SYMPOSIUM

New Frontiers in the Integrative Study of Animal Behavior: Nothing in Neuroscience Makes Sense Except in the Light of Behavior

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Introduction to symposium

The systematic study of animal behavior has been a diverse and dynamic discipline for more than a century. However, the study of animal behavior has often been limited to relatively simple processes and questions, which often failed to do justice to the complexity of animal behavior in nature. For example, behavioral studies in the field (e.g., mating behavior or group living) often fails to reveal the physiological and developmental mechanisms, whereas reductionist studies of behavior in the laboratory generally do not consider the adaptive value or evolutionary history of a given behavior. Expanding upon earlier insights, Tinbergen (1963) recognized over half a century ago that a comprehensive understanding of animal behavior required insights into both the proximate and ultimate mechanisms. These "levels of analysis" should be viewed as complementary to each other, rather than as alternatives to be pursued in isolation (Nesse 2013). However, to this date most studies of the proximate and ultimate explanations of animal behavior have typically proceeded independently. With the advent of new and powerful resources and tools in genomics, genome editing, physiology, neuroscience, movement tracking, etc., it is now possible to not only integrate across levels of analysis in the same studies, but also study increasingly more complex behaviors in more detail and in increasingly naturalistic contexts than ever before (Blumstein et al. 2010; MacDougall-Shackleton 2011; Hofmann et al. 2014).

How should we define integrative animal behavior?

As important as Tinbergen's "four questions" have been to guiding the animal behavior research agenda, the integrative study of animal behavior goes beyond integration across spatiotemporal scales and levels of analysis, which has become a goal of many modern scientific disciplines. Behavior is the ultimate complex and integrated trait, shaped not only by gene, protein, neural, and endocrine interactions, but also by interactions among animals of the same and even different species, and the abiotic environment; in this way behavior is the currency of selection. The integrative study of animal behavior can be conceptualized along four major axes of integration, spanning conceptual, biological, and analytical frameworks and including (but certainly are not limited to): (1) Tinbergenian levels of analysis; (2) levels of biological organization; (3) taxa and habitats, including across different temporal and spatial scales; and (4) research disciplines and their tools. The results of integrative studies in this sense should be mutually—but not necessarily equally—informative within and among these axes. This framework is hypothesis-driven as it encompasses both an iterative process of

'hypothesis-generation' as well as more traditional 'hypothesis-testing' (Rubenstein et al. 2014). Of course, the study of animal behavior has, to some degree, always been integrative as even in the early days of the discipline ethologists carried out empirical research in a wide variety of species in field settings while comparative psychologists studied model species such as rats and pigeons in the lab. Moreover, the study of animal behavior has always been intimately linked with mathematical and statistical modeling approaches, and remains to this day steeped in evolutionary theory. Yet, in recent years the study of animal behavior is becoming more integrative than ever before, largely because modern tools and techniques can increasingly be applied in non-traditional model systems (Blumstein et al. 2010; MacDougall-Shackleton 2011; Hofmann et al. 2014) and often even in naturalistic field settings (Taborsky et al. 2015). This integrative approach is enabling critical tests of long-standing theory, while also generating novel insights and opening up new areas of inquiry. Ultimately, integrative research can both generate novel hypotheses or reject or support long-standing ones, often in ways that traditional approaches cannot (Monaghan 2014; Rubenstein et al. 2014).

Toward integrative animal behavior studies

The idea for an SICB Symposium on the *Integrative Study of Animal Behavior* originated at a workshop on this topic that was organized by two of us (HAH, DRR) in August 2014, with support from the US National Science Foundation (Rubenstein et al. 2014). The workshop brought together mostly junior and mid-career scientists, who had distinguished themselves through innovative and integrative behavioral research. While some would call themselves ecologists or conservation biologists, others would say they are evolutionary biologists or geneticists; and still others would refer to themselves as neuroscientists, neuroendocrinologists, or engineers. Yet, they all study the behavior of animals in more than one way and from multiple angles. Many of the workshop participants agreed to participate in the SICB symposium (as well as a complementary symposium at the 2015 Animal Behavior Society meeting), and their contributions reflect the breadth of concepts and the multitude of approaches animal behaviorists use in their research. Many of these ideas were also reflected in other products from the workshop, including a white paper (Rubenstein et al. 2014) and an edited volume (Rubenstein and Hofmann 2015). Ultimately, our goal was to show

that no matter what the primary research focus, taking an integrative approach to animal behavior can enrich its study. The papers published in this volume represent the culmination of this multiyear reexamination of our field, but we hope that they spur a new generation of research studies and training methods in animal behavior.

