



SYMPOSIUM INTRODUCTION

Endocrine Modulation of Sending and Receiving Signals in Context-Dependent Social Communication

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Synopsis Animal communication requires senders to transmit signals through the environment to conspecific receivers, which then leads to context-dependent behavioral decisions. Sending and receiving sensory information in social contexts, however, can be dramatically influenced by an individual’s internal state, particularly in species that cycle in and out of breeding or other physiological condition like nutritional state or social status. Modulatory substances like steroids, peptides, and biogenic amines can influence both the substrates used for sending social signals (e.g., motivation centers, sensorimotor pathways, and muscles) as well as the peripheral sensory organs and central neural circuitry involved in the reception of this information and subsequent execution of behavioral responses. This issue highlights research from neuroethologists on the topic of modulation of sending and receiving social signals and demonstrates that it can occur in both males and females, in different senses at both peripheral sensory organs and the brain, at different levels of biological organization, on different temporal scales, in various social contexts, and across many diverse vertebrate taxa. Modifying a signal produced by a sender or how that signal is perceived in a receiver provides flexibility in communication and has broad implications for influencing social decisions like mate choice, which ultimately affects reproductive fitness and species persistence. This phenomenon of modulators and internal physiological state impacting communication abilities is likely more widespread than currently realized and we hope this issue inspires others working on diverse systems to examine this topic from different perspectives. An integrative and comparative approach will advance discovery in this field and is needed to better understand how endocrine modulation contributes to sexual selection and the evolution of animal communication in general.

Introduction

Communication in social contexts such as courtship and territoriality is crucial for reproductive success and survival in many animals. However, sending and receiving sensory information in these contexts can be profoundly influenced by an individual’s reproductive and hormonal state, particularly, in species that cycle in and out of breeding or other physiological condition like nutritional state or social status (Fig. 1A). For example, reproductive state plasticity in hormones, modulatory chemicals, or their receptors can change the quality of a bird’s song, how well a mouse hears courtship sounds, how electrical signals in weakly electric fishes are sent and perceived,

and how well frog muscles can generate vocal and visual displays. Furthermore, females of a species may only show a positive response toward a signaling male when they have elevated hormone levels and are in reproductive or breeding condition (Gordon and Gerhardt 2009; Zeddies et al. 2010); if not, they ignore male signals, demonstrating important behavioral flexibility regulated by internal physiological state. Importantly, true communication involves some coupling between senders and receivers to be effective, requiring research in this area to examine the mechanisms of both sending and receiving the signals. How might endocrine signaling impact the production of signals in different

