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EDITORIAL

The ultimate and proximate underpinnings of social behavior

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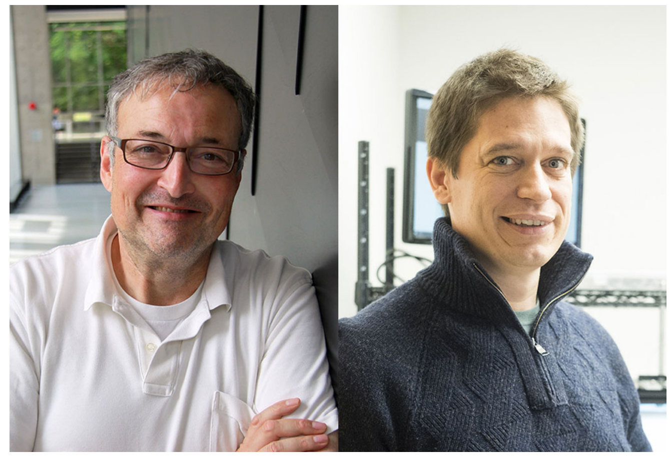
Social systems encompass individual components that come together and interact. How these interactions and resulting group-level phenomena unfold depends on the properties of the individuals, their experience, ambient conditions, as well as the interactions themselves. How evolution shapes social interactions and social behavior, and how social behavior plays out on a mechanistic level are questions of great general importance. These questions touch on sensitive issues related to human psychology and cognitive abilities, as well as how humans differ in these respects from other animals (Wilson, 1975; de Waal and Ferrari, 2010), but they also relate to fundamental aspects of evolutionary processes. In particular, social evolutionary theory provides a unifying framework in which social behavior and the evolutionary dynamics between interacting components can be understood at a variety of organizational levels, ranging from genes in a genome, to cells in multicellular organisms, individuals in a social group, and between-species interactions (Bourke, 2011).

This Special Issue of the Journal of Experimental Biology highlights how the same evolutionary concepts apply to different levels of biological organization and across the tree of life. While the altruistic behavior of worker ants that defend their colony while foregoing reproduction, or the mutualistic interaction between ants that milk and defend aphids is immediately apparent, other social evolutionary interactions are less obvious, yet governed by the same principles. For example, the first cases of ‘selfish genetic elements’ were perceived as genetic peculiarities, but the realization and formalization of the fact that the fitness of a genetic element does not necessarily coincide with the fitness of the organism it resides in (Hamilton, 1964) has led to a better understanding of why selfish genetic elements evolve and persist. This conceptual advance has also led to the development of new approaches to discover and study different types of selfish genetic elements, which are now known to be essentially ubiquitous (Burt and Trivers, 2008; Werren, 2011). Likewise, quorum sensing in bacteria, which was initially discovered in the particular context of bioluminescence, is now known across a wide range of bacterial species and biological contexts (Papenfort and Bassler, 2016). In fact, the study of social evolution and behavior in microbes has since become a vibrant field of research and, given the genetic accessibility and scope for experimental evolution in microbes, has provided important insights into how social interactions evolve (Foster, 2010; Strassmann et al., 2011). The search for common principles that recur across social systems has informed our approach to this Special Issue.

This Special Issue also aims to address how individuals interact at the mechanistic level, and how these interactions give rise to emergent properties at the group level. This approach will eventually allow us to tease apart general mechanisms that apply broadly across study systems from the idiosyncratic mechanisms of any particular system and its specific ecological context. More mechanistic studies of social behavior, both in traditional genetic model systems and in species that have been less tractable experimentally, have made great strides over the past years due to technical advances. In particular, recent developments in DNA and RNA sequencing (Goodwin et al., 2016), genome editing (Shalem et al., 2015), and individual automated behavioral tracking in groups of organisms (Schneider et al., 2012; Mersch et al., 2013; Herbert-Read, 2016), along with theoretical advances (Pinter-Wollman et al., 2014) now enable researchers to study species displaying complex social behavior at unprecedented behavioral and molecular resolution (LeBoeuf et al., 2013). Furthermore, these developments have revealed structured social interactions beyond mating and aggression in species previously considered solitary, such as *Drosophila melanogaster* (Schneider et al., 2012).



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There are several themes that emerge in this Special Issue. The appearance of new ways to communicate is inherent in major evolutionary transitions, and these cognitive innovations are reflected in the evolution of the social brain. A variety of epigenetic mechanisms are co-opted for the evolution of novel forms of differentiation, such as the production of different cell types in multicellular organisms or castes in social insects. We further note that sophisticated social behavior has also repeatedly evolved via modifications of molecular and neuronal circuitry that broadly underlies reproductive, feeding and foraging behavior in largely solitary species. Finally, complex group-level phenomena usually emerge from relatively simple local interactions between

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individual agents. Despite the fact that increasingly sophisticated tools have become available to investigate the structure of social groups as networks that do not assume hierarchical relationships or other features *a priori*, a unified statistical framework for evaluating properties that emerge from local interactions between individual units with unique properties is still largely lacking. Such a framework might ultimately transform our understanding of how selection has shaped the interactions in complex biological systems in general, from genes in genomes, to neurons in brains, to individual organisms in groups.

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