Examples of the integrative approach to animal behavior

Co-organizer Rubenstein started the event by providing a compelling and informative introduction to the topic, using his own research program as an example, and with an emphasis on both the history of the field as well as the opportunities awaiting us. In the first research talk, Ilany and Akcay underscored the importance of theoretical approaches to understanding behavioral processes. Specifically, he introduced a simple model of the effect of personality on social network structure and social role differentiation, demonstrating how social network analysis can move beyond purely descriptive approaches by developing predictive theory. Next, Chow took the audience on a *tour de force*, introducing various sophisticated and novel technologies for engineering cellular circuits on the one hand, and recording and manipulating neural activity in freely behaving animals on the other. Galbraith et al. then reviewed potential epigenomic mechanisms that regulate parent-specific gene expression in the generation altruistic behavior in social insects. Renn et al., also using genome-scale data, presented a meta-analysis that integrates data from numerous studies on the neuromolecular underpinnings of social dominance in wrasses and cichlid fishes to identify gene modules that are associated with dominant and subordinate behavior across sexes and species. Next, Woolley used a comparative framework to examine the neural underpinnings of vocal communication, with an emphasis on songbirds. Continuing this neurobiological theme, Kingsbury and Wilson presented a compelling example of an integrative analysis of social behavior in emberizid finches, showing how variation in the action of vasoactive intestinal polypeptide (VIP) and its receptors in specific socially relevant brain regions contribute to behavioral variation across sexes, individuals, species, and seasons. Also using finches as model system, Hutton and McGraw explored the impacts of urban environments on life-history variation, especially in relation to stress physiology, health, and head morphology. Finally, Martin et al. introduced the notion of physiological regulatory networks (PRNs) as whole-

Table 1 Core competencies for the integrative study of animal behavior

Core competencies[a]	Example	Application
Quantification of behavior	Field methods, behavioral observations, natural history	Knowing your animal, ethograms
Ecology/evolution	Ultimate causes, environmental determinants of behavior, measuring fitness	Putting research questions in broader biological context
Mathematical theory	Game theory, evolutionary simulations	Process-based models of evolutionary and behavioral dynamics
Statistics	Bayesian analysis	Hierarchical models
Computational methods	Bioinformatics, machine learning	Tracking, feature extraction, handling genomic data
Genetics/genomics	Functional genomics, gene expression	Genotyping, gene function, gene manipulation
Physiology/neurobiology	Endocrinology, electrophysiology	Characterizing neural/molecular mechanism

[a]Competency refers to being literate in a given area, not necessarily being an expert.

organism regulatory systems that mediate homeostasis and link suborganismal processes with the fitness of individuals. They applied this concept toward understanding how immunological and ecological factors contribute to individual variation and covariation in vector-borne disease-directed behaviors.

Training the next generation of integrative animal behaviorists

The discussion at the close of the symposium focused on training current and future researchers in animal behavior. A lively conversation ensued among the substantial number of attendees, indicating that there is great interest in this topic. Animal behaviorists already receive training in basic experimental design (e.g., statistical design or how to design a well-controlled behavioral test) and methods for observing and quantifying behaviors in the field or lab. And advanced expertise in varied techniques in both field (e.g., collecting specimens in challenging environments) and laboratory settings (e.g., physiological and molecular methods) will continue to be fundamental in this research. However, the need for more specialized training often arises at different career stages because fields evolve rapidly and because researchers may move toward integration at different points in their research program. Conducting effective integrative studies of animal behavior will require training in a breadth of core competencies, many of which are quantitative in nature (Table 1). We recognize that mathematical theories, statistical methodologies, and computational methods have increasingly central roles in integrative animal behavior research. For example, evolutionary game theory and population genetics have long been central to understanding ultimate causes of behavior for a long time. Likewise, modeling developmental, behavioral, gene

expression, and neural dynamics uses tools from stochastic processes theory and nonlinear dynamics. Moreover, statistical tools such as Bayesian hierarchal modeling are becoming increasingly important for behavioral ecologists. Obtaining a level of literacy in these mathematical and statistical tools (i.e., understanding their scopes and limitations) is therefore crucial in the training of animal behaviorists. Greater mathematical literacy in the methods used in animal behavior will help a new generation of researchers to integrate theory and empirical work, something in which the field has an uneven track record insofar.

In addition to mathematical literacy, training in computational biology should be considered an emerging core competency for integrative animal behaviorists. To handle efficiently large datasets that result from genomics projects, mass-array recordings, automated tracking, or video recordings, researchers will need to develop computational skills. Specifically, researchers should receive training in a scripting language that will facilitate the handling of these data, as well as in how to test and validate the results of all custom software. In addition, given the recent push toward the automated handling of tracking, physiology, and image data via machine learning techniques, training in this mode of quantitative thinking may be beneficial for researchers both implementing these methods as well as absorbing them via the primary literature. Finally, many researchers might benefit from expertise in programming microcontroller circuits on inexpensive open-source platforms (e.g., http://www.arduino.cc or http://www.raspberrypi.org) in order to manufacture custom-designed data loggers, tracking devices, or transmitters.