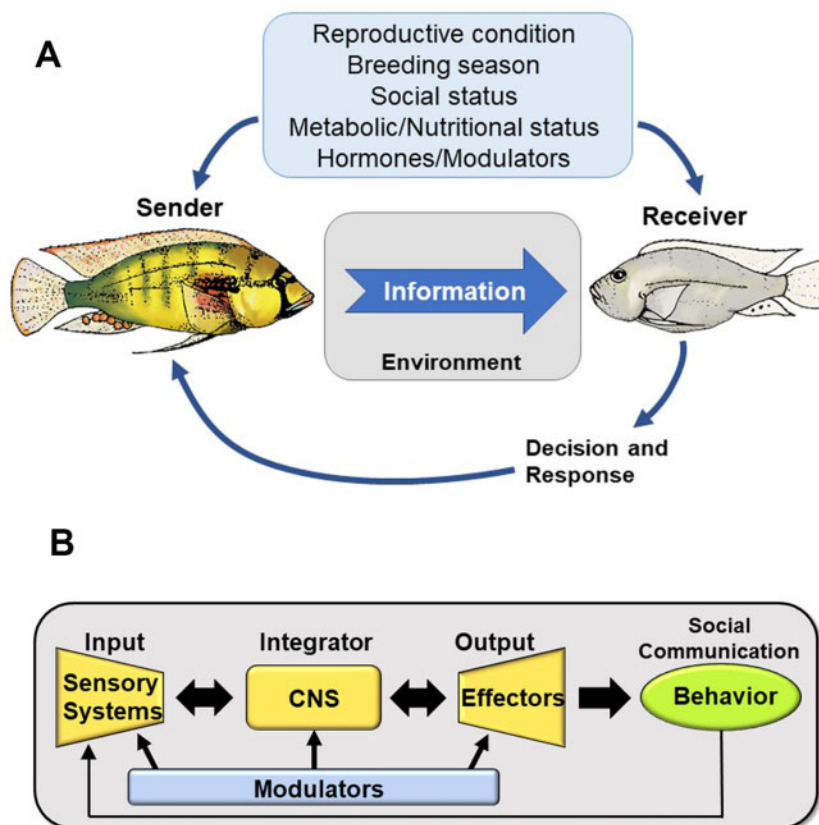


Fig. 1. (a) Animal communication involves information sent through the environment by a sender and then received and interpreted by a receiver, who then makes decisions about how to respond. Sending and receiving signals in social communication contexts can be influenced by many internal factors (shown in box) in both the sender and the receiver to change communication and resulting behaviors. (b) Context-dependent behaviors during social communication can be modeled as an input–output system in which different types of modulators can influence every level; the input or reception of signals (via peripheral sensory systems), their integration and decision-making processes (via the central nervous system, CNS), and the resulting output of adaptive behaviors (via effectors like sensorimotor systems and muscles). This arrangement adds flexibility to neural circuits so that different behavioral outcomes can result from the same neural circuitry or morphological substrates.

sensory channels of a sender, how does it influence reception and integration of sensory information in receivers, and how does this influence social communication and adaptive behaviors in general? Answers to these questions require insights from different fields and perspectives, including neuroscience, animal behavior, sensory biology, biomechanics, evolutionary biology, endocrinology, and others. Integration of knowledge and ideas from these disciplines promises to open exciting new avenues of discovery that we and future generations of scientists will reap rewards from now and for years to come.

This symposium and ICB issue broadly addresses the topic of hormone modulation of sensory function related to communication in a social context and is intentionally structured to take an integrative and comparative approach. The topic of endocrine impacts on sending and receiving signals is probably best investigated with a neuroethological approach

by examining communication with an emphasis on the mechanism, ontogeny, phylogeny, and adaptive significance of social interactions, as proposed by Tinbergen's four questions (Tinbergen 1963). We also use the term “endocrine” loosely in the context of this topic to include any modulatory substance (steroids, biogenic amines, peptides, etc.) released by any body tissue and acting at any body tissue (both local and distant). The symposium and resulting papers come from neuroethologists pushing the envelope of scientific inquiry using diverse animals that are well-suited to address specific research questions, as originally highlighted by Krogh's principle (i.e., for a large number of problems there will be some animal of choice, or a few such animals, on which it can be most conveniently studied) (Krogh 1929). One of our goals is to encourage others to consider this neuroethological approach, and to collaborate with neuroethologists to address how

animals interact in our changing world. In studying the molecular and cellular mechanisms of sensory plasticity, for example, it is important to interpret results in the context of the natural behavior and ecology of the animal. In other words, ask the question “what does this mean to the animal?” Taking this organismal and comparative approach will reveal how and why this signaling modulation exists and evolved and what impacts it has on fitness and survival.

Taking an integrative approach on the timely topic of modulation of sending and receiving signals

Because modulatory substances in the body can influence anatomical substrates necessary for production (e.g., sensorimotor, motor, and motivational systems) and reception (peripheral sensory organs and brain) of communication signals, it is imperative to examine how these substrates are modulated with an integrative perspective to truly understand the selective pressures driving animal communication. For example, seasonal or hormone-induced changes in vocal muscles or central pattern generators controlling vocalizations in the brain can change acoustic signals sent by male fishes, birds, and frogs (i.e., the sender) (Sassoon et al. 1987; Brantley et al. 1993; Bass and Remage-Healey 2008; Hall and Kelley 2020), and similar seasonal hormone-mediated changes in auditory processing influence perception and behavioral responses in female receivers in a reproductive context (Arch and Narins 2009; Sisneros 2009b; Remage-Healey et al. 2010). Unfortunately, many studies on animal communication and sensory processing at different biological levels do not consider potential modulatory influences. This symposium and ICB issue address this major knowledge gap through the integration of approaches from neuroscience, endocrinology, animal behavior, biomechanics, sensory ecology, and evolution.

