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The Social Transmission of Acquired Behavior[1]

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The social transmission of acquired behavior may be differentiated from other observable changes in behavior resulting from conspecific interaction by three criteria: (i) Behavior change is in the direction of homogeneity of behavior between interactants. (ii) Behavior change extends temporally beyond the period of interaction. (iii) Social interaction is a sufficient but not necessary condition for development of the behavior pattern of interest. Such behavioral transmission results, in most cases, from the introduction of one organism by another into a stimulus situation to which the first organism is predisposed to respond in a specific fashion. Social transmission processes serve to facilitate the rapid acquisition of adaptive responses by naive animals. The mechanisms by means of which weanling wild rats acquire the learned feeding preferences of adult colony members are discussed in terms of the preceding analysis of social transmission processes.

There are, broadly speaking, essentially three nonindependent methods by means of which the behavior characteristic of a population may be maintained from one generation to the next. First, adaptive behavior in population members may be largely endogenously organized and genetically transmitted as propensities influencing ontogeny. Second, similar patterns of behavior in population members may result from similar histories of individual transaction with the nonsocial environment. And, third, long-term homogeneity of population behavior may result from the social transmission of acquired patterns of behavior from individual to individual within a population. The purpose of the present symposium is to discuss the transfer of information between mother and young, which

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may be, of course, a special case of either the first or third modes of maintaining homogeneity of population behavioral phenotypes. That is, mothers may transmit behavioral propensities to their young either genetically or as a result of behavioral interaction with them.

I would like this afternoon to discuss briefly one aspect of the social transmission of behavior from individual to individual. In particular, I want to talk about cases in which an individual organism acquires some specific pattern of behavior as a result of direct transaction with the environment and then increases the probability of other species members exhibiting similar patterns of behavior as a result of social interaction with them. Although I will not be speaking exclusively about mother-young interaction and instead will be talking more generally about social transmission processes, there are two points to keep in mind. First, both my own work (Galef, unpublished) and review of the literature (Galef, in press) indicate that young organisms are more susceptable to social influence processes than are adults, and, second, that in many species the adult with whom the young interact most often is their mother. So it is reasonable to assume that mother-young interaction is a very important aspect of the social transmission of behavior.

Before attempting to discuss instances of transmission of acquired behavior, it is necessary to define the range of phenomena to be considered, to distinguish transmitted behavior from other observable changes in behavior resulting from interaction among conspecific individuals. The fundamental distinction I would like to make is between those cases in which social interaction is necessary or obligatory for the development of some pattern of behavior, and those cases in which social transmission processes provide an alternative to direct transaction with the nonsocial environment for behavior acquisition. The dichotomy is, thus, between cases in which social interaction is sufficient and those in which it is necessary for behavior acquisition.

Harlow's work on the development of normal affective systems in rhesus monkeys is an example of social interaction necessary for the development of species-typical behavior patterns. Rhesus monkey infants reared in isolation from interaction with conspecific peers and their natural mother fail to develop normal patterns of sexual or maternal behavior (Harlow and Harlow, 1965).

As an example of social interaction sufficient in the development of a behavior pattern, let me describe very briefly some results taken from my own work on wild rats. If one takes a colony of adult wild rats and trains them to avoid eating a highly palatable diet by introducing sublethal concentrations of poison into that diet, and forces the rats to eat a less palatable diet, young rats born to the colony will ingest only the less palatable diet which the adults are eating. The young avoid ingesting the highly palatable diet although they themselves have never experienced any adverse consequences as a result of ingesting it. Even after one removes the young from the enclosure with the adults and again offers them the choice of the original palatable and unpalatable diets they continue to avoid ingesting the palatable food (Galef and Clark, 1971a). It is

clear, I think, that the adults have transmitted a learned feeding preference to their offspring.

The important distinction to be made between the wild rat example and that of the development of affective systems in rhesus monkeys, which Harlow and Harlow (1965) described, is that in the wild rat case social interaction is not necessary for the development of the pattern of behavior in question. That is, the young wild rats could have acquired the avoidance of the poisoned palatable diet by repeating the adults' history of transaction with the diet; that is, by eating it and becoming ill. The rhesus monkeys, on the other hand, do not develop normal sexual and maternal behavior in the absence of social interaction in infancy. The rationale for making the distinction between social interactions necessary and sufficient for the development of behavior is that there appear to be marked differences in their role in the ontogeny of behavior. Let me expand on this point for a moment.

Organisms often require exposure to specific environmental conditions for the development of a given behavior pattern. If the environmental condition is a social one, as for example interaction with a parent, it is possible to confuse a social exposure necessary for normal development with a social transmission process. In the former case, the result of social interaction is normal development of a relatively invariant species-typical behavior. In the latter, idiosyncratic patterns acquired by the transmitter, as a result of its history of transaction with the environment, may be introduced into a population repertoire, resulting in the establishment of socially transmitted traditions within subpopulations of a species. In other words, the apparent function of necessary and sufficient social interactions differ in important ways.

