

Introduction

The Neuroscience of Social Behavior

Scott R. Wersinger

Tiger got to hunt, bird got to fly;
Man got to sit and wonder “why, why, why?”
Tiger got to sleep, bird got to land;
Man got to tell himself he understand.
— Kurt Vonnegut, *Cat’s Cradle*

The theme of this issue is the neural bases of social behavior. As the diversity of the behaviors discussed in the articles illustrates, the term social behavior applies to a broad range of behaviors whose expression is species specific. What are the common characteristics that make all these behaviors social?

When most people think of social behavior, they first think of human behavior. Humans are clearly social organisms, with complex, sophisticated societies and many “rules.” Innate behavior directs adherence to some rules, whereas other “rules” and appropriate social behavior must be learned.

To understand an individual culture, scientists study characteristics specific to that culture; to understand general principles that apply to all human culture, we must look for similarities among cultures. For example, languages differ greatly across societies, but all humans have language. Researchers can study differences between individual languages to try to understand specific cultures, or commonalities across all languages to try to understand how and why humans use language. People hear, learn, understand, and produce language. From a neurobiological perspective, this means all humans have the brain circuits necessary to do these things. *What* we hear, learn, understand, and produce varies among human societies; *how* we do these things does not. I believe this same principle applies to the study of social behavior in different species.

To function in society, humans (and other animals) must display appropriate social behavior. The ability to do so relies on the coordination of many processes—sensing and interpreting a social situation, remembering the appropriate behavioral response for that situation, coordinating the immediate sensations from the social environment and

neural circuits that control behavioral output, and, finally, engaging in the appropriate behavioral response. In order for these events to occur, the brain must function nearly perfectly (and, as one might expect, brain anomalies are associated with abnormal social behavior).

The ability to form complex social groups is not limited to humans. Nonhuman primates including gorillas, Bonobo chimpanzees, and rhesus macaques live in social groups, and simpler organisms, such as ants and honeybees, also form complex societies. Even organisms as simple as amoebas are capable of interactions that result in a rudimentary society, demonstrating that social organization and behavior can occur in the absence of a complex nervous system.

What Is Social Behavior?

This seems at first like an easily answered question. As it turns out, it is not. Many books and articles use the term “social behavior” without defining it, and those that do define it may not agree. For example, McGill (1965) defines social behavior as “the behavior of an animal, or a group of animals, in response to others of the same or different species.” Manning (1979) states that “It is perfectly valid to refer to any interaction between one individual of a species and another as ‘social behavior’.” Thus, McGill includes interactions between species as social behavior, whereas Manning does not. The fact that leaders of the field do not arrive at a consensus definition suggests three things. First, I will not be able to offer “the” definition of social behavior here. Second, it may be more useful to think of social behavior as a concept rather than a definable term. And third, given the wealth of research on the neurobiology of social behavior, the absence of a universal definition clearly does not impede its analysis.

I begin my conceptualization by presenting several cases and asking whether or not they represent social behavior. First, consider the numerous species of north temperate dung beetles. If one were to take a census of dung pads, as Hutton did (Hutton and Giller 2004), one would count many beetles of the same species on each pad (although members of different species also inhabit the pads). These nonrandom clusters of organisms are referred to as aggregations. Are these aggregations an example of social behavior? In this case, clustering on a dung pad is not social behavior because the

Scott R. Wersinger, PhD, is an assistant professor in the Department of Psychology at the University at Buffalo of the State University of New York.

Address correspondence and reprint requests to Dr. Scott R. Wersinger, Department of Psychology, B-72 Park Hall, University at Buffalo, SUNY, Buffalo, NY 14260 or email sw39@buffalo.edu.

gathering of dung beetles is a simple byproduct of attraction to a limited resource. As Allee (1927) noted, animals form aggregations for many nonsocial reasons; for example, organisms necessarily aggregate around limited resources such as food, water, or breeding grounds. Once organisms form aggregations, however, there is a high probability that they interact. One can easily imagine how the formation of aggregations could lead to the evolution of social behavior, an idea discussed in more detail below.

Consider another example, the Dictyostelia, or so-called social amoebas (see Dormann et al. 2000; Strassmann et al. 2000). These unicellular animals normally live as asexually reproducing amoebas. However, starvation triggers individual amoebas to release a chemoattractant that causes conspecific amoebas to move toward it. When the population is starved, millions of amoebas may aggregate in response to the chemoattractant and form a motile structure called a “slug,” which after several days of movement supports a mass of spores that are capable of establishing new colonies of amoebas. Amoebas in the slug differentiate into five different types, each with a specific role. I believe this is similar to the division of labor observed in honeybee colonies. Clearly the amoebas form a group of interacting organisms. Is this interaction an example of social behavior? There are several behaviors here: the formation of the aggregation, the differentiation of roles in the slug, and the coordinated movement of the slug, to name a few. Not all these behaviors may fit the definition of social behavior but, although the behaviors displayed by the social amoebas is rudimentary compared to those displayed by more familiar animals, I think they are social behaviors.

