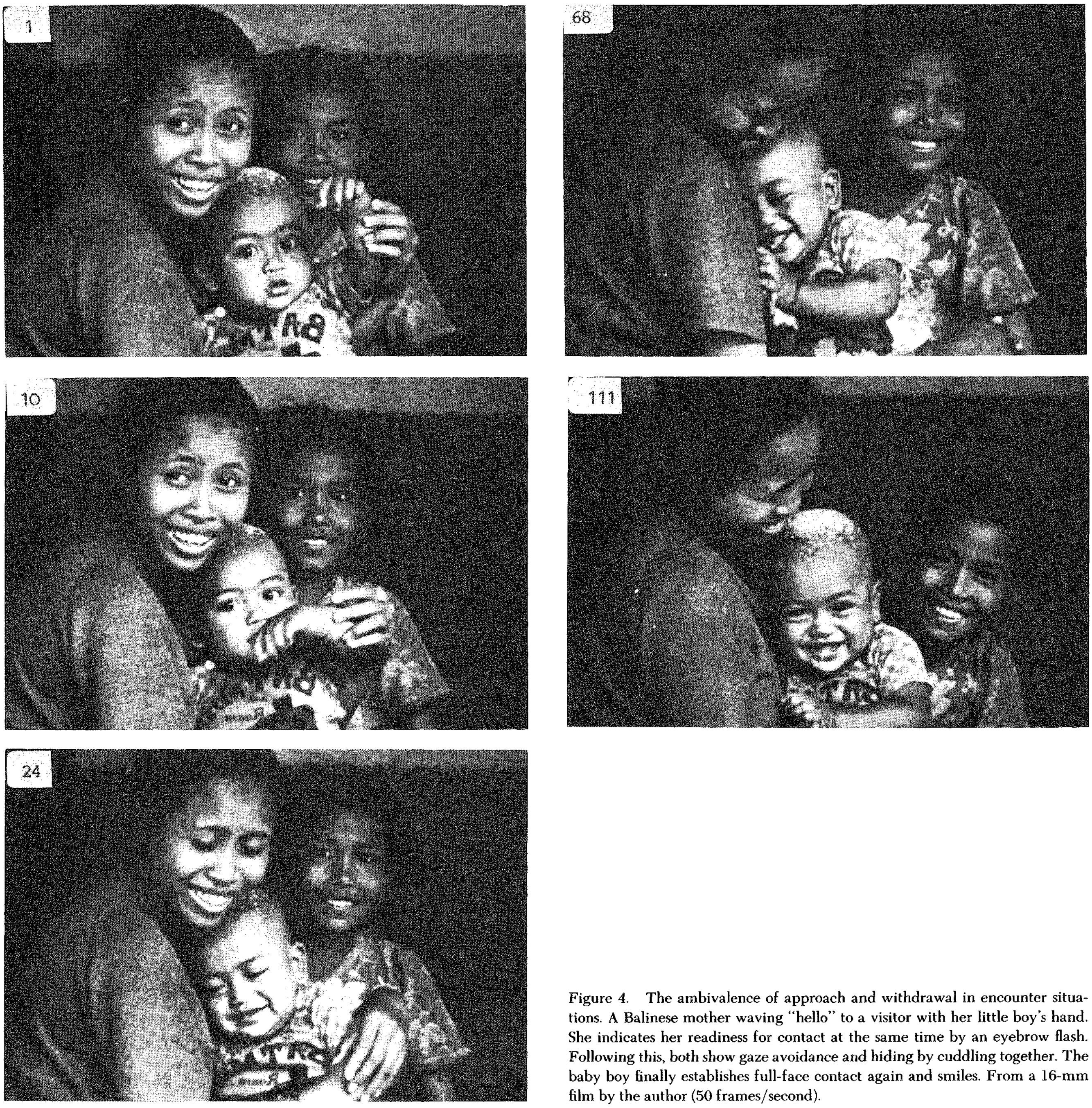


Figure 4. The ambivalence of approach and withdrawal in encounter situations. A Balinese mother waving "hello" to a visitor with her little boy's hand. She indicates her readiness for contact at the same time by an eyebrow flash. Following this, both show gaze avoidance and hiding by cuddling together. The baby boy finally establishes full-face contact again and smiles. From a 16-mm film by the author (50 frames/second).

categorize a great variety of observed behaviors, and connected to the motor system so as to generate the appropriate performance. The authors' discovery is in any case exciting proof of a highly specific phylogenetic adaptation in man.

c. **Avoidance of strangers.** A phenomenon that has puzzled many investigators is the "fear of strangers" which develops in babies at six to eight months. At this age, babies begin to discriminate between their familiar reference persons and strangers. If the latter approach, the child exhibits withdrawal responses, sometimes accompanied by signs of fear, such as crying, turning toward the mother, and hiding. In other cases we observe less pronounced "flight" reactions, but usually the child will show ambivalent behavior, including reactions of turning away.[5] This fear response develops in any baby that can attach itself to a familiar reference person, and does not depend on any particular aversive experience with strangers. I might add that I have encountered fear of strangers exhibited by all cultures I have visited so far (see Figure 4). Konner (1972) has provided detailed data on the phenomenon in !Kung bushmen. It is a universal trait, for which learning theory could hardly account. It can be reinforced by education, but it occurs with or without maternal training. The behavior has been interpreted as separation anxiety (see Rajecki et al., 1978), but a less psychologistic explanation would be that at a certain age the child responds with fear to the features of a fellow human. The fear-releasing quality of these stimuli is canceled out if the baby knows the person. But a certain amount of ambivalence often remains detectable even if the baby interacts with its mother, and it remains detectable in the behavior of the adult (cf. Figure 12). One of the signals that releases this fear response seems to be the eyes. There is much evidence that staring is perceived as a threat (Argyle and Cook, 1976) and that eyespot patterns in general have a highly arousing effect (Coss, 1972). This explains cutoffs during conversations. On the one hand, we have to look at our interlocutor in order to signal attention and readiness for communication, but we must interrupt eye contact at intervals in order to prevent the escalation into staring, which could easily be considered as an intent to dominate or even become aggressive.

One may argue that this fear of strangers can be overcome by education, and this is to a certain extent true. It would be wrong, however, to play down its importance in everyday life. To a considerable extent this apparently simple underlying program determines our social conduct. That we are inclined to live in closed individualized groups and tend to react with ambivalence and reservation or even hostility to a stranger, unless he is formally introduced, is a universally encountered fact. We can certainly identify with strangers, and we are actually taught to consider our fellow man in the anonymous crowd as a brother. But the fact remains that we view the stranger with strong ambivalence; one need only observe the gaze avoidance of strangers sharing an elevator (Goffman, 1966). Fear of strangers is one of the reasons why life in the anonymous society of a city exposes us to stress; city dwellers adapt by strategies of avoidance (cutoffs, noninvolvement) but still complain about overexposure to strangers, which continuously elicits stress (Newman and McCauley, 1977). Paradoxically, one hears at the same time that people feel alone. They miss the individualized groups of friends and family members, all scattered nowadays as a result of the celebrated mobility of modern man. City planners take man's inclination to avoid strangers into consideration by effectively isolating families in city blocks. What they do not realize is man's urge to bond, to get acquainted gradually with the stranger, and thus to form individualized groups.

Stranger avoidance has led man to live through most of his history in small, fairly closed groups, where all know one another; this has probably been one factor spurring cultural and biological evolution. Certainly it is an innate disposition of fundamental importance.

d. Basic social interaction strategies. I have promoted the hypothesis that many cultural rituals are differentiations and elaborations of basic, universally encountered social-interaction strategies and that they constitute phylogenetic adaptations (Eibl-Eibesfeldt, 1972, 1976). This is certainly in part speculative. However, cross-cultural study of ontogeny provides enough evidence to make it worthwhile to pursue this idea further. As examples, I wish to discuss strategies of agonistic buffering; patterns of sharing and giving, and the rituals derived from them; and focus of attention seeking. We will return to this subject in the later analysis of complex ritualistic events.

i. Agonistic buffering. The following example may serve to illustrate one universally observable strategy of conflict management. In this case a Yanomami girl is playing around a pole (Figure 5). Earlier she has had a brief conflict with the boy, who tried to chase her away. He approaches her again. The girl smiles prominently, with the intent to appease. This strategy fails; the boy hits the girl, who now lowers her gaze, pouts, and turns her head away. This behavior blocks the aggression of the boy, who turns away, leaving the girl unmolested.

The attempt to block aggression by smiling or by gaze aversion (cutoff) and pouting is universally encountered. In most cases it not only blocks aggression but also releases efforts to reestablish friendly relations on the part of the injuring party. The hypothesis that these constitute innate social interaction strategies is backed by a finding of Murray (1977). He told mothers during interaction sessions with their three-month-old babies to keep their faces motionless. This caused distress in the babies, and when the mothers, after the period of nonresponsiveness, attempted to talk to their children, the latter showed clear withdrawal by turning away as if resentful. For a gregarious organism a social cutoff is a serious threat since it isolates the individual by symbolically severing a bond. Such a threat induces efforts at bond-repair.

This strategy can be observed at the level of individual as well as group encounters. Man has the further capacity to verbalize this interaction. While children mostly act out in nonverbal behavior, an adult may say: "I will not speak to you any more." A sentence in this case acts as the functional equivalent of a nonverbal behavior. It is a characteristic of human ritualistic events that functional equivalents can substitute for one another. The cross-cultural analysis of greeting encounters provides numerous examples. Nonetheless, the basic rules by which such events are structured remain universally the same (Eibl-Eibesfeldt, 1979).

ii. Giving and sharing. Sharing and giving are widespread means of establishing friendly bonds. A wealth of anthropological literature refers to ritual gift exchange, which serves to establish bonds via obligations. Gift exchange is based on reciprocity, but usually with delay. In primitive societies like those of the bushmen, gifts chain-link people into a system of social security (Wiessner, 1977). Gifts are exchanged on occasions of meeting (see below). In our culture, birthdays and Christmas are two events when giving and exchanging gifts are of particular importance. Gift exchange is certainly a universal mode of establishing and reinforcing bonds. Since from early childhood children experience the rewarding effect of being given food by their mothers, one might assume that sharing and giving are learned as a bonding strategy. They are certainly reinforced by education as of early childhood, and to be "stingy" is considered bad in many societies and treated with reproach.

What intrigues me, however, is that as early as one year of age children already spontaneously part with objects when seeking friendly contact (Stanjek, 1978). They employ this strategy, for example, toward a visiting stranger, once initial shyness has been overcome. And even at an earlier age, one can see babies performing with the clear intention of feeding a morsel to a sibling or to the mother. While doing so they open their mouths in the same way their mothers do when feeding their babies. Again, this could be playful imitation. But the spontaneity with which the strategy is instrumentally employed to achieve friendly relations surpasses, in my opinion, the cognitive capacity of the child at this age, and seems to hint at a phylogenetic basis.

Children readily share when appropriately approached by their sibs or playmates. They do, however, resent attempts at forceful acquisition. The accompanying photographs illustrate this (Figure 6). Two Yanomami girls are eating berries. The one who finishes first tries to grab some berries from the other, who withdraws. The first child then discontinues her acquisitive attempt, and the other girl willingly shares with her. Whether consciously or not, children want their property to be respected, and only if this respect is accorded, will they fulfill a demand.

The second series of photographs (Figure 7) illustrates a similar sequence taken in a completely different culture, namely a recently contacted neolithic Papuan tribe (Eibl-Eibesfeldt, 1976). Two half-sibs are sitting side by side. The boy is eating a piece of roasted taro; the girl wants some and tries to grasp it, whereupon the boy withdraws. The mother of the boy then comes and takes the morsel, which is willingly given to her; she parts it in two halves and returns both to the boy with the verbal and gestural instruction to share, which he does without reluctance. In this case intervention and aid were necessary, since the boy was not capable of breaking the morsel in two. The readiness to share is evident, even though sometimes in conflict with egocentric inclinations. In such cases education endeavors to reinforce the altruistic tendencies. It is remarkable how this mother returns both pieces of taro to the boy in order to allow him to share with his half-sister.

At such an early stage objects serve as mediators of social relations, so we assume the existence of an innate disposition even though we are aware that incontrovertible evidence is not yet available (Figure 8). Supportive data come from man–animal comparisons. Meat-sharing plays an important role in bonding chimpanzee group members (Teleki, 1973a,b) and the analogous giving of greeting presents is found in many birds.

Objects are not only used as tokens for friendly bonding; at an early age children already employ them as mediators to place themselves at the center of attention. This behavior again finds its

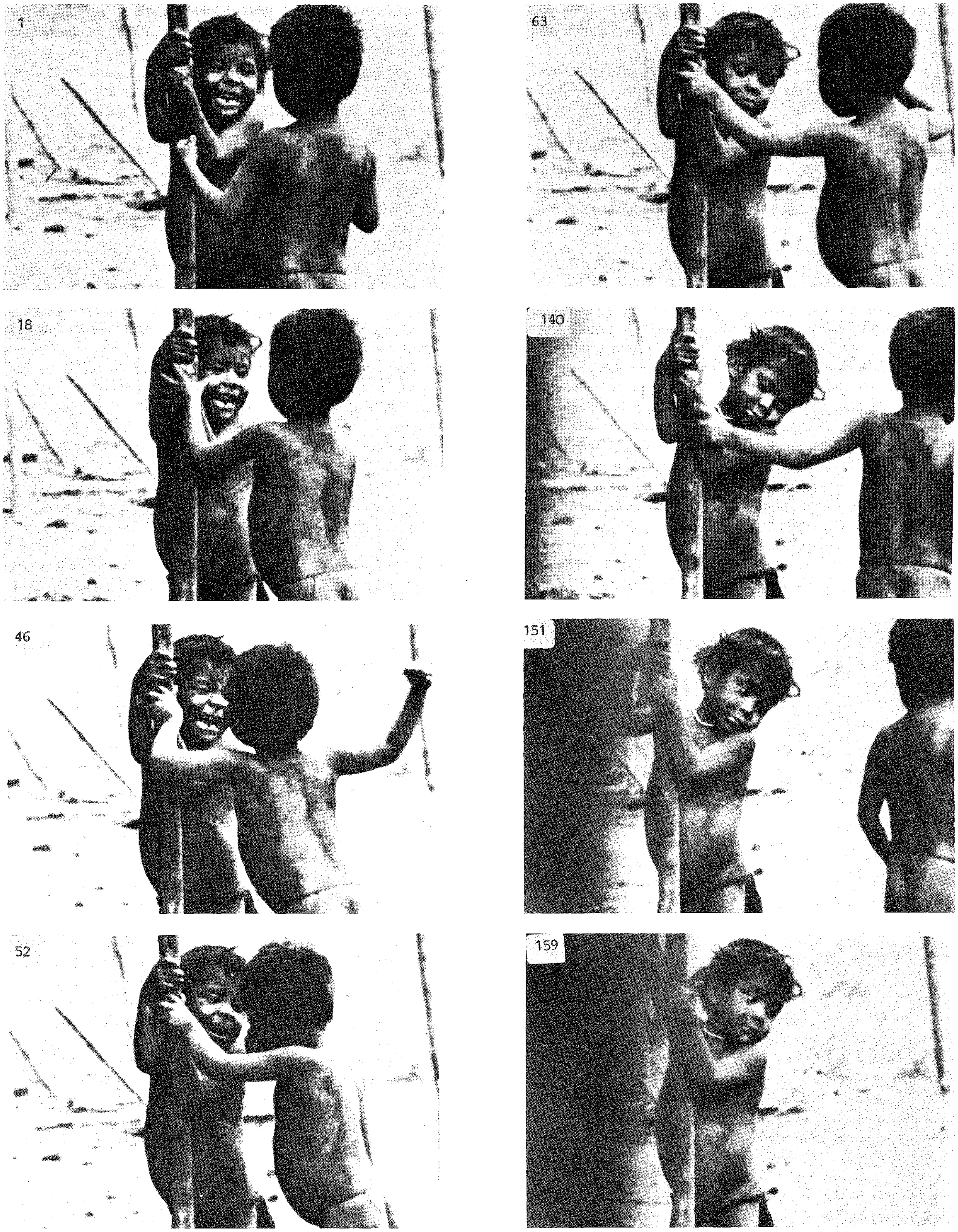


Figure 5. A Yanomami girl is approached by a boy with the aggressive intention of taking over the pole which she has been climbing. They have already engaged in this sort of competition (or struggle) before. The girl attempts to block the aggression by smiling, but her attempts are in vain. The boy hits her, she lowers her gaze in a clear cutoff, and pouts. Thereupon he withdraws. From a 16-mm film by the author (25 frames/second).

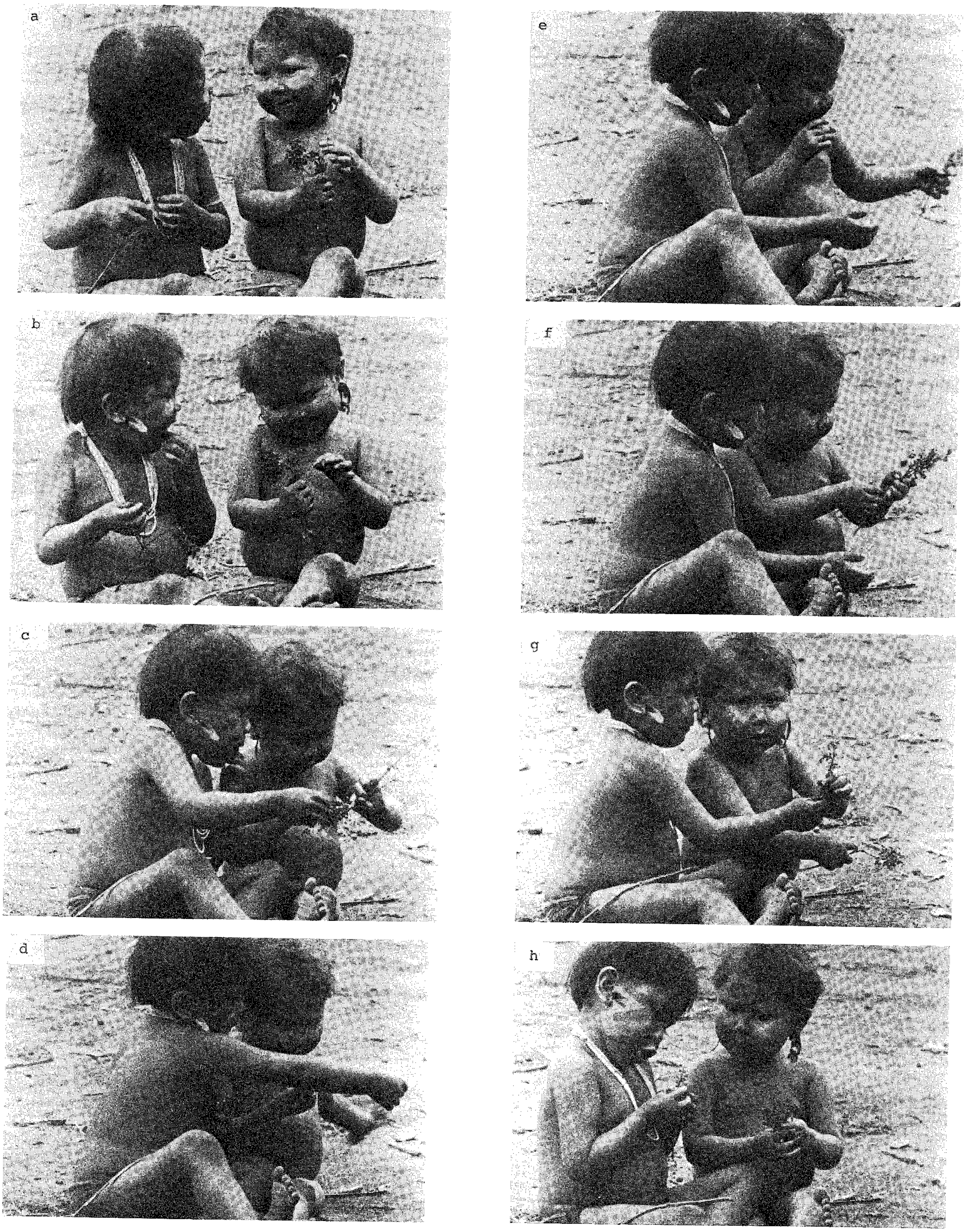


Figure 6. Two Yanomami girls eating blueberries. One shows her blue tongue to the other and then attempts to take some of her berries, This intrusion (attack) is responded to by a withdrawal movement. The attacker stops and waits, whereupon she is willingly given berries and both girls continue eating. From a 16-mm film by the author (frame rate not shown because the sequence was interrupted during filming).

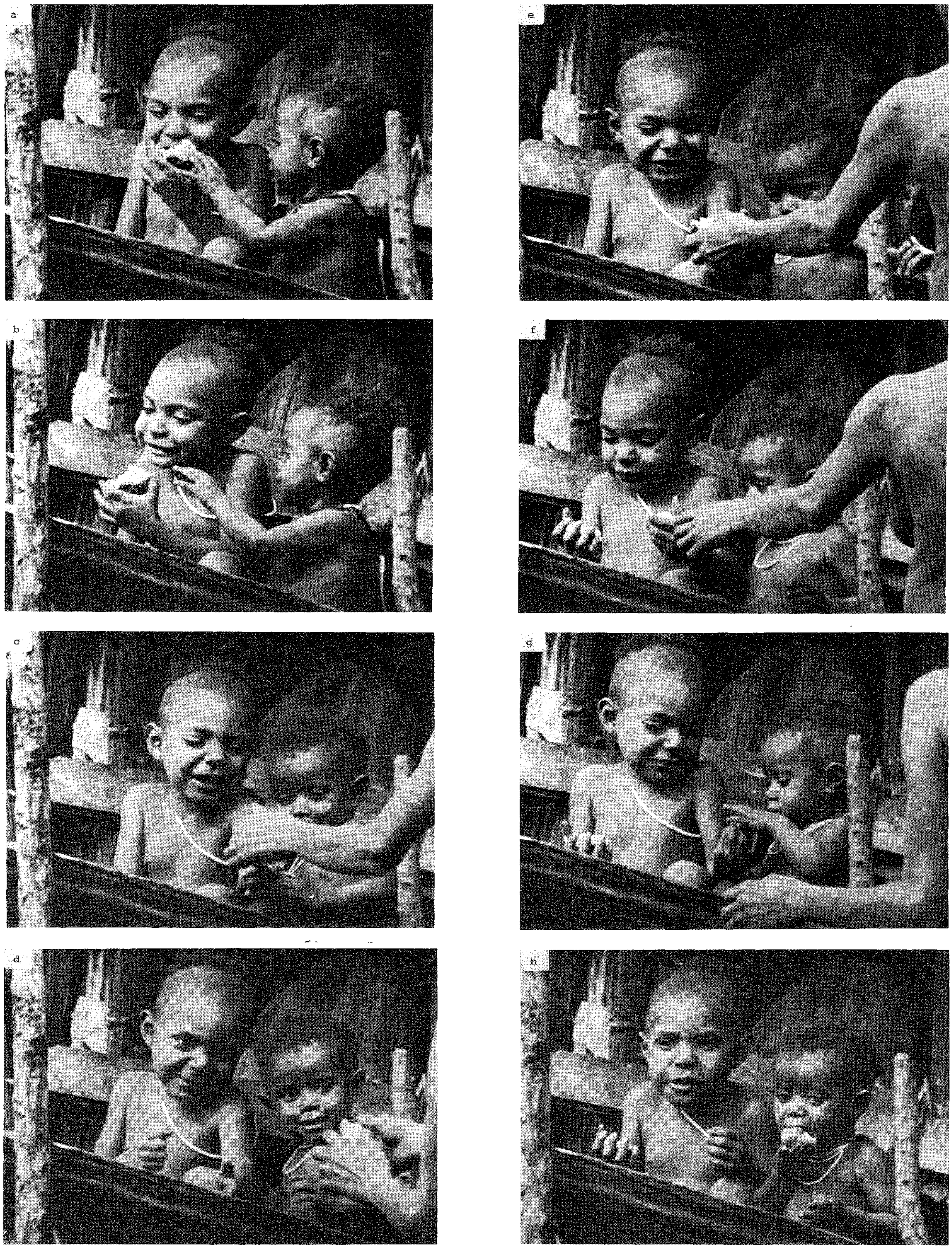


Figure 7. Two Eipo children (half sibs) sitting side by side, the boy at the left eating a piece of taro. When his half-sister tries to grab some, he reacts by withdrawing. Upon observing this, the mother of the boy intervenes by taking the taro, breaking it into two halves, and returning both to her son, who willingly gives one to his half-sister. From a 16-mm film by the author (25 frames/second; frame rate not shown because the sequence was interrupted during filming).

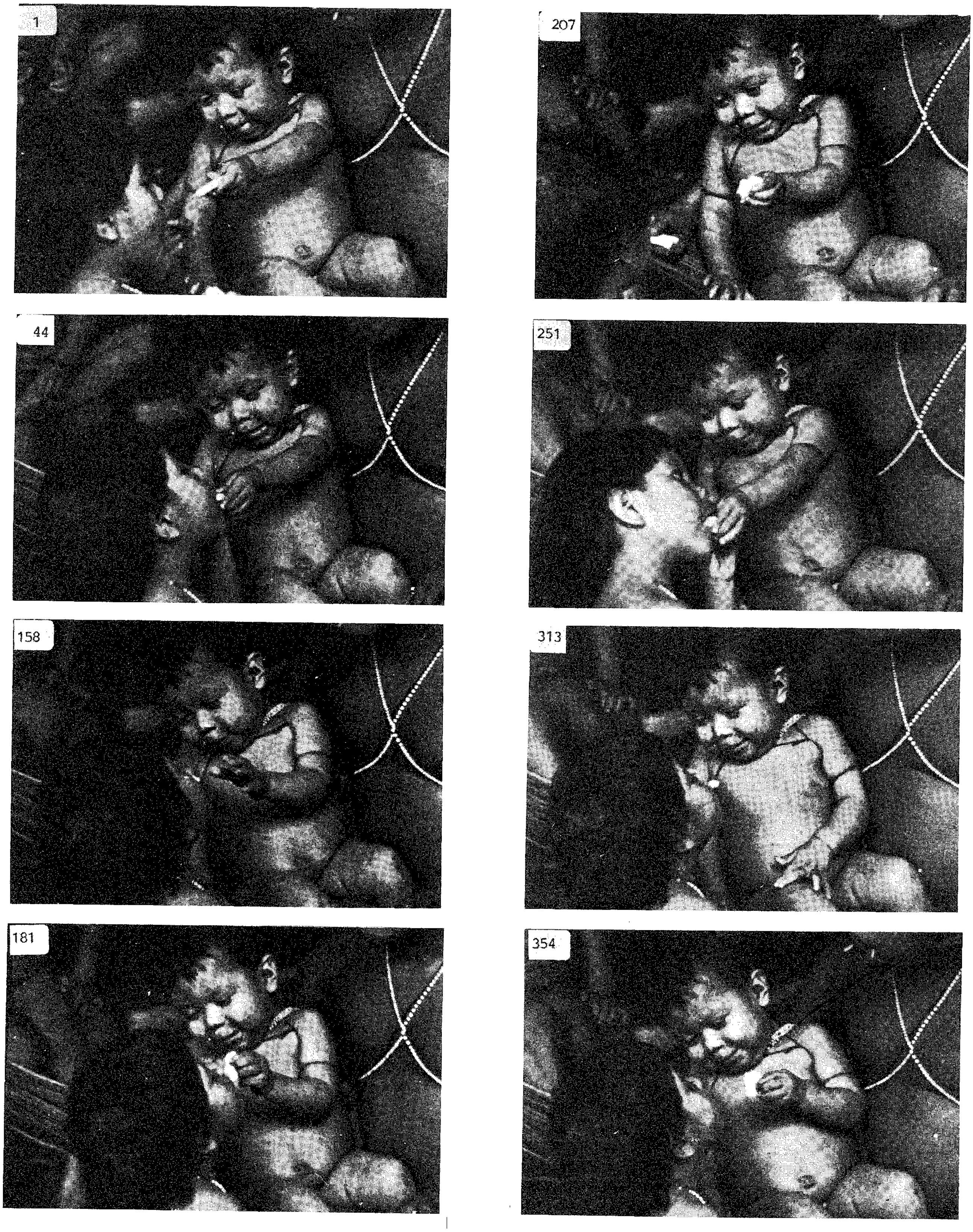


Figure 8. Dialogues of giving and taking are often initiated by very young children. Here a Yanomami baby offers her sister a morsel. The readiness with which small children in all cultures exhibit the pattern suggests a shared disposition. From a 16-mm film by the author (25 frames/second).

elaboration in a rich diversity of cultural rituals, the potlatch being one well-known example (see also Heeschen et al., in press).

iii. Focus of attention seeking. High-ranking monkeys and apes are characteristically the focus of attention (in terms of gaze patterns, etc.) for other members of the group (Chance and Larsen, 1976). They are mostly adult males, with a conspicuous outer appearance; a high-ranking hamadryas baboon, for instance, stands out visually by virtue of his impressive fur. In addition, high-ranking individuals position themselves in such a way that they are easily seen by other group members. Finally, they use a variety of displays to draw attention to themselves.

In studying groups of children, Hold (1976) was able to demonstrate that the structure-of-attention criterion is a valid one for indicating rank in man as well. Individuals who are the focus of attention are characterized by a number of behavioral traits. They are the ones who initiate and organize games, they comfort others in distress, they share more readily and show an above-average amount of aggression, although they are never the most aggressive. Others preferentially seek their company and like to engage them by displaying various objects of interest.

The strategies employed among children to achieve rank are a mixture of friendly bonding behaviors and display and agonistic patterns. Helping, comforting, sharing, and cooperating in games are combined with aggressive threats against competitors and children who attack others. Individuals seek attention by conspicuous forms of behavior, such as dress, the use of various objects for display purposes, and conspicuously positioning themselves. Very small boys already know how to show off. And it is not difficult to recognize most of these displays, whether in dress or in preferential seating behavior, at the adult stage of life.

Studies of sensorily deprived children.

Most of our facial expressions develop during ontogeny. Are these motor patterns learned or the result of maturation? Studies on the congenitally deaf and blind provide an answer. Children born deaf and blind grow up in eternal darkness and silence: they lack the opportunity to hear or see other individuals' actions, and if the environmentalist's conception were valid, their behavior would deviate very much from that of children not deprived of this basic information. We have examined such children and found that the basic facial expressions, such as smiling, laughing, crying, anger-frowns, clenching of teeth, pouting, and the like, occur in the same situations as with healthy children. The congenitally deaf and blind smile when their mothers play with them, cry when they have hurt themselves, and demonstrate fits of anger, to mention just a few examples (Figure 9).

It could be argued that the deaf and blind have derived information from their sense of touch and learned their facial expressions from tactile models. I have had the opportunity, however, to study congenitally deaf and blind thalidomide children, whose truncated limbs prevented them from exploring their environment with the help of a sense of touch (Eibl-Eibesfeldt, 1973a). They nonetheless exhibited the basic repertoire of facial expressions such as smiling, laughing, and crying. The argument remains that shaping could have occurred, for example, by the mother responding to smiling with friendly fondling and to crying with comforting. Such reinforcement can be expected to occur, but it must start with already recognizable patterns of facial expression for the mother to respond to. For the more complicated patterns of expression, such as anger, it is difficult to conceive how this could be determined by accidental shaping.

Information derived from the study of the congenitally deaf and blind is of great theoretical interest, but limited, however, since many of our social behavioral patterns are released by auditory and visual cues. As these channels are blocked in those born deaf and blind, we have to explore other ways if we want to find out whether more complicated patterns of social interaction belong to our phylogenetically acquired behavioral program. We have investigated this question in studies of the congenitally blind and through cross-cultural comparison.

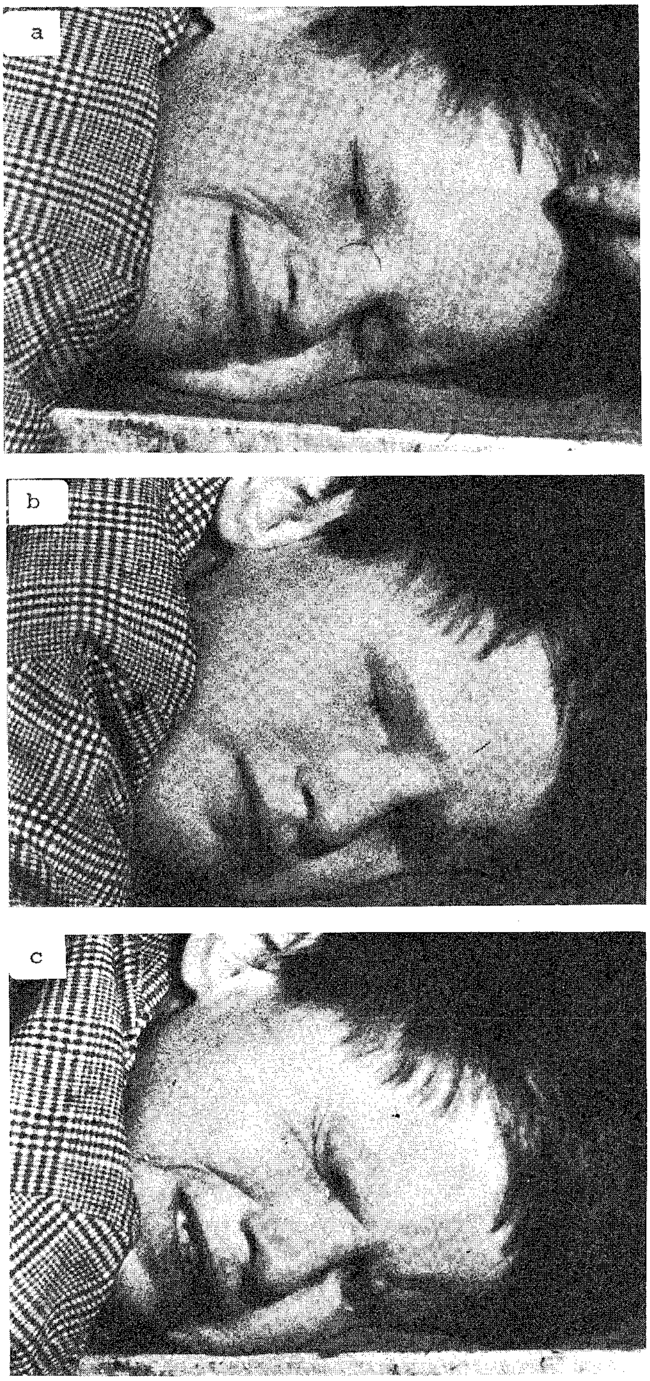


Figure 9. The expressions of a nine-year-old girl born deaf and blind: smiling; neutral; and distressed (crying). From a 16-mm film by the author.

In speaking to the congenitally blind, it is possible to release quite complex behavior patterns, for example, coyness. One need only make a compliment to a young girl to evoke blushing, lowering of the head, and turning away in a brief cutoff, alternating with patterns of approach such as turning toward the speaker, looking in his direction, and smiling. A congenitally blind boy hid his face behind his hands when slightly embarrassed.

Comparative studies of primate behavior.

The comparative study of primate behavior has revealed a large number of homologies between human and nonhuman primates.

The human smile is homologous to the silent bared-teeth display of monkeys and apes; human laughter is homologous to their play face or relaxed open-mouth display. In children and chimpanzees both expressions are strikingly similar, and van Hooff (1971), who studies these patterns of expression, has published a picture of a boy playing with a young chimpanzee, both displaying a nearly identical play face. I have filmed the play face in children of the Yanomami, the Kalahari !Ko Bushmen, and the Eipo (Papuan). Kortlandt (1972) and van Lawick-Goodall (1975) have pointed to the striking similarities in the greeting display of chimpanzee and man. On occasions of friendly encounter chimpanzees have been observed to embrace one another and kiss (see above: Human and animal rituals, section 2).

Very peculiar phallic displays have been reported in a number of monkeys and apes (Ploog et al., 1963; Wickler, 1967b). These function as aggressive threats against conspecifics and are derived from the male's intention to mount, an expression of dominance in many mammals (Eibl-Eibesfeldt and Wickler, 1968). When a group of vervet monkeys forages on the ground, some males sit on guard with their backs to the group, exposing their brilliantly colored genitals (red penis, blue scrotum); erection occurs when conspecifics of another group approach. This phallic threat serves a spacing function.