How hormones might influence sensory processing, signal production, and communication, in general is also an extremely timely topic. There are increasing examples of hormones, modulators, and reproductive state having significant impacts on an individual’s signaling and sensory abilities (Hurley et al. 2002; Remage-Healey and Bass 2006; Sinnett and Markham 2015; Forlano et al. 2016; Leary and Crocker-Buta 2018; Vahaba and Remage-Healey 2018; Butler et al. 2019). Studies are revealing changes in the production of sending sensory signals as well as the reception of the communication signals by receptors and brain regions involved in decisions. For example, in the cichlid fish, *Astatotilapia burtoni*, vision

and auditory sensitivity improve in females that are gravid or ovulated and close to spawning, possibly allowing them to make better mate choice decisions based on visual-acoustic signals from males before their heavy investment in maternal care (Maruska et al. 2012; Butler et al. 2019). Studies in songbirds show that steroid hormones modulate song production and the motivation to sing in male senders, as well as the reception of songs in auditory processing regions of female receivers, and the development of song learning and communication (Remage-Healey 2012; Chao et al. 2015; Brenowitz and Remage-Healey 2016; Vahaba and Remage-Healey 2018). In the midshipman fish, production of male “hum” vocalizations during the breeding season is mediated in part by modulators acting at both vocal control regions in the brain and the muscles controlling sound production (Brantley et al. 1993; Goodson and Bass 2000; Bass 2007; Rosner et al. 2018), and seasonal hormone-mediated changes in the auditory periphery improve female hearing during this time to better detect vocalizations from males (Sisneros 2009a; Forlano et al. 2016). Historically, many of the initial examples of endocrine modulation of signal production or reception were discovered by studying the dominant communication channel of an animal within a specific behavioral context like reproduction (e.g., acoustic communication in birds, frogs, and some fishes). However, it has become increasingly clear that non-dominant senses within a species can also show similar endocrine-mediated plasticity, raising the question of how modulation of multimodal communication has contributed to the evolution of sender–receiver physiologies. For example, while many frogs show plasticity in their most obvious signaling modality, acoustic communication, there is also evidence for endocrine modulation of visual function (Leslie et al. 2019, 2021) and visual signaling (Smith et al. 2021). Furthermore, many cichlid fishes use vision as their dominant sense, which shows reproductive-state plasticity (Butler et al. 2019; Butler and Maruska 2021), but they also have similar plasticity in auditory and olfactory systems (Maruska and Butler 2021). Because this general phenomenon of hormone-sensory modulation occurs in both males and females, in different senses such as vision, olfaction, and audition, and across many diverse vertebrate taxa, it has broad implications for influencing social decisions including mate choice, which can ultimately affect reproductive fitness, species persistence, and biodiversity in a wide range of organisms.

Our goal for this symposium and ICB collection of papers was to encourage more researchers working on diverse taxa and different sensory systems to examine potential effects of endocrine modulation in their