Some of this education will necessarily come through standard graduate training, relying on a curriculum that draws upon existing courses within home institutions, or through stand-alone courses

Table 2 Existing graduate courses and workshops.

Topics	Title	Location
Neuroscience	Neural Systems and Behavior http://www.mbl.edu/nsb/	MBL
	Neurobiology http://www.mbl.edu/education/summer-courses/neurobiology	MBL
	Computational Neuroscience http://www.mbl.edu/education/special-topics-courses/methods-in-computational-neuroscience	MBL
Genetics and Genomics	Big Data Short Courses and Summer School http://ccbb.biosci.utexas.edu	University of Texas at Austin
	The Genome Access Course http://meetings.cshl.edu/courses/2013/tgac13.shtml	CSHL
	Programming in Biology http://meetings.cshl.edu/courses/2014/c-info14.shtml	CSHL
	Computational and Comparative Genomics http://meetings.cshl.edu/courses/2014/c-ecg14.shtml	CSHL
	Advanced Sequencing Technologies and Applications http://meetings.cshl.edu/courses/2014/c-seqtec14.shtml	CSHL
	Next-Gen Sequence Analysis Workshop http://angus.readthedocs.org/en/2014/	Michigan State University
	Molecular Evolution Workshop http://www.mbl.edu/education/special-topics-courses/workshop-on-molecular-evolution	MBL
	Tutorial: Evolutionary Quantitative Genetics http://www.nimbios.org/tutorials/TT_eqg	NIMBioS
	Workshop in Applied Phylogenetics http://treethinkers.org	Bodega Bay
	Summer Institute in Statistical Genetics http://www.biostat.washington.edu/suminst/sisg/general	University of Washington
	Computational Macroevolution and Phylogenetic Comparative Methods http://cba.anu.edu.au/news-events/computational-macroevolution-and-phylogenetic-comparative-methods	Australian National University
Other	Analysis of Organismal Form http://www.flywings.org.uk/MorphoCourse http://www.nimbios.org/tutorials/TT_eqg	Manchester University
	Modeling Dynamics in Biology http://www.transmittingscience.org/courses/syst-bio/intro-system-bio	Barcelona
	Social Evolution http://biologie.cuso.ch/index.php?id=1128&clear_cache=1&tx_displaycontroller[table]=members&tx_displaycontroller[showUid]=1898	Switzerland

Note: This list of relevant courses is not meant to be comprehensive. MBL, Marine Biological Laboratory, Woods Hole; CSHL, Cold Springs Harbor Laboratory.

offered through various centers. Training in experimental techniques as well as computational and evolutionary analyses also exists in various summer courses and workshops (Table 2). Although many of these skills are currently offered at the identified courses, we can envision the creation of a new intensive, discovery-driven course, modeled after the iconic summer courses at the Marine Biological and Cold Spring Harbor Laboratories, and specifically designed for animal behavior researchers at a range of career stages. Such a course would help build a vibrant integrated animal behavior community and focus on the core competencies including experimental design, molecular, cellular, and organismal tools, in addition to quantitative statistical, theoretical, and bioinformatics tools. Thus, although we have identified many courses and funding opportunities in other fields that currently exist to fill the training void in integrative animal behavior, we conclude that the community would benefit from developing its own course for the integrative study of animal behavior.

The benefits of outreach and diversity

Another important topic that was raised during the discussion is the importance of educating public funding agencies and private foundations along with university administrators about both the value and necessity of interdisciplinary and collaborative research in animal behavior. Junior investigators in particular are eager to engage in these activities, but are confronted with a difficult funding climate as well as tenure expectations that often explicitly discourage collaborative work. The discussion also underscored the important role integrative animal behavior can play in diversifying science. In a diverse scientific work force, each researcher should be encouraged to bring their own perspectives and background to the fore, which can have particularly powerful impacts on behavioral studies. As a consequence, the animal behavior community should play

a much more active role in attracting members from underrepresented groups.

Conclusion

More than half a century after Tinbergen's seminal paper on the "four questions" in studies of animal behavior, progress is critically dependent on an integrative understanding of behavior. Clearly, an integrative understanding of animal behavior—and organismal biology more generally—will be essential for us to provide deeper insights into what drives behavior and how it comes about; to apply the study of behavior toward new biomedical and neurobiological discoveries; and to conserve biodiversity through knowledge of how animals adapt to global change and other anthropogenic stressors. Such an approach requires comprehensive analyses at a variety of levels of analysis, across levels of biological organization, in a diversity of taxonomic groups, and at a range of spatial and temporal scales (Rubenstein et al. 2014). The talks presented in the symposium, along with the papers in this issue, illustrate but a few examples of this integrative approach to studying animal behavior.

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