In man, phallic displays serve similar functions. Direct phallic displays occur in confrontation with enemies. The Eipo of Westirian (New Guinea) wear phallocrypts. When mocking the enemy, they first loosen the string that fastens the tip of the phallocrypt around the waist. Then they jump up and down at an elevated spot, which makes the phallocrypt swing up and down conspicuously. When startled, the Eipo click their thumbnails against their phallocrypts, thus drawing attention to their phallic display organ. This is an apotropaic (evil-averting) display, safeguarding against potential threat (Eibl-Eibesfeldt, 1976). Phallic figures or verbal threats are substitutes for phallic displays in man. Phallic figures serving as guardians to protect an edifice (Figures 10a–c,e) or the fields, (Figure 10d), or as personal amulets, are known from Europe, tropical Asia, New Guinea, South America, and Africa (Eibl-Eibesfeldt, 1970; see also Figure 10).

Results of cross-cultural comparison.

a. Universal motor patterns. In this section we wish to discuss some results of cross-cultural comparison with respect to our hypothesis that phylogenetic adaptations preprogram human behavior to a significant extent. Some observations concerning our cross-cultural work have already been presented in previous sections.

Our cross-cultural studies are based on film documentation. Although man is certainly the most filmed being on earth, we have rarely been able to make use of the film material of others for present purposes, since this has tended to be focused primarily upon aspects of survival strategies and material culture: how people hunt, fish, trap, build huts, weave, and so on is fairly well documented. Unique ritualistic activities have been filmed, too, but here the documentation is less complete; and when one is interested in unstaged social interactions, one rarely finds useful existing documentation, except for a few interspersed snapshots. To my knowledge only Bateson and Mead have made a pioneering effort to record everyday life on film (Bateson and Mead, 1942). Most ethnographic film and photography have focused on the "strange ways of life" of other cultures, but how people greet each other when they meet, how siblings interact, how mothers hug their babies have not been systematically filmed in an unstaged form, even though these features are of interest to the ethnocinematographer.

We have accordingly begun a cross-cultural documentation program, filming people, without their knowledge, by means of mirror lenses (for details see Eibl-Eibesfeldt, 1973b, 1975b; Eibl-Eibesfeldt and Hass, 1966, 1967). During the last ten years we have focused on rapidly vanishing cultures that still follow their original ways of life, selecting those that represent models for different stages of cultural evolution. At regular intervals we have visited the Kalahari Bushmen (!Ko, G/wi, !Kung), who live as hunters and gatherers; the Yanomami (Upper Orinoko), who are incipient agriculturists; the Eipo, Biami, and other neolithic agriculturists of New Guinea; the Himba (Kaokoveld, South-West Africa), representing pastoralists; the Balinese, representing rice farmers; and many other groups. We have principally collected films of unstaged social interaction. In order to allow later correlational analysis to be performed, every scene is accompanied by a protocol stating the context in which the recorded pattern occurred, what released it, what followed it, and what had happened beforehand. We have also attempted to avoid selectivity as much as possible by filming

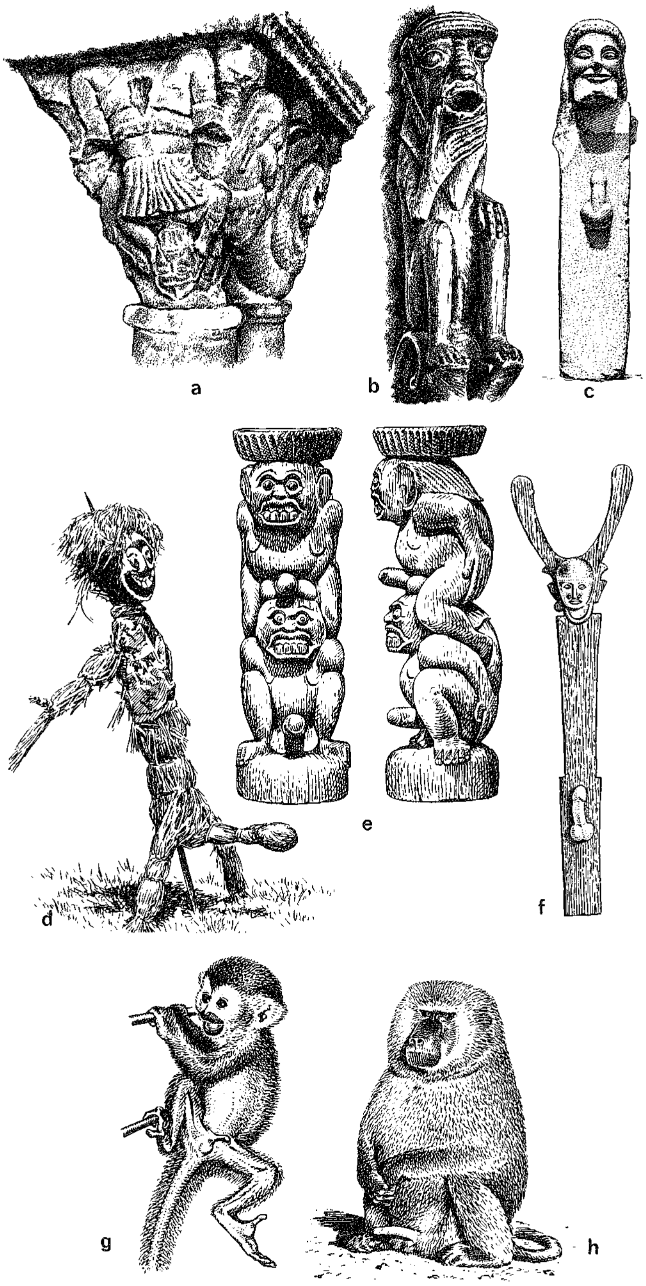


Figure 10. Examples of phallic displays in human artifacts and nonhuman primates. a) Phallic figure on the capital of a column in the cloister of St.-Rémy, France. The phallus of the figure, which stands on its head, has been chiseled away. b) Phallic figure under the pulpit of the Romanesque church in Lorch, Germany. c) Greek herm. d) Scarecrow from a Balinese rice field. e) Balinese guardian figure ("scare-devil"). f) House guardian from Borneo. g) Male sexual display posture of a squirrel monkey. h) Hamadryas baboon sitting guard for group protection. From Eibl-Eibesfeldt, 1970 (a, b, d, e); Wickler, 1967a (c, f); Ploog et al., 1967 (g).

whenever an interaction was expected to occur, for example, when people moved or turned toward one another, the filmer not knowing in advance whether the interaction would be friendly or aggressive. The uncut original is stored in an archive. Film publications are made from duplicates. An Archive of Human Ethology of the Max Planck Society was established in 1970. The publications accompanying the films appear in the journal *Homo*.[6]

Our cross-cultural films have revealed a large number of universal motor patterns. Their universality alone certainly does not allow us to deduce that these patterns are innate in man.[7] Similar experiences in the early life of a child could shape behavior in different cultures along similar lines. Darwin proposed that head-shaking, which accompanies a "no" in our culture, derived from the child's turning away his head when refusing the breast after satiation. This could well explain why head-shaking occurs in so many different cultures as a signal expressing "no" (but see below: b. Cultural convention and innate motor patterns). The actual study of ontogeny, however, must provide the final answer. Similarity in detail can in addition be the result of some shared function, thereby merely constituting analogy. Analogy is less probable, however, if the pattern is complicated and yet proves in cross-cultural comparisons to be similar in terms of detail, despite differing ecologies of the peoples compared. Certainly there are numerous motor patterns to be found in man whose particular form does not directly derive from a particular function. This is especially true of many nonverbal patterns of social expression. That smiling expresses friendly intent, crying and weeping sorrow, "laughing at" a particular form of aggression, may be primarily based on convention, comparable to the conventions that give words their specific meaning. Such a convention could be the product of cultural evolution. In such a case, however, man's tendency to "pseudo-speciate" culturally should bring about fast changes, as the rapid evolution of language clearly demonstrates. If, on the other hand, we find instead that patterns of socially expressive behavior remain the same across cultures, that they occur in the same context, that they are positively and exclusively correlated with certain other specific patterns, that they are embedded in the same sequences of other patterns, that they have the same signal value, and so on, then this is indeed strongly suggestive circumstantial evidence for the hypothesis that they constitute phylogenetic adaptations. Systematic study of ontogeny will again provide the final answer, but even circumstantial evidence provides some preliminary basis for statements concerning the nature of the pattern.

Since cultures pursue different educational strategies, we sometimes have the opportunity to note certain persistent patterns of behavior that are contrary to particular educational efforts. Thus aggression constitutes a problem for cultures like the Kalahari Bushmen, who pursue pacific ideals. Although, they fight it by education, they cannot prevent aggression and rivalry from occurring in early childhood. They likewise employ special strategies to achieve a fairly egalitarian group structure, but again possessiveness and striving for rank are problems with which they must cope. Were these inclinations merely a result of cultural imprinting, they would hardly show up in cultures that explicitly sought to pursue different ideals and attempted to socialize their children accordingly. Different cultures thus provide the natural experiments from which we can learn that certain human behavioral traits show resistance to the shaping efforts of the environment.

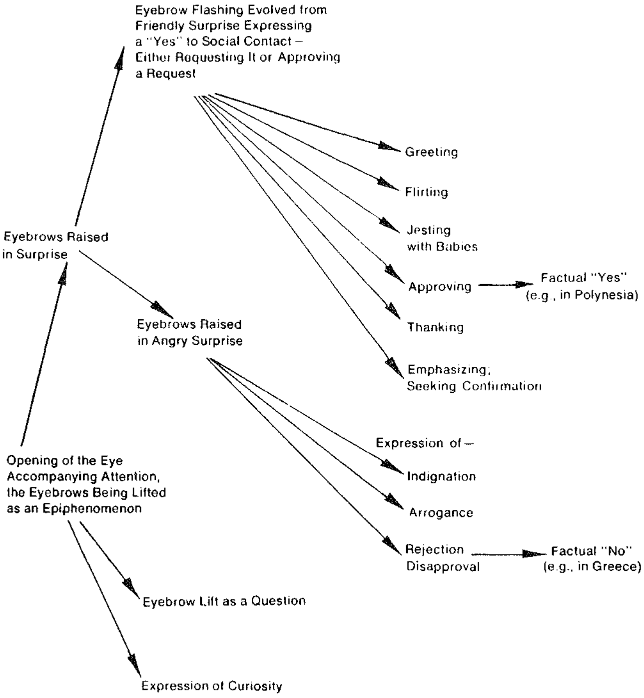
I wish to present here a few examples of expressive patterns to document universals which can be said, with a high degree of probability, to constitute phylogenetic adaptations. One concerns a pattern of greeting, which I have called the "eyebrow flash." It occurs in a very specific context and signals readiness for social contact. It is most often observed in a greeting encounter. A short head toss, whereby the head is raised and quickly jerked backward, initiates the eyebrow movement, which occurs nearly simultaneously: the eyebrows are raised for approximately one-sixth of a second. The pattern is often followed by head-nodding, and a smile is frequently superimposed upon the whole sequence. I have discussed the derivation and function of this pattern in detail elsewhere (Eibl-Eibesfeldt, 1975b). Briefly, the expression has derived from an expression of surprise – in this case friendly surprise as indicated by the accompanying smile – and thus readiness for contact. We observe it in greetings, flirting, in emphasizing agreement, and in other situations expressing contact readiness. There are also contrasting lines of ritualization in which raised eyebrows are combined with the threat-stare, indicating contempt. In this case the eyebrows remain raised during the encounter (see Table 1).

Cultural differences affect the readiness with which an eyebrow flash is signalled. Polynesians give eyebrow flashes readily. They greet strangers with this signal and couple it to a factual "yes." The Japanese, however, repress it during encounters with adults; it is considered improper, although small children, are freely addressed in this way. We in the West seem to hold an intermediate position. We use the signal in flirting, in greeting very good friends, and finally in emphasizing agreement. Its basic pattern would be considered by ethologists as *Erbkoordination* or "innate motor pattern."

Another behavioral pattern that occurs as a universal sign of affection is the kiss. In all cultures studied so far, I have found that mothers hug and kiss their little children, Papuans as well as Australian aborigines, Japanese, Balinese, bushmen, Himba, Yanomami, and many others. The observed cultural variation may affect the use of this pattern in adult communication. In some cultures it seems to be taboo, at least in public. As discussed earlier, the pattern derives from mouth-to-mouth feeding and is linked to homologous behaviors in nonhuman primates.

Let us now turn to more complicated patterns. It has been argued that mammalian behavior shows so much variability that one can hardly speak of any fixed patterns (Schenkel, 1947). Lorenz (1953) has answered by showing how the superposition of various intensities of the movements accompanying the intention to fight or to flee in the dog can generate a variety of different affective expressions (Figure 11). In a similar way, many human expressive patterns, which at first glance seem so variable, can be reduced to a number of "invariants" superimposed upon each other or occurring in alternation. Let us take the pattern of coyness as an example. We

Table 1. Schematic relationship among the various forms of eyebrow lifting. From Eibl-Eibesfeldt, 1975b.



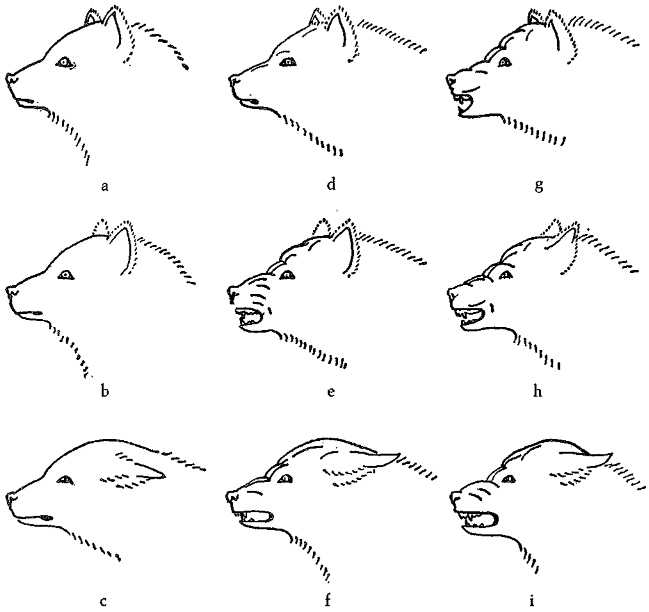


Figure 11. Canine facial expressions that result from a superposition of various intensities of fighting and flight intentions. a–c dimension: increasing readiness to flee; a–g dimension: increasing aggression and the corresponding superposition. From Lorenz, 1953.

have discussed man's ambivalent reaction toward his fellowman, already manifesting itself early in infancy as fear of strangers. This ambivalent reaction is also expressed in the coyness pattern.

A coy girl will look at a person, then lower her eyelids, turn her head away and, after averting her gaze, return it, either by looking from the corner of her eyes, her head still turned away, or after turning back to full face-to-face orientation. In the same situation a girl may smile while simultaneously activating the antagonistic muscles suppressing the smile, which results in what might be called a coy smile. She may hide her mouth behind her hand to hide the expression, or hide herself behind a friend or any object at hand, and even clasp the object as if seeking protection. She may perform a friendly eyebrow flash, but at the same time avoid eye contact by lowering her eyelids. She may look at the other person, but turn her chest away, showing her shoulder. And she may even show some patterns of aggression, like stamping her feet, jokingly hitting a nearby friend, laughing and biting her own fingers, nails, or lips. In short, it is evident that two systems are aroused at the same time, a friendly approach system and the agonistic system which controls the reactions of aggression and flight. The motor patterns of aggression and flight, on the one hand, are combined with the patterns of approach and expressions of readiness for social contact on the other. They can be combined simultaneously or in alternation. Since many different patterns of both systems can be combined, a great variety of expressions can occur.

Nonetheless we have no difficulties at all in interpreting and classifying the pattern, even when we encounter the situation in a completely different culture, (Figure 12). This fits in with the findings of Ekman et al. (1972), who present to people of literate and illiterate cultures photographs and videotape recordings of staged expressions. Subjects recognize the expressions of other cultures with a high degree of accuracy. For further examples of homologous motor patterns, see Eibl-Eibesfeldt (1976).

b. Cultural convention and innate motor patterns. Movements accompanying "yes" or "no" are sometimes puzzling. It is well known that cultural variation exists, but head-shaking is certainly the most widespread motor sign accompanying a "no." I have filmed this behavior (amongst others) in several Papuan groups, among the Yanomami Indians, the Kalahari Bushmen, and the Himba. The pattern occurs worldwide in a scattered distribution, but is certainly not the only way to express a "no." Greeks and many other people of the Mediterranean and Near East area express a "no" by jerking the head back and closing the eyes, often turning the head sideways and sometimes lifting one or both hands in a gesture of refusal. This pattern is observed in many other cultures as an expression of annoyance, for example, Westerners exhibit the same pattern when insulted by a proposal and expressing refusal under strong emotional conditions. As a factual "no," however, its use is quite restricted in the West.

The Ayoréo Indians of Paraguay have still another way of expressing "no." They wrinkle their noses, as if sensing some pungent smell, close their eyes, and often push their lips forward in a pout. As a factual "no" the pattern is again quite restricted, but if we observe people's reactions to offensive smells, we find universal eye-closing and nose-wrinkling. The pattern derives from an attempt to block off the annoying stimuli.

The Eipo of New Guinea use two motor patterns to express "no." The factual "no" is a head-shake, but when expressing refusal in a social encounter they push their lips forward – they pout. And pouting is again a universal pattern people exhibit when they are insulted and cut off the contact.

In other words, "no" can certainly be expressed in different ways, but several patterns can be adapted to this purpose, because they already express a "no," either in a social context, or in the refusal to accept a stimulus, or in simply shaking something off.[8] The latter has the least emotional loading and hence is more amenable to expressing a factual "no" than other patterns which might be interpreted as an insult. Sometimes, however, cultures pick up such patterns as a convention. The motor patterns in such cases are universals that obtain their specific meaning through cultural adaptation.

c. Analogies in terms of underlying principles. Quite a number of behavioral patterns prove similar on cross-cultural comparison, although the similarity is not so much one of form as of principle. Many are brought about by built-in biases on the receptor side, thus constituting a component of human phylogenetic adaptation. As we have discussed, animals as well as man are not only equipped with motor patterns, but also possess detector devices (innate releasing mechanisms) tuned to certain stimulus situations. The latter act as signals and release certain behaviors. There is no need for prior conditioning; the animal has, so to speak an innate "knowledge" of them.

Some of our innate releasing mechanisms are tuned to signals coming from other people. Babies, for example, are characterized by a number of features we perceive as "cute." Some of these are physical relationships, e.g., a large head in relation to the body, relatively short extremities, a protruding forehead in relation to a small face, and relatively large eyes. Furthermore, the cheeks seem to be signals. It is fairly easy to produce models which are cute, and exaggeration of one characteristic feature is enough to produce the effect required. We can see this in numerous Disney cartoons, for instance, where "cute" animals are produced by exaggerating the head size in relation to the body. Baby features are universally the same, and so is the response to "cute" features, which inhibit aggression. It is therefore not particularly surprising to find that making appeals via a child occurs in numerous encounter rituals indicating peaceful intent. When Yanomami Indians are invited to a feast, they take women and children along. When entering a village, visiting warriors first dance in a warlike display, prancing and showing off their bows and arrows. This aggressive display is counteracted by the contrasting presence of a child dancing and waving green palm leaves (Figure 13).

Another receptor bias has been identified by the thorough cross-cultural investigation of Koenig (1975), which has revealed the universal occurrence of eye-patterns in amulets and other designs serving to ward off evil. This is consistent with our observation that eyes are perceived with ambivalence. Many cross-cultural similarities in fashion, body decoration, and in ritualistic events may,

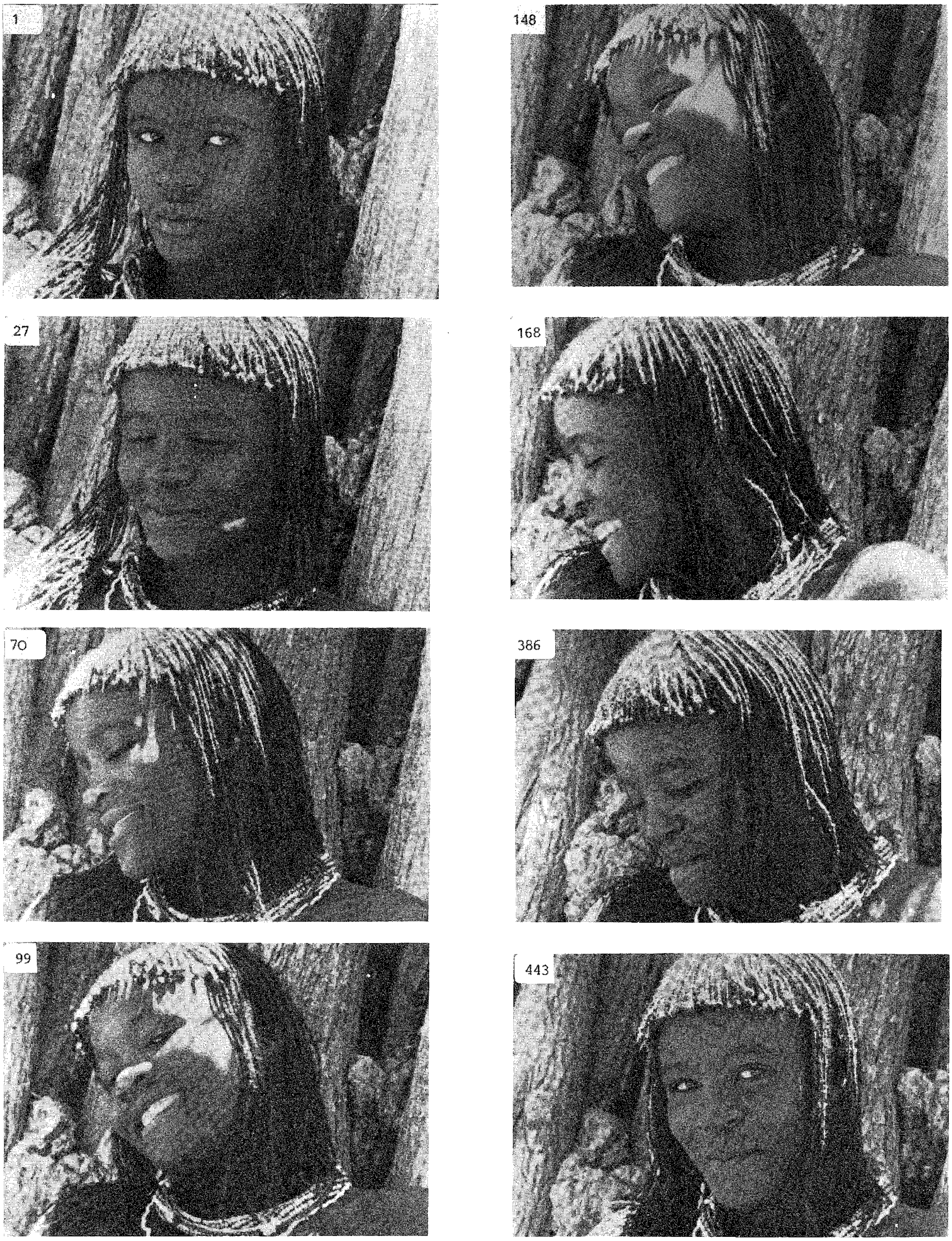


Figure 12. Coyness in a Himba girl illustrating successive states of ambivalence in response to a compliment. After establishing eye contact, a smile is signaled but suppressed; eye contact is cut off and her head is turned away. Following this, eye contact is reestablished from the corners of her eyes (this time with a full smile). Another cutoff follows and the smile is suppressed again. The sequence ends with eye contact and a coy smile. From a 16-mm film by the author (50 frames/second).

Figure 13. Yanomami visitor greeting his hosts by a warlike display dance. In contrast with this aggressive display, a child waving green leaves accompanies the warrior. Photograph by the author.

upon closer examination, be found to have a receptor bias as a shared basis.

d. Cross-cultural analyses of complex ritualistic events. Behavioral events can be structured in a variety of ways. Tinbergen's (1951) classic study of the sexual behavior of the stickleback revealed an interdependence of male and female behavior, each triggering in turn the response of the other. When the female appears, the male starts his zigzag courting dance. This releases presenting behavior on her part, which in turns elicits guiding to the nest, which she follows, and so forth. This chain of events ends with egg laying and fertilization, which initiates a new chain of parental behavior patterns, beginning with fanning of the eggs by the male.

External stimuli play a decisive role in structuring these events. The orderly sequence of behavioral acts is not however, always brought about in this way. Once released, fixed action patterns are executed in a stereotyped fashion, the coordination depending on central processes, often in combination with proprioceptive feedback, but sometimes without. This holds true even for some learned motor patterns (Taub and Berman, 1964).

In the more complex behavioral sequences external and internal stimuli as well as central mechanisms interact in bringing about an orderly sequence, and they do so according to rules either acquired during ontogeny or already available as phylogenetic adaptations.

Investigating rituals in man, one does encounter events conforming to the stimulus-response principle. The responses are partly innate motor patterns (like facial expressions), partly learned ones. In addition, rules imposed by culture can structure the whole sequence of acts. Whether this is also partly due to phylogenetically acquired programs is an open question. Undoubtedly, innate releasing mechanisms make us particularly responsive to certain signals, thus determining the general course of certain events.

In our discussion of basic social-interaction strategies we provided examples of events structured by rules, which on our hypothesis constitute innate phylogenetic adaptations, determining the nature of the response in relation to the external stimulus situation as well as the general behavioral sequencing pattern. We emphasized the cultural variability resulting in part from man's capacity to substitute for innate motor patterns certain cultural ones, including verbal behaviors, which then serve as functional equivalents, the general patterning of the strategy remaining essentially the same. The strategies discussed hitherto have been comparatively simple. We turn now to more complex events.

Rituals of friendly encounter serve to illustrate how such complex patterns are structured along cross-culturally similar lines. Complete rituals of friendly encounter are characterized universally by three phases (Eibl-Eibesfeldt, 1971a,b, 1973b, 1979; Ghosh, 1972): the opening phase (phase of salutation); the phase of interaction; and the phase of parting. Each of these phases is distinguished by a set of verbal and nonverbal behaviors correlated with a specific function.

The *opening phase* is characterized by a combination of aggressive displays and patterns of appeasement and bonding. The Yanomami Indian, as described above, enters his hosts' village on the occasion of a feast and dances in full war gear with aggressive displays. Functionally, this show is a demonstration and reassurance of his identity. An encounter situation is a challenge, and man is prone to accept any sign of weakness as an invitation to establish a dominance relationship. It is for this reason that man is usually on guard not to show weakness. By their displays interactants define their position in relation to one another (Goffman, 1966). Provocative displays are combined with mitigating signals of appeasement – witness the child waving green leaves who accompanies the dancing Yanomami warrior (see Figure 13).

The Yanomami salutation is certainly a culturally specific ritual. We in the West do not perform war dances on such an occasion. But consideration of the more general principles expressed does reveal comparable displays in our way of saluting. A visitor of state, for example, is greeted by a welcoming cannonade, and in addition is received by a child with a bouquet of flowers. In the most diverse salutations we discover the same principle. When two groups of Medlpa (Papua) meet on the occasion of a mourning ritual, the hosts rush toward the visitors, the males with raised spears in aggressive display, followed by women waving green Cordyline plants (Eibl-Eibesfeldt, 1978). So, too, in our culture the handshake – and squeeze – are partly display and partly challenge, mitigated by smiling, nodding, and embracing.

Cross-cultural examination of the salutation phase reveals that a number of behavioral patterns can substitute for one another: innate motor patterns as well as culturally evolved ones, including verbal behavior. In discussing strategies of agonistic buffering in children above, we provided some examples illustrating this interesting fact. What remains universal in the phase of salutation is the combination of displays with appeasing and friendly (bonding) appeals. Emphasis upon one or the other may vary with the rank of the persons involved, with the intimacy of acquaintanceship, and so on. The universal appeal via children or women can be explained by assuming that the signals involved buffer aggression through innate releasing mechanisms specifically tuned to them. Concerning the features of the child at least, there are strong indications that this is indeed the case (Lorenz, 1943; Hückstedt, 1965; Gardner and Wallach, 1965). In this context it is interesting to note that the same principles are involved in the strategies of Barbary macaques and other monkeys for blocking aggression in conspecifics. When a subordinate male wishes to approach safely a high-ranking male, he will borrow a young monkey and present it to the other (Deag and Crook, 1971).

The *interaction phase* is characterized by attempts to establish a close relationship. A variety of patterns of bonding are employed to achieve this. As in the phase of salutation, a variety of appeals can substitute for one another as functional equivalents. The recurring basic strategies consist of expressing concern for and interest in the other party. The phrase "how are you?" is certainly a widespread verbal cliché. Sympathy is expressed in a variety of ways. On occasions of festive meeting two Yanomami groups mourn their deceased together. In a more formal way, for example, upon the occasion of a state visit, a wreath is laid at a war memorial in our culture. Affection is expressed either by patterns like embracing and kissing or in a more formal way by entertaining and feeding the guest. Agreement (conformity) is demonstrated, for example, in the type of redundant dialogue which Morris (1968) aptly called "grooming talk." Among the means employed to establish a strong bond, aggression often plays an important role. Among the Yanomami guests and hosts sniff drugs, and in a state of intoxication jointly send spirits to the enemy villages where they are believed to do harm. Through all these bonding maneuvers the friendly atmosphere prerequisite to "talking business" is created.

Encounters do not end abruptly, but with a formalized *parting phase*. During this phase the bond is reinforced for the future through the exchange of gifts, either by really presenting objects, or verbally, in the form of good wishes ("good-bye," "farewell"). In addition, patterns of appeasement may occur.

The basic strategy of the encounter ritual can already be seen in small children. I have observed that at the age of one and a half a child will show off in front of another in a sort of introductory display, and will combine this with an effort to establish friendly relations by offering toys or things to eat. This phase is regularly followed by intensive playful interaction. Unity (conformity) is expressed in nonverbal acts in which one imitates the other (banging objects, somersaulting, spinning around, and so on).

6. Discussion

It has been suggested that the legitimate domain of human ethology is restricted to the primitive, animal-like design features of behavior, while higher levels of organization cannot be investigated by ethological methods. This is certainly a misconception (Shafton, 1976). We have shown here that cultural behavior can also be studied by applying the methods and theoretical approach of biology. While it clearly does not constitute the only approach in man's interdisciplinary efforts to understand man, the biological method is likely to illuminate unique facets of human behavior thus far overlooked. That we have focused here on the exploration of phylogenetic adaptations as determinants of human behavior is due to the fact that this very important factor has been hitherto neglected. Human ethologists have added the phylogenetic dimension to the historical one.

As was elaborated in the previous section, phylogenetic adaptations play a decisive structuring role, even in complex ritualistic events. On the basis of our motivational structure it already follows that encounter patterns are likely to take a particular course: our unconditioned fear of strangers is in conflict with our strong urge to establish friendly bonds. This ambivalence has a significant effect on our relationships with others. A repertoire of apparently innate signals is available for display and appeasement. Their demonstrably identical interpretation in different cultures supports our contention that we respond to some of them via innate releasing mechanisms. Certain basic social interaction strategies are accordingly constrained in terms of their general structure with strikingly similar expressions observable cross-culturally, since many complex rituals are actually elaborations of a limited number of basic strategies. Cultural variability results from man's unique ability to substitute for innate patterns of behavior various acquired functional equivalents, including verbal behavior, but the general framework of the ritual remains essentially the same. Patterns of social interaction may even be verbalized in their entirety: even then they obey the same rules that structure the corresponding nonverbal strategy. I suggest that there exists a universal "grammar" of human social behavior whose study will open promising avenues of cooperation between ethologists and sociolinguists in a field that might appropriately be dubbed "etholinguistics."

The basic question as to why we behave as we do is, of course, not restricted to phylogenetically adapted behavior patterns, but must be addressed to purely cultural patterns, too. The Himba, a cattle-breeding Bantu population in the Kaokoland south of Angola, are warriorlike people. This is adaptive for herders, who have to defend their stock and must occasionally conquer new pastures. Their ability to strike efficiently depends on a potential for rapid military organization under a hierarchy of headmen. This potential must be maintained in peacetime and rituals reinforcing obedience are accordingly exhibited in everyday life. Every morning the members of a kraal community bring the milk of their cows to the headman to be formally tasted. Only after the headman has sipped from or at least touched the container are others free to consume the milk (Eibl-Eibesfeldt, 1979). It is easy to see how people are continuously conditioned to submit to authority in this way. At the same time the particular authority reinforces his control over his subjects. Similar rituals exist in our own cultures, such as the daily raising and saluting of the flag by soldiers (and certain schoolchildren). Among the Himba heroic attitudes are reinforced at social gatherings by singing songs hailing the deeds of heroic ancestors.

Harris (1977) has elaborated brilliantly upon the adaptive function such culturally evolved patterns might fulfill and here the interests of anthropologists and ethologists clearly merge. There is a shared desire to understand how behaviors contribute to the survival of the individual (or group). To find the answers ethologists prefer nonparticipant observation techniques in the natural setting, as described earlier in this article. We apply comparative and experimental methods, tracing history and ontogeny, and accepting the methodological and theoretical insights increasingly emanating from neighboring disciplines, particularly psychology and social anthropology.

The topic of phylogenetic adaptations has been largely ignored until recently and, as I pointed out at the beginning of this article, there is still strong reluctance to accept the fact that man is far from being born as a blank slate. This reluctance is based upon the erroneous assumption that anything innate to man must then be accepted as some kind of inevitable fate. I accordingly wish to emphasize once again that ethologists have never promoted any "biological determinism" that would imply this. On the contrary, man's ability for self-control has been stressed again and again. It is important, however, to realize that man is not equally malleable in all directions, and those who fail to take into consideration the existence of a human nature do run the danger of developing inhuman educational programs that impose unnecessary frustrations upon man.

Anonymity, for example, has been found to impose a strain on man. Oblivious of this, certain educational schemes involving the elimination of the original classroom community are at present being tried out in central Europe on a large scale. If the gains were clearly to be greater than the loss, we would have to accept the new ways. But what is so frightening is that humane aspects are not given much consideration in reckoning the gain. Educational ideologists continue to proceed as if humanity were just wax in the hands of its shapers.

Tiger (1976) has expressed the same concern and provided a similar explanation for the preponderance of the environmentalistic ideology. He writes: "I suggest that the ideological leadership of both the communist and non-communist traditions were content with and supported a psychology which focused on their rights and options as manipulators rather than on the proclivities, needs, enthusiasms and 'biological rights' of the manipulated" (p. 262). The environmentalistic ideology can indeed be abused in many ways. If it were true, as is often assumed, that all our norms of conduct were a product of education only, an ethnocentric cultural relativism could result. Against this possible interpretation I find it comforting to be able to report that we have hitherto failed to find any basic differences in human behavior attributable to race.[9] On the contrary, many of the expressive behaviors which I have inferred to be innate to man are the same in groups as different as Kalahari Bushmen, Europeans, Papuans, and Yanomami Indians. This common heritage facilitates communication across the barriers set up by culture. Cultures separate people, but our shared biological heritage still supplies a strong frame of reference for cross-cultural identification (Eibl-Eibesfeldt, 1975a, 1977).

Finally, a few comments as to the relation between ethology and sociobiology. In his recent book, Wilson (1975) has drawn a puzzling scheme. It was presented as an admittedly subjective conception of the future contribution of ethology and physiological psychology on the one hand and sociobiology and behavioral ecology on the other hand. It was amusing to note how in the year 2000 the contribution of ethology and physiological psychology would dwindle in relation to that of the other two fields! It seems that Wilson is unaware that sociobiology and behavioral ecology are the basic constituents of ethology. Ethology has from the beginning been based upon the theory of selection. By concentrating on the question of how social structures and behavior contribute to genetic survival, in the sense of contributing to inclusive fitness, the new field of sociobiology has certainly justified its own existence as a part of ethology.

Of the stimulating ideas promoted by the new sociobiology, the hypotheses concerning the way selection operates deserve attention. Ethologists have for a long time used the phrase "survival of the species," which is not quite correct (as pointed out above). It is certainly of considerable value and interest when sociobiologists calculate energetic investments and resulting genetic survival, showing from the example of self-sacrificial behavior, for instance, that altruism can pay off if closely related siblings profit from it: genetic survival is what counts. This basic statement, however, is not so very new; what is new is the more exact calculation and the resulting new formulation of the problems involved. As far as human behavior is concerned, the sociobiological approach will certainly stimulate discussions concerning whose investment still pays or fails to pay whom. In a situation of reciprocity, altruistic investments will always pay off. Co-operation is a proven strategy in the "struggle for survival," as exemplified by the numerous mutual relationships that bond even genetically nonrelated animal species (e.g., symbiosis). As far as nonreciprocal altruism is concerned, animal behavior studies certainly support Hamilton's (1964) model of kin selection as the mechanism responsible for the evolution of altruistic behavior. A recent analysis of aiding in agonistic encounters has revealed, for example, that pigtail macaques clearly discriminate between relatives and nonrelatives, aiding closer relatives more often than more distantly related individuals (Massey, 1977).