experiments or study organisms to advance the field forward. Many studies examining sensory processing at cellular levels, for example, either do not report the sex or reproductive condition of the animals or will group animals of mixed conditions and sexes together in their analyses. Grouping individuals of mixed internal states can introduce large variance in datasets and lead to erroneous conclusions. Furthermore, documenting whether animals were fed or not before experiments can be important because there are many examples showing changes in the function of different sensory systems or signal producing mechanisms based on metabolic or energetic state (i.e., body condition) that are mediated by endocrine modulators (Mousley et al. 2006; Sinnett and Markham 2015; Nikonov et al. 2017). This constant bi-directional communication between the brain and body is therefore important for understanding how the function of different cells, tissues, and organs can impact the sending and receiving of social signals. By highlighting this topic here, we hope to make more scientists aware of this sensory plasticity. At a minimum, we hope to persuade researchers to document and report the sex and reproductive condition (or other physiological states like nutritional status, social experience) of animals used in all experiments, and to inspire others to investigate this understudied topic by *a priori* including sex and reproductive condition as factors in their analyses. Endocrine–sensory interactions are likely more common than we realize, but have not yet been examined in most systems, so the universality cannot currently be assessed or fully appreciated. The timeliness of this topic also nicely complements the recent push by biomedical researchers for the inclusion of females in scientific studies (Choleris et al. 2018; Shansky and Murphy 2021), particularly those in neuroscience, because mammalian models also show clear sex and reproductive-state differences in the brain and sensory processing (McEwen and Milner 2017; Balthazart et al. 2018). Collectively, we hope this assembly of papers will move the field of sensory biology forward by drawing attention to this topic and will allow researchers to address more interdisciplinary, comparative, and evolutionary questions related to sexual selection, speciation, signaling systems, and physiological mechanisms in the future.

Why is studying the modulation of social communication important?

There are several reasons why it is important to study and account for the modulation of social communication from sender and receiver perspectives. First, modulation allows for state-dependent

behaviors to occur in different contexts. In other words, modulation can add flexibility to existing neural circuits or whole organs, allowing different behavioral outcomes to occur from the same circuitry and morphology. This type of “biochemical switching” is especially important for modulation acting at rapid timescales, such as changing the relative firing of action potentials in neurons throughout the brain leading to changes in the valence of sensory inputs (Marder 2012). Although complex in reality, if we think of behaviors as a simplified input–output system with sensory systems as the inputs, the central nervous system as the integrator, and effectors like muscles as the outputs, modulators can influence every level of this system to modify the behavioral output in the context of social communication (Fig. 1B). This can dictate survival and reproductive success of individuals, ultimately controlling species persistence and biodiversity. Second, comparative studies on this subject are important because they can reveal both conserved mechanisms across species or sensory systems, as well as reveal unique adaptations that are species specific. This approach increases the possibility of also uncovering novel sensory abilities not previously described, which can also inspire technological developments with societal benefits (e.g., sonar in bats and marine mammals inspiring military sonar systems). Third, it is important for better understanding the evolution of communication systems in general, coevolution of senders and receivers, and the evolutionary selective pressures that contribute to speciation across diverse animal groups. While this collection of ICB papers is focused on vertebrates, there are examples of endocrine or internal-state modulation of sending and receiving signals in invertebrates that can also provide insights toward evolutionary mechanisms (Birmingham and Tauck 2003).

Examples of endocrine and reproductive-state modulation across taxa and sensory systems

Below we summarize some of the key themes, discoveries, and insights presented at the symposium and in this collection of papers and then briefly outline some important areas for future research. We separate the examples into two general topics: (1) how modulators influence signaling by the sender and (2) how modulators impact reception of sensory signals by the receiver. The research included here spans multiple sensory systems (vision, chemosensory, auditory, and electrosensory) and diverse vertebrate organisms (fishes, amphibians, reptiles, birds,

and mammals). Furthermore, examples include a focus on hormone effects at both peripheral organs (e.g., eye, ear, and olfactory organ) and central sensory processing areas, different classes of modulatory molecules (e.g., steroids, monoamines, neuropeptides, and prostaglandins), and at multiple levels of biological organization from molecular mechanisms to whole animal behavior. Inherent in many of these studies is a careful consideration of how an animal's internal physiology and hormonal state might influence sensory or signaling abilities at muscles, sensory organs, and the brain, and what the resulting modulation means to the natural ecology and behavior of the study animal. Thus, the insights gained from these neuroethological and neuroecological studies on sensory plasticity have the potential to fundamentally change how we think about the sensory function and animal communication in general.

How do modulators influence the sending of signals in different sensory channels?

