Feed-forward and the evolution of social behavior

C. N. Slobodchikoff

Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011. con.slobodchikoff@nau.edu www2.nau.edu/~cns3

Abstract: Feed-forward Pavlovian conditioning can serve as a proximate mechanism for the evolution of social behavior. Feed-forward can provide the impetus for animals to associate other individuals' presence, and cooperation with them, with the acquisition of resources, whether or not the animals are genetically related. Other social behaviors such as play and grooming may develop as conditioned stimuli in feed-forward social systems.

Feed-forward Pavlovian conditioning can function as a proximate mechanism for the evolution of social behavior. As Domjan et al. note, three types of hypotheses have been suggested for the evolution of social behavior (Slobodchikoff & Shields 1988): genetic, ecological, and phylogenetic. Of these, the phylogenetic one is the default hypothesis, invoked when we cannot come up with a plausible explanation for why social behavior evolved within a social group (Slobodchikoff 1988). The other two hypotheses offer more possibilities for explanation: The genetic one suggests that animals cooperate because of close relatedness and the genetically beneficial effects of helping relatives (Hamilton 1964), whereas the ecological hypothesis suggests that animals cooperate because of the benefits obtained from cooperative resource extraction (Slobodchikoff & Schulz 1988). In their present form, neither of the latter two hypotheses offers any mechanism for how animals would develop such cooperative behavior, either toward relatives or other individuals who can help with resource extraction and utilization. Feed-forward conditioning can provide such a mechanism.

Many animals living in a social group can make a choice: Stay in the social group, or leave the group and live as solitary individuals. Except for the eusocial insects with their sterile castes, such choices can be seen in the form of the flexible social systems found in a variety of different animals (Lott 1991). One approach to the matter of choice is to list the costs and benefits of social behavior (Alexander 1974) and make the assumption that animals are assessing these costs and benefits and making a decision on the basis of the cost/benefit ratio of staying in the social group (Wilson 1975). However, exactly how animals might be able to make this cost/benefit ratio assessment is not discussed.

Feed-forward conditioning offers a simple mechanism for explaining how social groups can become established. Let us suppose that two animals coexist spatially and temporally, either because they are related (i.e., the genetic hypothesis) or because they have been attracted to the same habitat for the purposes of resource extraction or utilization (i.e., the ecological hypothesis). In these circumstances, the two animals can respond to each other aggressively, with one animal chasing away the other, or they can respond neutrally, by ignoring each other, or they can respond cooperatively, by helping each other to construct a shelter or by sharing food or the location of food sources.

Decisions about sharing or cooperation appear to be made on the basis of ecological factors, such as the availability and abundance of resources, even among relatives. As Slobodchikoff (1984) has pointed out, a relatively small proportion of *Hymenoptera* (bees and wasps) is social, probably because of the availability of resources, although all species of *Hymenoptera* have the haplodiploid system of sex-determination that led Hamilton (1964) to speculate about the benefits of inclusive fitness in the evolution of sociality. Resources can be food, shelter, or the availability of other animals to serve an antipredatory function, such as that found among cooperative mammals such as meerkats (*Suricata suricatta;* Blumstein 1999; Clutton-Brock et al. 1999).

If the animals respond to each other cooperatively, then feed-forward can become an important proximate mechanism for strengthening the cooperative response. Here the reinforcer might be access to a resource (e.g., food). Each of the animals can then function as a CS, and the feed-forward mechanism leads to the procurement of more resources. This in turn can lead to behaviors that we see within social groups, such as play and social grooming. In this context, these behaviors can be viewed as CS byproducts of the feed-forward mechanism. The learned system of cooperation can then be transmitted culturally to subsequent generations, and if it increases the fitness of the members of the social group, it can serve as the basis for natural selection for behaviors that increase the strength of the cooperation.

Such feed-forward mechanisms can also serve as the initial impetus for the evolution of sterile castes among the eusocial animals. As pointed out by Slobodchikoff (1984) and Slobodchikoff and Schulz (1988), if an animal is going to have an expectation of zero fitness as a solitary individual, and an extremely small but greater than zero average fitness expectation as a member of a social group, the animal in an evolutionary sense should choose to be in the social group. Among the social insects, workers are functionally sterile, but the fitness expectation for any individual is not zero. In most social insects, whether an individual egg develops into a sterile worker or a reproductive adult is determined by dietary considerations and the needs of the colony (Michener 1974; Slobodchikoff & Schulz 1988; Wilson 1971). Thus, each egg has a small chance of becoming a reproductive adult, in which case that individual acquires an extremely high fitness. If an individual insect cannot survive as a solitary individual but can survive as part of a group, then evolution would favor the development of sociality, as long as each individual in the group had an average reproductive expectation that was greater than zero. Feed-forward conditioning can serve as the initial mechanism by which the group forms, and the resource requirements and availability can then determine how many individuals can reproduce (see Slobodchikoff & Schulz 1988).