The statement that "Altruistic behavior can evolve in the absence of competition between groups by a process called kin selection" (Wilson, 1976, p. 21) should, however, not be twisted into the generalization that this is the only way selection operates. Once closed groups evolve, group selection could take place. This development commenced with the evolution of parental behavior and the individualized bond (Eibl-Eibesfeldt, 1972). Closed groups grew from the family unit, parental behaviors and infantile appeals forming preadaptations from which the mechanisms of adult bonding derived. In such closed groups all individuals are closely related, in particular where incest avoidance ensures a constant mixing within the gene pool of the group. This is so particularly in man. One cannot overlook man's astonishing ability to identify with his larger group (band, village, people) to the extent of self-sacrifice. This can be explained by the fact that human breeding populations have been fairly small for most of man's history. Extant groups of hunters and gatherers or neolithic agriculturists as a rule consist of a few hundred or up to a few thousand people. Therefore breeding populations are basically comprised of fairly closely related individuals, so that investment should pay off for any group member and not just for immediate kin. To reckon only on the 50 percent of his genes that a person shares with his full sibling, or parent, or child, as one might be inclined to read Wilson (1976), is to oversimplify matters. What is meant, I am sure, is that the individuals in question are related to that percentage for the purposes of calculation, but the majority of a person's genes are shared with any other member of the group. History finally teaches that group selection took place in man.

7. Summary

1. Human ethology can be defined as the biology of human behavior, its interests distributed along the same paths that biological research pursues, namely morphology, ecology, genetics, phylogenetics, developmental biology, sociobiology, and physiology. Its methods and questions are elaborations of those employed in these fields, but specially adapted to the study of man. Human ethology is based upon the theory of selection.

2. The supposition that human ethologists consider only the animallike design features of human behavior as their legitimate domain is wrong. We also try to understand the evolution and functional aspects of cultural patterns, in the perspective of their contribution to overall fitness.

3. In terms of methodology, human ethology begins with the elaboration of the ethogram by studying and documenting human behavior in its "natural context," this being a tested approach in ethology and not only a prerequisite for any comparative morphology of behavior, but also the starting point for any ecological and other causal analytical approach.

4. One current focal point of interest in human ethology is the question concerning the extent to which man's behavior is determined by his genetic heritage.

5. Since any adaptation is based upon the acquisition of information by the adapted system, it is legitimate to ask for the source of the underlying information and to explore the process of information acquisition. An interaction must have taken place between the adapted system and the environmental mold with which its structure (behavior) fits, unless we are to believe in a pre-stabilized harmony.

6. Acquisition of information can take place during phylogeny, cultural evolution, and on the basis of individual experience. In both the latter cases learning is involved.

7. Phylogenetic adaptations determine behavioral events in various well-defined ways. They exist as innate motor patterns (fixed action patterns), innate releasing mechanisms, releasers, innate motivating mechanisms, and innate learning dispositions, innate being a shorthand description for the fact that the neuronal network and its connection with sensory and motor organs grow in a process of self-differentiation according to the blueprint given in the genome of the species.

8. Deprivation experiments are a way to determine whether or not a structure owes its adaptedness to phylogenetic processes, since one can withhold from animals the patterned information relevant to the adaptation in question, for example, the hearing of the species-specific song. If the pattern nevertheless occurs, this proves that the information underlying the patterning was phylogenetically acquired, irrespective of whether less specific environmental influences during ontogeny are needed in order for development to occur at all.

9. Animal–man comparison should not restrict itself to the study of homologies because analogies teach us about those laws deriving from function which, independently of any closer relationship, govern the expression of a particular pattern. This is true of organs (wings) as well as of behavior patterns and social structures (ranking, monogamy). Even culturally and phylogenetically evolved structures can be usefully compared in this way.

10. Phylogenetic adaptations also determine human behavior to a significant extent, and in the same ways as in animals. This is revealed by approaches such as the study of infant behavior, including that of the congenitally deaf and blind and others growing up under conditions of specific deprivation; it has been found, for example, that the congenitally deaf and blind exhibit a highly differentiated repertoire of facial expressions.

11. Fear of strangers develops as a basic human response during infancy and without the need of prior experience with strangers. This reveals that we react *a priori* to certain signals from conspecifics with agonistic behaviors. Personal acquaintance cancels out fear-arousing effects.

12. Some basic social-interaction strategies develop in nearly identical fashion in children of all cultures examined so far, e.g., patterns

of giving and sharing, or of attention seeking. Many adult cultural rituals appear to be elaborations of these strategies, which seem to be preprogrammed to a considerable extent by phylogenetic adaptations.

13. Cross-cultural documentation of unstaged social interactions and rituals reveals universals that are in part to be interpreted as homologous innate motor patterns. Comparative primate studies further support this notion.

14. In addition, cross-cultural comparison reveals analogies in principle that seem to be based upon shared innate releasing mechanisms. Thus, children are universally used in rituals of friendly encounter. Another example is the apotropaic phallic display, as can be seen in the Eipo and in expressive figures (see above: Comparative studies of primate behavior); this can be traced to an infrahuman primate heritage.

15. Cultural and phylogenetic forms of ritualization exhibit striking similarities owing to similar selection pressures guiding the evolution of signals and because both often start from similar preadaptations. Greeting and courtship rituals provide interesting examples.

16. Greeting rituals and festivals, despite their apparent cultural variability, share features of detail as well as a common basic structure. Within a given framework, however, functionally equivalent cultural patterns can substitute for innate patterns.

17. The discovery that certain verbal and nonverbal behaviors can substitute as functional equivalents for one another bridges the gap between these behaviors and opens the way for the study of a grammar of human social behavior, encompassing both modes. Basic social-interaction strategies indeed follow the same rules, regardless of whether verbalized or acted out nonverbally.

18. The biological unity of mankind, as expressed by a shared phylogenetic heritage determining our conduct to an important extent, is to be considered as a very positive feature because it provides the basis for a shared and emotionally felt concern as well as for a common understanding which transcends cultural barriers.

19. Proponents of a rigid environmentalism should be aware of the dangers that may arise from the neglect of human nature. Educational programs based upon exclusively environmentalist ideologies run the risk of being inhuman by imposing unnecessary frustrations, and strict cultural relativism may lead to ethnocentric political strategies.

NOTES

1. This is not quite correctly expressed. In animals, where traditions play a minor role, homologies, as a rule, point to shared genetic ancestry. In man, however, homologies of tradition have to be distinguished from homologies of phylogeny. The best-known examples of the former are provided by studies of language (for details, see Wickler, 1967a).

2. In view of the readiness with which learning theorists have generalized and extended principles from the study of rodents to humans, it is rather surprising that ethologists are so often criticized for cross-specific comparison.

3. One used to speak of the "survival of the species" in this context. But whether selection operates at the group level is at present a much debated issue. Individual selection seems to be an important principle in evolution (Hamilton, 1964; Wilson, 1975; Dawkins, 1976), but certainly not the sole one, as will be discussed later. Furthermore, species change and do not survive as such.

4. The German term is in my opinion better than the English translation, which implies a rigidity rarely encountered. Most fixed action patterns can be performed with varying intensity; speed of performance can vary, too. The sequence and phase distance of muscle contractions, however, remain basically the same.

5. There exists an extensive literature dealing with this phenomenon (see review in Sroufe, 1977). Some recent critiques of the concept (in particular Rheingold and Eckerman, 1973) point to inconsistencies in the reported age of onset and the percentage of infants showing fear. The authors question the validity of the concept, since crying and withdrawal in clear fright are less common than smiling and other expressions of contact readiness. The discussion by Sroufe (1977), however, demonstrates that "wariness of strangers" remains a viable concept withstanding existing criticism. Context and procedure strongly influence the response, which also varies individually, but negative reactions to strangers are evident even if expressed only by movements of withdrawal intention. That positive responses can also be observed is no contradiction. This ambivalence will be discussed further in the text.

6. Sorenson (1967, 1976) and Sorenson and Gajdusek (1966) have independently emphasized the value of filming everyday social interactions. They have presented thorough documentation on the Fore, and in 1974 Sorenson founded the National Anthropological Film Center at the Smithsonian Institution. At about the same time D. Freeman established a film archive on human ethology in Canberra.

7. This must be emphasized, since it is occasionally assumed that ethologists invariably conclude from the universality of a pattern that it must be innate.

8. The explanation given by Darwin (1859) cannot be supported by present data. It seems that the pattern derives from shaking something off, a motor pattern widespread in mammals and birds.

9. It is outside the scope of this review to deal with the IQ discussion.

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by **David P. Barash**

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Human ethology and human sociobiology. Professor Eibl-Eibesfeldt's excellent review makes it clear that human ethology has been making and will doubtless continue to make real contributions to our understanding of human behavior. However, I believe that rather than constituting *the* biology of human behavior, ethology's contribution will be more narrowly limited to methodologic innovation (in particular, detailed, non-participant observation) and the heuristic value of such terms as *releaser, IRM, fixed action pattern,* etc. Lorenzian ethology was of great value in emphasizing the role of innate factors in influencing behavior, and thus, in counterbalancing the American swing toward behaviorism during the first half of the twentieth century. But is has not provided the firm, conceptual underpinnings likely to carry the field from a description and ordering of behavior to a profound understanding of it. By contrast, the direct application of evolutionary biology to behavior – human as well as infra-human – offers just this possibility. The current amalgam of ethology, ecology, and evolutionary genetics has come to be called sociobiology (Wilson, *op. cit.,* 1975; Barash, 1977) and although we could argue interminably over whether ethology is a subset of sociobiology or *vice versa,* it seems clear to me that the exciting frontier of behavioral biology lies at this intersection of behavior and natural selection.

Borrowing from anthropologists Tiger and Fox (1972), E-E suggests that human ethology will reveal the "biogrammar" that underlies our behavior. His metaphor is somewhat mistaken: human ethology will help compile the lexicon of human behavior, but the grammar itself – the deep structural rules that underlie the organization of behavioral "sentences" – comes from natural selection and its direct application to behavior; accordingly, it is likely to be most clearly revealed by sociobiology. Insofar as particular releasers, fixed action patterns, and IRM's occur in the human behavioral repertoire, we may than ask why they are organized in this way rather than another. Thus, why are certain behaviors more inflexible than others, why do they emerge when and as they do, and why does our biogrammar predispose us to organize these building blocks into the recognizably pan-human behavior that characterizes all of *Homo sapiens*?

E-E's emphasis on "phylogenetic adaptation" appropriately highlights ethology's static rather than dynamic use of evolution. I agree with him that human ethology will help reveal a "structuring role" for behavior, but the discipline has been discouragingly unsuccessful in telling us why one structure is preferred over another. Thus, the author speaks of the value of human ethology in elucidating "social interaction strategies" while conspicuously omitting any discussion of "strategies for what?" My Random House dictionary defines strategy as a "plan, method or series of maneuvers for obtaining a specific goal or result." A sociobiologic perspective suggests that the goal is the maximization of inclusive fitness and that all behavior – including those details which are the focus of human ethology – serves as tactics directed toward that ultimate, strategic end. Thus, for example, the adaptive value of fear-of-strangers may possibly be inferred from its time of emergence: at six to eight months an infant is typically beginning to crawl and likely to encounter individuals less benevolently inclined than its mother. Similarly, Triver's (1971) discussion of reciprocity provides us with an analytic handle on sharing and gift-giving. Ethologic accounts of this phenomenon are important and, in fact, necessary; but without the conceptual power provided by sociobiology, such research comes perilously close to intellectual stamp-collecting. On the other hand, by combining the data of human ethology, anthropology, psychology, and sociology with sociobiology's growing insights into evolution as a *mechanism*, a real science of human behavior may well be in sight (Barash, in press; Wilson, 1978; van den Berghe, 1978; Chagnon and Irons, 1978; Alexander, 1977; van den Berghe and Barash, 1977).

Finally, I must also take issue with some of E-E's concluding statements regarding sociobiology itself. For example, we simply do not know whether group selection took place during the evolution of *Homo sapiens*. It is a possibility (Alexander, 1971), and mathematical models have suggested various conditions under which group selection (Levins, 1970; Boorman and Levitt, 1973) or a variant of it (D. S. Wilson, 1977; Wade, 1977; Bell, 1978) could occur. However, the theoretical arguments against group selection remain cogent (Williams, 1966, 1971; Wiens, 1966) and the received wisdom, at present, is that individual selection is likely to have been more important in shaping our nature, both physical and behavioral.

In summary, my criticisms should not be taken as a negative view of human ethology or E-E's review of it. This is a valuable summary of a useful tool in our efforts to understand ourselves. Like most tools, however, human ethology will be most constructive when wielded with an eye toward the overall, evolutionary blueprint for behavior.

by Jerome H. Barkow

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Human ethology: Empirical wealth, theoretical dearth. E-E's work is interesting for his empirical rather than his theoretical contributions. Most researchers have by now lost interest in the nature/nurture false dichotomy, and few still find useful the hydraulic model of classical ethology. E-E, even while declaring natural selection to be the theoretical context of his work, remains capable of discussing the child's tendency to initiate social relationships by offering objects, without referring to Triver's (1971) idea of reciprocal altruism. But just as E-E's keen eye (and camera) for motoric stereotypies across species and cultures in this case provide data relevant to Triver's theory, so does his corpus as a whole provide scarce data for the development of a general evolutionary theory of *Homo sapiens* and his cultures. It is true that E-E's conception of human ethology neglects feeling states and verbal and symbolic behavior in favor of the physical movements that are the primary data for the animal ethology from which his approach derives, but this limitation does not destroy the usefulness of the data he does collect.

For example, E-E documents the similarities between the rituals observed by ethologists and those observed by cultural anthropologists, similarities that should be taken into account by theorists concerned with the relationship of biological to cultural evolution (e.g., Barkow, forthcoming; Campbell, 1975; Cloak, 1975; Durham, 1976; Richerson and Boyd, 1978). His observations appear to support those, like Campbell (1975) and Cloak (1975), who would argue that both types of evolution are based on a similar blind-variation + selective-retention process, challenging those who would stress the importance of human rationality in cultural evolution (e.g., Boehm, 1978). From this theoretical perspective, the next question E-E and others concerned with ritual might ask would be what the unit of selection is: the gene (or group of coordinated genes) for animal rituals, perhaps, but then what is the unit of human ritual itself?

Other theoretical questions are raised by E-E's suggestion that cultural rituals seem at times to be highly elaborated versions of the behaviors of small children. Assuming that this observation is supported by future research, one wonders just how much of the cross-cultural similarity in human adult behavior can be explained by it. Could it be that many cross-cultural differences in adult behavior arise from different cultures having patterned action in terms of different aspects of the child's repertory? At a more mundane level, what is the relationship between inclusive fitness and such behaviors as the young child's turning his head away in rejection? How would we demonstrate such a relationship empirically?

The *Human Ethology Newsletter*[1] often includes efforts to define that discipline, efforts similar to those of E-E. But the need to define and redefine academic disciplines seems more a requirement of university curriculum committees than of active scholars and scientists, particularly those working in the context of evolutionary theory. The latter framework derives much of its power from its breadth, and the recent efforts to include within it the behavior of our own species are to be applauded. Let us get on with that work, and be distracted neither by definers of disciplines nor by environmental and genetic reductionists.

NOTE

[1] Those interested in receiving the *Human Ethology Newsletter* should write to Dr. Cheryl Travis, Department of Psychology, The University of Tennessee, Knoxville, TN 37916.

by Burton Benedict

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The dangers of analogy in human ethology. Chimps and children, gulls and Greeks, boobies and Balinese – the ethologists go on their merry way, comparing bits of human cultural behavior with bits of the genetically programmed behavior of sticklebacks, swamp sparrows, and chaffinches. Of course, it all depends on the questions one wants to ask. Humans are animals and they share certain anatomical features with other animals, more with those to whom they are closely related, like chimpanzees, than with those distantly related, like sticklebacks. Anatomy implies function and function implies behavior, but though the analogical game is fun (Washburn, 1978), it can seriously mislead if we fail to look at the whole context of which a particular item of behavior is a part. Thus E-E compares the presentation of a twig by a cormorant returning to his nest with gift-giving in man. Yet, if we are going to play analogies, the presentation of the twig by the cormorant simply inhibits attack and is comparable to other greeting or appeasement rituals found in many species of birds. Gift-giving in man, however, is concerned with the creation, continuance, or termination of *obligations* (Mauss, 1925). It has direction and purpose. It can appease, insult, bind, or terminate subsequent actions. It not only differs in form from culture to culture, but within the same culture in various social contexts. It depends on the use of language. It is embedded in a wide variety of institutions. Everything that is significant about it derives from its social context, not from an isolated piece of behavior.

Another danger of analogy is the comparison of species-specific behavior in nonhuman animals with culture-specific behavior in humans. Thus E-E compares the phallic displays of vervet monkeys with those of the Eipo of New Guinea; but very many cultures do not use such displays, and even where they are used, they do not have similar meanings. Again the social context in which phallic displays are used by human groups is glossed over.

The problem is compounded when E-E starts comparing human artifacts with features of the anatomy of nonhuman animals. Thus the lifting of a booby's beak is compared with a Masai thrusting his spear into the ground and with a twenty-one gun salute with guns averted. But boobies carry their beaks with them always and even Masai do not always carry spears. Spears are manufactured by some men in some societies, they are not a universal human feature. As for twenty-one gun salutes, they involve an elaborate institutional system redolent with many kinds of symbolism. The behavior which goes with spears or twenty-one gun salutes is not reducible to the behavior exhibited by a sky-pointing booby. Human social behavior depends on language, and this implies tradition, knowledge, belief, law morals, art, and so on. Booby sky-pointing does not depend on any of these. Ethologists can remind us (for they are writing for humans) that we are animals, and this is useful for its sets the biological and behavioral limits in which humans operate; but beyond this they can do little until they start to study humans as language-using animals [see also "Cognition and Consciousness in Nonhuman Species" *BBS* 1(4) 1978].

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A confusion about innateness. E-E argues that "what is innate to man is not a negligible quantity, but of fundamental importance, in particular with respect to social behavior." But what does he mean by "innate?" He tells us quite explicitly. He says that every adaptation involves the acquisition of information, and that when a system has acquired information, "it is legitimate to ask for the source of the . . . information." Sources of information for biological systems can be divided into two categories: (1) "acquisition of information can take place during phylogeny," in which case the information (and the behavioral capacities it underlies) are *innate*, or (2) information can be acquired during "cultural evolution and on the basis of individual experience," in which case "learning is involved." In sum, a characteristic is innate just in case "the acquired information is stored in the genome of the species and decoded during ontogeny."

So far, I make no complaints.[1] Conceptual problems lurk in every corner, but perhaps empirical investigation and theory construction can skirt them, at least for the time being. The confusion I want to talk about occurs later. After presenting evidence for innateness of various human characteristics, including aggression, E-E says:

> ". . . aggression constitutes a problem for cultures like the Kalahari bushmen, who pursue pacific ideals. Although they fight it by education, they cannot prevent aggression and rivalry from occuring in early childhood. They likewise employ special strategies to achieve a fairly egalitarian group structure, but again possessiveness and striving for rank are problems with which they must cope. Were these inclinations merely a result of cultural imprinting, they would hardly show up in cultures that explicitly sought to pursue different ideals and attempted to socialize their children accordingly. Different cultures thus provide the natural experiments from which we can learn that certain human behavioral traits show resistance to the shaping effects of the environment."

In context, it is clear what E-E wants to say is that *the reason* that aggression is resistant to change is that it is innate. Later in the discussion, he repeatedly makes remarks such as:

> "Proponents of a rigid environmentalism should be aware of the dangers that may arise from the neglect of human nature. Educational programs based upon exclusively environmentalist ideologies run the risk of being inhuman by imposing unnecessary frustrations. . . ."

Though it is never stated explicitly, the upshot of E-E's remarks is as follows: (1) many aspects of human mentality and behavior patterns are innate; (2) what is innate is resistant to change, and changeable only at a cost; and therefore (3) makers of social and educational policy ignore evidence of innateness at their peril.

The confusion I am after lies in (2). Innateness *per se* has nothing to do with "resistance to the shaping effects of the environment." An innate characteristic need not be resistant to change, and innateness provides no evidence for such resistance. Suppose, for example, that I have the information that plants with a certain appearance are likely to be edible. Where did this information come from? One possibility is that this information is learned in one way or another. For example, I may have had experience with many varieties of plants, and have always found this type to be good eating. Or I may have had no experience with this type of plant, but rather absorbed the belief from my cultural environment. However, it may also be that the information is innate, a product of the history of my species, and coded in my genes. But notice that the inateness hypothesis and the learning hypothesis *do not differ* in predictions about the plasticity of my belief or my behavior. If the belief is acquired through learning but is deeply entrenched in the ritual, myth, and symbolism of my culture, I may find it nearly impossible to accept evidence that the plant is not edible. On the other hand, the belief may be innate, yet easily eradicated by a few unpleasant experiences with such plants. I repeat: the source of the information in the genes or in the environment does not by itself determine the "fixity" of the belief.

The missing idea in E-E's discussion, as in so many discussions of genetic determination (see Lewontin, 1976 and Block and Dworkin, 1974) is the idea of a "norm of reaction." The norm of reaction for a behavioral variable (or any other characteristic) can be defined as the function that maps environmental and genotypic variables into the behavioral variable. For example, a plant of one genotype may do well at high altitudes and poorly at low altitudes, while another genotype may react to the environment in just the opposite manner. This idea is illustrated in Figure 1.

The earlier example concerning plant edibility is easily expressible in terms of the norm of reaction. If the belief is innate, then the norm of reaction may reflect this fact by mapping environments that lack evidence about edibility into (phenotypic) belief in the edibility of the plant (see Figure 2). If the information about edibility is genetically coded, then we can have *knowledge without evidence* – though, of course, something analogous to the acquisition of evidence would have occurred during phylogeny. But while the norm of reaction may thus reflect innateness, *it may also reflect malleability.* For it may also map environments that provide evidence of *non*edibility into actual belief in the nonedibility of the plant. This situation is also represented by the hypothetical norm of reaction in Figure 2. Further, as Figure 2 also indicates, a very small change in environment can cause a very large change in actual characteristics of organisms, even when the characteristic undergoing change is innate. Of course, for human characteristics – including those known to be substantially innate – we have little knowledge of the norms of reaction or of the relevant environmental parameters, and thus little theoretical knowledge relevant to malleability.

Note that I am not challenging E-E's claim that aggression is hard to eradicate. What I am insisting on, however, is that even if aggression is hard to eradicate

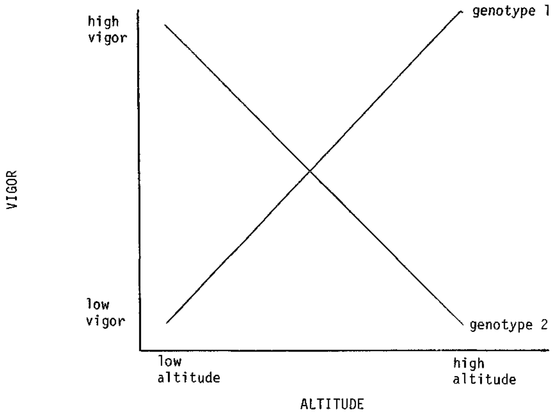

Figure 1 (Block).

and also innate,[2] the latter need not be the cause of the former. Consider, for example, E-E's discussion of aggression among the Bushmen. Assuming that adult Bushmen *do* exhibit aggression – If they do not, we have a malleability success story – the fact that they are not wholly pacific may be a crucial determinant of the next generation's aggression. For the norm of reaction for aggression may be such that any child raised in the context of genuinely pacific adults becomes genuinely pacific throughout his life. For example, the genetic program may amount to "Be aggressive unless adults around you are not aggressive, in which case, imitate them." So aggression could be innate, yet vanish without a trace in certain environments. It could have a norm of reaction analogous to that in Figure 2.

This point leads naturally to a comment on the notion of *potential* that bedevils the thinking of biologists about genetic determination. (E-E says that "what is inherited is a 'prospective potential.' ") It is tempting to believe that if a phenotypic disposition is innate in an organism with a certain genome, then an organism with that genome must inevitably have that disposition, even when the environment is such as to prevent the disposition from being realized. In environments in which the disposition is not realized, it is thought of as "potential." Thus, if human aggression is innate, many biologists would say that it must be present in any possible human society, *if only in potential.* But the innateness of aggression may consist only in a genetic instruction to develop aggression during childhood in certain circumstances; and *pacificity could be simultaneously innate as well,* in that the same gentically coded instruction may specify developing pacificity during other circumstances (see Figure 3). Yet it may not be possible for a pacific adult to become an aggressive adult or vice versa, if the environment has an effect only in childhood. So, in the sense of "potential" I am criticizing, pacificity and agression could both be potential in every human, even though no human who exemplified the one could switch over to the other. Such a sense of "potential" would seem more misleading than leading.

It should be clear that I do not accuse E-E of claiming that what is innate is

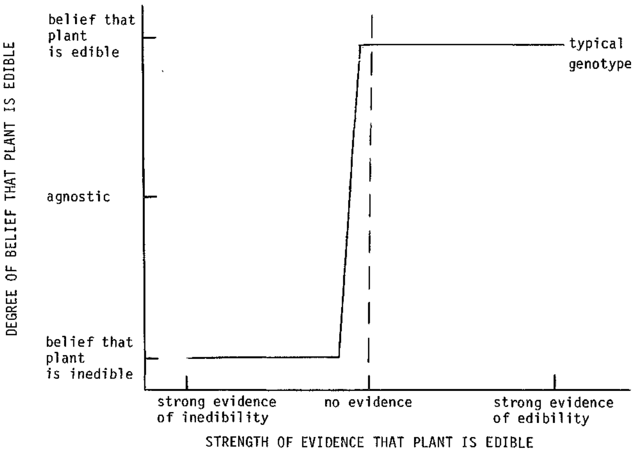

Figure 2 (Block).

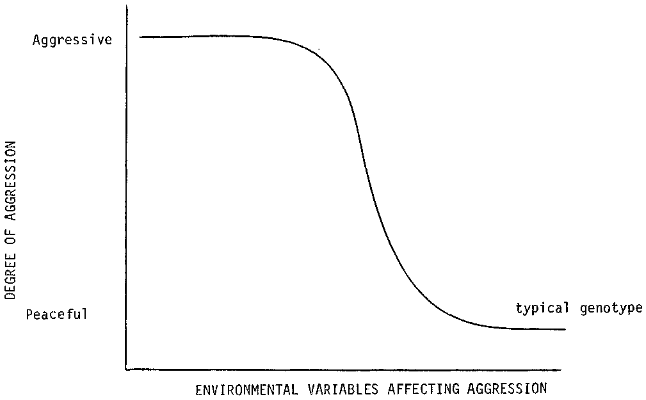

Figure 3 (Block).

utterly unchangeable. He explicitly denies this. His position, rather, is that what is innate inevitably resists change, and can be "suppressed" only at a cost. But, as Figure 2 illustrates, information can be innate, appearing in a belief in the absence of an environmental source, yet vanish totally in environments that present contrary information. So what is innate need not resist change, and if changed, need not cause "frustration."

Objection: your point is a purely theoretical one of no practical import. For while you are right that what is innate *need* not resist change, the fact is that what is innate *does* resist change.

Reply: I know of no evidence for such a claim; E-E certainly presents none in his article. Some innate characteristics resist change, others do not. Down's syndrome idiocy resists environmental intervention; phenylpyruvic idiocy does not. But both are gentically caused. Another example: if suspended in mid-air with no visible means of support, newborn kittens and babies seem to expect and fear that they will fall (as is indicated by "visual cliff" experiments). This result suggests an innate expectation of falling in response to certain configurations of visual stimuli. But astronauts report that such visually stimulated expectation and fear disappear quickly in no-gravity situations. Further, with acquired characteristics as with innate ones, some resist change while others do not. What is relevant to malleability is not innateness *per se* but rather the mechanisms of genetic determination, and the available means of environmental manipulation.

Of course, lack of gravity is not an environment common in the course of evolution, and this is part of what makes it useful for my purposes. It is of the nature of innate information to be realized in a range of circumstances common in our evolutionary history. But this fact provides no objection to what I have been saying. For purposes of social and educational policy, what we are typically interested in is the effect of *uncommon* environments. The social and educational policy issues in which considerations of innateness are typically brought to bear are cases in which what is in question is whether we can change the environment so as to change human attitudes or patterns of behavior. That is why innateness is a red herring as far as issues of social policy are concerned. The claim that aggression is innate, or that sex-role attitudes are innate is at best irrelevant. For even if true, its only policy implication is that in circumstances relevantly similar to those common in our evolutionary history, these characteristics occur. And without a specification of what relevant similarity comes to, this information adds nothing to what we already know. What we want to know for practical purposes is what sorts of departures from the hunter-gatherer environments in which human evolution took place can *make a* difference. To be told that such and such characteristics are innate is of no help.

The irrelevance of considerations of innateness to social policy is strikingly revealed in E-E's discussion of anonymity. He says:

> "Anonymity, for example, has been found to impose a strain on man. Oblivious of this, certain educational schemes involving the elimination of the original classroom community are at present being tried out in central Europe on a large scale . . . Educational ideologists continue to proceed as if humanity were just wax in the hands of its shapers."

Note, however, that what is relevant to social policy here is not innateness, but rather the *observation* that anonymity imposes a strain.

Given our boundless ignorance about the nature of aggression, sex-role attitudes, and so forth, and the environmental variables relevant to these characteristics, the best way to find out whether they can be changed is to *try to change them.* Comments by ethologists and others to the effect that such characteristics are innate and therefore resist change serve only to mislead us.[3]

ACKNOWLEDGMENTS

I am grateful to Richard Boyd, Susan Carey, Jerry Fodor, Paul Horwich, Dan Osherson, and Zenon Pylyshyn for comments on these ideas.

NOTES

1. Not that I don't *have* any complaints. For example, I have some qualms about the notion of genetic coding of information. Note that any pebble on the beach can be a gene for some logically possible creature. Of course, any sequence of scribbles is meaningful writing according to some logically possible system of orthography, but this point does not quiet my qualms, since the information required to decode writing lies in the decoder, while the information required to decode the genetic code is itself coded in the genes. Another qualm has to do with the extension of E-E's "information in the genes" account of innateness from states that have propositional content (such as belief) to states that have no propositional content, such as aggression. To the extent that aggression depends on information, all sorts of other characteristics – including peacefulness – may involve the *same* information.

2. As mentioned in the last two sentences of note 1, it is not clear that talk of innateness of aggression makes sense, on E-E's analysis of innateness. Perhaps one can broaden the "information in the genes" account, making it a "programmed in the genes" or "caused by the genes" account. If we can make sense of the idea that aggression is caused by or programmed in the genes, then we can make sense of the idea that aggression is innate. Since causation is a notoriously pragmatic notion, identifying innateness with genetic causation would make innateness a pragmatic notion as well.

3. I want to warn briefly against an enormously widespread confusion that E-E does *not* fall prey to, the confusion of *innate* with *heritable.* A characteristic is heritable if variation in it is caused by genetic variation. If identical twins, randomly placed in environments in the populaion, tend to have similar heights, that is evidence for the heritability of height. To see the difference between heritability and innateness, note that the number of legs is innate, but probably has *low* heritability, since probably its variation is mainly due to the distribution of environmental accidents. Heritability of number of legs is a matter of genetic causation of *differences* in number of legs in a population. Innateness, by contrast, is a matter of genetic determination of the number of legs itself. Heritability is a population statistic (like birth rate), while innateness is not.

by Robert C. Bolles

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The functional significance of behavior. I find it odd that E-E invests so much of his effort here in trying to convince us that there really is a phylogenic component to human behavior. I find it curious that the nature/nurture question, which is now so widely dismissed by behavioral scientists (because everything is now known to depend upon both), might be revived just because some behavioral scientists have gotten interested in human behavior. I find it peculiar to encounter anew all the old arguments about the universality of traits, their appearance in neonates, and the evidence from deprivation experiments. Perhaps my disappointment with this aspect of the paper merely reflects my own bias that, of course, there are phylogenic components, and important ones, too, in human behavior. Perhaps it is only because I have no doubts about that point that I wish the paper had gotten on more with the proper business of ethology.

The proper business, or at least the customary business, of ethology, as I understand it, is not to demonstrate once again that there is a phylogenic origin to some bit of behavior, but rather to show what the functional significance of the behavior is. Part of its significance can be revealed by an analysis of its motivational status, that is, by showing to what system the behavior belongs. What is the coy girl *doing* when she is being coy? Is she avoiding excessive social stimulation, (i.e., too much contact)? Or is she asking for more? Is she turning the other person off, or turning him on? Is the other person, the one who evokes the coyness, necessarily a male? For that matter, is coyness found only in girls? At a more general, or more molar or distal level, I wonder if coyness is a sexual thing, or only a social thing. Is the coy girl controlling a potential sexual relationship or only dealing with another human? Is this what E-E is calling a social interaction strategy? I wish he had elaborated that concept, because I suspect it may provide a very useful tool for looking at human behavior at an intermediate level of analysis. Then there is the ultimate functional question of how coyness contributes to fitness. If girls are coy because that is an "instinctive" reaction to male attention, then coy girls must have (or at one time must have had) some advantage over straight-talking, look-you-in-the-eye girls. They must select better mates with more resources, or be more attractive to such potential mates, or form more permanent pair-bonds, or something. How does coyness confer such an advantage? In short, what is the functional significance of coyness?

If some distinctive behavior actually has a phylogenic origin, then we may suppose that it has (or has had) some functional significance, and that it has benefited those who had it. But if we find some distinctive behavior that has a cultural origin, then it may or may not be functionally important; it could be just a cultural ritual that does neither good nor harm to anyone. It is hazardous indeed to suppose that a particular ritual reflects some continuing adaptation to the cultural niche, or that it confers any advantage upon those who practice it. E-E describes a ritual dance performed by young couples in New Guinea, which is said to play a role in mate selection. Do young people there really select mates on the basis of this dance? Or do they pair off the same way every one else does it, on the basis of propinquity and availability?

Or consider the eyebrow flash. The author had convinced me with his earlier writings that the eyebrow flash is as characteristic a human behavioral trait as having hairy eyebrows is a morphological trait. Now he tells me that the Japanese learn to suppress it. I am stunned. I now have to wonder about all the non-Japanese cultures; is it possible that we all learned it? I worry about the Japanese; how could they forego such a beautiful, expressive gesture? And why don't they see it as beautiful and expressive? Worse yet, are they likely to become extinct because they no longer have whatever advantage the eyebrow flash conferred upon all the rest of us (it must have been advantageous or we would not all have it, right)? But how can 100 million Japanese become extinct? For that matter, how could there be 100 million Japanese if they have such a handicap? The answer must lie in different selection pressures. The unique Japanese response must be an optimal adaptation to a unique environment (or there would not be 100 million of them), just as having the eyebrow flash must have been optimal for everyone else in the common environment that shaped everyone else. What was that unique environmental pressure that made nonflashing so successful? What does the eyebrow flash have to do with fitness, anyway? What are we talking about? Let us get on with the business of ethology.

by Gerald Borgia

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Levels of selection and human ethology. The first part of this commentary focuses on the last section of E-E's paper in which he describes his views on the relation of the various levels at which natural selection might operate and the study of human behavior. Although this represents a very small part of the material presented, this information is critical to my subsequent evaluation of the overview of human ethology he presents.

E-E correctly rejects the "survival of the species" notion which "ethologists have for a long time used" and he nominally embraces the inclusive fitness model as a means for explaining "altruistic" behavior. There is, however, some confusion in his presentation of this model, and, together with his inordinate reliance on models of group selection, he provides a rather curious view of patterns of benefit transfer in which "investment should pay off to any group member and not just immediate kin." What he views as man's tendency toward self-sacrifice, and a problem in the common interpretation of the inclusive fitness model, are the reasons he cites for this tendency toward group-wide altruism. But there are other means of explaining apparent self-sacrifice that are more likely and involve individuals maximizing inclusive fitness without relying on differential group extinction. This is significant because Williams (1966) provided cogent arguments concerning the unlikelihood of group selection as a source of adaptation when it conflicts with individual interests. Moreover, individual competition for mates, wealth, and status dominate social interactions in most human groups (Murdock, 1949). Such behavior implies much less within-group harmony than intimated by E-E and could be expected had group selection molded patterns of social interaction.