There are two further aspects of the wild rat example which are of some importance. First, the behavior which the young rats acquired as a result of interaction with the adults (feeding on the normally less preferred diet) persevered for some time following cessation of the social interaction. It extended temporally beyond the period of social contact. Second, the result of the interaction between adult and young was to produce behavioral homogeneity between transmitter and receiver.

I would like to call cases such as the wild rat one — in which social interaction results in increased homogeneity of behavior between interactants extending temporally beyond the period of interaction and in which interaction is not necessary or obligatory, but rather serves to facilitate development of the behavior in question — cases of "social transmission of acquired behavior."

In the remainder of this paper, I will consider two fundamental questions concerning the social transmission of acquired behavior: First, By what mechanisms may it proceed? and, second, What is the survival value or evolutionary significance of the social transmission of acquired behavior?

How then may organisms transmit patterns of acquired behavior to conspecifics? In the simplest case, organisms can alter the environment itself in such a way as to channel or direct the behavior of others. To return to our

example of the wild rat young acquiring the feeding preferences of adult colony members, it is the case that adults tend to deposit large amounts of urine and feces in the vicinity of feeding sites, and young rats are far more willing to take their first meals of solid food in an area that is marked in this way than one that has not been chemically altered by adults (Galef and Heiber, in preparation).

In more complex cases some form of direct interaction between transmitter and receiver is essential to the transmission process. Usually, general orienting or following responses on the part of the young directed towards adults introduce the young to selected aspects of the environment to which they then respond. For example, wild rat pups show a very strong tendency to approach adults at a distance from the nest site using visual cues and ordinarily take their first meal of solid food in the immediate vicinity of a feeding adult. The presence of an adult at one food source rather than another will, thus, serve to influence the young's choice of diet for early ingestion (Galef and Clark, 1971a; 1971b). Here again, the adults have altered a portion of the environment, by placing themselves in it, and have influenced the behavior of the young.

A second process involving direct interaction between transmitter and receiver is also possible. The young may respond directly to adult responses to environmental features and only later come to attach those responses to the environmental features to which the adults themselves initially responded. This would be a classical or pavlovian conditioning mechanism for social transmission. For example, an adult organism has learned to flee the approach of a potential predator, the young have an unconditioned tendency to run when they see an adult running, and it is only after a number of pairings of the conditioned stimulus (sight of the predator) with the unconditioned stimulus (adult fleeing) that the young come to flee independently when they perceive the predator approaching. Both Reiss (1972) and Angermeier *et al.* (1959) have reported evidence of such transmission in rats.

An alternative mechanism, the deliberate tuition of young by adults, is a type of social transmission of acquired behavior common in humans and, perhaps, present in some other primates. However, in most vertebrate species, the transmission of acquired behavior appears to result from the introduction of one organism by another into a stimulus situation to which the first organism is predisposed to respond in such a way as to acquire the behavior of the second organism. This behavioral predisposition may be the result either of previous experience or of instinctive tendencies. The observed behavioral transmission, then, results from a combination of social interaction and a predisposition to respond in a particular way to the stimuli encountered as a result of that social interaction (Galef, in press).

Returning to the example of the social transmission of acquired feeding patterns in wild rats, we have seen that adult rats can bring their young to initiate feeding on one diet rather than another by chemically altering the area in

which the young feed or by being physically present at one feeding site. However, the pups continue to eat only the diet the adults have been eating, even after removal from interaction with them. As you might suspect, and as our experiments have demonstrated, this is because the young learn the flavor of the diet to which the adults have led them and have an unconditioned tendency to avoid ingesting novel diets (Clark and Galef, 1972; Galef and Clark, 1971a, 1972). The transmission of behavior, thus, results from the combined effects of a social interaction and a tendency to respond to certain stimuli in specific ways once they are encountered.

What is the evolutionary significance or survival value of the ability of organisms to socially transmit acquired behavior? If laboratory learning paradigms are, in fact, accurate analogues of learning as it occurs in natural habitats, then the trial and error processes necessary for the acquisition of adaptive patterns of behavior must be both energy-consuming and error-filled undertakings for the acquirer. A naive, young animal, newly recruited to a population, must face particularly acute environmental challenges requiring rapid acquisition of behaviors necessary for survival within the particular area in which it achieves independence of its parents. It must locate and come to ingest needed dietary constituents once its mother ceases to feed it, it must avoid or escape potential predators, it must locate an area suitable for survival and reproductive activities in which to establish itself. Although the naive animal may have the capacity to acquire the learned adaptive behavior of more mature and experienced individuals by repeating their histories of transaction with the environment, it would clearly be advantageous to the young and, hence, reproductively advantageous to their parents, if the young could in some way incorporate into their own behavioral repertoires the learned adaptive behavior of more experienced conspecific individuals through some process less cumbersome than *de novo* trial and error learning. Facilitative social transmission processes of the type discussed here appear admirably suited for such a role.

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