



SYMPOSIUM INTRODUCTION

Spatio-temporal Dynamics in Animal Communication: A Special Issue Arising from a Unique Workshop-Symposium Model

Kim L. Hoke^{*1}, Nicholai Hensley[†], Jessleen K. Kanwal[‡], Sara Wasserman[§] and Nathan I. Morehouse[¶]

^{*}Department of Biology, Colorado State University, Fort Collins, CO 80523, USA; [†]Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, USA; [‡]Division of Biology and Biological Engineering, California Institute of Technology, Pasadena, CA 91125, USA; [§]Neuroscience Department, Wellesley College, Wellesley, MA 02481, USA; [¶]Department of Biological Sciences, University of Cincinnati, Cincinnati, OH 45221, USA

¹E-mail: kim.hoke@colostate.edu

Synopsis Investigating how animals navigate space and time is key to understanding communication. Small differences in spatial positioning or timing can mean the difference between a message received and a missed connection. However, these spatio-temporal dynamics are often overlooked or are subject to simplifying assumptions in investigations of animal signaling. This special issue addresses this significant knowledge gap by integrating work from researchers with disciplinary backgrounds in neuroscience, cognitive ecology, sensory ecology, computer science, evolutionary biology, animal behavior, and philosophy. This introduction to the special issue outlines the novel questions and approaches that will advance our understanding of spatio-temporal dynamics of animal communication. We highlight papers that consider the evolution of spatio-temporal dynamics of behavior across sensory modalities and social contexts. We summarize contributions that address the neural and physiological mechanisms in senders and receivers that shape communication. We then turn to papers that introduce cutting edge technologies that will revolutionize our ability to track spatio-temporal dynamics of individuals during social encounters. The interdisciplinary collaborations that gave rise to these papers emerged in part from a novel workshop-symposium model, which we briefly summarize for those interested in fostering syntheses across disciplines.

An animal's position in space and time determines its ability to collect information about the world around it. These spatio-temporal concerns are of particular importance to animals engaged in communication with each other: The relative spatial positioning of sender and receiver over time can either facilitate or reduce information exchange. However, much remains unknown about how such spatio-temporal dynamics are coordinated by those involved. For example, do individuals differ in their ability to navigate space and time in ways that impact their success in communication and associated decision making? How do neural systems shape this aspect of animal communication, and what impact does physiology have on evolutionary trajectories? What new tools and analytical approaches can we adapt to better measure the spatio-temporal dynamics of animal communication across individuals and species? Answers to these deceptively simple questions

require integration of insights from a number of disparate fields, including neuroscience, cognitive ecology, biomechanics, sensory ecology, computer science, evolutionary biology, animal behavior, and philosophy. We describe here a new model for cross-disciplinary integration of experimental frameworks and concepts in animal communication. We paired a workshop and symposium hosted at consecutive annual meetings of the Society for Integrative and Comparative Biology (SICB) to draw together researchers from these different disciplines in discussions about new transdisciplinary paradigms for investigating spatio-temporal dynamics in animal communication. In this introduction to the special issue that resulted from our symposium, we outline the current state of the field, introduce the nine associated manuscripts that emerged from the symposium, and describe our unique workshop-symposium model.

Spatio-temporal dynamics during communication can have major impacts on signal efficacy and receiver responses. The relative spatial positioning and postures of sender and receiver can work to promote information exchange or hamper it (Hutton et al. 2015; Patricelli et al. 2016). One key reason for this is that sensory systems and the signals that stimulate them are often highly directional (Hutton et al. 2015; Echeverri et al. 2017). Take, for example, the courtship display of the male broad-tailed hummingbird, which combines a dramatic high-speed dive, a loud feather-generated auditory signal, and a stunning flash of his iridescent gorget (Hogan and Stoddard 2018). For maximum effect on a prospective female mate, the male must time and place these elements of his display perfectly, coordinated with millisecond and millimeter precision. If he does not align his gorget just right in relation to the sun and the female's perch, his magenta flash doesn't quite go off. Furthermore, the female must be looking directly at the male as he performs this courtship display. If he is in the corner of her eye, she may miss most of the show. Although (literally) flashy examples like the broad-tailed hummingbird are dramatic, such spatio-temporal challenges are not unique to visual communication or iridescent signals. To the contrary, space and time play a critical role in the coordination of communication across a wide range of sensory modalities, signal types, and animal species.

Inspired by these (often understudied) communicatory complexities, our symposium focused on novel questions and approaches that emerge from a closer look at the role of spatio-temporal dynamics in communication, aided in part by a new surge in technological and analytical tools that help link neural system function with behavioral outcomes. The result was a series of presentations and associated papers that traverse this broad topic, from novel solutions to technological challenges to theoretical explorations of the role that spatio-temporal dynamics might play in shaping the evolution of behavior. We provide brief descriptions of these exciting new perspectives below.