Although E-E accepts the inclusive fitness model, there appears to be a basic misunderstanding about how it operates. He cites a study which gives it strong support (Massey, *op. cit.* 1977) but then argues that "To reckon only on the 50 percent of genes that a person shares with his full sibling, or parent, or child . . . is to oversimplify matters . . . the majority of a person's genes are shared with any other member of the group." There is a flaw in this argument which comes from the suggestion that the absolute level of genetic overlap between individuals should be used as the criterion of optimality for distributing benefits, rather than the relationship as calculated by identity in terms of descent. Hamilton (*op. cit.* 1964) pointed out that ordering benefit-giving priority according to identity by descent gives the most evolutionary stable pattern for beneficent behavior. Alleles specifying different patterns of beneficence are assumed to be in competition. Those that follow the pattern Hamilton specified gain most, on the average, from the combined effects of likewise beneficent copies of themselves while not wasting aid on potential competitors, and therefore become dominant in natural populations. (Seemingly indiscriminate beneficence within breeding units might also evolve were alleles able to recognize and direct benefits toward identical copies in other individuals, but such a pattern seems unlikely; see Hamilton, 1964; Alexander and Borgia, 1978.)

These considerations suggest that, contrary to E-E's suggestion, individuals commonly discriminate in aid-giving within social groups, and group selection cannot be considered the dominant force in shaping patterns of behavioral adaptation in human populations.

Consistent application of E-E's view that all members of a group exchange benefits without regard to differences in relationship leads to some curious predictions about intragroup behavior. For instance, one is disposed to assume that aggression within groups is initiated because of anticipated advantage to the aggressor which ultimately allows him to gain control of some scarce resource. However, strict adherence to the notion that human behavior is a product of group selection causes us to surmise that this behavior occurs for an entirely different reason. We might guess, for instance, that aggression functions to equalize the distribution of resources among group members. The lack of discussion of the functional significance of many supposed adaptations, together with ambiguity caused by E-E's assumptions about levels of selection, prevent the reader from correctly understanding his intent, particularly where there are several possible explanations for a behavior. Such problems intensify if one attempts to test some of the proposed models.

E-E uses common ethological terms such as appeasement, canalized aggression, and agonistic buffering, which were in use before the concept of inclusive fitness was generally applied to behavioral models. These were defined in terms of species or group level adaptation, and may hence refer to functions that were of putative benefit to the group or even to mechanisms whose existence would not be predicted if selection were considered only at lower levels. The use of these terms leads to ambiguity in the discussion of the adaptive basis of behavior.

For example, when E-E says that smiling or gaze aversion "blocks aggression," does he mean that expression of these facial gestures by a girl toward a boy who had previously hit her makes that boy *incapable* of hitting her again? We have to consider how this gesture might cause the boy not to strike her. Does he refrain from attack because the gesture communicates (1) that she is not a threat and has nothing he wants; (2) that she will report the attack to a higher authority and he will be punished; or (3) that she has been harmed and he has been programmed to avoid harming other group members? Unless we know why the boy refrains from hitting her, the term "blocks aggression" is meaningless, assuming that we are concerned with determining the evolutionary consequences of this act. Perhaps the only way to remove such ambiguity from behavioral analysis is to drop, or at least carefully redefine, much of the common ethological jargon.

E-E shows some concern about Wilson's (*op. cit.* 1975) claim that ethology will be incorporated as part of a new science to be called sociobiology. What we label the study of behavior seems relatively unimportant compared to the need to produce a discipline that develops testable predictive models of behavior. The continued use of ethology as a label for the study of behavior will depend on how successfully those who call themselves ethologists apply advances in selection theory to the study of behavior.

by William R. Charlesworth

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"It's true, but we don't know why:" Problems in validating human ethological hypotheses. E-E's paper represents in summary form a great portion of his total effort in the field of human ethology: the themes, arguments, illustrations, and photos will be familiar to those who have kept up with his work over the past ten years. During this time, E-E has logged at least 15,000 hours in the field filming human behavior in many different cultures, and he has spent at least twice that much time analyzing films. This vast and singular effort qualifies for serious consideration his claim as to the universality of certain behavior patterns.

In my opinion, there is no question that E-E has identified universal human behaviors. I recognize them on film and in vivo, and am confident that because of such universal behaviors people manage, despite great cultural and linguistic differences, to get along with each other at tourist resorts, in United Nations assemblies, and in close quarters on transcontinental trains. Actually, it is odd that behavioral scientists have not documented universal human behaviors earlier. For thousands of years people have been adapting to each other regardless of geographic and cultural differences. This should be a strong enough hint that humans all over share a basic grammar of behavior and behavior recognition. E-E's documents should dispel any doubt as to the existence of this grammar (or at least of some important words in the lexicon of behaviors regulated by this grammar). Of course, many may wish for more rigor in subject sampling (a larger, stratified/random sample?), inclusion of all noninstances of universal behavior, more information on the meaning of the social event for the persons involved, blind scoring of the filmed behavior, and generally more evidence that E-E uses objective, systematic methods for collecting and analyzing his records of behavior. It is to be hoped that, these desiderata will be satisfied in the future. In the meantime, E-E has mustered enough evidence to support his claim of behavioral universals. Why or how these universals have come to exist, though, is a different matter.

E-E's research strength is in documentation and discovery, and for this he should be given ample credit. He should not be given credit, however, for validating his hypothesis concerning the functional value of universal behaviors and the origin of the causal mechanisms underlying them. His hypothesis can be seen as twofold: (1) the causal mechanisms underlying behavioral universals involve brain structures whose construction during ontogenesis is more or less tightly controlled by genetic programs; and (2) the genetic programs are products of phylogenetic adaptations that evolved because the behaviors controlled by the programs were of positive functional value to all surviving species' members. Both parts of this hypothesis are plausible and make more sense than the hypothesis that geographically or culturally isolated peoples independently invent and pass on behavior patterns that enable them, by happy coincidence, to communicate with total strangers. However, neither E-E's hypothesis nor the alternative can be tested by documenting behaviors on film, discovering that the behaviors occur early in ontogenesis or in perceptually handicapped individuals, and then making inferences about their functions and origins. Actually, I see no way at present to test either E-E's hypothesis or the alternative in any rigorous manner. To do so one would have to carry out tightly controlled genetic/developmental/ecologic studies that are currently impossible or unethical to carry out with humans.

Unfortunately, E-E gives the impression throughout his paper that his hypothesis has substantial empirical support. Actually it does not. For example, in discussing function he claims that certain behavior patterns, such as eyebrow raising or the complex courtship ritual of the "Tanim Hed," serve particular vital functions. But what kind of evidence is there for this claim? Establishing the function of behavior is primarily an experimental task, and not an easy one at that, especially when complicated subjects such as humans are involved. It is an impossible task when only descriptions and "correlations" are involved. In most, if not all, of the examples E-E cites there is no experimental evidence for function, at least not in the sense of the term "experimental" as used by most biologists and psychologists.

E-E gets into further difficulty when he discusses the origin of universal behaviors within or across species. For example, he accounts for similarities in behavior between sky-pointing bobies, spear-wielding Massai, and twenty-one gun saluters by noting that they are "due rather to similar selective pressures that have shaped behavior during phylogenetic and cultural evolution alike, or else to a common heritage resulting from a shared ancestor." This is a very strong claim, which is not substantiated. Selection pressures are usually very difficult to identify with any certainty (especially in times long past) and establishing similarities between phylogenetic pressures and cultural pressures seems impossible because the underlying mechanisms (one physical, the other symbolic) are so different. And, as we know from zoology, establishing homologies is no easy matter, especially when behavior is involved.

E-E's difficulties magnify when he claims that similar patterns of maternal care and infantile appeals in birds and man "are derived from parental behavior," or that kissing derives from mouth-to-mouth feeding. Developmental derivations of behavior are virtually impossible to demonstrate with any certainty in humans because of the complicated causal networks involved. These networks contain numerous uncontrollable neurophysiological and muscle maturational factors which interact with numerous, usually unspecified, environmental and psychological factors – all operating over relatively long periods of time, which further complicates matters. For example, developmental psychologists are only beginning to chart systematically the ontogenetic pathways of such important human behavioral phenomena as infant attachment [see Rajecki et al.: "Toward a General Theory of Infantile Attachment" *BBS* 1(3) 1978], object and event concepts, and aggressive and prosocial behaviors, and have only minimal knowledge as to what maturational, environmental, and experiential mechanisms are implicated in their appearance and changes at different ages [see Brainerd: "The Stage Question in Cognitive-Developmental Theory" BBS 1(2) 1978].

One concluding point. What is conspicuously missing in E-E's reports is evidence of variability in the behavioral patterns he has observed. It is to be hoped that he will, in the near future, give us some idea of the frequency of behavioral variations or nonuniversal patterns that people in different cultures (or even within the same culture) engage in when confronted with the same social situation. Variations are the main source of evolutionary change, whether phylogenetic or cultural, and it would be surprising indeed if they did not turn up in such extensive studies of unstaged social behavior as E-E's. It should be quickly pointed out that differences by themselves support neither a phylogenetic nor a cultural explanation of their origin. Variances and invariances can be due predominantly to nature or predominantly to nurture. Now that E-E has established an important truth about the existence of behavioral universals, one hopes that ethologists will begin to put more emphasis upon studying the interaction of both nature and nurture during ontogenesis. This will help us understand better why behavioral universals exist.

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I am grateful to Judith Langlois for her helpful remarks and suggestions concerning this comment.

by **José M. R. Delgado**

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Cerebral building blocks and behavioral mechanisms. Genetic heritage and instincts are obviously important elements in the organization of cerebral mechanisms of behavior, but the age-old debate of nature versus nurture, its dichotomy of percentages (50–50?), and the possible existence of a unique human nature are losing scientific interest. The present trend is to be more specific in the study of the origin, properties, and consequences of the multifactor building blocks that intervene in the organization of the cerebral mechanisms of *each behavioral category*. These elements are different in visual perception, food intake, aggression, and other aspects of behavior. Generalizations may be misleading. Phylogeny is an important but not an exclusive factor.

One of the merits of the work of E-E is his careful analysis of specific patterns of behavior: kiss-feeding may be the instinctive origin of a tender human kiss and may be investigated in birds, apes, and man. Aggressive behavior may have comparable rituals throughout the animal kingdom. Innate releasing mechanisms can be studied in socially isolated monkeys, and there is preprogramming of some types of behavior by early imprinting. These facts do not validate extensive generalizations as to the importance of instincts as bases of human behavior, however, and the example of phallic displays is a case in point. Observations on such displays in monkeys and apes as a sign of domination, and similar practices in some primitive tribes, are of limited value in analyzing behavior in civilized societies. Similar comments apply to the study of fear of strangers, attention seeking, giving and sharing, which are all very interesting, but represent only a small part of the normal behavioral repertoire. The study of primitive societies is central for anthropological research and may provide excellent data for the understanding of specific aspects of behavior, but it should be parallelled by complementary and extensive research concerning many other behavioral characteristics typical of civilized societies. Precisely the aspects that characterize our present age but often escape anthropological interest are the scientific, technical, and industrial development of human activities which provide nature with human purpose and constitute decisive determinants in the evolution of our surroundings. Nature is being changed as man creates artificial environments. It is for this reason that the concept of "human ethology" is controversial.

The biology of animal behavior is usually investigated in the following situations. (a) Ethological studies are performed in the field where the natural spontaneity of behavior is preserved. The handicap is that observations may be interrupted by unforeseen circumstances, experimental planning is limited, and recording of biological data is rather difficult. (b) Laboratory studies are conducted in well-controlled environments; experiments may be carefully designed; and animals are continuously accessible for recording, stimulation, and other manipulations. The artificiality of the laboratory situation may distort animal behavior and great caution is necessary in the interpretation of results. (c) To bridge ethological and laboratory research, the use of intermediate, designed environments has been proposed and the same groups of animals have been investigated in the laboratory as well as in a seminatural setting (Delgado et al., 1978).

The interest in studying "the biology of human behavior" is evident, but to name this discipline *human ethology*" with its methodology and theory derived from the parent discipline" may not be correct. The distinction between the natural setting and artificial surroundings, characteristic of ethological and laboratory research respectively, is clear cut in most animal studies but cannot be applied to man.

Nature provides elements of uniformity and ecological dependence for animal life while the artificiality of civilization – from temporary nomadic settlements to huge metropolises – cannot be equated with "natural" ethological environments. Genetic heritage and instincts should not be confused with "natural settings."

In the study of the building blocks responsible for the organization of behavioral mechanisms, there are essential aspects which deserve greater attention and which may be exemplified by the human acquisition of motor skills. These skills are not instinctive or dormant somewhere in the brain, only waiting to be unveiled. The newborn brain does not have the anatomical support, functional mechanisms, or experiential background for skillful mobility. Each of these three elements is essential for motor skills to appear. The crucial fact is that the anatomical and functional development of the brain proceeds by genetic determination but *under the guidance of sensory experience*. Learning leaves material traces in the neuronal tissue, influencing synaptic anatomy, enzymatic activity, functional selectivity of pathways, and the chemical composition of the neurons.

Initial learning will modify brain structures and transmitting systems, making possible further and more complex learning. At birth, the brain is so immature that its learning capacity is very limited. Mechanisms for skilled performance must be constructed inside the brain. The cerebral areas which organize hand movements may have the potential to learn the ideokinetic formulas necessary for playing musical instruments, but these abilities do not exist in the naive brain, nor will they be acquired without training. Motor coordination and skillful performance do not emerge from the brain but must be absorbed through the experience provided by sensory inputs entering the central nervous system, together with trial and error learning. The information received which alters neuronal function through feedback and correlational processes will later be *expressed* by the functioning brain.

In a similar way, the speech areas are undeveloped at birth and it is impossible for a newborn infant to learn to talk in a few days. Languages are not dormant somewhere in the brain. Many months of training are necessary for a baby to learn, very slowly at first, to parrot some words and then to comprehend their meanings and to start constructing phrases. Early sensory experience is decisive for the physiological organization of speech areas.

An essential aspect in learning is that the outside world enters through the senses, in the form of individual experience of a referential system, and becomes a material and functional part of the maturing brain. The central nervous system cannot functional properly independently of its essential extracerebral constituents. Symbols and information can be considered the transmaterial entities necessary for the anatomical and functional structuring of the functioning brain [See Puccetti & Dykes: "Sensory Cortex and the Mind-Brain Problem" *BBS* 1(3) 1978].

The flow of sensory information from the environment to the individual brain requires both material vehicles and transmaterial, coded symbols. Matter is a nonspecific element in sensory reception, while the coded symbols are specific messages whose exact meaning may be conveyed by different material vehicles such as light, sound, and shapes. The meaning is in itself independent of the eventual material carrier. The message has no gravitational field or inertia; it cannot be smashed to release energy; nor has it any of the accepted properties of matter. The meaning of a message has no intrinsic existence because in the absence of decoding mechanisms, symbols have no significance, although their material vehicles may persist.

Symbols may be shared by man and animals. Cats and monkeys can learn that a red light means punishment and a green light represents reward. Development of personality is primarily the experiential accumulation of symbols and frames of reference for decoding sensory information. Neurological processes are influenced by the transmaterial symbols of sensory perception, directing the material structure of neurons. In these neurological processes, there is interaction between transmaterial symbolism and material structuring of memory traces. The usefulness of the concept of "transmaterial" is that we must deal with it as a research tool when we explore intracerebral mechanisms. (For extensive discussion of this subject, see Delgado, 1979.)

In summary:

1. Understanding of the biology of human behavior requires a combined study of genetic heritage, anatomical substrate, functional mechanisms, and experiential information.
2. Human ethology is not comparable to animal ethology because of the importance of manmade qualities of the human environment.
3. Anatomical and functional development of the brain proceeds by genetic determination but under the guidance of sensory experience. Skills are not "unveiled": their mechanisms must be constructed inside the brain.
4. Sensory reception requires material vehicles plus transmaterial information which will influence the material formation of neuronal structures. Experimental study of the multiplicity of extracerebral elements which impinge on the neuronal organization of specific patterns of behavior is possible and desirable.

by Gordon E. Finley

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Cross-cultural methodology and ethological universals. For the cross-cultural psychologist, E-E has written an exciting and refreshing review. Certainly, every discipline evolves its own particular set of professional blinders and, almost be definition, for the cross-cultural psychologist this is the neglect of the biological determinants of behavior in favor of the cultural. As recently defined, "Cross-cultural research refers to empirical studies carried out among members of various cultural groups who have had different experiences that lead to predictable and significant differences in behavior" (Brislin, 1976, p. 215). Thus, E-E's hypothesis that "phylogenetic adaptations preprogram human behavior to a significant extent" ought to rekindle a lively debate. Further, viewing a variety of common behaviors (for example, greeting rituals, courtship behavior, fear of strangers, and aggression) in phylogenetic perspective certainly questions the omnipotence of culture in the shaping of human behavior.

However, an evaluation of E-E's position on universals is made difficult by the data base and by the data-gathering strategies with which it appears to have been obtained. My office dictionary defines "universal" as "a mode of behavior existing in *all* cultures . . . a culture trait characteristic of *all* normal adult members of a particular society" (italics added) (Webster, 1972). In the present review, one reads of extremely exciting and insightful examples. But E-E writes of *universal* phylogenetic adaptations. How many examples make a universal? Are similarities in detail sufficient evidence for universals [cf. Corballis & Morgan: "On the Biological Basis of Laterality" *BBS* 1(2) 1978]?

Ultimately, if the behaviors in question are truly under genetic control, then one would need only a few confirming examples to demonstrate the point and, after that, data gathering would be redundant, boring, and uninformative. But if the behavior is only partially, or not at all, under genetic control, then more systematic data gathering would be most informative.

Relevant here are four issues of sampling and selectivity. First, cultures. Selecting sample cultures to represent different stages of cultural evolution is a very reasonable strategy. But why vanishing cultures? What about surviving cultures and highly technological cultures? Second, behavior. Of all the behaviors engaged in by man, why were the present ones selected for study? Are there behaviors that the ethological approach cannot account for? And what is the background of behavioral *differences* in light of which we should evaluate the reported *similarities*? Third, individuals. Are comparable samples of subjects taken across cultures? Are there inter- or intra-individual differences? If so, what determines when, where, how frequently, and under what conditions the behaviors occur? Do we have a count? Fourth, units of analysis. Are not unstaged social interactions very difficult units to make equivalent across cultures?

Historically, cross-cultural psychology began with the reports of missionaries, traders, and adventurers who documented and described their experiences in interesting and exotic lands. Likewise, some of the earliest empirical work in developmental psychology consisted of baby biographies. The methodological implications of Kessen's critique of the baby biography literature may well be relevant for the early cross-cultural work as well as for the current ethological position: "Darwin, like almost every baby biographer after him, not only saw children, he also saw a living expression of his theoretical position" (Kessen, 1965, pp. 117–118). What data-gathering strategies are sufficient to establish a universal?

For the reader interrested in exploring methodological issues in cross-cultural psychology, good discussions can be found in a recent special issue of the *International Journal of Psychology* (Triandis, 1976) devoted to methodological problems of comparative research and in two forthcoming volumes of the *Handbook of Cross-Cultural Psychology* (Triandis and Berry, 1979). Finally, three much-discussed topics in cross-cultural psychology likely to be of interest to the ethologist are the competence/performance (Cole and Bruner, 1971) etic/emic (Brislin, 1976) dichotomies and the plausible rival hypothesis interpretive procedure (Campbell, 1969 [see also Rosenthal & Rubin: "Interpersonal Expectancy Effects" *BBS* 1(3) 1978]).

by Peter J. Fraser

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Analogy and dimensions of behaviour. It seems strange at first sight that the value of studying analogous behaviour requires great emphasis. However, adaptive value has frequently been put forward from superficial evidence to the total exclusion of useful comparison with analogous systems. The sabre-toothed tiger has often captured the imagination of the public as a ferocious predator attacking huge thick-skinned prey. A careful search for analogous canine adaptations in living mammals where function can be deduced from observation would quickly show the sabre teeth to be adaptations for digging, as in walruses. A behavioural pattern has less substance than a structural part. Perhaps difficulties in presenting behavioural patterns in a wide range of animals to a wide audience have prevented ready acceptance of analogies.

It is hard to argue against similarity of function for optokinetic or semicircular-canal induced eye movements in crabs, rabbits, or primates, including humans. Most people would agree that the eye movement behaviour of crabs is analogous to that of rabbits or humans. The eyes, the muscles that control them, and the semicircular canal systems of rabbits and primates are considered homologous. Are the eye movement behaviours homologous? Close examination of connection has shown that semicircular canal pathways are connected to different homologous muscles. The eyes of rabbits and primates are set at different angles with respect to the skull. Both rabbit and primate compensate for rotation in a plane by moving their eyes in that plane in a direction opposite to their rotation, but because homologous muscles in rabbits and primates move the eyes in different planes there has been a rearrangement of connection between a given (homologous) canal and given (homologous) muscles. The behaviour is thus fixed, but the homologous muscles are now used in different feedback loops (see papers in Kornhuber, 1974). Do we say that the behaviours are homologous and the pathways plastic? I am sure that if we demand homologous parts and pathways (as we must) as a necessary condition for complete homology of behaviour, then we shall be left with few examples. Thus similarities between behavioural patterns in very closely related groups may well turn out to be analogies rather than homologies, and this may open the door for a complete acceptance of the value of examining analogous behaviours. Few would dispute the value of studying eye movements in crustacea and rabbits and primates. The case for a hypothesized function for a behaviour is greatly strengthened if it can be seen to have been arrived at in several independent ways. We can then distinguish parts that are necessary and parts that are there simply because of the history of evolution.

How fixed is a fixed action pattern? The terms "fixed action pattern" and "innate releasing mechanism" are easily applied to the optokinetic reflex in crustacea and mammals. The reflex in these animals is so constant that it is often used to study the underlying sensory systems. Yet if you force a mammal to wear reversing prisms [See Gyr et al.: "Motor-Sensory Feedback and Geometry of Visual Space" *BBS*, this issue] or magnifying lenses, this quickly alters the gain of the system to compensate (Melvill Jones, 1977). The effect thus tends to be constant but the behaviour (as measured by the output) different. It is not possible to use a single output of a negative feedback loop to describe the loop. The weakness of the idea of a fixed action pattern is this use of merely the output to define the behaviour. Behaviours are often described as unitary where they clearly have a multicomponent basis.

E-E quotes von Holst as having described the "neurogenic motivation" underlying swimming in fish. What is meant by swimming? In common with all locomotion (and many other behaviours), all output parameters are vector quantities having direction as well as magnitude. We must ask in what direction the spinal eels swim. It must be recognized that swimming is a three-dimensional behaviour, whereas a single neural pathway is one-dimensional (from a simple consideration of vector coding in the nervous system, there must at least be three separate neurogenic networks underlying swimming; see Fraser, 1978a).

Ethologists have found it convenient to regard fixed action patterns and orientation as separate. This may be true where the fixed action pattern has signal value only, but where it is expressed as a vector parameter (e.g., swimming) the orientation must be considered part of the fixed action pattern, and we can recognize different dimensions for the control of behaviour. Thus, escape on the part of a worm is one-dimensional, involving two fixed action patterns mediated by appropriate groups of giant fibres defining the two directions of escape in a straight line. Crab swimming is a three-dimensional behaviour controlled by at least six pathways defining positive and negative directions of torque and force in three orthogonal planes (Fraser, 1978b). In all behaviour other than simple one-dimensional control without feedback, the behaviour cannot merely be described by the output. In the absence of complete detailed descriptions of behavioural output, control pathways and inputs, the behavioural scientist must use function to describe a behaviour, and hence must use analogous behaviour.

It seems to me that the basic uncertainties of the fixed action pattern concept partly outlined above, along with a cultural fear of deterministic behaviour, have prevented analogous behaviour from being accepted as a valid parameter to assess human behaviour.

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Has human ethology rediscovered Darwinism? As I have said before (Ghiselin, 1973), "The history of the assimilation of Darwinism has been the history of failure to assimilate Darwinism." Although E-E's contribution to some extent helps supply the deficiency, his approach would benefit from being still more Darwinian in substance. The same may be said of virtually all efforts to study behavior from an evolutionary point of view. It is hard to say whether evolutionary biology has suffered more from its "friends" or its "enemies." E-E delivers a few jabs at the opposition, but delivers not telling blows with respect to the emotional, philosophical, and ideological controversies. As with so much polemical literature, especially in this area, disagreements about fundamentals are handled as if they could be resolved with a modest amount of empirical data. Herein I can only touch upon some of the issues, but more extensive discussion has been provided elsewhere (Ghiselin, 1969, 1974a). Various matters will have to be passed over in silence, simply because there is not room enough to do justice to them. The relationships between germ and soma, phenotypic plasticity, modes of selection in social contexts, the logic of analogy and of comparison, how insect nervous systems differ from those of vertebrates, schemata, and presuppositions about cerebral localization should be treated in depth or not at all.

E-E seems to take it for granted that his own approach is ideologically pure and methodologically above reproach. I will attempt to show that this is far from true (although, as I have said, I shall be obliged to leave out a great deal). As with the generality of schools, movements, and bandwagons, ethology has its myths and dogmas that are but rarely subjected to penetrating critical scrutiny. Much scientific controversy is misdirected because the participants fail to address such metascientific issues when they are the real basis of disagreement. Were the philosophy of ethology more openly and candidly discussed, the whole enterprise would be viewed with much greater scepticism. Most readers of E-E's article will probably not recognize the peculiar neo-Kantianism implicit in his use of the term "*a priori.*" As I have pointed out (Ghiselin, 1974a), modern philosophy has rejected synthetic *a priori* judgment in the Kantian sense, and substituting natural selection for sensory experience will not salvage the doctrine or its implications. Again (Ghiselin, 1969), the allegation that ethologists begin (or must or should or even can begin) their work with unbiased observation would hardly be taken seriously by a knowledgeable epistemologist – or, for that matter, by a well-trained, professional scholar in any other behavioral science. There is no substitute for rigorous hypothetico-deductive methodology, and no hope for so-called Baconian induction.

Another myth is that "Ethology has from the beginning been based upon the theory of selection." To be sure, a growing awareness of evolutionary theory characterizes ethology as well as many other behavioral sciences. But the historical documents unequivocally attest to the fact that ethology arose out of anti-selectionist, idealistic morphology, and has long suffered from virtually total disassociation from the mainstream of selectionist thought. A phylogenetic interpretation has merely been superimposed upon typological systematics, as was true of much traditional morphology. (Typologists believe in Platonic Ideas, Aristotelian essences, and the like – see Ghiselin, 1969 and references therein.) For the most part the sole use of natural selection has been as a substitute for God in explaining adaptation. The result has been an incredible amount of naive teleology (Ghiselin, 1974a).

E-E's paper shows that although he is beginning to undergo metamorphosis into a Darwinian, the transformation is far from complete. Vestiges of typological attitudes are evident in his discussion of the "universality" of behavioral traits. To have features "essentially the same" is necessary, for an Aristotelian at least, if they are to be part of "human nature" (another term of dubious metaphysical status). However, modern philosophy has largely managed to liberate itself from such notions as "essential similarity" and "nature" in the Aristotelian sense, and has developed much more effective ways of dealing with attributes and groups. And modern systematic biology embraces population-thinking, so that there is no reason why any intrinsic trait, inherited or not, should be present in all organisms or populations that form any species. Organisms as well as the populations of which species are composed differ in genetic makeup. What they share is a gene-pool. It follows from the fact that species are not classes, but individuals in the logical sense of composite wholes (Ghiselin, 1974b), that they do not have defining properties, much less essences. Diversity and polymorphism are only to be expected in a Darwinian universe wherein variation is a necessary condition for change. Whether variation be genetic or not, it should be as rampant in behavior as it is in anatomy. To be sure, phenotypic variation, including the effects of nutrition and learning, often renders the genetic component inconspicuous and hard to detect, and it would be rash to pontificate one way or another on just how much each contributes. E-E takes comfort in his negative results with respect to finding any "basic differences in human behavior attributable to race." Now, even though my great-grandfather fought for the Confederacy, I consider myself anything but a racist. Nonetheless, concealing the facts about human diversity, or ignoring them, will not help us to understand human biology. It is hard to say what E-E means by "basic" (all things to all men no doubt), but the assertion seems to reflect the sort of typological attitude toward classification that racists themselves find so attractive. By all analogy, human populations ought to be polymorphic and variable in everything influenced by chromosomes. It would be astonishing, for example, were phenylketonuria and color-blindness to have exactly the same frequency in every human deme. From what we know of blood-group frequencies, we can very reasonably expect to find geographic variation and clines in quite a variety of behavioral traits. Racist ideology should be answered with good philosophy, not bad science.

E-E dismisses the ethologists' use of the expression "survival of the species" as "not quite correct." This is a remarkably cavalier way to admit that they have not understood the first thing about selection theory, namely that it explains evolution as the result of reproductive competition between the parts of species. The unreflective assumption that species can undergo adaptation has led numerous biologists, especially ethologists, to misinterpret the function of many important biological features. It is truly remarkable how little attention has been paid to the fact, so well documented by Darwin, that evolutionary mechanisms profoundly influence the properties of organisms and that a knowledge of selection theory is useful for investigating these properties. E-E's remarks on familial selection and related topics treat a profound and difficult matter as if it could be dismissed in a few words. But virtually the whole literature on "sociobiology" displays equal superficiality. Instead of merely tossing out a few speculations, a responsible scholar will think matters through carefully and relate his hypotheses to data indicative of their validity. Unfortunately, it is not generally known how one tests hypotheses in evolutionary psychology.

It is pleasing to see that E-E realizes that evolution is not always adaptive, but he certainly does not go far enough. It would help if all students of behavior were better acquainted with the causes of what Haeckel called "dysteleology," such as historical accidents, pleiotropy, and sexual selection. Some readers may be interested in the semantic difficulties of "adaptation" (Ghiselin, 1966). The term is equivocal, and much of the literature on adaptation suffers from verbal confusion.

When we turn to the empirical aspects of the paper, all seems quite reasonable. Yet one might contend that well-nigh everything of significance, including the methods and the results, was clearly and explicitly expounded by Darwin (1872) in the definitive work on evolutionary psychology. The curious reader might well compare *The Expression of the Emotions in Man and Animals* with E-E's work. The parallels could hardly be more striking. Darwin discusses the congenitally deaf and blind, cross-cultural comparisons, and many other topics that E-E treats as if they were new (see also Ekman, 1973). Darwin's principles of emotional expression can serve as a basis for a "grammar" of communication, and much else besides. His experimental design and comparative approach have rendered his work the standard of excellence in the study of behavior. Selection theory, in this as in his many other works on evolutionary psychology, served to reveal the causes of behavior. Both its effects and its mechanisms could be understood by studying the two together. As Darwin (1874) emphasized in the last part of *The Descent of Man*, behavior must be regarded as a major cause of evolutionary change. A peacock's tail tells us something about the aesthetic tastes of peahens, in a situation where a peculiar mode of selection has long operated. However, if one does not study evolution and behavior from a unitary point of view, one will misinterpret both. The failure of those who came after Darwin to grasp this point is perhaps the main reason why it is taking them over a century to catch up with him. He did not just anticipate modern work, he laid the foundations for what will come next.

These are not hostile criticisms. On the contrary, everything I have said backs up E-E's fundamental thesis that evolutionary biology can teach us a great deal about human behavior. My only objection is that we need more attention to the subtleties of evolutionary mechanisms if our approach is to realize its full potential. The behavioral sciences can not only use Darwinism, but after a century of misunderstanding and neglect, they deserve it.

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Classical ethology's conception of ontogenetic development. E-E states his views on ontogenetic development with such clarity that they invite commentary in the hope of advancing our understanding of the significance (for developmental studies) of concepts such as "genetic heritage," "self-differentiation," "patterned information," "phylogenetically acquired," "phylogenetic adaptation," "preprogrammed," and "preadaptation."

E-E's views on development are "classical" in that they faithfully represent those of his teacher Konrad Lorenz, one of the founders of ethology. Not all ethologists share these particular views. The enormous success of classical ethology is due in no small part to the popular appeal of its relatively simple and straightforward theory of ontogenetic development – to wit, there are two sources of behavioral adaptation: heredity (phylogeny) and learning. (Although I shall not comment on E-E's behavioral observations, the absence of reference to Birdwhistell's extensive pioneering work on kinesics or "body language," summarized in 1970, seems a serious omission.)

According to E-E, a focal point of interest in human ethology is "the extent to which man's behavior is determined by his genetic heritage." How could anything we do be unrelated to our genetic heritage? All of our behavior (and that of every other species) is related to our genetics – it could not be otherwise. Thus, there is not one class of behavior that stems from the genome – all behavior stems from the genome.

So, if we may put genetic considerations aside for the moment, we can proceed to what I understand to be the nub of the problem. E-E seems to have in mind a particular route of *development* for innate behavior: "a process of self-differentiation according to the blueprint given in the genome of the species." According to E-E, ethologists are aware that development involves organismic-environmental interactions, so it is not the absence of environmental input that characterizes the self-differentiation of innate behavior. Rather, it is that "no patterned information concerning the adaptation needs to be available to the growing organism for the adaptive pattern to occur." This is certainly an hypothesis worthy of developmental experimentation; in fact, my own research program has been guided by related theoretical considerations.

The question I have asked is: Are there nonobvious experiential precursors operative in the course of the development of innate behavior? To render the question less paradoxical, my provisional definition of innate behavior has been the manifestation of adaptive or species-typical responsiveness to patterned stimuli (or stimulus objects) that the organism has not previously encountered, at least not in their present form. It occurred to me that once one identified the critical perceptual features of the stimulus, it might be that the organism had encountered these earlier, although in a different form. If such were the case, and if the later behavior could be shown to be dependent on the earlier exposure, then these would be instances of *nonobvious experiential precursors* to the manifestation of innate behavior. But perhaps we would want now to put the term innate in quotation marks. I don't know about that since this is not really an possibility that has been faced very squarely heretofore, although Schneirla (1956) and Lehrman (*op. cit.*, 1953), among others, have made similar suggestions in their critiques of the concept of innate behavior. The search for nonobvious experiential precursors to innate behavior has not been popular, but there is some evidence beginning to accumulate (e.g., Gottlieb, 1976a, 1978, and in press).

The finding of nonobvious precursors does not necessarily do away with the concept of innateness. Rather, what it does is force us to think in a new way about the role of experience in the development of species-specific or species-typical behavior. As has been documented elsewhere (Gottlieb, 1976b), there is not only one role of experience during species-typical development, there are at least three: maintenance, facilitation, and induction. The interesting thing about these three modes is that (1) they do not fit the definition of traditional (i.e., associationistic) learning, and (2) they entail specific patterns of stimulation to achieve the species-typical behavioral phenotype (e.g., Gottlieb, 1976a). Who would have thought, for example, that an already developed species-specific auditory perception would require a highly specific patterned experience to keep it functional? Or, even more unexpected, that a maintenance experience can antedate the behavior to be maintained (*ibid.*)?

The search for nonobvious experiential precursors to unlearned behavior is in line with evolutionary considerations. Natural selection works on behavioral phenotypes; it is completely indifferent to the particular pathway taken by the phenotype during the course of development. Since all forms (pathways) of development involve genetic activity, natural selection does not (need not) favor one developmental pathway over another for the ontogenesis of unlearned behavior. Natural selection involves a selection for the entire developmental manifold, including both the organic and normally occurring stimulative features of ontogeny. Thus, nonobvious experiential precursors of a patterned kind may be much more widespread than heretofore realized. Only developmental investigations of unlearned behavior can answer that question.

E-E's conception of phylogenetic adaptation is not incompatible with the operation of nonobvious experiential precursors in species-typical behavioral development. All the evidence to date favors "patterned information" and development constraints – there is no evidence for "blank slates" in the development of perception, even among the lower vertebrates (e.g., Wiens, 1970), much less in birds of mammals. One does feel that the classical ethologists' two-factor conception of ontogenetic development is too simplified to foster our understanding of the development of species-typical behavior and, thus, to direct the practice of development analysis.

by **Jack P. Hailman**

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The ethology behind human ethology. E-E's essay is a rebuttal of Pierre Charron's assertion (a century before Alexander Pope) that "The true science and study of mankind is man." Human ethology is somewhat like Mark Twain's weather in that many talk about it but few do anything. Happily, E-E is an exception.

When E-E says that "the formal application of ethological methods to the study of man began about fifteen years ago," he means *his* application. His methods are not fundamentally different from those of Darwin (1872), who set out (1) "In the first place, to observe infants"; (2) to study the insane; (3) to stimulate behavior electrically, to photograph it, and "to show several of the best plates, without a word of explanation, to above twenty educated persons" as judges; (4) to investigate "the great masters in painting and sculpture"; (5) to compare "all the races of mankind"; and finally, (6) to attend, as closely as he could, to "some of the commoner animals." In fact, Darwin also studied actors and the facial musculature mediating expressions, and used other methods he failed to list formally as separate approaches.

