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SYMPOSIUM INTRODUCTION

Introduction to The Symposium: "The Role of Mechanosensation in Robust Locomotion"

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Synopsis Mechanosensory information is a critical component of organismal movement control systems. Understanding the role mechanosensation plays in modulating organismal behavior requires inherently multidisciplinary research programs that reach across biological scales. Recently, there have been rapid advances in discerning how mechanosensory mechanisms are integrated into neural control systems and the impact mechanosensory information has on behavior. Thus, the Symposium "The Role of Mechanosensation in Robust Locomotion" at the 2023 Annual Meeting of the Society for Integrative and Comparative Biology was convened to discuss these recent advances, compare and contrast different systems, share experimental advice, and inspire collaborative approaches to expand and synthesize knowledge. The diverse set of speakers presented on a variety of vertebrate, invertebrate, and robotic systems. Discussion at the symposium resulted in a series of manuscripts presented in this issue that address issues facing the broader field, mechanisms of mechanosensation, organismal function and biomechanics, and sensing in ecological and social contexts.

Many animals exhibit extraordinarily robust behaviors in the face of extreme external disturbances. This Symposium, "The Role of Mechanosensation in Robust Locomotion" at the 2023 Annual Meeting of the Society for Integrative and Comparative Biology (SICB) focused on how mechanosensors, in particular, enable consistent, and robust motor control. The 2023 SICB Meeting was an opportune time to bring together organismal scientists studying mechanosensation, as mechanosensory research has rapidly progressed in recent years, especially in the realm of neuroethology, with studies that consider mechanosensory mechanisms in the context of organism behavior.

Mechanosensors transduce mechanical information (like tissue deformation or ciliary bending) into electrochemical neural signals, and the term "mechanosensation" broadly refers to this physiological process at all levels of biological organization. For example, a Golgi tendon organ is a mechanosensor in terrestrial vertebrates found at the end of a sensory afferent nerve embedded in the myotendinous junction. Contraction of the muscle causes tension in the Golgi tendon organ, which then compresses mechanically sensitive ion channels in the sensory afferent, causing them to depolarize. Thus, the mechanical information of the muscle contraction is transduced into neural information by the Golgi tendon organ mechanosensor. This neural information is then integrated into a motor control feedback loop (Jami 1992; Milneuslic and Loeb 2006; Granatosky et al. 2020).

A variety of mechanosensing systems are known across organisms. The vestibular organs in vertebrates and the lateral line specifically in fishes assist with body positioning and orientation, as do a variety of proprioceptors (including the vertebrate Golgi tendon organ) across vertebrates and invertebrates (e.g., Tuthill and Wilson 2016; Tuthill and Azim 2018; Hale 2021). In terrestrial vertebrates, proprioception regulates gait mechanics (e.g., Maas et al. 2007; Gordon et al. 2020). Proprioceptors also contribute to locomotor

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robustness (reviewed in Santuz and Akay 2023). Proprioceptive motor control networks can also integrate information from enteroceptive mechanosensors (e.g., in *Caenorhabditis elegans*, Kreig et al. 2022). In addition to proprioceptive cells at the periphery, vertebrates have mechanosensing cells in the central nervous system that are involved in locomotion (e.g., Grillner et al. 1991; Bohm et al. 2016; Massarelli et al. 2017; Katz et al. 2021; Picton et al. 2021; Wu et al. 2021). Mechanosensation is also manifest in tactile-sensing systems critical for navigation and foraging, among other complex behaviors [summarized in Prescott et al. 2011]. For instance, tactile mechanosensing is critical for behaviors related to food acquisition (e.g., Catania 2012; Schneider et al. 2014; Amichai et al. 2023), reproduction (Yamanouchi et al. 2023), and grooming (Zhang et al. 2020; Ravbar et al. 2021).

The mechanism of mechanotransduction occurs through several types of mechanically activated ion channels (summarized in Kefauver et al. 2020). The channel(s) implicated in mechanotransduction varies across mechanosensory systems, and revealing this mechanism is an active area of research in many systems. Because mechanosensors modulate motor control and thus behavioral motions, the implications of mechanosensory abilities reach beyond the molecular-scale mechanisms all the way to the organism-level and even inter-organismal interactions. Indeed, a full understanding of the function of molecular-scale mechanisms requires studying the higher levels of biological organization, while the mechanisms of higher-scale phenomena require study of the molecular- and cellular-levels. Thus, a full understanding of mechanosensory control requires crossing biological scales, which can be accomplished through interdisciplinary training, collaboration, and through interactions among the scientific community in gatherings such as this symposium.