The substrates for modulation of signal production can be in the central nervous system (brain and spinal cord) or in the muscles or other organs controlling signal displays. For example, [Smith et al. \(2021\)](#) demonstrate that visual signaling in Bornean rock frogs is modulated by androgens, and because androgen receptor levels are highest in the spinal cord and hind leg muscle of this species ([Mangiamele et al. 2016](#)), it is likely that both CNS and skeletal muscles may be critical sites for androgen influence on motor control necessary for visual signaling behaviors. These male frogs use multimodal displays (vocalizations and visual signals) for reproductive signaling and blocking androgen receptors with flutamide inhibited visual signaling behavior, including the conspicuous foot flagging display, but had no measurable response on vocal signaling or characteristics of the males' calls ([Smith et al. 2021](#)). This provides the first evidence for androgen control of visual signaling behavior in frogs and demonstrates divergent modulation on different signaling channels within a multimodal signaling species.

Can hormone modulation of signal production in a sender influence the responses in a receiver? [Leary et al. \(2021\)](#) provide evidence in the green treefrog that corticosterone (CORT)-mediated changes in male vocalizations influences their attractiveness to female receivers. Male–male agonistic calling in these frogs results in higher CORT levels in loser males, which is associated with reduced vocal effort and call quality ([Leary and Crocker-Buta 2018](#)). Using

playback experiments, [Leary et al. \(2021\)](#) show that females can discriminate between calling males with low vs high CORT levels based on differences in call rate and they show a preference for calls reflective of low CORT winner males. This demonstrates that hormone modulation in senders that impacts signal quality can also influence mate choice behaviors in receivers, with important implications for sexual selection.

Signaling to conspecifics can be energetically costly, so it makes sense that modulators involved in metabolism, appetite, and overall energetic state may also impact communication. For example, the peptide hormone leptin is primarily known for regulating energy balance and fat stores across vertebrates, but recent work shows that it also regulates communication signals in both weakly electric fish ([Sinnett and Markham 2015](#)) and singing mice ([Giglio and Phelps 2020](#)) by linking the energetic state with signal production. The fact that this modulation occurs in very different taxa (fishes and mammals) using different signaling modalities (electric organ discharge [EOD] and vocalizations) and by different mechanisms raises the possibility that leptin may play a broad role in regulating energetic communication costs. Markham and colleagues presented work on the role of leptin in EOD signaling in weakly electric fish and also provided a conceptual framework for predicting which vertebrate species may have leptinergic regulation of communication signals based on direct (metabolic signal investment) and indirect (predation and social conflict consequences of signaling) costs to the signaler. Using metabolic signaling molecules to help regulate the costs and benefits of signaling can help animals balance tradeoffs between energetics and social communication and deserves further widespread investigation.

Some modulators show wide distribution in the brain that is conserved across vertebrate taxa, suggesting multiple roles on signal production via both motivational and motor systems. For example, [Macedo-Lima and Remage-Healey \(2021\)](#) review the role of dopamine (DA) in influencing motor (and sensory) cortical circuits across vertebrates. The common existence of DA fibers and receptors in conserved cortical regions suggests that pallial DA effects are widespread among vertebrates. They provide evidence that DA-induced plasticity mechanisms exist across cortical systems and are associated with motor adaptations important for signaling behaviors such as vocal production in songbirds, as well as goal-directed, practice-dependent motor skill improvement in other taxa.

How do modulators influence the reception and processing of signals by different sensory systems at peripheral and central levels?