My other major comment is that the ethology E-E applies to man is not The Ethology, but rather traditional Austro-German ethology, the framework of which most of the field has long since outgrown. I will comment first on three issues of evolutionary ethology (function, homology, and comparisons) and then on three issues of developmental ethology (innateness, inheritance, and deprivation).

The "function" of behavior. E-E first asserts that from observing behavior one can draw "conclusions as to function," but later, more cautiously, he states that one can only infer "a fairly good guess as to adaptive function in most cases." As I have pointed out elsewhere (Hailman, 1971), E-E's guesses take on the aura of established conclusions. The adaptive significance of behavior can be established only by research on populations, not by observing individual animals (e.g., Hailman, 1976a; 1977a, pp. 11–13). A further mischief is engendered by the belief that each behavioral trait has an assignable "function" (see Hailman, 1977b). We are in danger of forgetting that natural selection works on whole animals or groups of them rather than on individual traits or genes. Because the animal is an adaptive whole, a particular behavioral pattern may have no discrete, assignable "function." Furthermore, E-E provides no explicit method for formulating "functional" guesses.

Homology versus analogy. E-E correctly states that cross-specific behavioral similarities that are due to similar selective pressures are analogies, whereas those due to common phyletic descent are homologies. But he fails to make clear that when one says two traits are homologous (or analogous) he must say homologous (or analogous) *as what?* To extend E-E's example concerning the wings of bats and birds, one can say that they are homologous as forearms because they are evolved from the forearm of a common ancestor, but they are merely analogous as wings because the common ancestor did not fly. A set- and information-theoretic analysis of evolutionary concepts such as homology and analogy is provided in detail elsewhere (Hailman, 1976b). In any case, E-E provides no methodology for separating homology from analogy.

The comparative method. The two foregoing problems – how to establish the functional significance of behavior (if one exists) through observation and how to distinguish homology from analogy – converge at the comparative method, which E-E sees as "a basic source of information." He fails, however, to clarify the design of the comparative method, and thereby creates problems for those unfamiliar with it. As I have set forth in greater detail elsewhere (Hailman, 1976a; 1977a, pp. 13–15), the comparative method is in its basic form a contingency table whose cells are filled with numbers of species (or other population units) exhibiting some particular trait. The rows of this table may be taken as different taxonomic groupings of the species, such as gulls, terns, and boobies (to use an example from birds). The columns are different environmental circumstances, such as flat ground or steep cliffs as nesting locations. If species with a given trait accumulate in some particular row – which is to say that the trait correlates with taxonomy regardless of environmental circumstances – the behavioral similarities are attributed to common descent: the possessed traits are homologies. On the other hand, if species with a given trait accumulate in some particular column – the trait correlates with environmental circumstances regardless of the taxonomic relatedness of the species – then the behavioral similarities are attributable to common selective pressures: the traits are analogies. For example, certain behavioral patterns first discovered by E. Cullen (1957) in the cliff-nesting kittiwake gull also occur in other cliff-nesting gulls (Hailman, 1965), terns (J. M. Cullen and Ashmole, 1963), and boobies (Nelson, 1967), but not in their ground-nesting relatives. On the other hand, different behavioral traits of these same birds correlate with taxonomic grouping rather than habitat (e.g., Tinbergen, 1959). The effectiveness of the comparative approach is proportional to the completeness with which its design is executed: *caveat emptor!*

"Innate" and "acquired." The lack of one-to-one correspondence between the genotype and phenotype of animals is a continual nuisance to evolutionary reasoning. Austro-German ethology tries to define away the nature/nurture problem, but the attempt is unsatisfactory. I said (Hailman, 1969) that my results showed "clearly that behavior cannot meaningfully be separated into unlearned and learned components." E-E here states that "the argument that a distinction between innate and acquired components of behavior cannot be made . . . can no longer be upheld." I originally continued," nor can a certain percentage of the behavior be attributed to learning," whereas E-E now continues, "the whole nature/nurture issue should not be considered as a matter of either/or, nor can the contribution of each be measured quantitatively, in terms of percentages." E-E previously attacked[1] the conclusions of my study on begging in gull chicks (Hailman, 1967) without challenging the empirical findings or showing that the conclusions fail to follow from them. He now seems to say that the "innate and acquired" cannot be separated quantitatively, yet they can still be separated. I find this reasoning sufficiently opaque that there is no recourse but to approach the problem through more concrete issues: *what* is inherited and what can be learned from "deprivation" experiments?

What is inherited? E-E quotes Eisenberg (*op. cit.*, 1971) as stating "that there is no behavior . . . in the zygote. . . . What the DNA specifies are chemical constituents." E-E adds "Ethologists certainly agree." Yet later he is saying that "prospective potentials" rather than macromolecules are inherited. Suppose his circumlocution means the following: given certain rearing conditions, an animal with a particular genome will develop particular behavioral traits – hardly a conclusion with which many would argue. The rub comes when E-E, arguing through selected examples, leaves one with the impression that the rearing conditions make no difference. He forgets to mention that the development of species-typical, stereotyped pecking movements in gull chicks depends upon the experience of simply standing; that the head-rotation becomes incorporated into the movement through experience; that the response is elicited by increasingly specific and complex stimuli as perceptual experience accumulates; that the initial movement differentiates into separate movements of pecking to food and begging to the parent as a result of experience; and so on (Hailman, 1967). Gull chicks inherit DNA molecules and other parts of the fertilized egg, and one might loosely say these provide "prospective potentials" for development of complicated sensory-motor behavior, given certain experiences. But the adaptive whole depends as much on these experiences as upon the genes: change either and the behavior changes. E-E states that genes, not behavior, are inherited, but then he proceeds as if behavior were inherited. His confusion concerning behavioral development is nicely exemplified by his subheading: "Gene-environment interaction." As I said (Hailman, 1969) in the passage paraphrased above the E-E, "Behavioral development is a mosaic created by continuing interaction of the *developing organism* and its environment" (emphases added here).

The deprivation experiment. The subject of deprivation has been so tirelessly argued that I will do little more than recall the issues. Every animal grows up in *some* environment, so that "deprivation" or "isolation" are relative terms. The essence of the experimental logic is to rear animals in two environments, and to conclude that any trait developing similarly in both is uninfluenced by factors not common to the two environments. E-E and I have always agreed on the following (see Hailman, 1967): there probably *are* behavioral patterns that would develop similarly regardless of the rearing environment (given that it is generally conducive to life and health). We appear to disagree as to how common such behavioral patterns are, E-E apparently believing them to be the rule among patterns are, E-E apparently believing them to be the rule among animals and I maintaining that very few (if any) unequivocal examples actually occur.

E-E seems to convince by marshalling examples, but the evidence is selective and misleading. For example, he ignores my gull studies (Hailman, 1967), with which he is familiar, his own excellent study of the role played by experience in adaptive opening of nuts by European red squirrels (Eibl-Eibesfeldt, 1951), and all other studies of the same genre. He also misleads by implying that bird song develops normally in songbirds reared in complete deprivation. The truth extracted from a large literature is: (1) most, if not all, songbirds must hear something in order for song to develop normally; (2) in many cases they must hear their own species' song; (3) in most cases this experience must occur at a definite time during ontogeny (the critical period); and (4) in some cases different parts of the song must be learned at different times. However, there are (as E-E asserts) cases in which the species-typical song develops normally in birds reared in soundproof boxes. What E-E fails to mention is that if one does a more complete deprivation by deafening birds so that they cannot hear even their own sounds, then song does *not* develop normally. E-E has tried to convince us that many behavioral patterns develop similarly regardless of early experience and rearing environment, but I remain quite unconvinced.

Conclusions. Although no substantial part of the old Austro-German ethology has kept pace with modern conceptual frameworks, one must not conclude that E-E's results are invalid. It is extremely important to know which human behavioral traits are universal, which are restricted to particular cultures and genetic groups, and which vary among individuals of a given culture or group. It is not necessary to invoke outdated instinct concepts to advance understanding of human behavior, but it will require further thinking about the comparative method and other issues to adapt the ethological approach to comparisons among human cultures. E-E has usefully enlarged upon Darwin's pioneering efforts, and to both of them we owe a great deal.[2]

NOTES

1. In a plenary talk at the 1970 International Ethological Conference in Washington, D.C., E-E attacked what he believed to be my conceptions of behavioral development; I have not seen a published version. His memorable opening remark was to the effect that "Hailman's view of instinct is like that of the man who said he didn't believe in ghosts and furthermore wasn't afraid of them." I take this opportunity to offer whatever comfort I can to those who not only believe in instincts but also are afraid of them.

2. And I owe thanks to Dr. Jeffrey R. Baylis for critically reading the manuscript draft and to my wife Liz for proofreading final copy.

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An eclectric history of ethological theory and methods. The accompanying article by Professor Eibl-Eibesfeldt summarizes and reviews several of the distinctive and defining features of ethological theory and methodology as applied both to humans and to other animals. Human ethology, in contrast to many other approaches to the understanding of human behavior, begins with the premise that some nonnegligible portion of man's behavior is strongly governed by innate mechanisms and tendencies; in brief, that there is in fact such a thing as "human nature." Additionally, E-E's article attempts to demonstrate that in both organized rituals and day-to-day social intercourse, components of behavior – innate and cultural, nonverbal and verbal – can serve as functional equivalents in a unitary grammar of human social behavior. Obviously, an attempt is also made to demonstrate that ethological theory and methods, especially comparative studies across cultures and species, are appropriate and heuristically valuable in determining the structure of this grammar as well as the function of discrete components or acts within overall behavioral sequences. Unfortunately, I believe that the main problem faced by this or any other attempt to apply ethological theory and methods to human behavior is, quite simply, that ethological theory is hopelessly outmoded with respect to many of its main conceptual foundations, especially as concerns the role of intuition in behavioral research, the organization of the nervous system, and the nature and mechanisms of evolution. Below, I sketch a brief and eclectic history of ethological theory and methodology to elucidate my views on this subject, and then offer some further comments concerning the relationship between ethology and sociobiology.

Origins, goals and methods of ethology. The roots of ethological theory and methodology can be traced, respectively, to the romantic philosophical tradition of nineteenth-century Europe, especially, Germany, and to classical comparative anatomy as practiced by professionals reared and educated in this tradition. Thus, for example, one of the most important aspects of ethological methodology, as described by Tinbergen (*op. cit.,* 1951), was the compilation of an ethogram, a complete listing of the repertoire of behavior of a given species. Much to my surprise, the concept of the ethogram and its importance to ethological research was hardly mentioned by E-E.

By way of brief historical review: Just as the nineteenth-century anatomist (e.g., Ruge, 1887) completed painstakingly detailed observations and descriptions of the nerves, muscles, and bones of each animal species, so too did the ethologist, via the ethogram, attempt to provide names and descriptions for all of the basic "bits and pieces" of the behavior of a species. The essential feature of these activities, however, was that both anatomists and ethologists realized the importance of a detailed understanding of the basic design or structure of a species, and, moreover, relied solely upon observation and description to reveal the nature of this structure, presumably characteristically unique for each species. In such pursuits, however, within-species variability in behavior and morphology was typically ignored and overlooked; the goal was simply to determine the characteristic structure of each species, and then to use this information to determine the phylogenetic relationship of one species to another.

The romantic philosophical tradition exerted another important influence on the development of ethological theory by imparting to the first ethologists a profound desire to understand, identify with, and, crudely, "get inside of" the mind of the animals they studied. This early and fundamentally important goal of the ethologists is clearly evident in the influential and insightful writings of Jakob von Uexküll (1934), one of the founders of the ethological tradition (see Lorenz, *op. cit.,* 1935), who, among other things, coined the term *Umwelt* to describe the amalgam of an organism's perceptual and physical (or operational) universes.

Thus, I believe that very early in the development of ethology, a basic methodology arose consisting of three elements: (1) observe the animal, (2) describe its behavior, and (3) use intelligent empathy to determine the causation and function of the behavior. The comparative method and experimental analysis of behavior, as described by E-E, do not to my mind constitute either important or defining characteristics of ethological methodology; these are merely basic tools of the trade for many of the behavioral sciences.

Ethology and intuition. The first and second of the above methodological principles have been adopted by many behavioral scientists. More important with regard to the article under Commentary, however, is the third principle above, that is, the explanation of man's behavior through the application of intelligent empathy by one human toward the activities of another. The heavy reliance on intelligent empathy and intuition in ethological research, particularly human ethology, poses enormous difficulties, as one example should suffice to demonstrate.

As an observer of primates and other mammals, I am led by my intuition and empathy to suspect that in humans kissing is an elaboration upon such basic mammalian behavior patterns as oral-oral olfactory inspection and mouth grooming, both of which often involve lip and tongue protrusion, combined with a marked tendency in the order Primates for face-to-face communication at close range. E-E, in contrast, derives kissing in humans from ritualized kiss-feeding, a phenomenon primarily observed in avian courtship displays. Whose application of empathy, intuition, bias, or opinion is correct? More importantly, how does one go about systematically eliminating one or more of the plausible alternative hypotheses concerning the evolution of this very interesting and enjoyable behavior in humans?

In sum, ethological methodology, as clearly demonstrated in this article by E-E, almost always eventually falls back on intuition and empathy. Yet, unfortunately, intuition and empathy alone are not sufficient evidence in support of any hypothesis about behavior or its evolution.

Ethology and the nervous system. With its unique combination of theory and method, ethology eventually became focused, in some broad sense, on the study of perceptual processes in animals, especially stimulus filtering and the role of conspecifics and their displays as keys, releasers, or sign stimuli. Of course, animals did not always respond with equal rapidity or intensity to the same stimulus over time, apart from habituation, and thus ethologists turned to the study of motivation and, thence, to the study of the nervous system over and above the mechanisms of perceptual filtering at the level of peripheral receptors. Ethological analysis of the nervous system, however, by and large also relied upon the tripartite methodology described above, and, in particular, an attempt was made to infer the structure of the nervous system from observations on the structure of behavioral sequences. The end result of this endeavor was a description of the nervous system based upon the notions of action-specific energies, energy blockage and overflow, and so on (Lorenz, 1939). Needless to say, such ethological theories of the structure and operation of the nervous system, as inferred from the structure of behavior, have not largely been discarded both by ethologists and by neurobiologists, save for the single principle of hierarchial organization of the nervous system [see Kupfermann & Weiss: "The Command Neuron Concept" *BBS* 1(1) 1978].

Ethology and Evolution. Likewise, I believe that the ethologically-based approach to taxonomy, phylogeny, and evolution has largely been outdated by development of the modern synthetic theory of evolution. Classification and evolution have, to my reading, had two high points in the history of ethology. The first of these was Lorenz's (1941) monograph on the classification of the Anatidae; the second, E. Cullen's (1957) study of the behavior of the kittiwake, a specialized cliff-nesting gull species. Lorenz's study showed that analysis and comparison of species-specific sequences of behavior, both at the level of fixed action patterns and at that of entire ethograms, could play a valuable role in taxonomic studies. However, it should be obvious that in very few cases will behavior alone be sufficient to establish the taxonomic relationships among a group of species not already known to be united at some higher taxonomic level. Cullen's widely cited study served to demonstrate that specific behavior patterns constituted adaptations in the sense of subserving some basic function within the life cycle of a species and, more importantly, that when the niche of a species underwent specialization, so too did the structure of behavior.

The most sophisticated and coherent formulation of the ethological conceptualization of evolutionary change and phylogeny, however, was presented by Lorenz in 1965 (op. cit.) and can be summarized as follows. Evolution and speciation consist of the shuffling of specific sequences of behavior (for example displays, fixed action patterns, or even maintenance behaviors) across motivational fields. In the course of this process, some behavior patterns may change their functional association with a particular motivational state (as in the change from an aggressive with a particular motivational state (as in the change from an aggressive behavior in one species to a sexual behavior in another), or they may merely change in intensity, speed, or other aspects of sequential patterning. The key elements in this conceptualization of evolutionary change and phylogeny are first, an emphasis on the importance of understanding the fine structuring of behavior, and second, the absence of attention to variability in behavior within species. In essence, taxonomic and comparative studies by ethologists analyzed and presented evolutionary explanations for the variation in behavior among species. Ethologists as a group, however, have been substantially less successful in providing explanations for, or even fully grasping the evolutionary significance of, within-species variability in behavior. It is, of course, precisely such within-species variability in behavior and other aspects of biology that forms the center of emphasis for contemporary population biology and evolutionary theory.

Ethology and sociobiology. Finally, a commentary such as the present one should not close without some mention of the relationship between ethology and sociobiology. Briefly, sociobiology is a subdiscipline of biology closely allied to population biology. As such, sociobiology is grounded in the theory of natural selection as well as contemporary elaborations of that theory, for example, the theories of kin selection and reciprocal altruism and the concept of inclusive fitness. The important point concerning sociobiology, however, is not the particular theories utilized, but rather the almost complete absence of implied methodology of research techniques in this discipline (Wilson *op. cit.* 1975). Thus, researchers and students with the best of training in sociobiology are often embarrassingly ignorant of ethological techniques for the observation and description of behavior, and, more generally, of the importance of these endeavors to hypothesis testing in sociobiology or other behavioral sciences. This state of affairs typically reflects the fact that these individuals, in contrast to ethologists, are often not interested in behavior in its own right, sometimes not even interested in the biology of the particular species under study, but are usually completely captivated by the specific hypotheses to be tested and their relationship to the main body of sociobiological theory. In sum, the subtleties of animal behavior and ethological techniques for its analysis are often lost on sociobiologists.

On the other hand, although sometimes tied to outmoded theories of evolution and nervous system operation, ethologists still remain one of the few groups of biologists to recognize that behavior possesses structure and that analysis of this structure constitutes an activity of interest and importance in its own right, as well as being of critical importance for understanding the process of organic evolution. Ethologists have thus contributed to contemporary behavioral biology both a conceptual framework for behavioral analysis and a wealth of observational techniques and details, not the least of which is the importance of direct observation and description of the behavior of animals in their natural environments. Sociobiology might therefore be viewed as a discipline that has important and testable evolutionary theories of behavior, but no methodology with which to do so. In contrast, ethology is a discipline in possession of techniques for testing such evolutionary hypotheses about behavior, but otherwise lacking sound evolutionary or neurobiological theories in need of testing. In sum, I believe that ethology stands to provide the methodological and technical foundations required for testing a wide range of important sociobiological theories. As such, I do not foresee one field devouring the other; perhaps "marriage" provides a better description of the process.

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The problem of human ethology from the perspective of an experimental psychologist. When viewed in the context of evolutionary theory there can be little doubt that many aspects of man's behavior are preprogrammed, in the sense that they are a product of his phylogenetic heritage. As elaborated by E-E, human ethology (the biology of human behavior) seeks to identify those genetically determined (i.e., innate) components of man's behavior that reflect this heritage, and to specify their adaptive significance. The fruits of this approach are perhaps nowhere better exemplified than in the numerous interesting examples presented here, and one can only agree with the author's comment that" the biological approach is likely to illuminate unique facets of human behavior thus far overlooked."

What then is the problem that human ethology poses for the experimental psychologist? In essence, it is the problem that experimental psychology has faced from its inception, namely, that of identifying the factors responsible for behavior, including the behavior that human ethology describes. To assert that a given behavior is genetically based, to specify its phylogenetic precursors, and to identify its possible adaptive significance, can set a given behavior into perspective for the experimental psychologist, but it cannot "explain" the behavior in the sense of identifying its basic components and their possible interactions.

In 1943 Clark Hull warned psychologists against what he described as a doctrine of despair: "Emergentism." According to Hull:

> "Emergentism, as applied to organismic behavior, is the name for the view that in the process of evolution there had "emerged" a form of behavior which is ultimately unanalyzable into logically more primitive elements – behavior which cannot possibly be deduced from any logically prior principles whatever." (C. L. Hull, 1943, p. 26.)

Though they do not say so directly, it is difficult to avoid the impression that the human ethologists, at least as exemplified here, have adopted Emergentism as a working principle. Consider E-E's comment that fear of strangers ". . . is a universal trait for which learning theory could hardly account." Undoubtedly this statement is intended to emphasize the point that fear of strangers cannot be attributed to any explicit training by the mother or even to a set of aversive experiences with strangers. But the statement also implies that learning plays no role at all, and hence that learning theory has nothing to offer by way of explanation. As will be shown, such an implication is not only premature, it is wrong. [see also Rajecki, Lamb & Obmascher: "Toward a General Theory of Infantile Attachment" *BBS* 1 (3) 1978].

According to learning theory, any comprehensive analysis of a given behavior must seek to identify those factors, whether innate or acquired, that are responsible for its occurrence at a given time and in a given setting. In general, the method of choice is to bring the behavior into the laboratory and systematically to vary one or the other of the factors thought to contribute to it. In this way, one can determine whether these factors, acting either singly or in combination, are critical for the behavior under investigation.

When fear of strangers is brought into the laboratory and examined from the perspective that learning theory provides, several interesting facts emerge. In particular, it becomes clear that, while fear of strangers has an important innate component (as E-E suggests), it also has an acquired (i.e., learned) component, and the learned component is as crucial to its occurrence as the innate one.

It is by now well known that a newly hatched duckling will immediately approach, follow, and otherwise react affirmatively to any of a wide variety of moving objects during the first 24 hours after it leaves its shell. Beginning sometime on Day 2, however, the duckling starts to react fearfully to moving objects that are novel, and by Day 5 it will persistently attempt to flee from such objects. In short, the duckling exhibits the fear of strangers phenomenon that E-E describes. A variety of experiments have been carried out in an effort to identify the factors responsible for this effect and a number of hypotheses have been tested.

It has, for example, been hypothesized that a three-or-four-day-old duckling's fear of a novel object is predicated on the occurrence of a mismatch between the visual stimulation provided by that object and the "neuronal model" that the subject has formed of the stimulation to which it was initially exposed (Bateson, 1966, 1971; Dimond, 1970; Salzen, 1970). According to this "perceptual" or "exposure learning" hypothesis, rather than representing a rigidly preprogrammed reaction that necessarily occurs at a particular time in ontogenetic development, a duckling's fear of strangers is dependent upon the subject's prior opportunity to form a neuronal model of a given source of visual stimulation. Evidence in support of this proposition is provided by a number of investigations (Sluckin and Salzen, 1961; Moltz & Stettner, 1961; Asdourian, 1967). These studies reveal that if a subject's exposure to visual stimulation is severely restricted from the time it hatches, it will immediately approach and follow an appropriate moving object even though the initial exposure to the object occurs well after the period when fear reactions would ordinarily be seen.

These data make it clear that adequate experience with appropriate stimulation (i.e., the kind of experience required to form a neuronal model) is a necessary condition for fear of strangers to emerge. They do not imply that this experience is also a sufficient condition for this event, however. In an experiment specifically designed to examine this issue, Schaffer (1966) asked whether the onset of the human infant's fear of strangers coincided with the point at which infants began to give evidence that they could recognize strangers. This work indicated that younger infants can readily discriminate their parents from strangers and yet not be fearful of strangers. Similarly, it has been found (Hoffman and Ratner, 1973a) that even when ducklings less than a day old show that they can discriminate between a novel and a familiar moving object, they still react affirmatively to the novel one. Both studies make it clear that the formation of a neuronal model (as revealed by the capacity to discriminate) is not itself a sufficient condition for fear of strangers to emerge; some maturation is also required.

Schneirla and Rosenblatt (1961) have postulated that age-related changes in behavior are grounded not only in the growth-dependent process of maturation but also in the opportunity for learning and experience. Clearly, fear for strangers is no exception to this principle. When it is studied in the laboratory, we discover that while fear of strangers may, as E-E asserts, be a universal trait, it can nonetheless be analyzed into more primitive elements, and one of these elements is learning.

At the beginning of this commentary it was suggested that when viewed from the perspective of an experimental psychologist, human ethology does not go far enough. It serves the important function of identifying behaviors that might otherwise be overlooked, and it puts those behaviors into perspective by describing the settings in which they occur and indicating their possible phylogenetic precursors. However, until those behaviors are subjected to the kind of close scrutiny that is usually only possible in the laboratory, it is unlikely that they will be well understood. In this regard, it seems important to suggest again what has been suggested before (Hoffman and Ratner, 1973b), namely, that the experimental approach and the controlled laboratory procedures it entails complement and amplify the naturalistic observations obtained through an ethological approach. There is no sense in advocating one approach over the other because it is obvious that only when the two approaches are taken together is it possible to view a given behavior in the context in which it occurs, and also to isolate its component parts and begin to understand its underlying mechanisms.

by **David L. Hull**

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Universality and species specificity. Ethologists are frequently criticized for the facility with which they claim that certain behaviors are "innate." To the contrary, I think that in certain respects their standards of evidence are unrealistically high, certainly higher than those used by geneticists when the latter treat ordinary morphological traits. In his paper E-E expresses a belief shared by both ethologists and their critics that some significant correlation exists between how "innate" a behavior is and its distribution in the species under study. For some reason, university and species specificity are critically important in the ethological literature, certainly more important than they are in the literature of population genetics. According to ethologists, a behavior is universal if *all* the organisms in a particular species exhibit it under appropriate circumstances; it is species specific if *only* the organisms in a particular species exhibit it. To be sure, the distribution of traits, including behavioral traits, is important as evidence for inferring taxonomic relationships. What I wish to discuss in this commentary is its relevance to the issue of "innateness."

As I understand the ethological use of the term "innate," it implies that a behavior is innate only if it is strongly genetically determined (that is, has a narrow reaction norm), is elicited by only minimal environmental cues, and has been selected for in the evolution of the species (Cassidy, 1979). The purpose of cross-cultural study in ethology is to show that a behavior is consistently exhibited in the face of considerable variation in the cultural experiences of the subjects; but as E-E notes, ethologists do not "invariably conclude from the universality of a pattern that it must be innate." After all, even though cultures vary in many respects, they might just happen to share the relevant experiential features. "Similar experiences in the early life of a child could shape a behavior in different cultures along similar lines." Deprivation experiments are designed to reduce the likelihood that such fortuitous experiential similarities are actually responsible for the behavioral universal. As ethologists themselves have emphasized, an organism cannot be deprived of all environmental input. It need not even be deprived of all contact with conspecifics. Such extreme deprivation can produce all sorts of bizarre behavior. The only environmental factors that must be filtered out for highly structured behaviors are those that might supply the structure.

Ethologists do not reason from the universal distribution of a behavior in a species to its being "innate." Absence of the universal distribution of significant experiential input is also required. Until recently, evolutionary biologists assumed that any trait universally distributed in a species must, with rarest exception, be an adaptation. Either it is contributing to the survival of the organisms that possess it and the perpetuation of their genes, or else it did so in the past. Hence, on the selectionists' view of evolution, the inference from universality to innateness, the necessary caveats duly noted, is justified. Recently, however, certain evolutionary biologists have argued that a high percentage of the traits that are universally distributed in a species were never selected for, but became fixed through such processes as drift. If the neutralists are right, then the inferences ethologists make from universality are not justified. Universally distributed behaviors may be strongly genetically determined, but they need not be adaptations. As things currently stand, however, the evidence seems to favor the selectionists over the neutralists.

Ethologists also seem to reason from a behavior's not being univeral to its not being "innate." The assumption seems to be that all adaptively significant behaviors must be universally distributed in a species. Until recently, evolutionary biologists thought that any trait that conferred a selective advantage on the organisms processing it would rapidly become fixed in a species. Thus, most loci should be homozygous for particular traits. To their surprise, they discovered considerable genetic heterogeneity. According to current estimates, 30–35 percent of all loci in any population taken at random are polymorphic (Lewontin, 1974). It is also true that much of this genetic heterogeneity may be masked at the phenotypic level (Wilson, 1978), but even so, species are both polymorphic and polytypic. In consequence, traits that vary in a population can be just as "genetically determined" as those that do not. More than that, according to certain evolutionary models, such variability can actually be selected for. For example, both blood type and eye color are about as genetically determined as any traits can be and yet they are not universals. Hence, it is possible for a highly variable trait to be "innate." In order to refute claims that a behavior is innate, critics must do more than simply discover an exception. A behavior may vary in a species because the relevant genes vary.

One can avoid facing up to the difficulties posed by genetic heterogeneity by redefining the offending traits to make them universal. For example, *which* protein is found in the blood is variable, but the presence of some protein or other is universal. Hence, the *real* trait is the presence of some blood protein or other. This evasion works for blood type, but not for eye color. People who have brown eyes possess a pigment in the iris of their eyes which reflects brown light. People with blue eyes have no pigment whatsoever. But at least they have eyes. Maybe eye pigmentation is not a trait, but possession of eyes is. I fail to see the point of such finagling.

The message of the preceding for ethologists is that a behavior need not be universal to be innate. E-E concludes that the "results of primate sociology make it appear probable that many of the universal features of human behavior (ranking, territoriality, incest avoidance) are rooted in our primate heritage." If current views about the evolutionary process are correct, variable features of our behavior can be just as rooted in our primate heritage as those that are universal.

Ethologists also pay considerable attention to species specificity. One explanation for this emphasis is the role that certain sorts of behavior play in reproductively isolating one species from another. If the only thing keeping two species from mating with each other is a difference in courtship behavior, that difference better be species specific. However, two points need to be made explicitly. First, not all behaviors function as isolating mechanisms. Those behaviors that do not, need to be no more species specific than any other trait. They can be commonly distributed between species and variable within species. As Emlin and Oring (1977, p. 222) note, "Until recently, many field biologists have worked under a preconception that species specificity was a characteristic not only of courtship behavior but of mating systems as well. We are now coming to realize that variability in social organization, including mating systems, is widespread." Second, no special connection exists between species specificity and innateness. Just as all possible combinations of universality and innateness are common, all possible combinations of species specificity and innateness are just as common (for further discussion, see Mayr, 1976).

Perhaps ethologists and their critics have stated elsewhere what they take to be the relation between universality and innateness and between species specificity and innateness. If not, it would be a great help to everyone concerned if they did.

by **Carroll E. Izard**

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Human ethology and the ontogeny of emotional expressions. Ethology has made significant contributions to the life sciences. The strength and meaningfulness of these additions to our knowledge have stood the test of time. Above all, perhaps, they have given us a fresh perspective on the relationships among living things and between life and the inanimate surround. The case for *human* ethology, though already replete with fascinating observations and insights, cannot yet claim so solid a foundation or such a unique place among the human sciences. — This is not to imply that ethology itself is unique, for it overlaps with comparative psychology (Schneirla, 1972; Yarczower and Hazlett, 1977).

The territory marked off as human ethology by E-E – biology of behavior – cuts across the domain of a number of other disciplines. There are parallels between the work of contemporary human ethologists and that of cultural anthropologists (e.g., Davis, Gardner, and Gardner, 1941; Warner and Lunt, 1941; Mead, 1950; Benedict, 1946), and even closer parallels with ecological psychology (e.g., Barker, 1968; Barker and Schoggin, 1973). E-E's territorial claim ignores several other disciplines or specialties that contribute to our knowledge of the biological foundations of behavior. The work of developmental psychologists, psychophysiologists, and neuroscientists also contributes to the biology of behavior.

In addition to this overly broad definition of human ethology, E-E's paper exhibits uncritical acceptance and misinterpretation of controversial research findings from other disciplines, overgeneralizations, and errors of fact. Some of these problems are illustrated in the treatment of studies relating to the ontogeny of emotional expression. In the first place, a discussion of "emotions" in prelinguistic infants should be in terms of emotional expressions, since emotional experience is an untestable inference at this age. For example, Bower's report of surprise in two-week-olds lacks the only kind of critical data that could substantiate it – evidence that he observed the universal facial expression of surprise. The surprise expression is relatively rare even in older infants and difficult to elicit with regularity. E-E assumes, with Bower, (*op. cit.,* 1977), that the infant's increased heart rate on failure to grasp an "apparent object" indicates the presence of an "innate expectation of tactile consequences." An equally plausible explanation is that the novelty of the experimental procedure elicited the emotion of interest. Further, while there is robust evidence for the innateness of fear and of the encoding and decoding of its expression, the uncritical acceptance of Bower's highly controversial claim that it has been observed in two- to eleven-week-old infants weakens this statement on human ethology. The weight of the evidence suggests that, on the average, fear does not emerge until the second half-year of life and a case has been made for the adaptiveness of this delay in the ontogeny of this highly toxic emotion (Izard, 1977, 1978).

The arguments based on Meltzoff and Moore's (*op. cit.,* 1977) finding of "imitation" in the twelve- to twentyone-day-old infants are a mixed bag. That the infant's reactions to the experimenter's facial expressions represent innate responses is probably correct, but recent research from Kagan's laboratory raises serious doubt as to whether they are evidence of imitation (Kagan, 1976).

E-E's assumptions and arguments based on the concept of "stranger fear" in eight- to ten-month-old infants are on shaky grounds. He does not take into account the variability in the quality of the response due to context, and he does not consider the behavioral criteria for classifying the response as fear. He is clearly incorrect in placing the emergence of social discrimination (distinguishing familiar from unfamiliar persons) and the stranger response at the same age. The former occurs much earlier (Schaffer, 1966).

The assumption that "stranger fear" in the infant is continuous with "stranger fear" in the adult is unwarranted for four reasons: (a) the emotional quality of the infant's stranger response is variable and not totally dependent on the stranger as stimulus; (b) although under certain conditions an eight- to ten-month-old responds negatively to strangers, it has not been determined whether the emotional expression is fear, sadness, anger, shyness, or a blend; (c) in some infants the negative stranger response diminishes in the months immediately after onset (Emde, Gaensbauer, and Harmon, 1976) and in the second year of life it is most frequently called shyness (Kagan, 1976); (d) in adults, strangers may elicit a variety of emotional responses including interest and contempt. As E-E suggests, fear may have played some role in the evolution of "individualized social groups," but interest, joy, and sadness or grief were probably more important (Averill, 1968; Jolly, 1966).

I expect that the key concept of phylogenetic adaptation as applied to human beings will prove to be heuristic. However, E-E's current list of behavioral adaptations has been hastily drawn. Some of the behaviors he discusses may not meet the criteria for such a classification, and in the case of some of the others (for instance, stranger response) he has given erroneous descriptions and misinterpreted their role in ontogeny and phylogeny.

Given the fact that E-E, a distinguished ethologist, has written this position paper on human ethology, its most serious shortcoming is the virtual neglect of what may prove the richest nesting place of phylogenetic adaptation – emotion-related facial behaviors. The universal facial expressions of emotion are perhaps the only satisfactorily documented phylogenetic adaptions in human beings. Many of the behaviors which E-E discusses can be interpreted as components or derivatives of these facial patterns. (He recognizes this in the case of the eyebrow flash, but he sees it as a derivative of surprise rather than the emotion of interest, which has more important functions in the encounters that elicit eyebrow flashes.) Although he discusses facial expressions, he demonstrates no appreciation of their relation to intrapersonal and social motivation or their role in human evolution and adaptation. Surely the evolution of social interaction strategies is based in part on expressive signals that covary with the conscious state (if not the intent) of the expressor. Deficiency in concepts related to individual motivation may account for human ethology's lack of theory and focus.

by **Peter H. Klopfer**

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What the ethologist's eye tells the ethologist's brain. When McCulloch and coworkers (Lettvin et al., 1959) entitled a paper "What the frog's eye tells its brain," he articulated a principle that no scientist dare ignore. Perceptions represent not new "facts" but inputs selected, altered, and integrated by peripheral receptors, such as the eye. Central/peripheral mechanisms operating at the level of the CNS influence the bias of the receptors, too, and therein lies the truth of the adage, "we see what we want to see." E-E and another observer may confront the same grey-lag goose and elicit an inappropriate nuptial display. E-E, however, may "see" the discharge of an Action Specific Energy that activates the

Fixed Action Pattern of the display. The other observer may not. Is the other observer less acute? Or has E-E's bias merely generated a different perception?

When the function (i.e., adaptiveness) of the behavior is the subject of discourse, the subjective interpretations are even more evident. Early in his paper E-E suggests that the twenty-one gun salute is a ritual whose function is to demonstrate peaceful intentions, analogous to the Massai's thrusting his spear into the ground. Later this salute becomes a welcoming cannonade that is analogous to the aggressive display of the Yanomani warrior. Surely, even now, the emerging study of human ethology has the means of transcend such subjective and contradictory interpretations.

We ethologists must realize that we come to our task describing and, at some level, "explaining" behavior with eyes little different, fundamentally, from those of frogs. Nor does the interposition of a movie camera alter matters. After all, film speed and grain, field depth and shutter speed have been designed to accord with our preexisting perceptual preferences. The camera, as used by E-E, cannot extend our limits of perception, it can only help to refine our analysis of what we see. The question is, How adequate is E-E's analysis? How justified his dogmatism? Dogmatism in the description we allow our observations to spawn is not becoming. More important, it may not be fruitful.

