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Editorial: Evolutionary Biomechanics of Sound Production and Reception

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Editorial on the Research Topic

Evolutionary Biomechanics of Sound Production and Reception

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INTRODUCTION

Animals are capable of producing and detecting a broad range of vibrations transmitted through air, fluids such as water, or solids. The production of vibrations for communication (i.e., signals) in the animal kingdom involves three successive steps: (1) the production of vibrations, (2) modifications of vibrations to target specific functions, and (3) the coupling of these vibrations to the medium in which vibrations propagate. Although all three steps represent a challenge, producing signals and coupling them to the medium is exceedingly difficult in an energetic sense (particularly signals transmitted through air), and is perhaps the main reason why only two large groups of animals have evolved airborne sound and vibratory communication: Arthropods and Vertebrates, and within these groups only some taxa are capable of producing airborne sound signals (Bradbury and Vehrencamp, 1998). In Arthropods, acoustic communication is limited to crustaceans, arachnids and insects (Dumortier, 1963), with airborne sound detection being most prominent in some insect orders (Yack, 2004), with some reports in the literature for airborne sound production and detection in crustaceans (Popper et al., 2001), and Arachnids (Shamble et al., 2016). The detection of vibrations in the medium involves three successive steps: (1) a detection system to capture the vibrations, (2) the coupling of vibrations to the organism, and (3) the processing of sensory stimuli. In vertebrates airborne sound production and hearing (airborne sound detection) is more noticeable, although some taxa have lost at least one of these two features (Goutte et al., 2017). Airborne sounds, and vibratory communication (also known as biotremology) play a critical role in the day-to-day routines and survival of many species, for example in social communication (including mating), territoriality, detecting predators and in the detection and orientation of prey capture including echolocation.

This special issue covers various topics of acoustic communication (sound production and hearing) in animals from invertebrates to mammals primarily focusing on airborne sound but including one article on substrate-borne vibrations in webs (Miller and Mortimer). Each of the articles in this issue examines the biomechanics of the various forms of mechanisms that animals use for airborne sound production and detection (mechano-sensation). Therefore, articles are not centred on one specific topic but instead cover a range of systems that highlight recent advancements in animal bioacoustics.

SOUND PRODUCTION IN ANIMALS

Animals produce vocal sounds when the acoustic vibrations originate in the respiratory system. But sound can also be produced mechanically by the interaction of body parts or by using external objects in the environment. Historically, most research has focused on vocal communication in animals, whereas other non-vocal sound mechanics (e.g., stridulation, percussion, tremulation) has attracted the attention of researchers and have advanced considerably in the last four decades.

Vocal sounds are restricted to vertebrate animals (Bradbury and Vehrencamp, 1998), although some insects use their respiratory system to eject air and produce sound (Drosopoulos and Claridge, 2005). Producing signals and coupling them to the medium is difficult, and there are physical and biomechanical constraints that shape both the production and detection of airborne sounds. Jakobsen et al., discuss the physical and physiological mechanisms that constrain the production, radiation and propagation of loud airborne sounds. Importantly, other factors can constrain the transmission of acoustic signals; Tanner and Bee demonstrate the critical role of ambient noise in affecting signal identity and hence sexual selection in frogs.

Non-vocal sounds are produced by many invertebrates and by some members of nearly all vertebrate classes and occur across a variety of behavioral contexts from signals that function to bring animals together (social signals e.g., mating signals) to those meant to keep them apart (asocial signals e.g., warning and aggression signals). A third type of signal is specific to animals that use echolocation ("auto-communication") and function to capture prey and navigate the environment. Non-vocal signals are generally poorly studied in vertebrates and their importance in some taxa needs greater exploration. In their opinion article, Verga and Ravignani, discuss the current and future study of non-vocal (percussive) signals in seals and the need for a holistic approach into the study of form and function in these signals. Similarly, there is a growing body of work on the drumming behavior of woodpeckers. Schuppe et al. synthesizes our current understanding of the evolutionary biomechanics of woodpecker drumming and highlight how the critical integration evolution, behavior, biomechanics and physiology is necessary to understand this signal. Invertebrates by contrast, have been extensively studied for non-vocal sound production. Even so, our understanding of sound production in well-studied models is incomplete. Jonsson et al. present the latest advancements in field crickets that explain how crickets synchronize wings vibrations to produce pure tone airborne sound signals.

Asocial signals can be used for a variety of functions including antipredatory and defensive signals. Low et al. present an overview of insect defensive signals and discuss their forms, function and evolutionary origins. More specifically moths have evolved sophisticated antipredatory behavior to counter detection by bat echolocation, including anti-bat sounds echolocation. This bat-moth story is one of the pillars of neuroethology (Conner and Corcoran, 2012), and in this special issue, O'Reilley et al. further this work by characterizing sound production in four microlepidopteran taxa which use wingbeat-powered ultrasound, and which may offer an anti-bat function.

SOUND RECEPTION IN ANIMALS

Mechanosensors activate and respond to stimuli representing different kinds of force such as touch, medium flow, airborne sound, substrate vibrations, and strain (see research article by Strauß et al.). According to Cocroft et al. (2014), biotremology and chemical signaling are the oldest forms of communication known, and both probably evolved from the original cell–cell mechanical and chemical interactions within early metazoans. Although biotremology and chemical signaling are some of the less well-known among all the sensory modes, the former has received more attention in the last decade. Miller and Mortimer present recent insights on how vibratory transmission constraints are mitigated to promote information transfer in spider webs.

Auditory airborne sensory organs are morphologically diverse across animals, with respect to their body location, accessory structures, and number of auditory units, but remarkably uniform in that most are innervated by specialized mechanosensory receptors. The evolution of hearing is a topic that is of interest to a broad audience, and there have been fascinating new insights over the past 30 years. Fossil evidence and modern comparative/evolutionary analyses have prompted a reinterpretation of the evolution of the middle ear bones, eardrum, and spaces around the inner ear (Köppl and Manley, 2014). In the same way, the basic units of hearing, the hair cells in tetrapods and the chordotonal organs of insects, share some common biophysical principles in spite of being separated by millions of years of evolution. These evolutionary insights have opened up an enormous amount of Research Topics in hearing, with plenty of new potential model organisms that should be considered. Warren and Nowotny, provide an important comparison between mammalian and insect ears, whilst Ketten et al. compare adaptations for echolocation in water vs. air. Both articles highlight the variety and shared specializations for hearing across insects and in terrestrial and aquatic mammals, from both evolutionary and biomechanical perspectives, including sound capturing, directional hearing, impedance conversion and frequency analysis. Further, directional hearing (assessing the location of different sound sources) is vital for many species to detect predators and prey and is especially challenging for small organisms such as insects. Mason revisits the sophisticated hyper-accurate ear of the small acoustic parasitoid fly *Ormia ochracea* and shows that they solve this problem using pure-time differences in neural responses to prey sound cues.

CONCLUSIONS

During the last 50 years, our understanding of sound production and sound reception has advanced considerably, and we now know much more on the biomechanics of sound production and hearing, as well as the evolutionary diversity (including shared adaptations) of the systems used by animals. This special issue brings together a cutting-edge collection of papers that broadly synthesizes key areas in evolutionary biomechanics and critically provide a number of key areas of future research.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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