Guest Editorial

# Social Behavior: From Cooperation to Language

Social behavior is an integral part of complex life. According to Maynard Smith and Szathmáry (1997), it encompasses the last two major transitions in the evolution of life: the transition from solitary to social organisms, giving rise to the formation of social groups, and the transition from primate societies to human societies, enabling the emergence of language. The pivotal role of social behavior is especially apparent from the wide scope it spans over many natural phenomena, ranging from signaling in bacteria to altruism in social insects and to human cooperation, which has led to modern society as we know it. The articles in this thematic issue of *Biological Theory* on social behavior provide an interdisciplinary view, reaching across the full spectrum of its complexity, while nevertheless following a common thread.

Given its central role, it is hardly surprising that research on social behavior has given rise to a vast field, scattered across disciplines, and comprising a range of different research methods and model organisms. Traditionally, understanding the emergence and organization of social behavior has been tackled separately for humans and other living organisms, separately by biologists and social scientists, and separately by researchers using models and those conducting field studies. In many cases, there has been relatively little communication between these camps, making it difficult to see the forest for the trees.

More recently, however, there has been a general trend toward a more integrative approach to understanding social behavior (Laland et al. 2000; Caporael 2001; Hammerstein 2003), of which the articles in this issue are representative. The selection of articles presented here shows that common denominators of social behavior can be found despite variations in discipline, approach, and species studied. In this editorial we will briefly outline the traditional divisions in the study of social behavior, highlight emerging parallels, and discuss how the articles in this thematic issue may be indicative of a movement toward a common view on social behavior.

The first traditional divide to be conquered is between the exploration of sociality in human and nonhuman animals. Much of the work on social behavior in nonhuman animals has focused on explaining the cooperative nature of social behavior. Due to its central role in the evolution of complex life, the evolution and stability of cooperative behavior has been described as one of the defining questions of modern biology (Fehr and Fischbacher 2003). Cooperative behavior has been studied in aggregations of slime molds, schooling in fish, dominance hierarchies of chickens, and parental care in primates, among many other examples (Wilson 1975). The champions of sociality, however, are clearly the social insects, which is why much work in understanding nonhuman social behavior has been carried out in that domain (Wilson 1975).

Social insect societies provide the most advanced examples of social organization known, paralleled in scale and complexity only by human societies. As d'Ettorre points out in this thematic issue, ants are a major model for studying the evolution of cooperation and the transition from nonsocial to social behavior, owing to their strikingly complex societies. Ants comprise an exceptional diversity of social behaviors found across the 12,000 classified species, which have colonized almost every landmass on Earth and compose about 15–20% of the animal biomass in most terrestrial environments (Hölldobler and Wilson 1994). They also provide some of the most remarkable examples of division of labor, with many ant species forming castes of workers, soldiers, or other specialized groups, and using highly specific chemical signals for individual and broadcast communication (Wilson 1971; Hölldobler and Wilson 1994; Bourke and Franks 1995). Two key features of the organization of these complex societies are individual recognition and communication. In her contribution, d'Ettorre reviews different levels of recognition and their evolution from the comparably simple distinction between friend and foe to individual recognition and communication. The paper provides an overview of the basic circumstances that could have favored the emergence of these social behaviors and reveals their chemical and neurological basis.

Apart from the social insects, it has often been remarked that primates, and especially our own species, *Homo sapiens*, represent a pinnacle of sociality. It has been argued that human social systems are much more intricate than those of any other animal because of the extreme degree of cooperative and altruistic behavior found in humans (Wilson 1975; Fehr and Fischbacher 2003; Warneken and Tomasello 2006), sometimes referred to as *prosocial behavior* (Batson 1998). Human social behavior is typically studied distinctly from sociality in other animals within the fields of social psychology, economics, political science, or anthropology. One reason may be the diversity and complexity of human prosocial behavior found in modern societies, spanning examples from traditional family businesses to multinational organizations, welfare states, charities, or online projects like Wikipedia. However, while the range of human social behaviors may be more impressive than that of other social animals, some argue that the difference may be just quantitative rather than qualitative (Darwin 1859; Bekoff 2001).