Thus, when we observe an animal we find ourselves monitoring it with biased sensors whose bias may well be acquired and cultivated. In other words, we generate an hypothesis or set of expectations for which we instruct our sensors to search especially zealously. If what they sense fails to match expectations, we may have grounds to reject our hypothesis. Our progress, if progress there is in science, is marked only by the corpses of rejected hypotheses.

The great merit of Lorenz's and Tinbergen's original ideas on the organization and "causation" of behavior lay in the explicitness of the hypotheses they generated. The waning of their subsequent influence has been due to their followers' failure to attempt to reject those hypotheses. They have sought rather to rigidify and preserve them. The unhappy consequence is articles that are a veritable stew of personal observations, recorded data, explicit assumptions, and unacknowledged prejudices.

Consider, for example, the eyebrow flash. It is deemed an *Erbkoordination* primarily because of its prevalence across cultures. The evidence for this conclusion is anecdotal, and, in my judgment, unconvincing. We are given no series of slow-motion sequences that have been analyzed according to accepted quantitative procedures, no electromyographic data, no measures of response latency to standard stimuli, and most important of all, *no measures of variability* and variance. Ethology has finally become too rigorous to rely on the natural history approach of an earlier century. We can rightly expect replicable measurements in place of casual observations and intuition. However, let us grant E-E's observations on the eyebrow flash. He uses these observations to justify the conclusion that the flash is a phylogenetic adaptation which, in turn, means that it is due to an Innate Releasing Mechanism. Once we recognize that the eyebrow flashing is due to an IRM and is an adaption, of course it follows that we can expect it to be homologous across cultures!

Aside from the evident circularity in this line of reasoning, it ignores the fact that cross-cultural studies are in fact (and contra E-E) not methodologically equivalent to the work in comparative anatomy. The comparative method requires information on degree of relationship that is independent of the structures being compared. Ideally, it is represented by a 2 × 2 factorial design, in which the structures of species A and species B (the species being of known relationship) are compared under the conditions of two different environments. Under some conditions, this may allow a conclusion as to whether features held in common by the two species are to be regarded as homologous or analogous. At best, however, this is an uncertain procedure, for a great deal depends on the level of analysis. Two structures can sometimes be regarded as both analogous and homologous, depending on whether they are viewed at the molecular, cellular, or organ level (Klopfer, 1976). Furthermore, listing a few cultures which employ a common motor pattern is no basis for establishing that the pattern in question is a genetically programmed *Erbkoordination.* Finally, even when we do identify a true *Erbkoordination,* such as a knee-jerk reflex, there is an enormous developmental and conceptual distance between such relatively stereotyped responses and the complex behavior patterns which are truly the focus of ethological interest – "nonverbal and verbal communication, aggression, mechanisms of bonding, and aspects of social structure . . ." (E-E).

All that has been written over the past years about the intricate interplay of genetic and environmental factors, about the concepts of phenotypic plasticity, norms of reaction, genetic assimilation, and cultural variability seems to have swept by E-E, or so this particular paper, at least, suggests. The methods of quantitative analysis of behavioral patterns seem to have escaped him as well. He acknowledges the work but appears to ignore its implications. Human ethology, he claims, inquires into the selective processes that have shaped behavior, yet he apparently fails to realize that the nature of the selective benefit the eyebrow flash bestows is only grist for speculation. E-E does not, in fact, cite a single study of selection. Nor is the application of ethological methods to human behavior as novel as he suggests. Margaret Mead and Gregory Bateson used these methods – including prism lenses – in the twenties, considerably antedating the fifteen years' span cited by E-E. Furthermore, it has been argued that "homology" and "analogy" can be useful only if operationally defined. Nowhere has E-E clearly and carefully distinguished these terms. And, finally, there is the problem of genetic influence on behavior. When an isolated bird develops normal song and there is "no indication" as to how the sensory stimuli impinging upon it have shaped its behavior, does it follow that *therefore* the behavior must be fully encoded in the gene?

Obviously, these last are minor cavils and it should be emphasized that E-E does a service in urging the application of ethological methods to human behavior. He sorely needs, however, to refine those methods and the concepts that underlie them.

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by **Joseph K. Kovach**

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"It just depends on what one wants to know": Eibl-Eibesfeldt's Human Ethology. E-E has compiled a substantial list of controversial issues for ethologists and students of human behavior to ponder. I regard his present contribution as a timely step toward a much needed synthesis of concepts, methods, and data that may ultimately pinpoint the various vectors and coordinates of ethology in the protean world of the "sciences of man." Also, I most strongly agree that the naturalistic approaches and comparative methods of ethology, of which E-E is a major proponent, have already made and will continue to make significant contributions to the study of human behavior. Yet I take exception to the defensive posture espoused by E-E in this paper, and to his undue emphasis on concepts and data that are framed in terms of the old nature/nurture controversy. In the comments that follow I hope to substantiate my general sense of unease with this article, which is aptly captured in the quotation that I took from it and elevated (admittedly quibbling) to the status of my title.

In my opinion, this article harks back to the times when the general scientific accreditation of ethology was still very much in question (Lehrman, *op. cit.* 1953; Kennedy, 1954). A mutually enriching accommodation has taken place between the concepts and procedures of European ethology and American comparative psychology during the quarter of a century that has elapsed since that time. After an initial stage of predominant concern with innate and genetically programmed aspects of behavior, human ethology too "is now moving to a position where it begins to map the interplay between our genetic blueprint and phenotypic flexibility, and to spot the pressures which overstretch even our exceptional adjustability" (Tinbergen, 1976, p. 520). In the light of these new developments in ethology, E-E's compendium of concepts, procedures, and data appears to be too restrictive, and his arguments outdated. I have in mind especially his focus on phylogenetically adapted behaviors defined in terms of fixed action patterns, innate releasing mechanisms, central motor generators, and the like. But pursuing this theme any further would do no more than restate the statement I have just quoted from Tinbergen. Instead, I take on the task of commenting on E-E's systematics for human ethology, and on the related concepts of biological determination and innateness of behavior.

The idea of systematics applies to E-E's description of human ethology in two ways: (1) in regard to his placement of ethology within a hierarchical system of biology and its subdisciplines; and (2) in regard to the comparative structure of concepts and data that he offers for characterizing the ethological investigation of human behavior. Although I consider the question as to whether or not the study of behavior necessitates reduction to the terms of biology still very much open, I accept the utility of a primarily biological approach and shall restrict my comments to E-E's comparative systematics.

E-E's comparative systematics is built from behavioral elements that are amenable to nonparticipant, naturalistic observation. It is anchored in the traditional concepts of ethology concerning the phylogenetic adaptedness of behavior. Its procedures are comparative evaluation and systematic ordering of naturalistic data according to behavioral alternatives of rigidly stereotyped versus plastic and variable, innate versus acquired, and phylogenetically preadapted versus culturally determined. Experimentation plays a role in this system primarily in order to illustrate a concept or anchor an observation in a concept. Thus, the deprivation experiment is described as illustrating the innateness of stereotyped motor patterns, and the imprinting experiment as an illustration of phylogenetic preadaptedness in learning. There does not seem to be much room in this system for another, more broadly used experimentation: to test (verify or reject) paradigmatic assumptions about causation and systematic relationships by controlled manipulation of interactive variables.

The emphasis in E-E's system is placed almost entirely on inferences and illustrations. Yet, let there be no mistake about it, the comparative procedure espoused by E-E is a powerful one. Darwin's use of it is the best witness, and so is the enormous contribution ethologists have made through introducing the method into the general structure of behavioral sciences. But there are some elementary steps in comparative systematics which, I think, are not observed by E-E.

Firstly, the comparative evaluation and systematic ordering of naturalistic data must be based on an *a priori* assumption concerning relationships that the system is proposed to demonstrate and test. Secondly, it must rely on a set of concepts that are capable of weighing the goodness of fit of data with the assumed relationships. Thirdly, it demands a tight logical coherence between concepts such that the lack of fit of data in one area would reflect on the entire system (i.e., it would reject the system or pinpoint a faulty concept within it). And finally, the identification of a faulty concept demands paradigm testing by controlled experimental manipulation of the relevant empirical material and variables. A quick survey of related steps in Darwin's work will illustrate these points.

Darwin's *a priori* assumption was inherent in the already prevalent ideas of evolution (Darlington, 1959). A set of concepts relating to his new insight of natural selection formed the basis for assessing the fit of his observations. His concepts were so tightly knit that the lack of fit of data in a single area undermined the entire system, forcing Darwin to engage in rearguard actions and to fall back on explanations that contradicted his very concept of natural selection. This is best exemplified by his argument that the various social instincts of man evolved as a result of "natural selection aided by inherited habits" (Darwin, 1871). It was Mendel's paradigm-testing experimentation that pinpointed the faulty concept, the concept of blending inheritance, and thus saved Darwin's theory of evolution via natural selection.

E-E's system of human ethology falls short of this model on several counts. It does not specify clearly the assumptions it proposes to demonstrate and test. It does not stress the coherence and logical continuity of concepts. And it does not seem to have much use for the paradigm-testing experiment that would verify or reject, as opposed to illustrating, a particular concept.

The proposal that phylogenetic adaptation influences the ontogenetic expression of behavior has already been accepted by all. The question that remains open is "How?" The experiential deprivation and imprinting experiments cited by E-E may demonstrate that certain responses are present in certain organisms without prior experience of eliciting stimuli, or that some responses are learned more readily than others. But these experiments tell us little about how an individual's genotype may influence the complex manifestations of its behavioral phenotype. Likewise, cross-cultural uniformity or lack of it in the expression of a particular behavior pattern tells us nothing about its phylogenetic adaptedness, or about the phylogenetic adaptedness of the complex behaviors within which such a pattern may occur. To answer the question of how phylogeny may influence the ontogeny of behavior one must turn to behavior-genetic experimentation: to identifying units of information in the DNA code and testing their influences in the manifestations of a behavior in particular environments and conditions of development.

In focusing on the question "whether biological heritage has determined human behavior to any significant degree" and proposing that it be settled by demonstrating innate elements in human behavior, E-E has in fact placed his arguments on the antiquated scale of the nature/nurture controversy, despite his protestations to the contrary. The nine lives of this controversy draw sustenance from a continued fascination with two equally unserviceable ideas: (1) that man's enormous capacity for learning and cultural evolution makes no difference with respect to his basically animal nature and biological limitations; and (2) that man has already freed himself from his biological heritage, and is ready to move into a world of unlimited behavioral and cultural progress. Issues so deeply rooted in man's image of himself will not be settled by science alone. But we can and must demand from ourselves the utmost care in guarding against the perpetuation of misleading interpretations and hasty inferences from incomplete data.

E-E is certainly aware of these issues. He states: "I wish to emphasize that the whole nature/nurture issue should not be considered as a matter of either/or, nor can the contribution of each be measured quantitatively in terms of percentages. It is a matter of how both contribute to the development of certain characteristics." But he quickly forgets his own dictum when, after stating that "what is innate to man is not a negligible quantity, but of fundamental importance," he proceeds to characterize such highly complex, culturally determined behaviors as gift giving and rituals in terms of innate and learned elements.

We are told that the pattern of "eyebrow flash" would be considered by ethologists as an *Erbkoordination* – an innate motor pattern. Then we are presented with a chart of functional differences, which reveals that even this simple behavior is quite variable, has a great variety of expressive functions, and is embedded in complex forms of social interaction. No, we simply cannot have it both ways! Behavior is either the joint product of an individual's genotype and environment, or it is a concatenation of innate and learned elements where the purely genetic and the purely environmental are discernible. But this is the point at which the issue "it just depends on what one wants to know" comes to the fore.

It should be apparent from what I have said so far that I do not regard the breakdown of behavior into innate and learned elements, or the crosscultural comparison of simple motor patterns, as particularly revealing of how our phylogenetic heritage may have influenced our behaviors in ontogeny. It may accordingly come as a surprise that I agree with E-E on several points, including the point that the endlessly reiterated fact of joint determination of behavior by heredity and environment contributes nothing to solving problems of phylogenetic adaptation. Am I then in conflict with the gist of my preceding paragraph? I do not think so. My work has long since convinced me that a concept may sidestep certain implications of a demonstrated fact, if by doing so it contributes to understanding some aspects of the fact, possibly even those which were initially sidestepped. In other words, I regard the nature/nurture tangle, including the related contradictions in the paper presently under scrutiny, as being due entirely to a lack of proper attention to the inherent mutuality of a concept and the question its creator tries to answer.

Whether we approach a behavior as genetically or environmentally determined, or as a joint product of gene and environment interactions, is entirely a function of what we want to know about that behavior. The question of genetic determination, of "innateness" in E-E's terminology, is certainly approachable with the axiom that, given total uniformity of the environments (past and present), individual variations of a behavioral phenotype may be regarded as genetic in origin. And vice versa, the question of environmental determination is approachable with the axiom that, given total uniformity of genotypes, all nonrandom variations of a phenotype may be regarded as being due to environmental influences. These axioms give access to particular genetic and environmental determinants in the phenotypic manifestation of a behavior. They are especially relevant to studies of the neurochemical or bioelectrical mediation of genetic and environmental influences in a behavior. However, the questions to be answered by experiments derived from these axioms may be restricted to small fractions of the total genotypic or environmental influences in the manifestation of the studied behavior.

Let us assume, for the sake of an example, that the phenotypic expression of a behavior is influenced by 100 genes at 50 loci, and that each of 48 loci is represented by two identical allelomorphs throughout the population. The behavioral-phenotypic variations of this population would, in a uniform environment, reflect on the activities of only 4 genes at 2 loci. This may say precious little about the role of phylogenetic adaptedness or the totality of genetic influences in the behavioral phenotype. For questions addressed to the latter, our best bet may well be the deprivation experiment championed by E-E, or its simplified variant in which the behaviors of experientially naive neonates are studied (Kovach, 1979). In such experiments the stimulus information that elicits the behavior, and all other environmental information that may conceivably contribute to the development of the behavior, are excluded from experiences prior to testing. Under such conditions, the above example of phenotypic variation would reflect the activities of 4 genes, plus their interactions with the uniform background genotype of 96 genes, without contamination from prior experience with eliciting stimuli. This would certainly represent a further step toward the answer to our question of phylogenetic adaptedness.

It is in such a light that the ethological concepts of "innate behavior" and "genetically blueprinted behavior" are useful. But they should not be treated as independent behavioral constructs. Rather, they should be regarded as concepts of considerable utility in relation to what one may want specifically to know about a behavior.

By way of further qualification, I agree with E-E that the comparative study of analogous behaviors equals in importance the study of behavioral homology. The large store of information ethologists have accumulated on the ways different species manage comparable environmental demands has a lot to teach us about the management of our own behaviors. There is far more similarity than difference in the ecological demands and behavioral adaptations of animals and man, especially when it comes to comparing ourselves with our primate relatives. But here, too, as correctly emphasized by E-E, the task is to search for questions and concepts that may be translated and tested in the context of human behavior.

by H. P. Lipp

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Brain complexity enhances speed of behavioral evolution. I wish to comment on two issues raised by E-E. They concern the phylogenetic acquisition of neuronal structures governing "innate" behavior, and the usefulness of comparative primate studies for the detection of common primate "inheritance" in man.

I am in sympathy with ethological thinking and am thus in favor of E-E's conception that even very complex behavioral patterns may have a preprogrammed genetic base. I doubt, however, the value of comparative studies in subhuman primates as far as the detection of preprogrammed behavior in man is concerned.

Both opinions are derived from a neurobiological concept of behavioral evolution which differs somewhat from a widespread notion among ethologists and ethologically oriented scientists. There is a common belief that phylogenetically acquired (and thus genetically preprogrammed) behavioral patterns survive resiliently as archetypal neuronal programs through long evolutionary periods, at least among members of the same order (see also point 14 on phallic display in E-E's summary). In man such programs are thought to influence human behavior, either overtly or covertly.

I have reasons to believe that the neuronal structures governing "innate" behavior have varying degrees of phylogenetic stability, and the more *complex* the neuronal structures involved, the more *quickly* new behavioral programs evolve *and* disappear. Thus, if any arguments are based on "common inheritance" of ancestral traits, at least three questions should be elucidated, if not answered: (1) How are new behavioral patterns phylogenetically acquired? (2) How stable are they during evolution? and (3) How resistant are they to ontogenetic modification? I propose first a simplified concept of CNS and behavior, and then possible answers to questions (1) and (2).

Jerison's "miniature nervous systems" in ethological terms. Jerison's concept (1976) of cerebral evolution based on the progressing combination of "miniature nervous systems" can, without undue strain, be translated into ethological terms. Peripheral sensory organs and peripheral sensory analysis appear rather similar across mammalian species. The same seems true for the organization of basic motor and vegetative patterns (for example, extensor tonus and penile erection). The underlying neuronal systems (not necessarily simply wired) may thus be conceived as the modal units of behavioral evolution [see Kupfermann & Weiss: "The Command Neuron Concept" *BBS* 1(1) 1978]. Varying interconnections between such modules formed by specific neuronal populations could create a variety of sensory and motor "subroutines" which might well be equivalent to innate releasing mechanisms (IRMs) or fixed action patterns (FAPs). Central neuronal populations may match and coordinate selected modules and "subroutines," according to environmental and physiological parameters. Such neuronal populations are commonly referred to as "motivational" systems. There is fair evidence that such systems really exist. Electrical stimulation of the hypothalamus elicits species-typical patterns which show high contextual variability in patterning as well as modifiability by sensory and motivational factors (for example, see Lipp and Hunsperger, 1978): it seems unlikely that such a crude nonspecific stimulus could produce all the observed effects. There is, in addition, some evidence that such specific coordination systems maintain a tonic activity, which counterbalances the activity of other systems (Fonberg, 1967), as has been postulated by von Holst and St. Paul (1960). Neuroanatomically, they seem to occupy most parts of the limbic system (in its broadest sense), and are functionally linked to striatal and extrapyramidal neuronal circuitry. Evidently these systems possess extensive neuronal connections.

How are new behavioral patterns acquired during evolution? I shall argue that this concept of a limited number of central coordinating systems "playing" on various sensory, motor, and vegetative modules and "subroutines" implies the following conclusion: The key-mechanisms for the evolution of behavior are those that govern the correct development of fiber connections between neuronal populations forming the various modules and coordination systems. It is clear that the ontogenetic development of the brain depends not only on fiber growth, but also on many other factors such as cell proliferation, cell death, and synapse formation (see Van der Loos, 1976), but these factors will be omitted for simplicity. Clearly, a variety of new patterns and new releasing mechanisms could be created by connecting basic modules in different ways. Changing fiber connections between the coordination systems could give rise to new associations of species-specific patterns and releasing stimuli.

Suppose, for example, that a hypothetical ancestral mammal is already equipped with neuronal networks mediating food intake (scanning, locomotion, food intake, all accompanied by pleasurable feelings) and defensive aggression (snapping elicited by painful stimuli). If, during ontogenetic development, a number of collateral fibers sprouted from the medial forebrain bundle into the adjacent intermediate zone of the hypothalamus, this could create a pattern of scanning, locomotion, and reinforced snapping. The new pattern combination could serve as an evolutionary base for predatory or territorial behavior. The fiber-sprouting could simply be caused by mutagenic failure of cholinergic fibers to reach their preprogrammed region (for such possibilities, see Reis et al., 1978).

Which innate patterns are stable during evolution? The tremendous complexity and precision of neuronal connections within a mammalian brain might suggest a highly rigid genetic pregrogramming in order to avoid mismatches (Sperry, *op. cit.*, 1971). However, Jacobson (1978, pp. 348–350), recognizes differences in developmental rigidity. Determination is extremely rigid in systems with little tolerance for mutagenic malfunction, but less precise in systems capable of compensating for such malfunction. I suggest that basic modules of behavioral organization will have a highly rigid genetic determination, since they are essential for the proper functioning of the more complex systems. Mutations concerning the development of basic modules are thus not likely to survive in the gene pool of a population, and this may explain their relative uniformity across mammalian species. Mutations affecting the "wiring-programs" building up FAPs and IRMs may not immediately threaten the life of an individual, but they may severely handicap reproduction. Thus these genetic programs should be fairly rigid within a particular species, at least for those FAPs and IRMs that are subject to selective pressures.

Probably the least rigid genetic determination ("macro-heterogeneity" *sensu* Jacobson) will be found in the "wiring-genes" which program the formation of neuronal connections within and between motivational systems. Owing to their complex interconnections, motivational systems undoubtedly have great power for compensating malfunctions (as is indicated by countless lesion studies). Affected animals may in most cases reproduce, and it is likely, therefore, that a great number of mutated "wiring-genes" responsible for motivational structures will survive in the gene pool of a population. This is supported by the observation that wild animal populations show considerable variation of emotional traits. Further confirmation stems from behavioral genetics: many inbred (nonpathological) mouse strains show behavioral and physiological characteristics related to limbic structures (Cardo, 1978). Even strong selection for learning abilities in rats results in strains with profound motivational differences (Lipp, forthcoming).

Thus, it is possible to conclude that the more complex the brain of a mammalian species, the more likely it is that new wiring patterns within and between central coordinating systems will emerge. Selective pressure will shape new genetically preprogrammed sets of behavioral patterns, with their accompanying emotional attributes and IRMs, and these will spread through a population during a short evolutionary period. Should the selective pressure vanish, the new patterns would be likely to disappear again within a short evolutionary time span. The phylogenetically more stable "subroutines," and especially the basic modules, would persist, perhaps becoming integrated in to newly formed complex systems. The more complex these systems, the greater the individual variability and modifiability.

by Ashley Montagu

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"Instincts," infants, adults, and behavior. Let me begin first by saying that by "human" I understand the functioning of all those traits that distinctively characterize the members of the species *Homo sapiens.* I take this to mean that all species-specific human behavior must be learned from other humans. This does not mean that, as E-E elsewhere has me say, except for a few reflexes of the newborn, "nothing" is inborn in man (Eibl-Eibesfeldt, 1972). Such a statement would, of course, be utter nonsense. If nothing were inborn in man he would be nothing, indeed, nonexistent. Truth will not be advanced by misquotation or misrepresentation.

I will pass over E-E's comments on believers in the *tabula rasa* myth, for I know of no such believers in the behavioral sciences. If E-E knows of any, I wish he would name them.

Can we not agree upon the basic simple fact that all humans are morphologically and behaviorally the product of the interaction between genes and environment; that heredity is *not* what is laid down in the genes, but constitutes the resultant of the interaction between genes and their environments?

If we can agree upon these elementary points then, surely, it becomes generally incorrect to speak of genes as "determining" anything. I do not think it can be too often emphasized that what genes do is to *influence, not* determine, the physiological, morphological, and behavioral development of traits.

Whether empirically demonstrable or not, it is clear that there must exist genetically based potentialities for many forms of human behavior. I do not know what the character of those potentialities is, nor do I think that anyone else does. It is for that reason that I am wary of such terms as "instincts," "innate," "blueprints," "programs," "biograms," "wiring," "circuits," "energies," and the like. High walls may not a prison make but stereotypic terms do. And, as Goethe remarked, where an idea is wanting a word can always be found to take its place. Apart from the ambiguity and fogginess of such terms they all, more or less, beg the question; as such they constellate ahead of the evidence, and constitute impediments to clear thinking and much-needed inquiry. Even such terms as "disposition" or "predisposition" are of doubtful utility since they may be too loosely employed. I prefer "potentialities," a term which seems to me to be relatively neutral, that is to say, not assuming or implying more than we know.

"Instinct," which implies preprogramming, a fixed action pattern, I find difficult to accept for any form of human behavior, with the possible exception of a few transitory infant reactions. E-E states that he will show that it is "basically incorrect to claim that "human behavior is entirely instinctless," or that "if human beings ever had any remnants of instincts to begin with, they would have lost them."

But E-E does nothing of the sort. All the examples he cites of "instinctive" or "innate" behavior are drawn from observations on infants. But in all the instances cited, can E-E be quite certain that there has not been some prenatal learning? We do have evidence that the human fetus is capable of learning (Spelt, 1948). Whatever their genetic substrates, the reactions cited by E-E do not in many individuals persist into later life unless they are encouraged to do so. Will E-E supply examples of instinctive behavior that stereotypically occur in all humans?

As for fear of strangers, I do not believe that this is a universal trait. The manner in which Australian aborigines, Eskimos, Polynesians, American Indians, and other peoples welcomed whites when they first met them is a matter of history. The most notable record of such an encounter is perhaps the famous Columbus Letter in which Columbus gives an account of the hospitality with which he and his men were received by the aborigines, "a loving uncovetous people, so docile in all things that there is no better people or country. . . . They loved their neighbors as themselves . . ." (Newhall, 1953, p. 8).

I question the statement that "Stranger avoidance has led man to live through most of his history in small, fairly close groups, where all know one another," or that "this is an innate disposition of fundamental importance." Throughout the millions of years of human evolution during which humans lived as gatherer-hunters, the optimum supportable population size was between thirty and fifty people to a band. To judge from existing gatherer-hunter groups, anything larger than this puts an economic and social strain on the members of the group. Such bands are not "fairly closed groups," as E-E should know, for he has worked among the Kalahari Bushmen who maintain friendly relations with other Bushmen bands, marry into them, and make quite long visits with them (Heinz and Lee, 1979). I do not believe that there is any evidence that human beings, except possibly some infants, have an unconditioned innate fear of strangers.

May I, in conclusion, say that I share with E-E the hope that, even if the academic millennium of total harmony is never reached, we may soon achieve a closer approximation to that understanding we seek concerning the nature of human nature.

by **Steven A. Peterson**
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On human ethology: some methodological comments. In his target article E-E makes several noteworthy contributions. First and foremost, he delineates clearly the application of classical ethology to the study of man. This is hardly an innovation, of course, since others have trod the same ground before. However, this essay contains a concise summary of that approach, with examples of data supportive of the thesis that one can profitably look at man's behavior from an ethological perspective. Second, the author includes in the work some empirical support for his arguments, although one might disagree with the interpretations given. This is a delightful change from the ancedotal approach which one often encounters. Third, one can only admire the effort to obtain solid cross-cultural data on behavior. The use of photography is potentially valuable, although we note some difficulties below. Finally, the author acknowledges "man's ability for self-control," a statement that one occasionally finds omitted from ventures in human ethology. These contributions stated, let us now turn to a consideration of some difficulties with the analysis.

(1) There is a sampling problem inherent in the work. E-E often refers to "universals" in human behavior. However, it is not clear on what basis these universals are derived. Filming a limited number of societies (the nature of the total sample, by the way, should be clearly specified, at least in a footnote) cannot really support assertions about universality. There appear to be relatively few societies filmed. I do not wish to imply that because of this there are no universals – merely that there are no data presented to bolster this assertion. Much work in human ethology is based on contentions of universality. However, investigators seldom invest serious effort into actually demonstrating this. If one wishes to determine, through photography, the existence of basic continuities across cultures at different levels of sociocultural integration, one should at least employ a probability sampling method.

(2) There may be an ethical issue involved in the author's use of photography. He notes that one element in his method is "filming people, without their knowledge." I do not consider this a major point, but I think that it should be addressed.

(3) The author seems to confuse hypothesis-generation with empirical testing of hypotheses. There are many conclusions throughout the paper that a particular human behavior reflects an "innate" propensity.[1] These do not seem to be directly tested, however. Eyebrow flashes and kisses may, in fact, be genetically influenced patterns of behavior, examples of *Erbkoordination*. However, E-E demonstrates only that such interpretations are plausible hypotheses. There is no direct test of these propositions. There is a broader issue here, namely, what are the criteria for acceptable explanation of behavior in human ethology? *De minimis,* it would seem that four basic questions would have to be answered: (i) What is the phylogeny of the behavior? (ii) What is the ontogeny of the behavior? (iii) What is the survival value of the behavior? (iv) What are the mechanisms underlying the behavior? (Cf. Tinbergen, 1963. For a discussion of an application to human political ethology, see Peterson, 1978). The first criterion is extremely hard to meet, although one can derive information from cross-species comparison and the human fossil record. However, this can only yield inferences, although these may be fairly strong. The ontogeny of behavior and the mechanisms underlying it are more amenable to study. Survival value, on the other hand, seems bound to remain inferential (although, once more, inferences may be strong). E-E, in this essay, does not really address all of these issues with respect to such posited universals as eyebrow flashing or kissing.

(4) Closely related to the preceding, there is no strong evidence that the homologies that E-E detects are really homologies. Often, as with kissing, they remain assertions. These assertions may be reasonable and correct, but we are given no strong reason for believing them.

(5) One basic method in E-E's agenda for human ethology is cross-species comparison. This is a perfectly legitimate enterprise, but one that is fraught with more peril than the author acknowledges. For example, valid comparison demands valid data from the different species being compared. Although ethological studies are impressive, there remain some problems that should be noted, such as sampling (how adequate are the animals or groups of animals as representative of the species-as-a-whole?), measurement (is the ethologist actually measuring what he thinks is being measured?), and recording (are all significant, appropriate, and relevant data being recorded?). Furthermore, establishing generalizations about human behavior across cultures is more troublesome than is often recognized. Again, we face the three problems just mentioned: sampling, measurement, and recording. Once we have answered these questions, we must then demonstrate clearly that the behaviors across species are really comparable. The basic question is this: What are the criteria for comparability (cf. Peterson, 1978; Peterson and Somit, 1978)? The issues in this paragraph may seem tedious and trivial, but if our explanations based upon comparison are to be adequate, they must be satisfactorily addressed.

(6) Finally, we must acknowledge the ubiquitous question of culture's role. This comment is one that I make with some hesitation, because E-E does note the

issue and because it seems to represent in many minds a knee-jerk response to efforts at biological analyses of man. I think, however, that E-E may devote too little attention to culture as a part of human ethology. The determination of what is "innate" in man is rendered quite troublesome because of man's development of language and culture. Some social scientists even speak of a "social construction of reality" as a result of these two intertwined notions (see, for instance, Berger and Luckmann, 1966). Campbell argues that cultural behavior may have become emancipated from genetic control (Campbell, 1975; see also Dawkins, *op. cit.*, 1976). We do not deny the fact that human cultural abilities are related to human biology. Nonetheless, the proposed program for a human ethology must address seriously such contentions as are raised by Campbell and others. Despite this critical comment, I think that E-E warrants some credit, since he faces the issue more clearly than others (see, for example, Wilson's disappointingly limp *On human nature*, 1978, a work which makes one suspect that there may be some merit in critics' suggestions that the author should have remained content studying insects).

Summary. In fine, we believe that E-E's essay performs a useful service for the scholarly community interested in human ethology. He summarizes the classical ethological approach toward human behavior, adduces some types of empirical support consistent with that approach (which, at a minimum, makes clearer to the reader the nature of that perspective), essays a data-based approach to deriving cross-cultural generalizations, and correctly notes the role of the culture and learning in *Homo sapiens*. On the other hand, we find certain points which warrant critical comment. These include the sampling issue, a possible ethical issue in unobtrusively photographing natural behavior in human societies, a confusion between hypothesis-testing and hypothesis-generation, lack of evidence for posited homologies between man and other animals, basic difficulties with the comparative method and, perhaps, and underestimation of man's "social construction of reality" through the medium of language and culture. Hopefully, the type of dialogue reported in this *BBS* treatment – article, commentaries, and response – will advance the biological study of man.

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NOTES

I might add, parenthetically, that E-E forcefully addresses the generally accepted "interactionist" developmental approach. This serves to remind the reader that the nature/nurture dispute continues to remain at issue, although in ever more subtle incarnations. For the standard developmental arguments, see Lehrman, *op cit.*, 1953, 1970.

by Glendon Schubert*

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Classical Ethology: concepts and implications for human ethology. If Friedrich Engels had written an article on "Marxism – Concepts and Implications for the Social Sciences," which somehow (like Mendel's records of his experiments) came to light only after decades of cryptic storage and was then published in some journal of open peer commentary like *Current Anthropology*, the effect would surely be sensational. Historians of ideas would have a field day, together, of course, with radicals from various of the social sciences (for whom the event would take on the significance of the Second Coming). On the other hand, it would have no effect whatsoever upon the current rulers of such countries as the U.S.S.R., the People's Republic of China, and Cuba; or their respective subject peoples. But social scientists who are neither historians nor ideologues would find more perplexing the task of commenting, from the perspectives of contemporary theory and methodology, upon Engles's prescriptions. A social-scientist/human-ethologist, confronted with the paper that E-E has written, finds himself in a somewhat similar position.

E-E is internationally known and respected for his prolific writing, both professional and popular, concerning nonverbal communication among primitive and sensorily deprived humans as well as the expression of emotions in contemporary human societies. He is the leading student and associate of Konard Lorenz, the founding father of classical ethology; and he is the author of a leading undergraduate textbook on ethology, published in English by an American publisher. One turns to his article expecting to learn much from what he has to say about the theory and promise, for the life sciences, of ethological approaches to the study of human behavior. But the reader soon discovers that this article has little new to say; much that it does say seems appropriately directed to some other and less professional audience; and many of its figures have been published and discussed many times before (e.g., Table 1 and Figs 9–11, 13: Hass, 1972; Eibl-Eibesfeldt, 1972, 1975b *op. cit.*)

The first part of my commentary will examine E-E's assertions, and discuss the extent to which this article rehashes both ideas and data that have long since passed into the public domain, at least for the readership of this journal. The remaining three parts of my commentary will discuss: the relationship between ethology and experimental psychology; that between ethology and sociobiology; and in conclusion that between ethology and ethnology.

Stonewalling straw men. Virtually all of the introductory sections of the article fall in the straw man category, together with much that follows. It is most unlikely, for example, that "Whether the concepts of phylogeny, selection, and inheritance are applicable to human behavior . . . is still a matter of considerable controversy" for readers interested in the behavioral and brain sciences, which the Editor has associated with the fields of "psychology, neuroscience, behavioral biology, or cognitive science." Perhaps E-E could provoke a debate at this level of distraction among readers of *Current Anthropology, American Sociological Review*, or *Psychology Today;* and there *is* indication that he is confused about his intended readership, because the title of his article directs his remarks to "The Sciences of Man" – which this journal's first Editorial (*BBS* 1(1) p. 1), material, and Call for Papers have explicitly identified with *CA* rather than *BBS*. Anyhow, E-E's article is replete with similar rhetoric, such as the claim that "one of [human ethology's] principal questions is whether biological heritage has determined human behavior to any significant degree"; whereas, one ought to presume that the relevant questions for the behavioral and brain sciences, as distinguished from at least substantial parts of the sciences of man, and not whether, but rather how, why, and by means of what processes of developmental interaction. The same point is repeated in the Summary (sec. 7.4), although some might question whether "genetic" determinism is synonymous with "biological." But even if the author were right about his audience, he seems to underestimate the extent of sophistication about evolutionary theory – even in such relatively retarded life sciences as political science (White, 1972; Masters, 1975; Somit, 1976) – that has emerged in phase with the preceding decade and a half which E-E concedes to the "formal" study of human ethology.

It is surprising to encounter, in the discussion of environmentalistic ideology (as restated in the concluding Summary, sec. 7.19) the argument that "strict cultural relativism may lead to ethnocentric political strategies." It is the conviction of many scientists of man that it was the proponents of biological determinism in the form of racial eugenics who, well within the memory of many still-living survivors, became conspicuous for both the promotion and the execution of ethnocentric political strategies; although, of course, the same sort of thing can be said about American treatment of blacks, tribal genocide among blacks in half of the countries of Africa today, and so on throughout the world and (so far as we know) throughout human history in recent millenia (see Harris *op. cit.*, 1977). To the extent that we understand such matters scientifically, it is because of – not in spite of – cultural relativism. The usual understanding is that cultural relativism has debunked ethnocentric political strategies, not fomented them.

There must be very few human ethologists today who would deem it necessary either to rebut Ashley Montagu or to defend – to say nothing of building directly upon – Lorenz (see Blurton-Jones, 1976; Travis et al., 1977). Montagu continues to maintain the beneficence of innate human nonagression just as Ardrey continues to argue the opposite; but much of their debate is at the level of public rather than of scientific interest. A focus upon the critique of Wilson by his colleagues Lewontin and Herrnstein, or of Trivers by Sahlins, might not be any more enlightening [see Sahlins, 1976; Caplan, 1978; Gregory & Silvers, 1978]; but at least it would better illustrate the cutting edge of debate concerning the interactive effects of phylogeny and environment in the course of human development. An example of contemporary discussion is provided by the "forum" of the current issue of *Human Ethology Newsletter*, which includes three such articles, all on the sociobiology of human sexuality, by Daly and Wilson (1978), Travis (1978), and Barkow (1978). The announced topics for the next two issues are: methodology for studying human adaptation (January 1979); and the relevance of modern hunter-gatherers to the evolution of human behavior, particularly from the points of view of theory and methodology (March 1979). But in E-E's article here, sociobiology appears only as the last three paragraphs of his "Discussion"; it is such an afterthought that it is neither anticipated by any of the preceding data, nor does it get summarized: sec. 7.20 is conspicuous by its absence, and so are considerations of or references to most of the contemporary protagonists and antagonists of sociobiology. The more one reads E-E's article, the more the conviction grows that probably its principal difficulty is that the time is now out of joint; its publication comes at least a decade too late.