The speakers in this symposium (outlined below) exemplify this integrative organismal perspective on mechanosensory research, which was a major theme of the symposium. Other exciting, cutting-edge research areas in mechanosensation and organismal biology include building an understanding of how mechanosensation shapes and is shaped by organismal development (e.g., Sternberg et al. 2018; Williams and Ribera 2020; Agrawal and Tuthill 2022), the integration of mechanosensation in regenerating systems (e.g., Monroe et al. 2015; Hamlet et al. 2023b; Katz and Hamlet 2023, this issue), and how mechanosensory specializations have evolved (e.g., tuned to the biomechanics of organisms, Aiello et al. 2017).

Future advances in the field will be enabled by forming a cohesive and comparative understanding of how different mechanosensory organs and systems function across organisms. Thus, SICB 2023 was an excellent time to bring together researchers to compare and contrast their different systems (at cellular, organ, and organismal-levels); share experimental advice and methods; and inspire collaborative, cross-species approaches to understanding the role of mechanosensation in movement control systems. Goals for the Symposium included (1) encouraging a comparative approach to understanding how mechanosensors are incorporated in organismal control systems, including how robotic systems can help us learn biological principles and vice versa; and (2) developing an evolutionary approach to understanding the basic biology of mechanosensors, considering the potential for analogous (or homologous) sensor structure and function across taxa. By assembling researchers who study mechanosensation in different organisms and at different biological scales, and by encouraging a comparative approach to mechanosensory research, we hoped to enable breakthroughs in understanding the general principles of mechanosensory control of behavior.

The symposium

We assembled a diverse group of speakers who presented their research on a variety of mechanosensing mechanisms in both a main symposium session as well as in a complementary session. These presentations covered a wide range of topics, including proprioceptive and tactile sensing systems; sensors at the periphery and in the central nervous system; insect, vertebrate, and robotic models; and the integration of mechanosensation, biomechanics, and behavior.

The symposium began with presentations on how mechanosensory feedback is integrated into locomotor systems, including several examples. Brad Dickerson discussed how a common control system architecture from engineering control theory can be used to study sensory system dynamics and animal behavior (Dickerson et al. 2023; further reading: Dickerson et al. 2014; Dickerson et al. 2019; Dickerson 2020; and Dickerson et al. 2021). Kaushik Jayaram described how the study of distributed mechanosensors across animals can inform the design of bioinspired robots with distributed mechanosensory capabilities the improve locomotor function (Jayaram et al. 2023; further reading: Jayaram and Full 2016; Jayaram et al. 2018a and 2018b; Kabutz and Jayaram 2021; Hari Prasad and Jayaram 2022; McDonnell and Jayaram 2022).

The *Drosophila melanogaster* (fruit fly) model system has been recently used to reveal the complex mechanisms involved in mechanosensory locomotor control, facilitated by the availability of targeted genetic tools and very high-resolution anatomical data (e.g., Phelps et al. 2021). Several speakers discussed their cutting-edge research on mechanosensation in Drosophila. Chris Dallmann discussed how sensory information from fly proprioceptors—namely, from the proprioceptive femoral chordotonal organ—is modulated depending on behavioral context (Dallmann and Tuthill 2023; further reading: Dallmann et al. 2016, 2017, 2021). Sweta Agrawal continued the conversation on fly proprioceptors by presenting a reconstruction of the fly leg mechanosensory circuits (Agrawal et al. 2023; further reading: Agrawal et al. 2020; Chen et al. 2021). Julie Simpson revealed how neurons that sense debris shape grooming behaviors in flies and outlined current efforts to map and characterize these behavioral-modulating mechanosensory circuits (Simpson 2023; further reading: Hampel et al., 2011, 2015, 2017; Zhang et al. 2020; Ravbar et al. 2021; Guo et al. 2022; Mueller et al., 2021).