On the African savannah, there is often interaction among species around a freshly killed animal. In pictures one generally sees many species, such as lions, hyenas, and vultures, around the carcass and there is interaction among them—for example, the lions keep the hyenas and vultures at bay until they have finished. Is this social behavior? According to McGill’s definition, yes, although most definitions of social behavior state that the interaction must occur among members of the same species.

In one of my laboratory meetings I asked if a person talking to a pet dog constitutes social behavior. About half of my laboratory staff answered yes, about half no. I asked them to explain the rationale for their answers and, in the end, we agreed that although an individual simply feeding or walking a dog is not necessarily social behavior, talking to and petting the dog is. Why? It was difficult to articulate, but the motivation for feeding and walking a dog may simply be to keep the dog well-nourished and to keep one’s carpets clean, whereas the motivation for speaking to a dog may be for social interaction of some sort. But motivation is very difficult, if not impossible, to measure in animals. Therefore, although motivation can be part of the concept of social behavior, scientists cannot use it to differentiate social from nonsocial behavior. We must adopt an operational definition, an objective and quantifiable behavior that is recognized as the measure of social behavior.

All sexually reproducing species must interact with a conspecific to reproduce. Inasmuch as sexual behavior is an interaction between conspecific organisms, it would appear to be social behavior. However, some, myself included, wonder whether this necessarily makes all sexual behavior social behavior. Two examples illustrate this uncertainty. (1) During mating the male cimicid (a taxon of insect species that includes bedbugs) uses a sharp, specialized organ to pierce the female’s abdominal wall to inject sperm (Reinhardt and Siva-Jothy 2007). The female need not display behavioral receptivity and may be inseminated by more than one male. Several lines of evidence suggest that the male approaches any stimulus resembling a cimicid and determines whether the stimulus is a female through a series of movements; if so, he proceeds. (Male cimicids are good at this process, since they rarely inseminate a male.) This is certainly sexual behavior. But is it social behavior? (2) Humans and other primate species masturbate when alone. Is this sexual behavior a social behavior? Some argue yes, if the individual is “thinking” about a conspecific; others argue no, since that may not be the case; and still others can’t decide because we are not privy to the “thoughts” of the organism and therefore can’t use them to classify the behavior. I am not attempting to offer a solution. Rather, I am attempting to illustrate some of the complexities of the field.

In summary, scientists are unable to classify behavior as social or nonsocial behavior without a definition of the term. But there is no single, universally accepted definition of social behavior. Therefore, I offer only a reasonable working definition: Social behavior is *an action directed toward, or in response to, a conspecific*.

The Evolution of Social Behavior

The fact that social behavior is ubiquitous suggests that there are great benefits to it. Why and how did it evolve? What are its benefits? What is its adaptive significance? What modifications to existing brain circuits occurred to support social behavior?

A detailed discussion of the evolution of social behavior is beyond the scope of this introduction (see Alexander 1974). A brief discussion, however, is necessary to distinguish “living in groups” from “social behavior.” As mentioned above, organisms may live in groups without engaging in social behavior. Likewise, some species do not live in groups (e.g., the Syrian hamster) but engage in social behavior such as courtship and maternal behavior at some point in their life.

Living in groups has benefits and costs. The benefits include a reduction in predation (e.g., by improved detection or repulsion of predators), enhanced survival of offspring (e.g., by group feeding and protection), better defense of territory or resources, and more efficient foraging for prey (Alcock 1998). The costs include increased competition with conspecifics, interference in parental behavior, and, perhaps most importantly, increased risk of parasitism and transmission of disease (Alcock 1998).

Which came first, social behavior or group living? Social behavior may have evolved in group-living animals because it increases the benefits or reduces the costs of group living or offers benefits of its own. As mentioned above, it is easy to imagine how the beetles aggregated on dung might benefit from social behavior. So it seems likely that social behavior is a result of group living. But the opposite may also be true. Group living in some spider societies may have evolved as a byproduct of prolonged maternal care (Whitehouse and Lubin 2005). It is thus likely that both hypotheses explain the evolution of behavior.

Neural Bases of Social Behavior

At its most basic level, social behavior requires only that an animal detect a cue from a conspecific and respond to it. The social amoebas (the *Dictyostelia*) illustrate this principle well: they detect a chemical from a conspecific and move toward it. Their response does not even require a nervous system! Complex social behavior, such as is typically seen in vertebrates, requires a highly developed nervous system, and the processes underlying it require a great deal of brain. Therefore, the evolution of the brain and of social behavior are likely related.

How, then, is the brain related to social behavior? Since social behavior is a general term that encompasses many behaviors, this question can be answered at many levels. In the first article of this issue, Elizabeth Adkins-Regan reviews the neuroendocrinology of social behavior. As she points out, long-lasting social bonds develop in members of many species. These bonds may form the foundation of the species' social structure and are therefore central to understanding their social behavior. There has been great progress in studies of the hormones, neurotransmitters, and brain regions underlying these bonds to determine how they are formed and maintained. How well do the findings of these studies generalize? Here, the comparative approach taken by Dr. Adkins-Regan is especially powerful. Her comparison of the function of these neural systems in species that naturally adopt different social structures provides insight into the relationship between neural systems and social structure.