In order to examine that hypothesis on a less intuitive basis, I undertook to compare the bibliography of E-E's article with an alternative and putatively representative collection of contemporary research in human ethology. The current issue of *Human Ethology Newsletter* (No. 23, October 1978, p. 2) refers to "Human Ethology Abstracts" of which two of three parts have been published so far. The first part was readily accessible, so I used that. E-E is listed in the same column of the same page of the *Newsletter* as a member of the executive board of the International Society for Human Ethology, as the organization publishing the newsletter recently had decided to redesignate itself.

The 134 references of Eibl's article are apportioned, roughly by decades, as follows: 78 for 1968–78, 34 earlier during the sixties, 10 during the fifties, 4 during the thirties, and a couple of others before that. The year 1968 is the mean for citations during the past half century, so the works cited are about a decade old on the average, even though a majority of them are less than that. A virtually identical total of 133 of the annotated "Human Ethology Abstracts" (Travis et al., 1977) are works published during the decade 1968–77; four others fall in the preceding decade, and nineteen are references to undated manuscripts. The average age of these references is five rather than ten years, so they are somewhat more contemporary as research literature.

The scope of human ethology is twice defined by E-E to be congruent with "biological research," to wit: "morphology, ecology, genetics, phylogenetics, developmental biology, sociobiology, and physiology." The Abstracts classify items under rather different concepts: general human ethology (theory and methods, general reference, group formation and mating strategies, sex differences); agression and altruism (aggression, altruism, and cooperation); children and infants (neonate behavior, attachment and separation, attention and cognition, general behavior, play and peer interaction); communication (vocalization and language, the face, gesture, and posture); and social spacing (personal space, social distance, environmental design). Even though "biology" conceptualizes human behavior rather differently than does "human ethology," there appears to be no obvious reason why both systems could not be used to classify similar sets of "references on human ethology." But that is clearly not what happened: of the 157 items listed by the Abstracts, only five appear among the 134 references to E-E's article; and of those five, two are to works authored either by E-E himself (*op. cit.*, 1974), or else by persons associated with his own research institute (Pitcairn and Schleidt, *op. cit.*, 1976). The other three works, appearing in both bibliographies, include: Wilson (*op. cit.*, 1975), Blurton-Jones (*op. cit.*, 1972), and McGrew (*op. cit.*, 1972). This is hardly impressive evidence that the two bibliographies purport to deal with the same subject.[1] I shall now turn to the very good reasons why they do in fact deal with quite different subjects.

Ethology and experimental psychology. One difficulty lies in the disciplinary chauvinism supporting the educational systems out of which classical ethology developed (see Presthus, 1977; H. T. Wilson, 1977) and which still tends to characterize the thinking of its remaining spokesmen. Classical ethology was (and to a large extent still is) a naturalistic activity pursued by persons trained as zoologists, who do their own experimental work and engage in relatively little collaboration with experimental psychologists. In the United States, to the contrary, such organizations as the Animal Behavior Society (ABS) and the American Society for Primatologists are much more equally divided between zoologists and comparative psychologists (among other supporting disciplinary components) and the representatives of both groups are accustomed to a symbiotic relationship very different from what is found in continental Western Europe. The United Kingdom is somewhere in between, as symbolized by the subtitle of Hinde's textbook (1970); and it has been more to the U.K. than to the U.S. that continental ethology has turned. *Human* ethologists are organized neither on the continent nor in the U.K.; but they have been for at least five years in the U.S., piggybacking the annual meetings of ABS.

Probably it is innocence of what American human ethology involves that explains the prominence E-E gives to such putative goals as "to bridge the gulf between ethologists and opposing [sic] groups of behavioral scientists." But this article frequently manifests a barely repressed fear of experimental psychologist strangers (such as Tobach and Eisenberg); as Charlie Brown says, "We have met the enemy and he is us."

Rapprochement is not likely to be facilitated by the persistence of classical ethologists in the use of theory, methods, and concepts that are idiosyncratic and that have long since been given up or greatly modified (and always in the direction of indeterminancy and flexibility) by an intervening generation of students of animal behavior. The Lorenzian hydraulic model of animal motivation discussed by E-E, for example, is treated as a relic in modern textbooks on animal behavior (Hinde 1970, pp. 201–202; Beer, 1973, p. 34; Alcock, 1975, pp. 189–191; Mortenson, 1975, pp. 41–42, describes it as the "flush-toilet model," and portrays a figure of it [see Figure 1] and Dawkirs, 1976, p. 8, includes it in his assertion of "the general, deserved destruction of simplistic energy models"). Concepts of fixed action patterns, innate releasing mechanisms, drives, and releasers are too rooted in Newtonian mechanics (see Landau, 1965) to be useful in guiding contemporary research (Hinde, 1970, pp. 21, 121–213; Beer, 1973, pp. 37–38: "The hierarchy theory . . . was the culmination of the development of theory at the heart of classical ethology. . . . Later thought and study questioned and tested the assumptions and implications of the theory, and in so doing carried ethology from its classical period into a period in which theoretical unity gave way to differentiation in theoretical interests and in research"; Mortenson, 1975, pp. 41–43). At least this is true in the study of mammals; and it is worth remembering that the animals with which both Lorenz and Tinbergen (as well as most of their students) worked primarily were either fish or birds, whereas the thrust of interest in recent animal research in the U.S. has been in mammals, for which the early ethological research apparatus was not designed. Even at the level of stickleback courtship discussed by E-E, it is by no means evident that it makes the slightest difference whether it is stated that the male's zigzag course through the water ("courting dance") *releases* or that it *stimulates* presenting behavior on the part of the female conspecific – except that "stimulates" articulates with a very much larger corpus of research on human behavior, while "releases" does not.

Imprinting, perhaps the best-known concept of classical ethology, is now understood to be very much more complex and subject to many more qualifications than could have been realized at the time Lorenz reported his early observations [see Rajecki et al. Toward a General Theory of Infantile Attachment *BBS* 1(3) 1978]. It is one thing to find "imprinted" goslings waddling after Lorenz, or even jackdaws trying to feed him warm minced worms; it is quite another to hypothesize that a prenatal human imprints on the mother's heartbeat. Everything that we know about the phylogeny of humans ought to impel us to anticipate a great deal more flexibility in perception and response alike than has evolved in the behavior repertoires of either geese or jackdaws. The latter, incidentally, are animals whose social behavior I have investigated at first hand (see Röell, 1978). Many of these differences in human flexibility are discussed in a paper by Blurton-Jones (1976) which is also on the subject of the implications of ethology for social science, but in which Lorenz is neither mentioned nor cited.

E-E's emphasis upon animal "drives" is the wrong way to establish ties for or with human ethology; it would be much easier to link up with more of the life sciences if the concept of "needs" were substituted. It then immediately becomes necessary to reconsider E-E's remark that "The formal application of ethological methods to the study of man began about fifteen years ago." That statement may hold for Lorenzian ethology; but there are certainly many instances of earlier beginnings in human ethology. Tomkins (1962) was reporting at international congresses his theory of human facial nonverbal communication, a decade before then; Bowlby (1958) was discussing ethological approaches to attachment behavior; and various amateur primatologists (Marais, 1934) and humanist precursors (Day, 1920) were much earlier in discussing animal models of human behavior. Most important was Maslow (1954) who, trained as a primatologist, had formulated his theory of human needs as early as 1943: his influence has spread beyond psychology to include many social biologists (see Corning, 1977; Davies, 1977).

Human ethograms. E-E's assertion that "there exists a universal 'grammar' of human social behavior" suggests a dubious way to conceptualize the basis for a theory of human (and probably also most other forms of mammalian) social behavior. How dubious, is exemplified by the basic primate political biogrammar proposed by Tiger and Fox (1971, p. 32) as a model for for human political behavior. Grammars constitute systematic analyses of the structure and functioning of communication systems, especially natural languages; and however important communication is to social interaction, and vice versa, they are by no means the same thing (see Burke, 1945). Dawkins (1976, pp. 43–47, esp. p. 46) has provided an elegant discussion of grammatical models, with analysis of some of the problems involved in biogrammars, concluding that: "The problem is this. In the case of human language the criterion for grammatical correctness is the judgment of a native speaker of the language. In the case of animal behaviour 'correct' and 'incorrect' have no such meaning."

Sociobiology represents a type of grammar, at least in the guise of the models of population and behavior genetics applied to humans, and as understood by its most vociferous opponents (The Ann Arbor Science for the People Editorial Collective, 1977). The Hamilton-Trivers-Dawkins grammar of hard-core sociobiology specifies how rational actors will behave if they are to maximize their individual genetic contributions to the survival basis of their species. But sociobiology also has a more general and omnivorous form, as synthesized by Wilson [q.v.], who is said to speak openly and often about the "cannibalization" of other disciplines (including the social sciences) that are to be subsumed under the aegis and imprimatur of a dominant (if not rampant) supersociobiology. Such excesses indeed invite retorts such as E-E's that "the new field of sociobiology has certainly justified its own existence as a part of ethology." But aside from tit for tat, E-E's comment is simply wrong and misleading. Evolutionary biologists, population geneticists, behavioral geneticists, and others who have contributed – also, pretty much, during the past fifteen years – to the postulation of the hypotheses associated with hard-core sociobiology certainly have not been a "part of ethology" in the past; and E-E is the first to suggest that their work should be so classified in the future. It seems more likely that ethologists, including human ethologists (Daly and Wilson, 1978; Travis, 1978; Barkow, 1978), may well be involved for some time to come, together with experimental psychologists, primatologists, and many other life scientists, in attempts to test empirically the hypotheses of sociobiology.

By chance (see Aubert, 1959), one of the many ongoing real-world experiments in alternative life styles has recently provided some negative evidence bearing upon certain of E-E's sociobiological speculations, with particular regard to Trivers's (1971) most basic hard-core propositions about altruism. Suicide may indeed be the ultimate form of altruism; and E-E is probably right that typically in hunter-gatherer bands the populations consisted of "fairly closely related individuals, so that investment [in suicide] should pay off [in terms of genetic 'inclusive fitness'] for any group member and not just for immediate kin." But in the largest-scale and best-documented report of mass suicide in recent human history, the population members, although otherwise conforming to the size scale and at least some of the other criteria for neolithic horticulturists, were all unrelated genetically except at the level of nuclear family groups, of which many were mother-infant combinations. Jonestown indeed testifies to what E-E terms "man's astonishing ability to identify with his larger group (band, village, people) to the extent of self-sacrifice." Unfortunately for Trivers's theory, the motives of the deceased had to be strictly cultural: they died for social and ideological reasons, not for their genes. From a cultural point of view, they were an aggregation of poorly adapted and relatively unfit persons who, from a genetic point of view, took the action best designed to assure the minimization of their inclusive fitness, both individually and collectively.

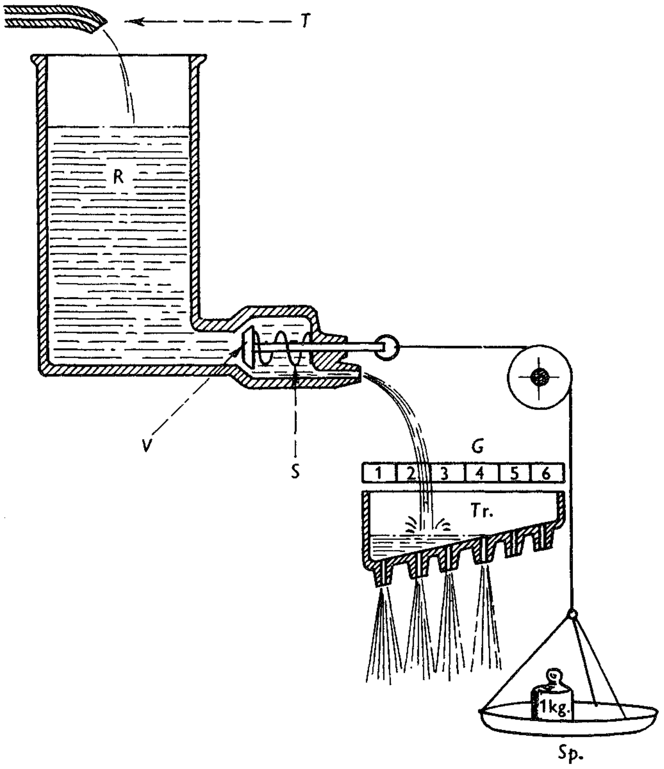

Figure 1. (Schubert). Lorenz's hydromechanical model for motivation. Tap T: action-specific energy; Reservoir R: available energy; Valve V: releasing mechanism; Spring S: higher sensory inhibition; Scale pan Sp: releasing stimulus; Gauge G: intensity of response; Trough Tr: sequence intensity. (From Lorenz, 1950, p. 255–6; reproduced with permission of Society for Experimental Biology.)

Human ethnograms. It may well be that "ethologists prefer nonparticipant observation techniques in the natural setting," but where in the world are they going to be able to indulge such preferences? A mirror-lens camera may be perceived, by primitives unsophisticated about cameras, to be less intrusive than cameras that are aimed at them (Hass, 1972, chap. 7: "A Voyage of Self-Exploration," describes how the photos were taken); but a primatologist who attaches himself to a band of nonhuman primates is engaged in participant observation, just as surely as Max Gluckman (1955) was a participant in the council of *indunas* when he sat in on their deliberations, while explorating legal ethnography during the colonial era in what is now Zambia.

Still, there is no doubt of the value, at least to ethnologists, of E-E's recurring global expeditions during the past couple of decades to undertake filming of NVC (nonverbal communicative) behavior sequences, of the surviving remnants of various scattered hunter-gatherer bands that have been "side-tracked into a cultural blind alley" (as Morris, *op. cit.,* 1968, p. 10, has described them). They are evolutionary losers only in the genetic sense of inclusive fitness; from the perspectives of group and kin selection, they have usually been very well adapted, which leads most ethnographers to object vehemently to their characterization by Morris. But the question still remains as to how much more value such film records have than, say, the surviving prints of Fitzpatrick travelogues, as contributions to the theory and method of human ethology.

It seems apparent that E-E visited his primitive subjects with various hypotheses about nonverbal communication (NVC) in mind; or, as he might prefer to put it, with mental templates of the fixed action patterns (FAPs) that he hoped to release for purposes of his photography, the task of which was to record on film what he perceived to be acceptable examples of the occurrence of such FAP-NVC behaviors in the subject populations. But the same behaviors may have been associated with different social contexts; other social situations may have produced the same behaviors; or the same social situations may not have produced the target behavior on other occasions. The problem is that even if he did undertake to film (as Fitzpatrick might well, however inadvertently, have done) the – no doubt long – stretches of facial and gestural communication when nothing relevant was being signalled, such data are neither analyzed nor discussed in his reports of the behavior. Instead of evidence pro and con, we are offered examples of good behavior – or what amounts to the same thing, good examples of the behavior. Hence the *nominal* objects of his observation, "unstaged social interaction" as he calls it, must be qualified by the phrase "highly selective" for purposes of recording, or at least those of publication. The quest for data not inconsistent with an hypothesis may produce data that exemplify the theory; but they cannot help in the more mundane – but also scientifically crucial – task of assisting in the endeavor to refute the hypothesis if possible.

Are the resulting film images better classified as ethograms or as ethnograms? Certainly the task to which E-E aspires (sec. 7.2) of trying "to understand the evolution and functional aspects of cultural patterns, in the perspective of their contribution to overall fitness" is one that is ordinarily undertaken by social anthropologists, and hence, in the ordinary understanding of the words, constitutes the practice of ethnography rather than ethology.

NOTE

*Author's Response will appear in Continuing Commentary.

1. The second part of the "Human Ethology Abstracts" (Travis, 1977) is an annotated bibliography of 222 items, almost entirely from the seventies, of which precisely one (Ashley Montagu's *Man and Aggression,* 1973 ed.) appears also among E-E's references, cited in an earlier edition (*op. cit.,* 1968).

by **Pierre L. van den Berghe**

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Ethology versus sociobiology: competitive displays. E-E's paper confirms my conviction that the social sciences are on the threshold of an exciting new era. Several lines of inquiry, ranging from biochemistry to ethology, have transformed the exclusive cultural-determinist credo of the social sciences into a veritable theoretical sieve. The doctrine now holds no more water than the creationist view of evolution. The only general explanation of behavior that "works" as a scientific theory is the Neo-Darwinian synthesis, a model based on the *interaction* of genes and environment. It is equally clear that, for humans, culture (including symbolic language) increasingly constitutes an extremely important (but not *all*-important) part of the environment. Culture may be defined as the man-made part of the environment; its inheritance is Lamarckian, to be sure, but the capacity for it grew out of a process of Darwinian selection and continues to be linked to it.

A social science divorced from biology is becoming as unthinkable and as absurd as biology without chemistry. There is simply no intelligent argument possible any more over *whether* genes influence human behavior; now it is only a question of establishing in what ways and with what degree of determinacy. Let us hope that all the archaic nature/nurture debates are buried for good. We are (or at least should be) in the business of explaining variations in human behavior as the result of genetic and cultural selection in response to ecological constraints (including the ones of our own making). The end result contains a large and perhaps irreducible element of indeterminacy due to the multiplicity of environmental factors involved, but then so does the evolution of other organisms. We could no more have predicted whales and bats 100 million years ago than, say, the French Revolution 500 years ago.

Fundamentally then, there is little to argue about. Instead of displaying to one another in journals, in an arcane ritual of dominance, we should get down to the business of studying each other. Yet, we have an *Anlage* to display: I found the invitation to comment on the paper under consideration simply irresistible. So have, I am sure, several of my colleagues. Perhaps one of the most common ploys in these competitive attempts to become the center of the private attention structures described by Michael Chance (Chance and Larsen, *op. cit.,* 1976) is to mimic disagreement, preferably with the alpha male. By publishing the right book at the right time and place, in the right language, E. O. Wilson (*op. cit.,* 1975) has captured a share of attention that he himself, I believe, will gladly concede to be somewhat disproportionate to his (substantial) accomplishments. The label "sociobiology" seems to be in the process of supplanting that of "ethology," and the label happily stuck to Wilson. He is, therefore, a prime target for his competing primates, both in and out of academia, much as Lorenz was just before him.

So the stage is set for competitive displays: Wilson described ethology as an obsolescent description of the behavior of animals in "natural" settings, a kind of natural prehistory of sociobiology. Inevitably, E-E, heir apparent to the Lorenzian mantle, retaliates by saying that sociobiology is a mere branch of ethology. In actuality, both protagonists define ethology/sociobiology as the biology of behavior, and both apply to their discipline the uncontested Neo-Darwinian paradigm of evolution by natural selection. In principle, there is little of substance to argue over, and it is a matter of total indifference whether the study of behavior is called "ethology," "sociobiology," "biosociology," "behavioral biology," or, as Richard Dawkins (1978) jokingly suggested in a recent rejoinder to a review, "selfish genery." Notwithstanding all this, these cultural substitutes for penile displays do go on.

Let me, at the outset, confess that my associations have been mostly with people who have been labeled "sociobiologists" rather than "ethologists." The differences between these two sets of behavioral biologists have been not so much on fundamental tenets as in the day-to-day conduct of their trade. Ethologists and sociobiologists have been talking different languages and engaging in somewhat different styles of research. Most sociobiologists talk English; they have developed such concepts as inclusive fitness, kin selection, reciprocal altruism, parental investment, and evolutionarily stable strategies; they are often enamored of elegant mathematical models that they like running through computers. They devise clever experiments to test their models; they tend to be less concerned with the ontogeny of behavior and the modalities of the proximate mechanisms that bring forth the phenotype; and they are often impatient of the complexity of the real world, unless it has a direct bearing on a neat theoretical problem.

By contrast, ethologists tend to talk German; they speak of *Anlagen, Erbkoordinationen,* and similar agglutinative mouthfuls that translate badly into English; they are more descriptive and concerned with the nitty-gritty details of ontogeny, signals, rituals, and proximate mechanisms; they insist on a rigorous methodology of nonparticipant observation of animals in "natural" environments; they are less concerned with elegant and parsimonious theoretical formulations; and they positively delight in the all the messy complexity and diversity of the world around them.

Naturally, most people fall between these two overdrawn caricatures, and many like neither label, preferring to call themselves ecologists, behaviorists, population geneticists, developmental psychologists, entomologists, or whatever. We need more of both types, and all shades in between. However, since E-E presents himself as an ethologist and represents a fair approximation to one of the profiles I have just drawn, I shall query some of his statements from an admittedly sociobiological angle.

First, there is a low blow to Wilson (*op. cit.,* 1976). One would have to be very simple-minded to read Wilson as restricting inclusive fitness to relatives sharing 50 percent of genes. Again, this is a not-too-subtle attempt at mimicking disagreement, a crude penile display.

E-E's appeal for a greater use and more systematic collection of photographic evidence in human ethology is well taken, but there is already more of it than he suggests. I should like to refer him, for instance, to publications of the Society for the Anthropology of Visual Communication, such as Erving Goffman (1976). (This is the "I-read-the-literature-better-than-you" display, the scholarly primate's way of saying: "I pay attention to our attention structure, therefore I deserve to be at the center of it.")

E-E states that fear of strangers is maladaptive in the modern urban setting. It may be in Seewiesen, but not to anyone familiar with the jungle of a modern megalopolis. (This is the *ad hominem* display.)

The argument about the linkage between the head-shaking signal for "no" in most cultures and the satiated baby's head turning at the breast is shaky. It is that kind of loose speculation that both ethologists and sociobiologists are constantly being taken to task for by social scientists. Let me put in my two bits' worth of ethology on this point. I have observed hungry human neonates (less than one month old) swiveling their heads laterally in apparent *search* for the nipple *before* feeding. They certainly looked as if they were saying: "I'll never touch the stuff again!" (Here we have a good example of the simple "I-am-better-than-you" display. The use of it is especially effective here because the challenger takes on his rival in the latter's chosen field of competence: the observation of "unstaged" or "natural" interaction.)

Joking aside, I would like to conclude with two more substantial points. The first concerns the ethologist's repeated emphasis on the importance of *nonparticipant* observation of *unstaged* social interactions in *natural* settings. Even for studying nonhumans, such a prescription is unnecessarily rigid, and conceptually limiting. The concept of a nonparticipant observer not only seems to exclude experimentation (which, I am sure, is not E-E's intent), but is also epistemologically naive. The presence of the observer often markedly affects the situation being observed. For humans, in whom the phenomenon of consciousness comes in, this is doubly true [cf. "Cognition and Consciousness in Nonhuman Species" *BBS* 1 (4) 1978]. What is a "natural" setting for humans? Serengeti National Park? The New York subway? The Gulag Archipelago? Indeed, a strong argument could be made for paying special attention to *extraordinary* groups in order to test hypotheses. Behavior in such settings as concentration camps, "natural" catastrophes, or famine is especially illuminating *because* these environments are beyond the normal range. So are extraordinary groups like utopian communes. How much has been learned, for instance, about incest from Joseph Shepher's (1972) study of the "unnatural" child-rearing system of the Kibbutz! Desmond Morris (1969) went as far as to suggest that the whole of industrial society far from being a "natural" setting for humans, is in fact a huge zoo of our own creation. Clearly, there can be even less of a sharp dichotomy between "free" and "captive" conditions for humans than for other animals.

What is an "unstaged" social interaction? In a fundamental sense, human consciousness makes many, if not most, of our interactions staged. Indeed, a major approach to the observation of human behavior has been premised on the notion that the world is a stage. I am referring, of course, to the work of Goffman (*op. cit.,* 1963) and of the "ethnomethodology" school. The only tenable position for a study of human behavior is that our species lives in a wide range of environments, many profoundly modified by our own actions; that most of our interactions are to some extent conscious and therefore staged; and that nothing is gained by regarding some settings as less "natural" and therefore less worthy of study. Nor is the strategy of nonparticipating observation necessarily the most fruitful one. Biologists studying other species constantly intervene in the situation they observe. Why should human ethologists systematically refrain from doing so (for other than ethical considerations)?

The last issue concerns group selection, a concept for which E-E shows lingering ambivalence. Developments of the last decade show the increasing success of the reductionist strategy in seeking the ultimate unit of selection. As Dawkins (*op. cit.,* 1976) forcefully suggested, even the organism – the usual conceptual unit of selection in much of the literature – is merely an ephemeral package of genes, and the ultimate units of selection are the alternate alleles at a given locus. Still, since the behavior of organisms is much more readily observable than that of genes, and since organisms are such readily definable and well-bounded units, it is a convenient shorthand for many purposes to speak of natural selection at the level of organisms.

Group selection is a little different. Societies do not have skins or exoskeletons. For highly related colonial invertebrates and eusocial insects, societal boundaries are fairly unproblematic; but for vertebrates, and most assuredly for humans, the definitional questions alone make group selection arguments much more problematic. Still, let us concede that as a heuristic shorthand device it is moderately useful for certain purposes and at certain gross levels of ecological analysis to refer to conspecific animal populations as competing against each other, or even (to push the argument one step further) to speak of different species as competing against each other. This is group selection *in the loose sense,* that is, conceived as a gross shorthand description of the outcome of individual and genic selection. The case for group selection, *in the strict sense* of a supraorganic level of selection which *conflicts* with individual selection, is extremely weak at best for nonhumans, though it is, I would concede, still an open question for human societies. E-E fails to make clear whether he means group selection in the loose or in the strict sense, but, to be on the safe side, the less we speak in "benefit-of-the-species" terms, the better off we are.

In conclusion, notwithstanding any of the above remarks, I greatly admire E-E's pioneer efforts in human ethology. Like all who dare venture on unbeaten paths, he is almost certain to be wrong on a number of specifics, but he powerfully contributes to revealing exciting prospects. If nothing else, he confounds critics who describe ethologists as those students of behavior who pretend that people cannot talk. (The last paragraph is obviously an appeasement display superimposed on aggressive displays. The target animal must have high enough rank to be worth challenging, but his high rank makes it unwise to antagonize him permanently, hence the final appeasement display.)

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Some logical fallacies in the classical ethological point of view. E-E has written a concise exposition of the classical ethological view of human behavior. The ethology of Lorenz and his followers has been incisively criticized by Lehrman and others, but it appears from E-E's essay that these criticisms have brought about no major modifications of the thinking of classical ethology.

I would like to discuss certain logical fallacies that are evident in E-E's interpretations of key experiments and studies, specifically the deprivation experiment and the study of cross-culturally universal behaviors.

According to both E-E and Lorenz (*op. cit.,* 1965), if an individual is deprived of an opportunity to learn a species-typical behavior, be it a song or a smile, by observing conspecifics performing that behavior, and if that individual nonetheless performs the species-typical behavior, then the behavior must be "innate," "encoded in the genome" or the genetic "blueprint" for a nervous system. I maintain that it is fallacious to draw any conclusion about the genetic inheritance of a behavior pattern from an environmental deprivation experiment. The improper inference made by classical ethologists follows from a dogmatic restriction of the causes of species-typical behavior to two classes of phenomena: observation learning, or imitation, and genetic coding, presumably in DNA molecules.

If all possible causes of a behavior pattern can legitimately be dichotomized, then of course an experiment which yields results that exclude one cause therefore compels the researcher to affirm the complementary cause, and it does so with all the authority of simple logical reasoning. If the possible causes cannot be neatly dichotomized, then no conclusion about the cause of a behavior can be drawn from an experiment which allows the exclusion of only one cause.

Suppose there is an urn known to contain only black and white marbles. If one marble is drawn and it is found to be not black, it is therefore white. No further investigation is necessary to assert this conclusion, because prior investigation has already established that the entire stock of marbles from which the sample was drawn consists of only two kinds. However, if the urn contains black, white, red, green, yellow, and blue marbles, and if it is established only that a marble drawn from the urn is not black, then there is no way of determining its actual color without further investigation. It could quite plausibly be either white, red, green, yellow, or blue.

If we look at the life of an animal, it is obvious that a vast array of mechanisms are active in its development from conception to the time it first displays some species-typical behavior. Some well-known mechanisms include the following: (1) the set of chromosomes, or the "genome," determined at fertilization; (2) the host of organelles and macromolecules in the cytoplasm of the zygote; (3) the spatial configuration of the cellular components of the zygote; (4) the external environment of the zygote with its characteristic temperature, pH, salinity, osmolarity, and so forth; (5) environmental factors such as nutrients and viruses, which are absorbed and in some cases assimilated by the organism; (6) the web of interactions among components within each cell during development; (7) the numerous interactions among the diverse cells comprising the developing organism; (8) in birds and mammals, maternal or parental care; (9) exercise by the organism; and so on. A further mechanism may also be observation of conspecifics performing a species-typical behavior.

If a deprivation experiment is carefully conducted so that two random samples of animals from a single population are reared in two environments which differ in only one respect – opportunity to observe a conspecific performing a particular behavior – and if the animals in the deprived environment nonetheless perform the species-typical behavior, then one and only one thing can be concluded: observation of performance by a conspecific is *not necessary* for normal performance of the behavior. Such an experimental result does *not* prove that the behavior is encoded in the genes (mechanism 1 above). Neither does it prove it to be encoded in the cytoplasmic organelles (mechanism 2) or any other of mechanisms 3 through 9 cited above.

This basic point has been made by Jensen (1961), Kuo (1967), Whalen (1971) and, most lucidly and eloquently, by Lehrman (*op. cit.,* 1953, 1970); yet the classical ethologists maintain their dogmatic view of the deprivation experiment.

When Lorenz and E-E conclude from this kind of result that the behavior is "encoded in the genome," they are in effect uncritically accepting the null hypothesis, which may constitute what is termed a Type II error in statistical inference. They in effect hypothesize *a priori* that the behavior is "innate," and from this null hypothesis they predict that the animals reared in normal and deprived environments will behave the same way. If there is no significant difference between the two groups, then they accept the null hypothesis as true. This is a serious error of logical reasoning.

The only way to draw a valid conclusion about the role of genes in species-typical behavior is to vary the genes themselves, perhaps through a mutation or selective breeding, and demonstrate that the behavior varies as a consequence. Because heredity consists of more than Mendelian genes in chromosomes, special crossing experiments must be done to dissect the contributions of Mendelian inheritance from numerous other mechanisms of inheritance (see Wahlsten, 1979) and establish that the behavior is indeed "encoded in the genome."

Investigations of the songs of isolated birds, the babbling of human neonates, the smiles of the blind, or the greeting gestures of primitive peoples are relevant and informative for students of behavior, but none of these studies can provide proof that behavior is "encoded in the genome" or "innate." The deprivation experiment is only one of many techniques for the analysis of behavior, and the knowledge which can be gleaned from its results is narrowly circumscribed.

Consider further the case where experiential deprivation does indeed disrupt species-typical behavior. This certainly demonstrates the plasticity of the behavior in question, but it does not in any way prove that the "genome" is *irrelevant* for performance of the behavior. The chromosomes may play an important role in the development of a nervous system capable of rapidly acquiring information through observation.

It seems to me that the classical ethologists have responded to previous criticisms of their doctrine by adopting an eclectic approach in order to blunt the effects of further criticism. On the one hand, they stubbornly cling to their original ideas, while on the other, they incorporate criticisms into their writings in the form of disclaimers that they really mean what their words appear to mean. This is apparent in the essay by E-E.

For example, in his abstract he presents a very clear dichotomy of causes of behavior by asserting that "innate and culturally evolved patterns of behavior can often substitute as functional equivalents for one another." Then at the end of section 3 he contradicts himself: "I wish to emphasize that the whole nature/nurture issue should not be considered as a matter of either/or, nor can the contribution of each be measured quantitatively, in terms of percentages." Now, what is *substitution,* if not a matter of "either/or?"

In the section on cross-cultural comparison, E-E begins with this disclaimer: "The fact of their universal appearance alone does not allow us to deduce that these patterns are innate in man." There seems to be a two-step process of reasoning implicit in this statement. First is the inductive inference that a behavioral pattern which appears in every one of a sample of cultures is universal, that is, occurs with probability 1.0. Second is the deduction drawn from the classical ethological theory that universality means the pattern is innate.

An inductive inference may be made on the basis of "circumstantial" evidence, and it always has a certain probability of being incorrect because of sampling error. A deduction from theory, on the other hand, should be made with mathematical certainty. It is a very inadequate theory that yields deductions which are only "probable," such that they may or may not follow from the theory.

Consequently, E-E becomes mired when he further states that patterns of expressive behavior which are virtually the same in all respects in many cultures provide "strongly suggestive circumstantial evidence for the hypothesis that they constitute phylogenetic adaptations," and when he speaks of "universals which can be said, with a high degree of probability, to constitute phylogenetic adaptations." These phrases clearly show that E-E has no doubts that the patterns are universal. Rather, he vacillates over the statement: Universal, therefore innate.

Evidence presented in this essay and other publications by E-E is not sufficient to convince me that the behavioral patterns in question are in fact universal, but in any event, the universality of a behavior does not prove its genetic encoding. The method of cross-cultural comparison has the same drawback as the deprivation experiment; it provides no direct evidence for genetic determination of the specific pattern of behavior. At best it provides "circumstantial evidence" in support of the hypothesis of "innate" behavior. Nevertheless, circumstantial evidence, unlike direct evidence obtained by manipulating genes themselves, cannot constitute proof that the hypothesis is true. It is logically fallacious to assert otherwise.

by S. L. Washburn

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Ethologists do not study human evolution. As so clearly outlined by E-E, human ethology has derived its methods and theory from the parent "discipline," ethology. When applied to human beings, these methods are inadequate and lead to trivial research. For example, it has long been recognized that bipedal locomotion is the fundamental behavioral adaptation which led to the separation of apes and humans some millions of years ago. The hands were freed, making possible the evolution of manipulative skills. Large brains evolved long after the making of complex stone tools. Although claiming to be concerned with evolution, the article under Commentary does not give a single reference to the known events of human evolution. Over the last dozen years the relationships of the contemporary primates have been clarified by molecular biology, the finding of numerous fossils, and radiometric dates which give a validated chronological framework. Ethologists pay no attention to locomotion, or archaeology, and little to the brain. They are so accustomed to using analogies, very general concepts, and uncontrolled comparisons that they do not seem to realize that this whole habit of thought is misleading when applied to human beings.

The problem is not only one of evolution; the methods of ethology effectively remove most of what is known about the biological basis of human behavior. For example, humans can easily learn a variety of facial expressions, and when it is that each is socially appropriate. Ethology attempts to find universal expressions with common meanings. But what is observed superficially depends on the brain, which makes possible the diversity of learning. Massive removal of the cortex in monkeys does not affect facial expression, but even a moderate insult may cause facial paralysis in humans. Clearly, in comparing facial expressions in human beings and even the most closely related of other animals, it is necessary to stress the differences in the cortex of the brain. For comparison, externally visible behaviors must be accurately described, but most of the biology is not externally visible, and it is for this reason that ethology omits most of human biology, just as it omits the study of human evolution. For example, the comparison of human hand skills with those of the apes requires a comparison of motions and of the joints and muscles that make them possible. It also requires a consideration of the great difference in the parts of the brain controlling the motor functions. An evolutionary speculation might be that tool using, bipedal locomotion, hand skills, and the brain evolved in a feedback relation. More speculatively, social life, hunting, and delayed maturity may be part of the same complex. If so, a traditional ethogram (biogram) would destroy the very complex functional pattern, the understanding of which is the goal of the research.

If comparisons begin with problems of human behavior, the issues appear very different from those of traditional ethology. Speech (phonemes combined in morphemes and into sentences) is unique to human beings and is dependent on a large part of the brain. The comparison of design features in human and other animals gives no information on the basic biology, or on the vast difference between what humans can communicate and the very limited possibilities of communication in other animals.