Mechanosensory neurons within the central nervous systems (as opposed to at the periphery) were another theme of the symposium. Claire Wyart discussed her extensive line of work on the mechanosensory (and chemosensory) cerebrospinal fluid-contacting neurons, which modulate spinal posture and locomotion (Wyart et al. 2023; further reading: Wyart et al. 2009; Bohm et al. 2016; Orts-del'Immagine and Wyart 2017; Sternberg et al. 2018; Cantaut-Belarif et al. 2020; Orts-del'Immagine et al. 2020; Wu et al. 2021). Katie Stanchak described current work on the avian lumbosacral organ, a putatively mechanosensory organ in the lower spinal cord of birds, including efforts to test a set of mechanistic functional hypotheses (Stanchak et al. 2023a, 2023b; Sta further reading: Stanchak et al. 2020 and 2022; Stanchak et al., 2023b, this issue). Hilary Katz characterized the mechanosensory Rohon-Beard neurons in the larval zebrafish, which sense at the periphery but have cell bodies within the spinal cord (Katz et al. 2021; Katz 2023). Dr. Katz then connected this sensory system to functional regeneration of spinal cord in lamprey (Katz et al. 2020; further reading: Katz and Hamlet 2023, this issue).

Christina Hamlet addressed injury recovery and regeneration from a neuromechanical perspective and presented a computational model of an anguilliform swimmer in fluid with proprioceptive feedback (Hamlet et al. 2023a; further reading: Hamlet et al. 2018; Hamlet et al. 2023b; Katz and Hamlet 2023, this issue). Eric Tytell then elaborated on this topic by comparing computational simulations with new experimental results of lamprey swimming in fluids of different viscosities (Tytell et al. 2023; further reading: Tytell et al. 2010; Tytell et al. 2011; Massarelli et al. 2017; Hamlet et al. 2018; Tytell et al. 2018; Hamlet et al. 2023b). Other speakers addressed mechanosensory systems for locomoting through a different fluid: air. Jasmin Wong presented new vibration analysis results to characterize the mechanical filtering properties of bird feathers (Wong et al., 2023). Brooke Quinn showed new experimental data demonstrating that the hair sensors on bat wings help regulate flight in turbulent conditions (Quinn et al. 2023; further reading: Amichai et al. 2023; Rummel et al. 2023).

The symposium extended beyond the biological level of the individual organism and explored how mechanosensation can influence animal ecology and sociality. Eve Schneider explained how the mechanosensitive bills of domesticated ducks help them distinguish food items (West et al. 2023; further reading: 2014; 2017; Schneider et al. 2019; West et al. 2022). Michael Smith then presented on the sensitivity of chameleons to vibrations and their ability to produce these tremors in the presence of other individuals (Denny et al. 2023; further reading: Huskey et al., 2020; Tegge et al. 2020; Denny et al. 2023a and 2023b, this issue).

Associated manuscripts

This issue of Integrative and Comparative Biology includes a series of papers stemming from the symposium session, including collaborative pieces among speakers that were inspired by the discussion during the Annual Meeting. The first piece is a collaborative perspective from several speakers that argues that mechanosensation is critical for robust locomotion and discusses how collaboration between experimental biologists and engineers can inform the implementation of mechanosensory feedback control systems in robotics (Dallmann et al., 2023, this issue). The second is another collaborative piece that focuses on advances in mathematical models of anguilliform locomotion and how these more complex models with integrated sensory feedback can support biological investigation (Katz and Hamlet 2023, this issue). Following that is an outline of hypotheses on how the avian lumbosacral organ might sense organismal movement, which provides a framework for further research on putative mechanosensory mechanisms of the LSO (Stanchak et al., 2023b, this issue). Finally is a set of experimental studies on how veiled chameleons communicate through biotremors (Denny et al. 2023a and 2023b, this issue). Collectively, these papers cover a wide range of topics in mechanosensation at different conceptual and biological scales: issues facing the broader field, cellular-level mechanisms of sensation, organismal function and biomechanics, and sensing in ecological and social contexts. Our hope is that these papers will inspire more integrative and interdisciplinary research on mechanosensation.

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Conflicts of interest

The authors have no conflicts of interest to declare.

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