Why do animals engage in social behavior? At the evolutionary (also termed the ultimate) level, there may be many reasons that eventually boil down to the following: individuals that engage in the behavior produce more offspring that survive and reproduce than animals that do not. Similarly, at the mechanistic (also termed the proximate) level, there may be many answers to this question. As a general principle, animals consistently engage in social and other behaviors that result in the acquisition of a rewarding stimulus and avoid engaging in behaviors that result in an aversive outcome. Thus, the expression of social behavior is tied to the function of the brain's reward system.

Raúl Paredes reviews reward in the context of one type of social behavior, sexual behavior. The field encompassing reward and reinforcement is complex and often contentious.

Dr. Paredes provides a clear definition of these two terms and describes methods for measuring reward. It is clear that social behavior in general and sexual behavior in particular are rewarding. What stimuli make sexual behavior rewarding? This question does not have a simple answer. Dr. Paredes reviews the literature addressing this question, including much of his own work. His perspective is important for the field, especially as, along with a few researchers like Mary Erskine (1989) and James Pfaus (Coria-Avila and Pfaus 2007), he considers sexual reward and reproductive behavior from the female perspective. Dr. Paredes compares the characteristics of the mating bout that female rats find rewarding with those that male rats find rewarding. He concludes with a discussion of the neurotransmitters and brain regions involved in sexual reward.

As mentioned in Dr. Paredes' article, social and sexual odor cues are rewarding in rats and mice, and in many species, including laboratory rodents, they mediate and regulate a great deal of social behavior. Kevin Kelliher and I review the effect of chemosensory cues on reproductive behavior and physiology in the mouse, a species in which chemical cues from other mice exert profound effects. We begin by explaining the basic structure and function of the olfactory system in the mouse, as this system regulates all chemosensory cues that affect behavior. We next discuss the effects of chemosensory cues on the reproductive physiology and behavior of the mouse. We describe each phenomenon, the chemical cues that induce it, and what is known about the neural mechanism underlying each effect. We also discuss the ramifications of these effects for the laboratory animal facility. Although we limit our review to mice, the concepts apply to a broad range of species.

Another group of stimuli that play a prominent role in rodent social interactions are ultrasonic vocalizations, high-frequency (greater than 20,000 kHz) sounds that humans are unable to hear. Stefan Brudzynski focuses on the ultrasonic communication of adult rats. He begins by reviewing possible reasons for the evolution of this form of communication in rodent species. There are several classes of ultrasonic vocalization that rodents emit under different circumstances, and Dr. Brudzynski describes how to measure them in the laboratory and which parameters are relevant. He then discusses the neurobiology and neurochemistry of each.

Complex social behavior may involve many of the processes described in the first four articles. Mark Kristal considers the biopsychology and development of one such behavior, maternal behavior, and critiques the current model of maternal behavior of the laboratory rat. He describes the external and internal factors that trigger the development of the complex constellation of behaviors that constitute maternal behavior. Throughout his review, Dr. Kristal notes critical theoretical flaws present in the literature and suggests ways to avoid these pitfalls.

How does the relationship between neural systems and social behaviors apply to the laboratory animal facility? First, it is important to consider whether domestication has

altered social behavior and mating systems in ways that matter for research. Second, information about an animal's social life in the field can help guide decisions about housing and breeding conditions as well as explain the impact of certain housing conditions in the laboratory. Studying social behavior in the laboratory can be challenging because many factors affect social behavior, some of which are very difficult to control. However, if these factors are not controlled, the behavior the researcher is studying may not be representative of the natural behavior.

Lisa Martin and I address the conditions under which social behavior should be studied in the laboratory. We attempt to help the researcher and the laboratory animal facility personnel partner to optimize the housing conditions of subjects used in behavioral analysis. After defining the goals of the investigator and the laboratory animal facility personnel, we briefly discuss how social behavior is commonly studied in the laboratory and the importance of considering the animals' natural ecology to optimize husbandry conditions. We illustrate how husbandry conditions affect social behavior in the context of aggressive behavior and sexual behavior. Finally, we discuss a variety of concerns that commonly arise during the analysis of social behavior and present suggestions to prevent or circumvent them.

Last, Randall Nelson draws on all the articles to offer an overarching perspective for IACUC members. In his essay he considers the challenges and opportunities for IACUCs in the context of protocols for social behavior.

I hope the articles in this issue give the reader an appreciation for the complexity of social behavior in all organisms, both in and outside the laboratory. The general principles illustrated by the specific examples apply to many other species, including other common laboratory animals. The experiences and insights presented here can help the reader to be more cognizant of the multitude of factors that influence social behavior but are beyond human senses and consciousness, and of the potentially dramatic impacts of these factors on the behavior and physiology of laboratory animals. Although the practical considerations discussed in this issue are in the context of social behavior, they also apply to many other fields

and may usefully guide general husbandry practices in existing facilities and the design of new facilities.

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