One approach that attempts to address human and nonhuman social behavior on a theoretical, abstract level beyond species specificity is evolutionary game theory. Historically, evolutionary game theory was conceived as a combination of game theory, the discipline of strategic behavior in social contexts, and evolutionary theory (Maynard Smith and Price 1973). It has since grown into a major tool for the study of cooperation and has been used to address a large variety of questions across disciplines (Hammerstein and Selten 1994). In this issue, Hauert et al. present an evolutionary game theoretical model that investigates the origins of cooperation among unrelated individuals. Both punishment and voluntary participation are mechanisms known to lead to cooperation in public goods games (Hauert et al. 2002; Fehr and Fischbacher 2004). However, it is unclear how punishment can establish itself in a population, and although voluntary participation can lead to cooperation, it cannot guarantee a stable outcome. Furthermore, evolutionary game theoretical models typically use infinite populations, an unrealistic assumption. In their contribution to this issue, Hauert et al. give a detailed analysis of the role of punishment and voluntary participation in both finite and infinite populations, showing that given finite populations, voluntary participation can provide a path for the establishment of punishment and cooperation.

The article by Hagen et al. in this issue gives an example of parallels between nonhuman and human social behavior, by highlighting similarities between animal communication strategies and deliberate self-harm (DSH) in humans. Their contribution draws on fields as far apart as economics, psychology, and animal signaling, and postulates that the same basic forces apply to both humans and nonhuman animals in need of proving the honesty of messages they communicate. They review the literature to support their hypothesis that DSH can be seen as a costly signal to credibly communicate suffering to social partners. They point out that the idea that costly signaling can be used as a guarantee for honesty represents one of the main theories in animal signaling known as Zahavi's handicap principle (Zahavi and Zahavi 1997). Although Zahavi's theory was developed very soon after a very similar theory in economics by Spence (1973), parallels between the two fields are rarely drawn.

A characteristic that has been attributed to human social behavior is that it is not only determined by genes, but also by thoughts and ideas, which unlike genes easily flow from one person to another by imitation. This allows human social behavior to be modified and adapted during an individual's lifetime, for example through individual learning or cultural transmission (Tomasello 1999). We have now arrived at a second junction, where the study of human social behavior has traditionally been divided into research on cultural propagation on the one hand, and biological evolution on the other.

The idea that parallels exist between cultural evolution and evolution by natural selection goes back to Charles Darwin (1871), whose theory of common descent seems to have been inspired by John Herschel's ideas on the common descent of human languages (Whitfield 2008). Thirty years ago, Richard Dawkins (1976) made the parallels between both concepts more tangible by developing the notion of "memes," referring to a unit of imitation, such as a song, skill, or religious belief. Exploiting the parallels between cultural and genetic evolution has since been repeatedly advocated as a means to advance our understanding of both through collaboration between research fields (Cavalli-Sforza and Feldman 1981; Blackmore 1999; Laland et al. 2000; Hull 2001; Fehr and Fischbacher 2003; Hammerstein 2003; Whitfield 2008). Nevertheless, there seem to be relatively few studies in the literature that have put this into practice (see Croft 2008 for a review).

The opening paper of this thematic issue by Caporael presents a model of society that bridges the gap between genes and culture by proposing repeated assemblies as an abstraction that describes evolutionary processes (either in the genetic or cultural sense). As an illustration of the concept, she uses the framework of repeated assembly to organize human society into overlapping social networks of different sizes that have been established over human history through repeated face-to-face interactions in coordinated groups. Her voice can thus be added to those arguing for the establishment of more general evolutionary models that bridge the gene–culture divide.

