Review

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An evolutionary framework for studying mechanisms of social behavior

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Social interactions are central to most animals and have a fundamental impact upon the phenotype of an individual. Social behavior (social interactions among conspecifics) represents a central challenge to the integration of the functional and mechanistic bases of complex behavior. Traditionally, studies of proximate and ultimate elements of social behavior have been conducted by distinct groups of researchers, with little communication across perceived disciplinary boundaries. However, recent technological advances, coupled with increased recognition of the substantial variation in mechanisms underlying social interactions, should compel investigators from divergent disciplines to pursue more integrative analyses of social behavior. We propose an integrative conceptual framework intended to guide researchers towards a comprehensive understanding of the evolution and maintenance of mechanisms governing variation in sociality.

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The study of social behavior in the 21st century

All animals interact with conspecifics at some point in their lives. Members of the same species tend to be each other's fiercest competitors and strongest allies, as evidenced by the intense cooperation and conflict that characterize many intraspecific interactions [1]. These interactions are the products of genetic, epigenetic, endocrine, and neural mechanisms that – in conjunction with environmental conditions – affect Darwinian fitness and evolve via natural selection. Building upon Aristotle's four questions, Tinbergen [2] posited that understanding behavior requires the integration of studies of mechanism and function. Only by asking questions both from a proximate perspective (i.e., focusing on causation and development) and an ultimate perspective (i.e., focusing on adaptive value and evolutionary descent) can behavior be fully understood. Social behavior in particular lends itself to such an integrative approach not only because it commands the attention of many disciplines [3] but also because even many behaviors commonly considered nonsocial often occur in a social context (e.g., mating, fighting, parental care). Social behavior is also special because the selective agents are other members of the same species, and this results in intriguing evolutionary dynamics. Nevertheless, in the intervening decades since Tinbergen's

seminal work [2] studies of behavioral mechanisms have proceeded largely independently of analyses of ultimate-level explanations for social behavior [4]. Among the factors contributing to this disconnect are the challenges of applying laboratory methods to field research where most complex social behaviors are studied, as well as long-standing differences in terminology, conceptual foci, and study taxa [3,5–7]. Progress towards an integrated understanding of the evolution of social behavior has been limited.

Only now, 50 years after Tinbergen's seminal 1963 publication [8], efforts to integrate neural, genetic, epigenetic, physiological, ecological, and evolutionary studies of behavior are gaining increased prominence [7,9–11,101], facilitated by multiple factors, including innovative technologies (e.g., high-throughput sequencing [12]), and analytical procedures (e.g., improved statistical methods for modeling and comparative analyses [13]) as well as the increasing ease of application of these advances to field studies (e.g., biotelemetry [14,15]). As a result, it is increasingly possible to address all four of Tinbergen's questions concurrently for the same species [3,7,10,11,16], which is most effective when using modern comparative methods [13]. Such integration is crucial if studies of behavior are to contribute to solutions to pressing biological problems. For example, only by understanding the evolutionary origins of diverse mechanisms can we begin to predict how species will respond to global change [17]. Similarly, a thorough understanding of the adaptive consequences of diverse mechanisms can help to identify novel model systems for studies of specific neuropsychiatric disorders [18]. Integrating Tinbergian levels of analysis is especially appropriate for the study of social behavior which, given its complexity, must be approached from an integrative perspective.

Historical perspectives

Although most current textbooks on animal behavior prominently feature Tinbergen's four questions [19–21], researchers have been slower to adopt the type of truly integrative approach that Tinbergen originally proposed [2]. Indeed, studies of behavior remain to some extent divided into efforts to understand ultimate- versus proximate-level reasons for variation in social interactions [3]. Each tradition offers important impulses for the integrative conceptual framework we outline below.

Ecological and evolutionary traditions

Ethologists and behavioral ecologists have emphasized field studies of ultimate-level aspects of social behavior. Crucial concepts addressed by such studies include the roles of kinship and inclusive fitness in shaping social interactions, as well as the effects of specific ecological parameters on social structure [8,22]. Such studies have the advantage of documenting patterns of behavior and the associated adaptive consequences in the environments, and under the selective regimes experienced by the study organisms. However, such analyses have tended to ignore the physiological, neural, and genetic mechanisms underlying these behavioral patterns as part of a 'phenotypic gambit', a heuristic construct positing that detailed knowledge of the mechanistic bases for behavior is not required for an understanding of its function and evolution [23,24]. As a result, such studies have been typically unable to determine how underlying mechanisms shape observed behavioral responses to external environments, including generating significant individual variation in response to similar external environments.

Neuroendocrine and genetic foundations

Psychologists and neuroscientists interested in social behavior have followed an often parallel but distinct research tradition that emphasizes its physiological, neuroendocrine, and genetic bases. Prominent themes have included the roles of learning and ontogenetic experience on social interactions, as well as the effects of hormone levels in both generating and mediating specific patterns of behavior. Such studies are typically conducted under laboratory conditions and involve a limited number of 'model' study organisms, thereby offering important opportunities for controlled experimentation, often employing tools specific to the organisms under study. However, these analyses have tended to employ highly inbred study organisms that live in simplistic laboratory environments [25], thereby largely precluding consideration of the functional contexts in which behavior – particularly complex social behavior – occurs and has evolved [26]. As a result, studies of proximate-level mechanisms of social behavior generally cannot address the potential impacts of variable environmental conditions.

The power of integration

Although numerous opportunities exist for multidisciplinary research, at present we lack an appropriate conceptual framework – including a common language for describing social behavior – to develop an integrative understanding of the evolution of social behavior. To capitalize upon emerging opportunities we need predictive models of social interactions that integrate function and mechanism, and that can be applied to diverse taxa over a range of social and ecological contexts. We offer here such an integrative framework of sociality (Figure 1A), one that incorporates individual variations in ecology, fitness, and experience as well as the neural, physiological, genetic, and developmental mechanisms underlying social behavior. We outline ways in which researchers can use this framework to dissect mechanisms of social behavior in free-living animals exposed to the real-world ecological and evolutionary factors that shape such behavior. We do so in a manner that will open up innovative avenues for comparison across disparate taxonomic groups. Importantly, this framework can be extended to other types of complex behaviors (e.g., finding food or a suitable habitat, migratory behavior, learning and memory formation) and therefore acts as a blueprint for the integrative study of behavior.

An integrative framework

Clearly, combining proximate and ultimate approaches to the same phenomenon generates opportunities for understanding social behavior that are not possible through either tradition alone. For example, because the genetic, molecular, and neural mechanisms underlying behavior are subject to selection and have a phylogenetic