Chemosensory signaling is the oldest and most phylogenetically widespread communication system, and there are several examples of endocrine modulation of olfaction. Pheromone signaling in goldfish is perhaps one of the most complete described examples of true chemosensory communication in vertebrates (Stacey 2011; Ghosal and Sorensen 2016), but new discoveries continue to highlight how modulators are involved. Sorensen and Levesque (2021) describe one of the first examples of a pheromone released by males (androstenedione plus polar body metabolites) that has behavioral actions on females in a reproductive context. Importantly, they show that prostaglandin $\text{PGF2}\alpha$ (released at ovulation) in ovulated receptive females increases their responsiveness to sexually mature males, which is likely mediated by changes in the olfactory system (Sorensen and Levesque 2021). Thus, $\text{PGF2}\alpha$ in females, which changes with the reproductive cycle, specifically induces behavioral specificity to a male pheromone (Sorensen and Levesque 2021). In the cichlid fish, *A. burtoni*, there is also evidence for intra- and inter-specific chemosensory communication (Maruska and Fernald 2012; Field and Maruska 2017), and Maruska and Butler (2021) review the plasticity present in olfactory abilities associated with the reproductive, nutritional, and social state in this species. Lizards also use chemosensory communication in multiple social contexts, and Campos and Belkasim (2021) review the evidence for the nonapeptide arginine vasotocin (AVT) playing a role in modulating lizard chemical communication. Studies in the green anole, for example, show that AVT increases a male's interest in chemical information available during social interactions, and in several reptile species, there is AVT innervation to olfactory processing areas, and sex and reproductive state differences in AVT neuron populations. Despite the importance and broad taxonomic distribution of chemosensory communication in vertebrates, we know relatively little about endocrine modulation of olfaction outside of mammals (Johnston 1980; Ferkin et al. 2004; Coombes et al. 2018), and even less about the system of taste or other specialized chemosensory detectors (Martin et al. 2009).

Vision is a critical sense for communication in many vertebrates, but despite its importance, there is relatively little information on how modulators influence visual capabilities, particularly, at the level

of the eye. In the cichlid fish, *A. burtoni*, male courtship visual signals (behaviors and coloration) are important for female choice. Females also show improved vision at the time of ovulation that is associated with elevations in modulatory receptors in the eye, and $\text{PGF2}\alpha$ injections that induce ovulation further improve female visual sensitivity (measured by electroretinograms) in the wavelengths of male coloration (Butler et al. 2019; Maruska and Butler 2021). Butler and Maruska (2021) explore this retinal plasticity further by measuring opsin gene expression in the eye and demonstrate reproductive-state differences of specific wavelength opsins that is correlated with circulating steroid levels in females. These experiments in the cichlid collectively demonstrate reproductive-state plasticity and potential modulatory impacts in the eye at multiple levels (photoreceptors, cells of inner nuclear layer, ganglion cells). Electroretinogram studies in frogs also illustrate improved visual capabilities induced by treatment with human chorionic gonadotropin (hCG) hormone, which stimulates ovulation during the breeding season (Leslie et al. 2019). Leslie et al. (2021) further test the role of estrogen signaling in this visual plasticity of the eye and demonstrate that blocking estradiol synthesis with the aromatase inhibitor fadrozole abolishes the hCG-induced increase in visual sensitivity in females. This provides support for the role of estradiol in reproductive-state visual plasticity in the frog retina. These studies demonstrate endocrine modulation of the visual periphery in representative species where vision is the dominant (cichlid) and the non-dominant (frog) sense in the context of reproductive signaling.

Many species use sound production for communication in different social contexts, and of all the sensory systems present in vertebrates, the auditory system has the most well-described examples of endocrine modulation at both peripheral and central levels. Several papers in this issue add new information to this body of knowledge by addressing modulation of audition in fishes, frogs, birds, and mammals. In the midshipman fish, DA input to the inner ear is decreased in summer reproductive females, and because DA inhibits auditory sensitivity at the ear, this contributes to the improved hearing in breeding females as they attend to male hum vocalizations (Perelmuter et al. 2019). Perelmuter et al. (2021) now provide evidence that a pre-spawning increase in testosterone initiates this seasonal change in DA innervation to the ear, demonstrating steroid regulation of the DA-mediated peripheral auditory plasticity. The review by Macedo-Lima and Remage-Healey (2021)

