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SYMPOSIUM INTRODUCTION

Sensory Feedback and Animal Locomotion: Perspectives from Biology and Biorobotics: An Introduction to the Symposium

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Synopsis The successful completion of many behaviors relies on sensory feedback. This symposium brought together researchers using novel techniques to study how different stimuli are encoded, how and where multimodal feedback is integrated, and how feedback modulates motor output in diverse modes of locomotion (aerial, aquatic, and terrestrial) in a diverse range of taxa (insects, fish, tetrapods), and in robots. Similar to biological organisms, robots can be equipped with integrated sensors and can rely on sensory feedback to adjust the output signal of a controller. Engineers often look to biology for inspiration on how animals have evolved solutions to problems similar to those experienced in robotic movement. Similarly, biologists too must proactively engage with engineers to apply computer and robotic models to test hypotheses and answer questions on the capacity and roles of sensory feedback in generating effective movement. Through a diverse group of researchers, including both biologists and engineers, the symposium attempted to catalyze new interdisciplinary collaborations and identify future research directions for the development of bioinspired sensory control systems, as well as the use of robots to test hypotheses in neuromechanics.

Introduction

The symposium Sensory Feedback and Animal Locomotion: Perspectives from Biology and Biorobotics (January 2018, Annual meeting for the Society for Integrative and Comparative Biology, SICB) sought to answer a question fundamental to both biology and robotics: how is sensory feedback used to modulate motor output? This question is particularly relevant in the context of locomotion, because, for most animals, locomotor capability is essential to survival. More generally, all organisms possess a means of mechanosensation (Kung 2005), and even sessile organisms as diverse as Venus flytraps, hydra, and adult mussels rely on body movements for their survival. Animal movement is often the result of the coordinated activation of specific suites of muscles. The neural commands for these patterns can be complex, and they are not a unidirectional cascade: they are further complicated by the need for, and integration of, rapid sensory feedback. This feedback helps control and modulate the three-dimensional movements that enable animals to successfully complete behaviors ranging from the closure of a mussel's bivalve shell, to the movement of a hydra's appendage, to the navigation of an unstable and unpredictable environment during locomotion (e.g., Sainburg et al. 1995; Sane et al. 2007; Mongeau et al. 2015; Williams and Hale 2015).

The successful completion of complex behaviors relies on a range of sensory modalities to acquire information and provide feedback from the external world, the animal's own movement in space, and the animal's physical interaction with the environment. Across a diversity of behaviors, multiple sensory pathways, including visual, chemical, thermal, and mechanical sensation, can be used in parallel to finely control the motor output driving a given movement (Sherman and Dickinson 2003; Raguso and Willis 2005; Taylor and Krapp 2007; van Breugel et al. 2015). The contribution of a single modality or the relative contribution of multiple modalities to produce a movement can vary across behaviors. The completion of the reach-and-grasp behavior in primates, for example, uses visual feedback while planning the movement and mechanosensory feedback to control and adjust the movement in space (Sober and Sabes 2005). Further, while the ability of a moth to track a moving flower during feeding occurs through multimodal feedback from both visual and mechanosensory pathways, each of these modalities is sufficient for successful flower tracking on its own (Roth et al. 2016). While some animals strongly rely on visual feedback during locomotion, environmental and behavioral conditions can limit its effectiveness. For example, in organisms that have lost vision, such as the Mexican cavefish (*Astyanax mexicanus*), or those that live in the deep sea where light cannot penetrate, other sensory modalities like mechanosensation and chemosensation must dominate (Soares and Niemiller 2013). Furthermore, during the performance of extremely rapid behaviors like wing movement during insect flight, visual processing speeds are too slow to provide within-cycle feedback (Theobald et al. 2010; Sponberg et al. 2015), and mechanosensation is necessary to maintain stability (Sherman and Dickinson 2003, 2004).

The locomotor appendages of animals, from insect wings to fish fins to tetrapod limbs, perform dual roles as sensors and propulsors, and mechanosensory feedback from appendages and/or the central body axis has been shown to be critical to an animal's motor performance. Mechanosensory feedback can modulate the motor output of a central pattern generator (CPG) (Grillner and Zangger 1984) to maintain normal movement in the event of an unexpected perturbation during rhythmic behaviors like walking and swimming (Grillner and Zangger 1984; Giuliani and Smith 1987; Sainburg et al. 1993). Following the removal of sensory feedback, CPG-driven movement occurs with atypical kinematics (Gettrup and Wilson 1964; Polit and Bizzi 1978, 1979; Pearson and Wolf 1987; Bosco and Poppele 2001; Williams and Hale 2015) and reduced accuracy and adaptability (Grillner 1975; Sanes et al. 1985; Nathan et al. 1986). Following such disruption, other sensory modalities, like vision, are needed to provide compensatory feedback about appendage movements (Sanes et al. 1985).