The first set of papers from the symposium focuses on conceptual frameworks that structure our understanding of how animal movements and positions in the landscape alter signaling strategies and receiver responses in the real world. Echeverri and colleagues advocate for deeper appreciation of how the geometric relationships between signaling partners shape communication systems across sensory modalities. They characterize the diverse ways that relative distances and orientations of senders and receivers alter signal amplitude, form and reception, and they discuss how these geometric considerations intersect with physical and social environments. Echeverri et al. (2021) illustrate

how incomplete consideration of signal-receiver geometry can obscure meaningful selective pressures on communication systems. Reichert and colleagues then offer an in-depth analysis of signaling within more complex social environments as they argue for the study of communication to move beyond a simple sender-receiver dyad. They highlight analytical approaches to characterize communication within complex social groups and further develop themes about the geometry of signaling in different sensory modalities that shape entire communication networks. Reichert et al. (2021) go on to propose a series of next steps to better characterize signal function across spatial scales and receivers and to determine how sensory processing mechanisms handle complex social environments. In considering recognition and discrimination tasks, as receivers must during communication, Sung, Harris, and colleagues tackle issues arising from the use of cognitive template metaphors, which imply the existence of certain neural entities that compute complex cognitive tasks but for which there is currently no clear evidence. They review approaches used in the search for cognitive templates across disciplines of modern behavioral biology and philosophy as well as the neuroscience literature. Sung and Harris et al. (2021) argue for replacing the metaphor of a cognitive template (and related metaphors such as mental maps) with a distributed systems conception, as this view better aligns with the insights emerging from current neuroscience research about how animals and their nervous systems engage in recognition and discrimination behaviors.

The second set of papers focuses on expanding our basic principles of sensory and motor neuroscience to better reflect the complex reality within which nervous systems operate during dynamic communication. Mongeau and colleagues consider how animals integrate multimodal cues when navigating across several scales of space and time. They describe the neural mechanisms underlying multimodal integration that lead to low-, mid-, and high-level implementation of motor behaviors. Mongeau et al. (2021) identify summation (such as gating) and sensory weighting mechanisms that facilitate multimodal integration across multiple spatio-temporal scales of locomotion, and likely contribute to multimodal communication. Barkan and colleagues then synthesize work on neuromodulation to consider how combinations of neuromodulators tailor animal signaling to the appropriate context. They summarize experiments that identify which neuromodulators act on circuits underlying motor patterning and synthesize work on neuromodulatory impacts on sensory processing. Barkan et al. (2021) propose that neuromodulators create an "internal state" by which social context influences the sensory-motor processing

that generates context-dependent behaviors. Internal state representations are further explored by Kanwal, Coddington, and colleagues, who propose shifting and broadening the focus of internal state representations in the brain to encompass the dynamic communication loops and signaling molecules that act between the body and brain. Kanwal and Coddington et al. (2021) integrate historical and modern perspectives from ethology, physiology, endocrinology, and neurobiology to outline body-to-brain communication pathways that represent internal states. Further, they discuss how internal state is comprised of modular sequences of neural and endocrine mechanisms across multiple timescales that work in synergy to inform behavioral modules necessary for animal communication.

The third set of papers highlights how advances in machine vision and machine learning, alongside the increasing availability of low-cost, high-speed, and high-resolution measurement instruments, are providing new paradigms for automated tracking of freely behaving animals. These, in turn, are allowing us to probe new questions regarding individual differences in the control of movement and communication. Symes and colleagues present an empirical application of machine learning to long-term acoustic recordings, a modality with distinct challenges in mapping signaling behavior in communication networks. Symes et al. (2021) use automatic sound detection of long-term recordings of calling behavior to link signal rate of different katydid species to acoustic features of the calls and to movement of signalers within the landscape. Through this new approach, they are able to characterize species-specific signaling strategies in which males of some species produce longer calls, calling more infrequently and moving to signal from more locations. In contrast, males of other species are more stationary and produce short, frequently repeated calls. Vidal and colleagues introduce new opportunities for machine learning algorithms that build on the strength of pose estimation software to automatically detect and measure postures through time. One challenge in using machine vision algorithms to spatially track communicating animals is that the software must accurately distinguish individuals. Vidal et al. (2021) summarize current approaches to classify individuals and link the computational challenges in individual recognition with similar challenges that the field of pose estimation has recently made great strides in solving. Straw tackles a related challenge, explaining the optical constraints that limit our ability to obtain detailed position, orientation, and pose information from freely moving animals. To overcome the tradeoff between resolution and field of view, and the problems of motion blur, new approaches are needed to allow movement of lenses or

cameras to achieve high resolution video of moving animals. Straw (2021) outlines the technological challenges and one potential solution for this rapidly advancing field.