highlighting the distribution of DA innervation to auditory (and visual and olfactory) cortical regions (and homologs) stresses the potential importance of this modulator in higher-order sensory processing across vertebrates. Male cichlids also produce sounds as part of their courtship displays, and gravid females close to spawning have lower hearing thresholds compared with non-reproductive females (Maruska et al. 2012). This improved auditory sensitivity is also correlated with circulating estradiol levels, and there is evidence that estradiol signaling and other modulators may be involved in this reproductive-state auditory plasticity at both peripheral and central levels in *A. burtoni* (Maruska and Butler 2021). Frogs and birds are well-known producers of vocal signals, many of which also cycle in and out of breeding condition. Gall et al. (2021) review the examples of plasticity in auditory processing with a focus on modulation at peripheral auditory structures. They highlight that several aspects of auditory information such as sensitivity, frequency selectivity, and temporal resolution may be modulated by steroid hormones that fluctuate on a seasonal basis to help animals determine the salience of signals in social contexts. Endocrine modulation of vocal–acoustic communication in different species has already provided many key discoveries, and continued work on these systems (e.g., midshipman, cichlids, frogs, and songbirds) and inclusion of others will reveal new information on the proximate and ultimate mechanisms of modulation and its importance.

One aspect of endocrine modulation of sending and receiving signals that are less well explored is how an individual's early life experiences or developmental and ontogenetic factors might influence their communication abilities later in life. Davis et al. explore this issue in mice, testing whether early life experience (social isolation or group housing) impacts the responses of neurons in the auditory inferior colliculus in individuals that had serotonin levels pharmacologically manipulated (Davis et al. 2021). Their work shows that serotonin plays a role in modulating the effects of early social experience in a central auditory processing region on a long-term time scale, suggesting that serotonin links social history with sensory processing. The notion that an individual's past experiences can influence how modulators control signal production and reception of sensory information in adult social contexts, at multiple levels of organization, and on different timescales adds an interesting and additional layer of complexity to studying this topic, with important biological and evolutionary implications.

Future questions and directions

We have only begun to appreciate the widespread existence and importance of endocrine modulation of context-dependent social communication from different perspectives. There is, however, a long history of changes in sensory perception and signaling with reproductive state or endocrine modulation in different animals. For example, reproductive state of rodents influences both scent-marking behaviors and olfactory perception (Johnston 1980; Ferkin et al. 2004), and reproductive condition and sex-steroids influence both calling behaviors and auditory reception in frogs (Kelley 1980; Miranda and Wilczynski 2009; Yang et al. 2018; Hall and Kelley 2020). While this reproductive plasticity occurs across diverse taxa, many questions still remain that are worthy of pursuit. For example, how conserved are the mechanisms mediating endocrine modulation of sending and receiving signals, and are there commonalities across systems that led to their evolution? Furthermore, how might endocrine modulation impact sending and receiving of *multimodal* signals sent simultaneously in different channels? Because many animals signal in multiple sensory channels either simultaneously or sequentially, do hormones modulate peripheral senses separately, or at their level of integration in the brain, or both? Many of the examples of endocrine modulation of sending and receiving signals also occur in courtship and reproductive contexts, but what about endocrine modulation in other contexts like aggression/territoriality, parental care, and other social communication behaviors? How do factors like past experience, body condition, or even body size impact modulation of communication? A comparative and integrative approach across different species and sensory modalities will shed light on many of these topics, as will experimental approaches designed to reveal the molecular, cellular, and circuit-level mechanisms involved.

How common is modulation at both peripheral and central levels for a given sense, and how is this information integrated to change behaviors? There are relatively few studies that examine modulation at both peripheral sensory organs and centrally in the brain for a given sense, behavioral context, and within a single species, but these studies will provide insight toward answering these questions. Furthermore, what are the relative effects of modulation on motivation circuits versus on the circuits responsible for the reception or processing of specific sensory stimuli? While there are accumulating examples of modulation of communication, for example by pharmacological manipulation of modulators,