Perhaps some of the biggest controversies in the field are sparked by discussions on the origins of human language, whether it is unique to humans and whether it originated as a cultural or genetic phenomenon (Pinker and Bloom 1990; Christiansen and Kirby 2003; Számadó and Szathmáry 2006). Language represents a universal human trait that has emerged in all known human societies (Pinker and Bloom 1990; Hauser 1997), and has evolved into the almost 7000 known languages in the world (Gordon 2005). Understanding the origins of human language has challenged researchers for centuries, but has seen a recent revival with advances in the field of neuroscience; it has now grown into a large interdisciplinary field of study (Christiansen and Kirby 2003; Számadó and Szathmáry 2006). The term *language evolution* usually refers to one of two things: either the inquiry into the origins of language, or the study of language change over time. Three articles in this issue explore questions regarding the latter: Gong et al. show how a spatial model can allow a vocabulary to self-organize into one or more separate clusters of "languages" through playing local naming and category games. Kandler and Steele present an ecological model to analyze how competing languages behave in a population to determine the conditions under which the dominated language would go extinct. In a third article, Roberts reports on an empirical study with human subjects using an artificial language to test the hypothesis that subtle cues in language use can communicate information about the social group a speaker belongs to. Roberts's article discusses how cooperation and competition between individuals can shape their use of language, thereby highlighting a link between cooperation and language that is rarely made.

Apart from such causal links, in this issue we also find parallels between cooperation and language in the processes leading to their stabilization in populations of agents. Interestingly, Pestelacci et al.'s contribution on the evolution of cooperation arrives at conclusions that are similar to those found in the article by Gong et al. in this issue. By looking at cultural evolution through imitation, Pestelacci et al. also find that the use of a spatial model applied to the prisoner's dilemma and stag hunt games can result in clustering effects that lead to the convergence of multiple cooperative communities, as opposed to the theoretical prediction of stable global defection in the standard model.

Many of the articles in this issue follow a modeling approach, which brings us to yet another divide in the field, concerning the methods used to study social behavior. Scientific methods can generally be broken down into empirical studies conducted directly on the actual system of interest (e.g., experiments with animals in the wild) and studies in which reductionist models are built to represent some aspects of the real system (e.g., statistical models, game-theoretical models, or computer simulations) (Wartofsky 1979; Webb 2001). *Biological Theory*, as the name suggests, subscribes rather to the latter approach, of which the articles in this thematic issue are representative. A useful model reduces the real system of interest to its key parameters, such that its mechanisms are simple enough to understand, yet generates predictions that fit the empirical data measured on the real system (Webb 2001). A model that is fully understood can then gradually be complexified to incorporate more aspects of the real system to fine-tune correspondence with real-world observations, and deepen the understanding of the system.

The collection of articles in this issue exhibits such a trend toward more complex and realistic models whose results match empirical observations more closely. The articles by Pestelacci et al. and Gong et al. point out that adding a spatial component to their models results in clustering effects often observed in communities of living organisms. Kandler and Steele find that adding more realistic assumptions to their ecological model, such as spatial heterogeneity, influences their results to provide a better model of empirical data. Similarly, Caporael presents a model of evolutionary change that can explain human social systems better than the traditional "flat" view. Finally, in the model presented by Hauert et al., the use of finite populations, punishment, and a choice in participating in public goods games—again a step toward real-life scenarios—results in higher and more stable levels of cooperation. The increasing realism of the models presented thus serves to capture the defining properties of their real counterparts, hence guiding future empirical studies.

This thematic issue on social behavior assembles a diverse collection of articles addressing different aspects of social behavior. The many parallels observed in the articles, between sociality in humans and other living organisms, between genetic and cultural evolution, and between the results obtained in the theoretical studies presented here and empirical data, indicate that we are well on our way to an integrated approach to the study and understanding of social behavior. We expect that such convergence, achieved through interdisciplinary research and collaboration, will lead to a coherent view of the general mechanisms governing social behavior.

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