Stressing what is known about human speech, then comparing, keeps fundamental biology under consideration. Ethological methods and principles cannot be usefully applied to human behavior if ethology omits both the basic biology that humans share with other primates, and the biology that is unique to human beings.

by Edward O. Wilson

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Ethology and sociobiology: a point of definition. E-E's excellent review illustrates very well the richness of new discoveries that he and other investigators have made under the rubric of human ethology. The implications of this work for the social sciences will be obvious to anyone with an open mind. I am concerned at this time only with a point of metascience: the possibility of a confusion between the definitions of the two disciplines of *ethology* and *sociobiology*, which have been perhaps more clearly distinguished in the United States (since the 1950s) than in Europe. Here is what I stated in my recent book *On human nature* (1978):

> "The communal beings of the three pinnacles [of social evolution] are among the principal objects of the new discipline of sociobiology, defined as the systematic study of the biological basis of all forms of social behavior, in all kinds of organisms, including man. The enterprise has old roots. Much of its basic information and some of its most vital ideas have come from ethology, the study of whole patterns of behavior of organisms under natural conditions. Ethology was pioneered by Julian Huxley, Karl von Frisch, Konrad Lorenz, Nikolaas Tinbergen, and a few others and is now being pursued by a large new generation of innovative and productive investigators. It has remained most concerned with the particularity of the behavior patterns shown by each species, the ways these patterns adapt animals to the special challenges of their environments, and the steps by which one pattern gives rise to another as the species themselves undergo genetic evolution. Increasingly, modern ethology is being linked to studies of the nervous system and the effects of hormones on behavior. Its investigators have become deeply involved with developmental processes and even learning, formerly the nearly exclusive domain of psychology, and they have begun to include man among the species most closely scrutinized. The emphasis of ethology remains on the individual organism and the physiology of organisms.
>
> Sociobiology, in contrast, is a more explicitly hybrid discipline that incorporates knowledge from ethology (the naturalistic study of whole patterns of behavior), ecology (the study of the relationships of organisms to their environment), and genetics in order to derive general principles concerning the biological properties of entire societies. What is truly new about sociobiology is the way it has extracted the most important facts about social organization from their traditional matrix of ethology and psychology and reassembled them on a foundation of ecology and genetics studied at the population level in order to show how social groups adapt to the environment by evolution. Only within the past few years have ecology and genetics themselves become sophisticated and strong enough to provide such a foundation."

As I suggested in *Sociobiology: The new synthesis* (*op. cit.*, 1975), much of the content of ethology is destined to be absorbed into the explanatory systems of integrative neurobiology on the one side and behavioral ecology and sociobiology on the other, for the reason that these are the subjects most directly linked through chains of analysis and causal explanation to the remainder of biology. Integrative neurobiology is to be increasingly regarded as an extension of cellular biology and developmental genetics, while the basic theory of behavioral ecology and sociobiology stems from population biology. But this programmatic trajectory in no way lessens the pioneering role of ethology in discovering and conducting the essential first stage of analysis of patterns of behavior, a function well exemplified in E-E's review.

Author's Response

by **I. Eibl-Eibesfeldt**

Human ethology: methods and limits

The commentaries cover a wide range, both in style and in content. In general, my intention to evoke replies from which I could learn was achieved. Only very few responses do not seem to be germane to the points I was trying to make.

Van den Berghe has charmingly pointed to the arcane dominance rituals expressed in our journals, those cultural substitutes for penile displays. There are certainly ethological features for study in our efforts to communicate. However, focal attention seeking and display constitute but one aspect of the rituals that open an encounter, and I hope that my own intent to bond has been perceived as well. I certainly want to thank all who have contributed to the discussion. The commentaries converge upon a number of points, which I wish to answer in succession.

Ethology versus sociobiology. As to the claims of human ethology, some commentators thought that the definition was overly broad (e.g., **Izard**); some that culture should not be the subject of ethological research (e.g. **Bolles**) others that only the sociobiological approach would contribute to a "profound" understanding of behavior (**Barash**). I think that the last viewpoint involves a basic confusion concerning the question of proximate and ultimate causes. One main concern of ethology is the investigation of proximate causes. What makes a behavior occur in a concrete situation? How does the machinery work? What starts and stops it? The physiology of behavior is a very important aspect of ethology, and certainly in one way this research contributes to deepening our understanding. But, as Tinbergen has repeatedly emphasized, the question as to why an animal behaves in the way it does must also be answered by the study of individual development. Is this question of lesser importance? I do not think so. In the end, we must seek an explanation for the ultimate causes that have brought any particular behavior in to being. This inquiry about phylogenetic (and in man, cultural) evolution is inseparable from the question as to the ways in which a behavior contributes to survival. But to argue that it is only this search for the ultimate cause that contributes to our understanding does not make much sense. All aspects must eventually be covered. Ethology, traditionally defined as the biology of behavior, has explicitly declared that its program is to answer all these questions through a diversity of subfields like neuroethology, ethoecology, and the like (Eibl-Eibesfeldt, *op. cit.*, 1975b). Sociobiology certainly aims at an understanding of ultimate causes, and in this spirit, exciting theories and research strategies have recently been developed. One should keep in mind, however, that Tinbergen was the first to demonstrate by ethological techniques the selective value of certain behaviors. I am the last to belittle the contribution of sociobiologists, but nonetheless I fail to see sociobiology replacing ethology, even in combination with neuroethology.

Kin selection versus group selection. As to the question of the level – kin or group – at which selection operates, I am certainly open to the facts. So far, however, the evidence is controversial. Nice mathematical models are available but nobody has yet been able to tell me what proportion of my genes I actually share with my brother, compared with the proportion I share with any other group member. My *guess* is that the latter do not differ much from my close kin. For most of man's history groups speaking a common language have consisted of no more than several hundred to a few thousand people. And since special cultural institutions (marriage rules) cause constant mixing of the gene pool and prevent inbreeding, individual fitness can only result in a gradual enrichment of the gene pool with particular genes, the final selection taking place at the group level. For man, history proves this to be the case. Undoubtedly parents invest more in their children than in others, but this can be explained in terms other than some sort of genetic mystique. The young need to be cared for. One adaptive solution is that this be done by specific individuals who become emotionally bonded to them. And since the mother is present, as a rule, just when the young hatch or are born, it seems practical that this bonding should occur primarily between mother and child [see Rajecki et al.: "Toward a theory of infantile attachment" *BBS* 1(3) 1978].

Once the capacity for individual bonding evolved, the family ethos could be expanded to incorporate others and to form closed groups that acted as units (for details see Eibl-Eibesfeldt, *op. cit.*, 1972). From that stage onward at least we have to consider groups as having been competing units. Before that the kin selection principle, as proposed by the sociobiologists, may well have been dominant.

I basically agree on many points with the sociobiologists (and I in particular appreciate **Wilson**'s contribution as outstanding), but what sometimes irritates me are certain simplistic conceptions camouflaged by impressive mathematical models. Mathematical models such as those used by sociobiologists can certainly lead to more precise testing of various hypotheses. But there are many phenomena that do not lend themselves to this approach, and these too must be investigated. Furthermore, I feel that, for the moment at least, such models are highly speculative, and their expression in print has been sloppy, to say the least. Statistically speaking, I ought to share with my children 50% of those genes that came about by mutation (as **Hamilton** states correctly). But how often does one read that one in fact shares 50% of one's genes with one's children! Likewise, one often reads that it would only pay for an individual to sacrifice his life for the survival of two children or four grandchildren and the like, and that this would explain nepotism. But does nepotism really maximize inclusive fitness to the degree postulated by the sociobiologist, when members of each ethnic group share so many genes?

There are also other statements to which I object. To speak, for example, of "genetic selfishness," or to say that organisms (including man) are just machines for the reproduction of genes, fails to recognize the fact that there are different levels of existence (*Seinsebenen*) each characterized by new system attributes (*Systemeigenschaften*) which emerge but cannot be deduced from the characteristics of the components of the lower level of integration. Molecular evolution certainly led to the formation of self-replicating molecules. The newly discovered viroids are just naked molecules. They have no protective cover, no organelles at all; they lack metabolism (*Betriebsstoffwechsel*). In short, they are not organisms. To be sure, organismic evolution did start out by ensuring the replication of the molecules that carried the genetic code by the development of a variety of additional machinery. But, more and more, the emphasis shifted, and I would not hesitate for a moment simply to turn the statement of the sociobiologists on its head by saying that the genes, from a certain stage of evolution onward, are a means of reproducing organisms. At least in the case of man this view is tenable, since man certainly perceives genes as such. He is theoretically able to control his genes, to "engineer" them in a variety of ways, if he wishes to do so. With man, evolution evidently became conscious of itself and thus became capable of self control. Is a hen an egg's way toproduce more eggs? Perhaps, but as a biologist I would not accept such a simplistic view for man, and I am reluctant to do so even in the case of the hen.

Research strategy. It is certainly true that human ethologists have not yet sunk their probes in all the possible directions of research, but ethology does provide the theoretical background for the development of a program (even though in my target article some of this was admittedly presented in a sketchy way) and the references that I cited point to a number of detailed analyses. I emphasized that it is not just biologists who are developing the new study but that a number of scientists from different backgrounds and fields converge therein. In fact, there are by now so many that I had to restrict myself to mentioning only a few, thus not doing justice to others who have contributed equally. This I hope to correct on another occasion. For the moment, I had to be highly selective, and of course by bias led me to present those works that I consider the most compelling (consisting primarily of developmental and deprivation studies, as well as our own program of cross-cultural cinematographic documentation). This approach certainly has its precursors, and since **Hailman** feels that Darwin or Mead should be mentioned in this context, I can give assurances that I have done so on other occasions, such as in my ethology textbook (Eibl-Eibesfeldt, *op. cit.*, 1975b). However, at that time a systematic documentation of social interactions on a cross-cultural basis had not yet begun. Only recently have the interests of anthropologists converged on this point.

As to the documentation program itself, **Finley** has asked why I concentrate on primitive cultures. The answer is that they constitute interesting models for different culturally evolved survival strategies in a wide variety of rapidly vanishing cultures. I therefore consider this research a kind of "data rescue work" within the framework of urgent problems in anthropology. (In addition, I have begun documentation projects in Japan and Europe.) Since the burden of this task falls chiefly on my own shoulders and means three to four months of fieldwork per year, I have to restrict my focus to the five cultures mentioned in my paper, repeatedly returning to particular villages. This may explain why I have not, for example, collected electromyographic data on the eyebrow flash, as suggested by **Klopfer,** or carried out experimental research on the function of this signal. Even though I recognize a need, I simply cannot do everything! I am happy simply to be able to uncover cinematographically such phenomena as eyebrow flashes, and to determine their function from numerous observations.

My emphasis on the "natural setting" was questioned by **van den Berghe** and **Delgado.** Is there such a thing? I was probably mistaken. I meant a setting not experimentally manipulated and staged by the investigator. A group on a street corner, people in a church – in my terminology these are all in "natural settings." As to interference by the observer: I am certainly seen with my camera, but it makes an enormous difference whether one focuses directly on a person (he or she normally evades the attempt to be photographed) or whether one observes through the mirror lens. My films show the intimate details of social interactions and thus demonstrate the value of the method. I hoped that the tender interactions shown in the first figures would illustrate this point. In this context **van den Berghe** and **Peterson** raise the question of ethics. I have considered this thoroughly and have come to the following conclusions. First of all, I film only behavior occurring in public. Furthermore, my documentation is in no way derogatory; on the contrary, by showing how alike people are in so many charming ways, I attempt to evoke a sense of familiarity. So far the prevailing tendency has been to depict other people as "exotic."

Evolutionary function of social interaction patterns. Concerning the question of cultural factors, **Bolles** and others feel that the biological approach may not be adequate for their study. I certainly see it differently. We can indeed inquire into the ways that cultural patterns contribute to survival. We must, however, distinguish intended function (what people think they are achieving by performing a ritual) from observed function. We may very well find that a religious ritual intended to appease deities in fact serves the function of group cohesion, identification, and so forth.

Bolles, Borgia, and **Klopfer** have asked how a function can be proven to exist; others have emphasized the need for experimentation. I agree; but from observing what is regularly achieved by a certain behavioral pattern, and by applying the comparative approach, we get evidence at least as good as that of the morphologist, who rarely investigates function experimentally, often deriving it solely from detailed anatomical investigation. Anthropologists like Harris (1974) deduce function in a similar way; Godelier (1977, 1978) and others, in investigating "social relations of production," describe how man forms alliances, creating groups that function as systems of production, thus adapting to the environment. Our own conclusion, for example, that the ritual of Tanim Het helps the couples to "find" each other is derived from observation, detailed film analysis, and inquiry. The frame-by-frame analyses demonstrate that the partners synchronize their movements and that between some partners harmony is established faster than between others, thereby providing one of the factors that determine individual preferences. Inquiry has supported the thesis that this ritual constitutes the familiarizing process that leads to marriage. There is, of course, the need to perform a long-term study for the final proof.

To understand the selective advantage of social patterns is certainly a most important task. But to argue, as **Bolles** does, that the proper business is not to show that phylogenetic adaptations are present, which no one doubts, but to show their "functional significance," is a bit onesided. After all, some still do seem to have doubts.

We certainly have to consider that not every social pattern may be functional. Yet functional hypotheses are good to start with and can help indicate what to search for. Our studies in the "natural context" at least provide us with reasonable hypotheses. **Bolles** was "stunned" when he heard that the Japanese learn to suppress the eyebrow flash. But he failed to specify just *why* he was stunned, and hence it is now *I* who am "puzzled." If I have understood him correctly, he felt it odd that a successful ethnic group comprising 100 million people should drop such an important signal if it has survival value (as I do suggest). After all, we know from many instances that certain affective expressions get suppressed in a number of cultures, as well as in various contexts, such as in communicating with strangers. For example, in our own culture we are not supposed to cry in the street or to express ourselves too freely. Etiquette demands that we keep ourselves reserved and controlled. A plausible explanation, backed by circumstantial evidence, is that life in the anonymous society fosters the avoidance of contact as on adaptation against possible exploitation by strangers. The suppression of the eyebrow flash (which occurs to a certain degree in our culture as well) can be interpreted as one pattern of contact avoidance in a crowded society, and thus as adaptation to a new situation.

The experimental study of function is certainly within the scope of our program but it should be clear that we have to start out with some realizable goal in mind. For the moment, we assign priority to the documentation and attendant uncovering of phenomena as well as the study of their ontogeny in a cross-cultural perspective. The question "and why didn't you do this and that?" would be understandable only if the target paper had not taken this matter into consideration. However, I did in fact emphasize the need for experimental investigation to determine proximate and ultimate causes, and I further referred to a number of publications dealing with these issues in more detail.

Homology versus analogy. One question repeatedly raised by the commentators concerns the question of universality (**Finley, Peterson, Hull, Wahlsten,** and others). When do I consider a pattern to be universal and what does such an ascription mean? I mentioned that I concentrate on a number of model populations which are selected to represent different geographical areas, different cultures and races, and different levels of cultural evolution. Besides these cultures, in which we have over the years been accumulating as complete a documentation as possible, we also make single visits to other ethnic groups to obtain selected samples of specific patterns such as greeting or surprise reactions, responses to smell and taste, and the like. We also obtain samples of social interaction patterns encountered by chance. Such samples have been obtained with the Gidjingali, Pintubi, and Walbiri of Australia; with the Tasaday, Tboli, Blit, and Agta of the Philippines, with the Japanese, Chinese, Ceylonese and Singhalese, with Niloto Hamitic tribes (the Turkana, Massai, and Karamojo), Pygmies, Samoans (and other Polynesians), the Ayoreo, Quechua, Polar Eskimos, and others.

In our own culture, we extensively document children and parent-child interactions in investigations of behavioral ontogeny. Were we now to discover a pattern that tended in both form and detail to occur repeatedly in the same context, we would certainly ask whether the similarity was a result of analogous development or whether we ought to assume a common origin. In determining this we proceed in a fashion similar to that of the cultural anthropologist who, upon finding stone axes of similar shape in tropical Asia, Africa, and South America, would not (nowadays at least) jump to the conclusion that this was indicative of cultural contact. The shape of the axe is dictated by its function and, independently, man would tend to invent similar tools. But if the anthropologist found a number of similar-sounding words (such as; one, two, three; uno, due, tre) in different cultures, he would interpret this as evidence for common cultural origin, irrespective of whether many intermediate cultures would have to be posited in such a case to serve as links between the two languages (Wickler, 1965). Independent invention of such a language similar in sound and meaning would be highly improbable.

In part, this reasoning also holds for nonverbal expressive patterns such as facial expressions. If in groups as remote from each other as Eskimos, Kalahari Bushmen, and Papuans, we find identical patterns of expressive behavior, we can assume either traditional (cultural) or phylogenetic homologies at their base. The latter have a greater probability, since it is well known that ritual patterns based on cultural traditions change rapidly as demonstrated by the fast evolution of languages. So far, results of developmental studies on experiential deprivation and comparative studies on primates conform very nicely to this homology assumption. Of course, much still remains "speculative," as a hypothesis to be tested for its value. I would also like to point out that these universals in expressive patterns, aside from their specific role in communicating concrete intentions, also have the much more general function of communicating across ethnic barriers. Although the Japanese suppress the eyebrow flash in adult communication, they still understand it as indicating friendly intent when emitted by visitors from America or Europe.

Commentators repeatedly asked the question of how I come to infer that a particular pattern is homologous; and doubts were expressed as to the interpretation of particular cases that I used to illustrate my points (**Delgado, Benedict, Fraser, Petersen, Hausfater**). I thought I had already provided the answer: My inferences are based on the application of the concept of homology, as elaborated by the morphologist. These are: (1) the criterion of special quality; (2) the criterion of the relative position within the structural system; and (3) the most important criterion of the linkage by intermediate forms.

Let us elaborate with an example. **Hausfater** expressed the opinion that intuition and empathy led me to assume that human kissing derived from kiss feeding. His intuition, however, would tell him that the kiss is derived from grooming behavior, which involves licking movements with the tongue. Can we decide? If we look at the special quality of the movement we will soon discover that the movement patterns of kissing are very similar to those of kiss feeding. Upon mouth to mouth contact, a pushing activity of the tongue (not to be confused with licking) occurs and, in response, there occur movements similar to those by which the child accepts the proffered food. In fact, saliva is often exchanged during kissing (for example, between lovers), and the Kama Sutra mentions the exchanging of wines. Furthermore, there are forms intermediate between kiss feeding and the kiss. In fact, the example of the bush girl feeding her sister a morsel to comfort her (target article: figure 1) is shortly afterwards followed by a kiss without an attempt at food exchange, but with the same pushing movements of the tongue. Both events are fortunately recorded on film.

If we turn to nonhuman primates, we frequently observe kiss feeding and kissing in maternal behavior as well as in expression of seeking friendly contact. This being the case, we arrive at the conclusion that kiss feeding and kissing are homologous patterns. Grooming patterns and their derivates look different. These have been repeatedly ritualized into friendly bonding behaviors. Thus the Mongoose lemur uses ritualized grooming in greeting. He performs the fur combing movements of the lower jaw in the air, at the same time performing licking movements. Many mammals use their lower and upper teeth in a tender action nibbling while combing their fur. And indeed, this can be observed in nearly identical form as a sign of affection in man. Another ritualization which might be derived from grooming movements is a special form of tongue display, one of whose functions is to establish heterosexual bonds.

Some intuition is certainly necessary for a scientist (Lorenz, 1977). but there also exist proven procedures for discovering certain relations. Applying these methods makes it clear that the interpretation of phallic displays as ritualized mounting threats is not just a wild speculation (as **Delgado** seems to suggest). Again, all three criteria of homology are fulfilled, but owing to space limitations I must refer the reader to the original publications (Ploog et al. *op. cit.*, 1963; Wickler, *op. cit.*, 1967a; Eibl-Eibesfeldt and Wickler, *op. cit.*, 1968; Eibl-Eibesfeldt, *op. cit.*, 1970). In man, the mounting threat finds a new expression in certain cultural substitutes. We referred to the unique ability of man to "translate" social interaction strategies, for example, by verbalizing the event or by substituting cultural patterns for innate ones. In such cases we must ask in what respect the observed behaviors are homologous.

Let us construct a theoretical example. In the service of communication, mutual adaptation of the sender and receiver of a signal has often taken place. Releasers (e.g., "expressive movements") and innate releasing mechanisms (IRMs) have evolved. In a changing environment, new selection pressures may cause a signal to become more rudimentary, with the unchanged IRM of the receiver still remaining tuned to the original signal (there are specific examples from animal behavior studies). In such cases the sender's activities may develop an analogous bias to compensate for its own modified signal. We have some indication that cross-cultural similarities in male fashion (emphasis on shoulders) as well as in female fashion come about this way (Eibl-Eibesfeldt, *op. cit.*, 1972). In this case, analogies are brought about by a homologous **IRM.**

Relevant in this context is **Fraser**'s question as to whether, if the pathways of a movement pattern are plastic, the behavior can still be considered to be homogous. Homologous movements will in most cases have homologous neuronal substrates and will be performed by homologous muscles. But changes may take place during evolution, and in this case the question as to whether or not similar behavior patterns with different pathways are homologous can only be answered if we find a link in intermediate forms (by far the most important criterion of homology). Fortunately, most cases are not so complicated, otherwise morphologists and taxonomists would simply despair. But the problem is well known to them. Structures, too, can be homologous to one another at one level and analogous at another. The flippers of penguins and whales are analogous structures, if looked at as flippers, but homologous if looked at as vertebrate front extremities.

The nature/nurture problem. Ghiselin felt that I was too much of a typologist, and that this constituted a vestige of early ethological tradition. It is true that some of the early founders like Jacob von Uexküll were antiselectionists. But I do not see how my discussion of the "universality" of behavioral traits would indicate a similar attitude. I admit that terms like "human nature" are more ambiguous in this context, but the term is often used to point to features of man that characterize him as a "species." This may not serve as excuse, however, since "species" is after all a similar construct. Nonetheless, it is used by taxonomists, and no one would charge them with being antievolutionists. I am certainly open to the view that the polymorphism of the human populations is also expressed in behavior (see also the comment of **Hull**). In fact, Freedman and Freedman (1969) found that Mongolian and Caucasian neonates born in New York under practically identical situations show differences in their behavior. These differences are not in the actual patterns of behavior, but only in the frequency of their occurence (for example, restlessness). So far, I too have failed to find any qualitative differences, and whether observed quantitative differences (such as more expressiveness) are due to differences in genetic or in cultural background cannot be said at the moment. In the area of expressive behavior the cultural cast seems so far to be the main factor contributing to behavioral diversity, but this field is practically unexplored.

Numerous commentators discussed the nature/nurture issue (**Hailman, Charlesworth, Montagu, Klopfer, Block, Wahlsten**). One of the arguments advanced was that there may be precursors of innate behavior which became integrated – for instance, during early ontogenetic stages – into functional wholes (**Gottlieb**). I do not doubt this. However, the concept of phylogenetic adaptation versus adaptation by individual learning is not changed by such findings. In one of my earlier papers (Eibl-Eibesfeldt, 1963) I demonstrated that European red squirrels develop the stereotyped movement pattern of nut hiding even if raised on a diet of semiliquid food, in wiremesh cages, and deprived of any opportunity to dig or handle solid objects. The pattern consists of searching for a hiding place (preferably near a vertical obstacle, which allows easier rediscovery of the hidden food), digging a hole, depositing the nut, tamping it down by rapid blows with the snout, covering it with earth by sweeping movements of the paws, and, finally, pressing the earth down with the paws. Squirrels deprived of any opportunity to imitate a conspecific or to learn this behavior by themselves through trial and error still hide nuts on their first given occasion. They search for a hiding place and show preference for digging at the base of vertical obstacles. The stereotypy of the movements is especially evident when the animals attempt to hide a nut on the solid floor, such as in one corner of the room. After some scratching movements the nut is deposited, tamped down with the snout, and, even though nothing has been dug up, sweeping movements are performed as in an attempt to cover the nut with earth, finally, the imaginary earth is pressed down. This trait can only have derived its adaptedness as a result of phylogenetic adaptation. As I pointed out, this would hold true even if someone were to prove that at a lower level of integration the coordination of the antagonistic muscles of the limbs used in the nut-hiding performance were really learned in early ontogenetic stages. Nonetheless, the adaptedness at the higher level of integration would be considered a phylogenetic one.

Similarly, should it be demonstrated that a bird, having learned the coordination of breathing movements – certainly a prerequisite of singing – and having been raised in complete social isolation, could produce the species-specific courtship or territorial song, we would be forced to conclude that the patterning of song movements results from phylogenetic adaptation. There are different levels of adaptation, and our statements refer to the origin of specific adaptedness. We cannot escape the logic that, in order for a copy of a pattern to occur, information concerning the "original" (the template) must be acquired by the adapted system. Hence, deprivation experiments are indeed of great heuristic value, even though they constitute only the first (but most important) step in the analysis. Judging from the commentaries of **Hailman** and **Gottlieb**, I feel that in fact our points of view no longer diverge so much in this respect. I agree with their emphasis on the importance of further studying ontogeny, and am also sure that Hailman understood my point. I am all the more puzzled, therefore, by Hailman's assertion that "Austro-German" ethology tries to define away the nature/nurture problem.

Block remarks that "innate" should not be equated with "resistant to change" and he misses the idea of the "norm of reaction." It may comfort him that on p. 30 in my ethology text book (Eibl-Eibesfeldt, *op. cit.*, 1975b) I write "Characteristics in themselves are not inherited but are developed within the bounds of inherited variation." The potentiality (range of modifiability) may include a number of alternatives. For example, it could well be that, as Block suggests, the program for aggression consists in the instruction: be aggressive unless adults are around who are not aggressive. But this does not imply that statements as to the innateness of a response are irrelevant to social policy, since sometimes the range of modifiability and the openness for alternatives are very limited indeed.

If we punish a rooster with an electric shock whenever he displays, he will eventually stop doing so, and as a result he will also lose his rank. If we apply the same punishing stimulus whenever the rooster shows submissive behavior, this will not result in a similar extinction of the response. On the contrary, the more the cock is punished for his submissive behavior, the more he will act submissively, since that is how the cock is phylogenetically programmed to behave. In combat, submission functions to save the loser from further attack; the more severe the defeat (punishment), the more submissively the animal must act in order to escape further attacks. Behavior therapists ought to consider the possibility of similar constraints in the responses of man.

Charlesworth feels that only certain kinds of experiments that cannot be carried out in man could prove the existence of phylogenetic adaptation in man. He considers my data important, but not sufficient to prove my case. I certainly see it differently. Congenitally deaf and blind children grow up under deprivation more rigid than the deprivation schedules applied in the experiments of animal ethologists. Furthermore, cultural differences in child-rearing constitute experiments that can be evaluated.

Kovach expresses the opinion that only behavior genetic experiments could ascertain how phylogeny may influence the ontogeny of behavior. How does he propose to do this in man? It is certainly important to explore the genes in order to determine the contribution of heredity, but we have to be aware that there are a diversity of questions to be asked, and that they aim at different levels.

May I point in this context to the fact that there exists a field called the psychology of learning, which successfully explores the laws of learning? Now, is the value of these laws at all compromised by the fact that nobody knows for sure the "nature" of the engram? And I may draw the attention of those who are overexacting in the demonstration of facts to a stimulating publication by Hull (1978) in which, in discussing this very issue, he refers to T. H. Huxley, who pointed out that the inductive foundations of evolutionary theory would remain insecure until the evolution of a new species was actually observed – which nobody has done to this day. Are we therefore less sure that evolution took place? Certainly not. The circumstantial evidence is simply overwhelming.

Wahlsten criticizes "the ethologists," and me in particular, for stubbornly clinging to their original ideas, while merely incorporating criticisms into their writings in the form of disclaimers. It may occasionally sound this way, but I hope that by once again specifying what we mean by the source of specific adaptations, it may become clear what we mean by "phylogenetically adapted" or "innate": The source is the process by which template information is acquired by the adapted system, so that the latter can copy it. Once again, I emphasize that the term innate refers to a specific level of adaptation, and that this is why it would be wrong to deduce, once phylogenetic adaptation has been demonstrated at one level, that the behavior in its totality is to be considered innate. Nor does it make sense to calculate in percentage terms the contribution of the genes versus that of the environment. It does make sense, however, to ask whether phylogenetic adaptations determine certain aspects of territoriality and ranking, or any other aspect of man's social behavior. And it is indeed important to know whether or not a pattern grows in a process of self-differentiation. It is, after all, different if a bird – to return to our example – needs to hear a conspecific in order to sing like him, as opposed to developing his song without need of patterned information during ontogeny.

We can indeed demonstrate that some patterns develop even under a great variety of deprivation schedules, thus exhibiting resistence to environmentally induced modification. It should also be clear from my discussion that the deprivation experiment does not just provide supportive evidence for the hypothesis of phylogenetic adaptedness – as claimed by **Wahlsten**, but must be considered to be as good a proof as can be gained by manipulating the genes themselves: We observe that an adaptation copies a template. We deprive the organism of the template and of any other opportunity individually to acquire information pertaining to it. It nonetheless develops the copy. The only logical conclusion is that information concerning the features of the template must have been fed into the system at some time other than during ontogeny, and the only possibility remaining is phylogeny (unless we are to believe in a prestabilized harmony due to a Creator who made organs and behaviors just so as to fit).

As to **Wahlsten's** remark that I first disclaim universality as a criterion for innateness, and then later deduce innateness from universality, I am a bit at loss, since I specifically say that universality alone will not do, and that we must also determine whether universally similar environmental conditions or some universal function could independently have shaped the behavior along similar lines. Only if this has been shown to be improbable can we hypothesize innateness. Supportive evidence must come from the study of ontogeny and from comparative primate studies; and finally it may also be helpful to study the pattern in question in cultures, which, for some reason, consider the behaviour in question inappropriate, and thus discourage its development by education. This occurs in some cultures with respect to certain aspects of aggression, striving for rank, and possessive behavior, which still seem to develop, despite negative cultural pressure.

Fear of strangers. The fear-of-strangers response, which I used to illustrate how a comparatively simple innate response significantly influences human social conduct, was the target of several comments. **Izard** argues that fear in the infant and adult are not continuous but two different phenomena, since the emotional quality is variable in the infant and we do not know whether the negative response is due to "fear," "sadness," "shyness," and so forth. Moreover, the response diminishes one month after onset and in the second year is most frequently called "shyness." Finally, a stranger may elicit a variety of emotional responses, including interest and contempt.

This involves a confusion in the argument. First of all, I explicitly stated that a variety of responses are released by the stranger, and in fact by any fellow human. Otherwise, how could I have spoken of "ambivalence?" In using the term "fear" I followed the traditional terminology, but from what I wrote it should be clear that I do not interpret the baby's response in subjective terms. I group the responses descriptively as approach behaviors (contact-seizing: turning toward, moving toward, signalling readiness for contact) and behaviors belonging to the agonistic system (aggression, flight, submission), which are again characterized by a number of patterns. However, I find these in the child's responses, as well as in the adult's. The degree of "strangeness" determines the degree to which the so-called "negative" responses show up as opposed to the "positive" ones. (This should also answer **Bolles**'s question as to the motivational basis of the response). I am at a loss to see what difference it makes, whether one speaks of fear or shyness in the adult; apparently **Izard** considers these to be different (on what grounds?) Nowhere did I say (as Izard seems to think) that I consider fear of strangers to be the sole reason for man's forming individualized groups. In fact, in my book *Love and Hate* (Eibl-Eibesfeldt, *op. cit.*, 1972) I discuss in detail various roots of sociality, with emphasis on those developed in context with parental behavior.

My statement that negative experience is not needed for fear of strangers to develop was attacked by **Hoffman** on the basis of experimental studies on a response in ducks. Once ducks have followed an object, they stick to that class and show fear response to novel objects. If kept in isolation long enough, however, they do not show this fear, but follow any object, which according to Hoffmann proves that the subject's fear response is dependent upon his prior opportunity to form a neuronal model of a given source of visual stimulation.

But, first of all, this is not the "fear of strangers" phenomenon that Eibl-Eibesfeldt describes, but another type of response in another species! The ducks react to another class of objects with fear, once they have become imprinted to a particular object. Human beings, however, react with "fear" to the same class of objects (namely humans) to which they are individually bonded, the response showing gradations according to familiarity.

As to the selective advantage of the fear response (**Bolles**), we have reason to assume that primarily it served to strengthen the bond between mother and child as individuals. It might secondarily have been advantageous to emphasize contrast between group members and nongroup members [see also Rajecki et al.: "Toward a General Theory of Infantile Attachment" BBS 1(3)1978.]

Montagu tries to convince us that fear of strangers is not universal since it occasionally happens that strangers are received in a friendly way, as derived from the study of old travel logs. Again, I must return to my statement that people release friendly and aversive responses in other people. On our travels we have had the experience again and again of people's fear, after a short period of tension, melting away once our friendly intent has been realized. This must certainly also have happened to the old explorers, who may not always describe in their reports when there was slight tension at the beginning of an encounter.

Sins of omission. A number of commentators felt that particular points were not treated adequately or were even omitted. **Hausfater** missed my mentioning the value of the ethogram as a starting point for analysis. But did this not become clear from my emphasis on documentation? I did not go into the historical background, of course, since I had to be brief. But I have repeatedly emphasized the importance of the ethogram (see, for example, Eibl-Eibesfeldt, *op. cit.*,). **Izard** found it a "most serious shortcoming" that I virtually neglected the "richest nesting place of phylogenetic adaptation," namely emotion-related facial behaviors. Again, I wanted to discuss different phenomena. I doubt that much discussion would have been aroused on the topic of facial expression; I wanted instead to get responses to more controversial issues. I have dealt in more detail with universals in facial expression in other publications (see, for instance, in my ethology textbook, *op. cit.*).

Concerning the study of the grammar of human social interaction, I have started a collaboration with sociolinguists. Volker Heeschen, whom I mentioned, is a linguist, and we also have close contacts with the research group of Willem Levelt in Holland. The methodology is presented in the paper of Heeschen et al. (*op. cit.* 1979) that I cited. In this context, I would also emphasize that what I call a "grammar of social interactions" is quite a different thing from what is termed "biogrammar" of Count or Tiger (see the commentary of **Barash**). I refer to rules by which specific social interaction strategies are structured. My thesis, that these rules apply to verbal and nonverbal behaviors alike, of course needs further cross-cultural investigation. But should it prove correct, I would consider the discovery as of major importance. To clarify my point: These common strategies of social interaction and the general principles of behavioral organization can certainly not be elucidated at the level of the fixed action pattern. I emphasize this since some commentators (e.g. **Kovach**) felt that the ethological concepts were too restrictive. Fixed action patterns, innate releasing mechanisms, and central motor generators are important constituents of behavior. Their integration into larger functional wholes is mediated by other mechanisms, including those underlying the "higher" mental functions, which I, for reasons of space, omitted from my review, especially since Lorenz (1977) has presented a thorough discussion of the biology of cognition. We may ask at each level of integration, and with specific reference to that level, the question concerning the origin of particular adaptations.

Birdwhistell (1970), whom I failed to cite in context with our efforts to study the grammar of social interaction, worked at a different level. He started from the assumption that the motor patterns of expressive behavior are composed of elements that can be treated like phonemes. So far it appears as if this assumption has not stood close examination and it is my opinion that the commonality of verbal and nonverbal behavior begins at a much higher level of organization.

Washburn criticized me for not discussing primate evolution and the process of hominization. But the phylogeny of human behavior was not the theme of my presentation. My concern was with the *phylogenetic adaptations* in human behavior, and that is quite a different matter. Once again, my textbook (*op. cit.*, 1975b) discusses the questions concerning human evolution, the importance of upright gait, the skills of the human hand, and so forth. Contrary to Washburn's accusation "ethologists" do not neglect human biology;

they consider what is common with other primates and what is unique to man. Since such considerations are not published in some remote journal, I felt that there was no reason to repeat them. This holds true for many other comments on points I did not mention in the article.

My aim was to present many aspects for discussion, but still the article was far from being comprehensive. For example, I did not discuss such aspects of human behavior as obedience, rank ordering, the formation of groups, the determination of gender roles, and the like, even though there exists a rich literature pointing to the decisive contribution of genetic factors. Nor did I discuss the evidence on innate neurohormonal mechanisms activating many behaviors. Space being limited, I cannot now discuss all the contributions of the commentators and apologize to those to whom I have not responded here. There remarks were certainly considered and appreciated, and I will reply to them in my future works.

In closing, however, I would like to address those who in my opinion made too sweeping (and I feel, sometimes unqualified) statements as to the value of ethological theory. Some spoke of the concepts developed by the founders (Lorenz, Tinbergen, von Holst, von Frisch) as if they were outdated, but instead of being supported with arguments, these statements seem to be profferred on the basis of belief. I am certainly not trying to convert believers. The contribution of ethology, and of Lorenz and Tinbergen in particular, has been acknowledged, and if someone comments on basic issues he has to be more specific and to avoid sweeping statements if he wants to be taken seriously.

With regard to my own special concerns, however, it is a relief to read in a summarizing evaluation: "Although no substantial part of the Old Austro-German ethology kept pace with modern conceptual frameworks, one must not conclude that Eibl's results are invalid . . ." (**Hailman**). That certainly sounds encouraging – if a touch of mockery (including self-mockery) is not out of place. But humor, of course, is always useful in friendly bonding, which is a most important aspect of communication with fellow colleagues across the territorial boundaries of personal bias.

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