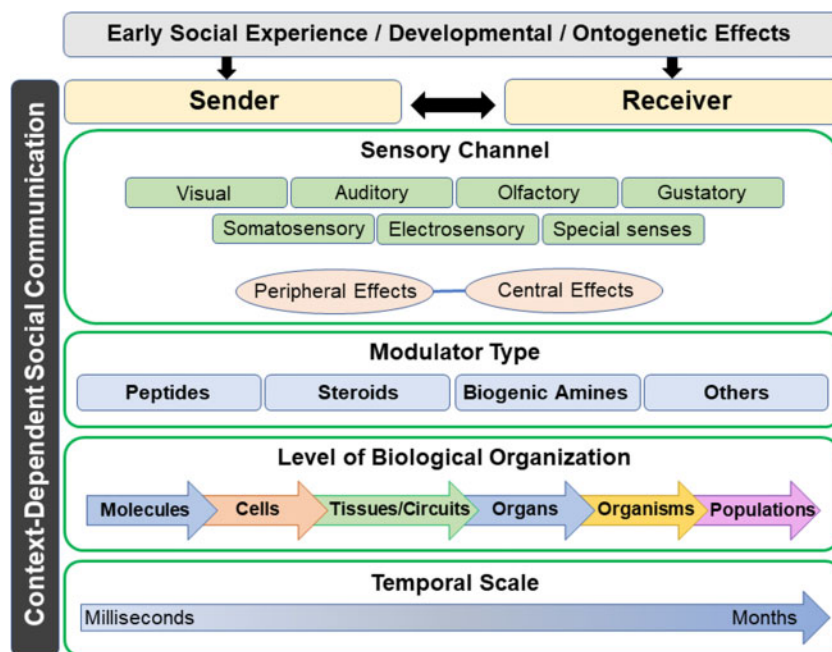


Fig. 2. Conceptual framework for examining endocrine modulation of context-dependent social communication. Plasticity in communication abilities can occur in both the sender and receiver and in multiple sensory channels at both peripheral sensory organs (or other peripheral tissue-like muscles in senders) and centrally in the brain. Early experience and developmental or ontogenetic factors can also influence social communication later in life, with effects on both the sender and receiver: Impacts on sending and receiving signals can be mediated by different types of modulators released from diverse tissues/organs, act at multiple levels of biological organization, and on rapid to long-term temporal scales.

there is still a gap in our understanding of exactly where the modulatory effects occur and what mechanisms are at play on different timescales. Furthermore, how is the endocrine modulation of sending and receiving signals related to an individual's reproductive fitness? Linking aspects of an individual's communication abilities with their fitness is often difficult but needs to be done to understand the ultimate impacts on species persistence and evolution. A related question is how might a changing environment impact endocrine modulation of sending and receiving signals? Endocrine disruptors, pollutants, and climate change may alter both hormone levels and communication abilities in different sensory channels (e.g., changes in transmissibility of signals through the environment). Studies in *Xenopus laevis*, for example, show that both estrogenic (e.g., the contraceptive compound 17α -ethinylestradiol, EE2) and androgenic (e.g., flutamide) endocrine-disrupting chemicals (EDCs) affect temporal and spectral parameters of male advertisement calls, leading to disruption of mating behaviors (Behrends et al. 2010) and reduced reproductive success (Hoffmann and Kloas 2012). What impact will these pollutants have on an organism's ability to adapt, survive, and communicate in these new conditions? While these are only a few of the remaining

questions, many others are presented throughout the collection of papers in this issue.

Conclusions

This collection of ICB papers that includes reviews and original research (and the references cited therein) will be an invaluable resource for students and researchers in many different fields. The modulatory effects of hormones on sensory processing and signaling ability are likely widespread across taxa, yet, relatively few research laboratories are currently studying the mechanisms involved. Figure 2 provides a conceptual framework for examining endocrine modulation of context-dependent social communication to highlight the complexity and many perspectives and levels at which we can approach and study this topic. While it is unrealistic for a single laboratory group to investigate all aspects of this framework, it further emphasizes the importance of collaborations across disciplines. The field overall will benefit from all studies focused on any of these areas and collectively will lead us to a better understanding of animal communication. The rapid advancement of new techniques (e.g., CRISPR/Cas9, optogenetics, functional genomics, and transcriptomics), that can be applied to addressing questions in

this framework in a wide variety of species will be particularly exciting moving forward. We hope this issue furthers scientific discovery on this topic by making it visible to the scientific community and encourages the existing and next generation of scientists to consider studying endocrine modulation and sensory plasticity in the context of social communication as part of their research programs.

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Conflict of interest

The authors have no known or potential conflicts of interest.

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