Across animals, we can observe large interspecific variations in environment (e.g., aquatic, terrestrial, aerial), the type and material properties of the appendages, the kinematics of appendages and their interactions with the environment, and the number and type of sensory modalities used to acquire sensory feedback from the environment. Even sensory organs that have evolved to encode similar mechanical stimuli can vary widely across taxa: for example, to sense fluid flow and self-movement, fishes and sharks utilize the mechanosensitive lateral line (Dijkgraaf 1963; Liao 2010), while many flying insects rely on antennae for similar purposes (Sane et al. 2007). Together, variations in environment and body mechanics, as well as the physiological and anatomical differences of sensory organs, suggest that processes of sensorimotor feedback and integration can also widely vary across animals. In other words, animals have evolved a diverse range of satisfactory mechanisms for gathering sensory feedback. Thus, comparative studies can be very useful in the development of engineered solutions for robotic movement, and robots can be very useful in determining the universal encoding features common across the diversity of sensors.

Robots are powerful tools for studying sensory feedback in animals. Similar to animals, the propulsors of robots are often outfitted with integrated sensors to collect feedback that can be used to adjust the output signal of the controller. Robots can thus be used to test hypotheses about locomotor feedback by implementing neural circuitry and processing algorithms in robotic controllers. For example, the use of robots allows biologists to systematically explore and identify the bounds of parameter space, or enable subtle behaviors or small movements to be amplified in order to test hypotheses on sensory feedback in animals (Eberle et al. 2015). Further, the physical interaction between a robot and a natural environment allows researchers to test hypotheses under the physical conditions experienced by biological organisms, an advantage over mathematical or computer models. The natural environment provides a realistic source of sensory noise and other complex conditions that may be simplified or nonexistent in simulations (Webb 2002). Ultimately, the use of robots could lead to more realistic models and representations of the neural circuitry, stimulus encoding, and processing that exists in animals.

The limitations of information processing and control systems in robots are often similar to the type of problems for which animals have evolved solutions. This allows circuitry and processing algorithms similar to those found in freely behaving animals to be implemented in robots (Webb and Scutt 2000). Single sensory modality robotic sensorimotor systems have been developed (Lund et al. 1998; Damper et al. 2000; Hoshino et al. 2000; Phelan et al. 2010). However, the processing time associated with some sensory modalities (i.e., vision) is often large relative to the duration of a propulsive cycle, and is limited in its effectiveness under certain conditions (Warzecha and Egelhaaf 2000). The next step in robotics is to not only model and incorporate visual feedback, but also combine this sense with other modalities (i.e., mechanosenation) to produce robots with multimodal sensory feedback (Chapman 2001). The study of sensorimotor integration in animals will be very useful for the successful and efficient implementation of multimodal sensory feedback in robots. Studies are already being conducted to determine how convergent sensory feedback pathways are weighted and how feedback from each sensory modality or source will modulate motor output independently and in combination with other senses (Hinterwirth and Daniel 2010; Roth et al. 2016). Yet, the most effective implantation of bioinspired circuitry, stimulus encoding, information processing, and sensorimotor integration will depend on large-scale and long-term collaborations between biologists and engineers. We believe that these collaborations should focus on the following questions: (1) how and where is multimodal sensory feedback integrated, (2) do different sensory modalities provide complementary feedback and what modalities are necessary, sufficient, or require complementary input to produce a given behavior, and (3) how can the number and distribution of sensors for a given modality in an animal inform the placement of sensors across the surface of a robot?

The symposium

The symposium was focused on addressing the questions above (among others) through presentations focused on novel techniques to study sensorimotor integration from the perspectives of both biology and engineering. The broad goals of the symposium were to (1) identify mechanisms of stability that rely solely on the passive mechanics of the musculoskeletal system of animals, (2) identify general principles of sensory feedback and their roles in animal locomotion, (3) identify how sensory feedback and locomotion can be studied from an engineering perspective, and (4) explore how sensory feedback can be incorporated into the development of sensors and control algorithms to be used in the design of bioinspired autonomous robotic vehicles. To reach these goals, the symposium included a broad range of speakers explaining how sensation is encoded, how and where multimodal feedback is integrated, and how feedback impacts the activity of other sensory modalities as well as motor output in diverse modes of locomotion (aerial, aquatic, and terrestrial) across a diverse range of taxa that include insects (Loveless and Webb 2018; Rauscher and Fox 2018; Sponberg 2018), lamprey (Tytell et al. 2018), fishes (Aiello et al. 2018; Haehnel-Taguchi et al. 2018), tetrapods (Cox et al. 2018; Daley 2018; Hartmann 2018; Quinn et al. 2018), and robots (Carryon et al. 2018; Haehnel-Taguchi et al. 2018; Loveless and Webb 2018). Further, stabilization mechanisms that rely solely on the musculoskeletal system (not neurally mediated) and can operate on very short time scales (Daley 2018; Tytell et al. 2018) were also highlighted.

The study of the animal stability mechanisms from both a biological and engineering perspective provides reciprocal insights into sensorimotor integration. Engineers often look to biology for inspiration on how animals have evolved solutions to problems similar to those experienced in robotic movement, and biologists too must proactively engage with engineers to apply computer and robotic models to help answer questions on the capacity of animal sensory systems as well as the role(s) different variables play in generating effective movement. We hope this symposium catalyzed new interactions between biologists, computer scientists, and engineers, stimulated productive discussions on the development of bioinspired sensory control systems and algorithms, and helped identify future directions for research collaborations.

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