In creating this symposium, we began with the principle that capturing the complex dynamics of communication requires transdisciplinary approaches. The papers arising from our symposium and collected here are a testament to the value of this commitment to inter- and trans-disciplinarity. Although challenging, integration across disciplines promises to open exciting new avenues of inquiry that should pay dividends across individual fields of study and beyond. Such integration is also timely, as answers to many of the questions related to spatio-temporal dynamics are emerging at the leading edge of each of these fields. With so many of these fields poised to tackle different facets of spatio-temporal dynamics in animal communication, interdisciplinary crosstalk seems essential to set the agenda for future work. It is exactly this opportunity that we hoped to capitalize on by organizing a workshop and symposium, hosted at consecutive annual meetings of SICB. We carefully considered the spatio-temporal dynamics of our own communication in the plan to initiate novel transdisciplinary paradigms for investigating spatio-temporal dynamics in animal communication. To promote interchange among disciplines, we opted for smaller, more frequent opportunities for communication among participants. We hosted a 6-h workshop at SICB 2020 that brought together a balanced group of faculty, postdocs, graduate students, and undergraduates to collaboratively outline the biggest challenges and opportunities in the field. The symposium organizers then adapted our original symposium schedule to accommodate new topics that emerged from the workshop, including the formation of four new working groups with 26 researchers of all career stages who contributed to manuscripts and symposium presentations that extended our original symposium plan. We established regular check-ins between the SICB 2020 workshop and SICB 2021 symposium. These efforts initiated meaningful dialog across disciplines and produced the thoughtful contributions published in this issue. The result, at least in part, is the collection of wide-ranging manuscripts in this issue. But what is not captured here are many of the ongoing discussions and collaborations stimulated by workshop and symposium participants. Thus, much of the value of our perspective and our efforts over these past two years has yet to be realized. We hope that the papers contained herein begin to point this exciting area of study in promising new directions as we work as a community to better understand the rich complexity that communicating animals all around us weave across space and time.

Funding

This work was supported by the [National Science Foundation](#) [grant IOS-2010768] for funding our workshop-symposium model.

Acknowledgments

We thank the Society for Integrative Biology (DAB, DCP, DIZ, DNNSB, and DEE) and National Science Foundation. Their support for student travel and food enabled participants from diverse career stages and backgrounds to spend an extra day at SICB for exchange of scientific ideas and networking. We would also like to thank MC Hammer and Paula Abdul for serving as inspiration during planning sessions.

References

- Barkan CL, Leininger EC, Zornik E. 2021. Everything in modulation: neuromodulators as keys to understanding communication dynamics. *Integr Comp Biol*, icab102, <https://doi.org/10.1093/icb/icab102>.
- Echeverri SA, Miller AE, Chen JZ, McQueen E, Plakke MS, Spicer ME, Hoke KL, Stoddard MC, Morehouse NI. 2021. How signaling geometry shapes the efficacy and evolution of animal communication systems. *Integr Comp Biol*, icab090, <https://doi.org/10.1093/icb/icab090>.
- Echeverri SA, Morehouse NI, Zurek DB. 2017. Control of signaling alignment during the dynamic courtship display of a jumping spider. *Behavioral Ecology* 28:1445–53.
- Hogan BG, Stoddard MC. 2018. Synchronization of speed, sound and iridescent color in a hummingbird aerial courtship dive. *Nat Commun* 9:5260.
- Hutton P, Seymoure BM, McGraw KJ, Ligon RA, Simpson RK. 2015. Dynamic color communication. *Current Opinion in Behavioral Sciences* 6:41–9.
- Kanwal JK, Coddington E, Frazer R, Limbania D, Turner G, Davila KJ, Givens MA, Williams V, Datta SR, Wasserman S. 2021. Internal state: dynamic, interconnected communication loops distributed across body, brain, and time. *Integr Comp Biol*, icab101, <https://doi.org/10.1093/icb/icab101>.
- Mongeau JM, Schweikert LE, Davis AL, Reichert MS, Kanwal JK. 2021. Multimodal integration across spatiotemporal scales to guide invertebrate locomotion. *Integr Comp Biol*, icab041, <https://doi.org/10.1093/icb/icab041>.
- Patricelli GL, Krakauer AH, Taff CC. 2016. Variable signals in a complex world: Shifting views of within-individual variability in sexual display traits. *Advances in the Study of Behavior* 48:319–86.
- Reichert MS, Enriquez MS, Carlson NV. 2021. New dimensions for animal communication networks: space and time. *Integr Comp Biol*, icab013, <https://doi.org/10.1093/icb/icab013>.
- Straw AD. 2021. Review of methods for animal videography using camera systems that automatically move to follow the animal. *Integr Comp Biol*, icab126, <https://doi.org/10.1093/icb/icab126>.
- Sung JY, Harris OK, Hensley NM, Chemero AP, Morehouse NI. 2021. Beyond cognitive templates: re-examining template metaphors used for animal recognition and navigation. *Integr Comp Biol*, icab040, <https://doi.org/10.1093/icb/icab040>.
- Symes LB, Robillard T, Martinson SJ, Dong J, Kernan CE, Miller CR, Ter Hofstede HM. 2021. Daily signaling rate and the duration of sound per signal are negatively related in Neotropical forest katydids. *Integr Comp Biol*, icab138, <https://doi.org/10.1093/icb/icab138>.
- Vidal M, Wolf N, Rosenberg B, Harris BP, Mathis A. 2021. Perspectives on individual animal identification from biology and computer vision. *Integr Comp Biol*, icab107, <https://doi.org/10.1093/icb/icab107>.