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# Modulation of sensory–motor integration as a general mechanism for context dependence of behavior

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ABSTRACT

Social communication is context-dependent, with both the production of signals and the responses of receivers tailored to each animal's internal needs and external environmental conditions. We propose that this context dependence arises because of neural modulation of the sensory–motor transformation that underlies the social behavior. Neural systems that are restricted to individual behaviors may be modulated at early stages of the sensory or motor pathways for optimal energy expenditure. However, when neural systems contribute to multiple important behaviors, we argue that the sensory–motor relay is the likely site of modulation. Plasticity in the sensory–motor relay enables subtle context dependence of the social behavior while preserving other functions of the sensory and motor systems. We review evidence that the robust responses of anurans to conspecific signals are dependent on reproductive state, sex, prior experience, and current context. A well-characterized midbrain sensory–motor relay establishes signal selectivity and gates locomotive responses to sound. The social decision-making network may modulate this auditory–motor transformation to confer context dependence of anuran reproductive responses to sound. We argue that similar modulation may be a general mechanism by which vertebrates prioritize their behaviors.



## 1. Introduction

Social communication at its simplest involves the production and reception of signals, but one of its most fascinating features is the variability and context dependence of social interactions. Signals and responses to those signals differ between sexes, among seasons, populations or species, and based on recent experience or developmental conditions. Researchers have relied upon these sources of variation in social communication to produce important insights into the neural bases of sensory processing and motor control. However, this variation also presents a challenge for the animals: communication is often only one task among many tasks that rely on the sensory or motor pathways that underlie these social behaviors. When animals adjust their behavior in a seasonal, sex- or species-typical, or experience-dependent manner, how do the neural mechanisms that regulate signal production or response change while preserving other critical functions of the same neural pathways, such as sensing approaching predators?

If social communication relies on separate channels dedicated to conspecific interactions, modifications that tailor communication behaviors to the animal's current priorities would have little or no effect on other behaviors. Such a parcellation is easy to envision for chemical senses, in which particular classes of odors may be relevant to a single behavior, or vocalization pathways, in which the muscles that generate sound may serve no other function. In contrast, neural pathways underlying communication may be multifunctional, which we define to mean that a single neuron may be engaged in multiple behavioral tasks, although its processing may be quite similar across tasks. The distributed nature of auditory and visual processing could produce a subset of neurons dedicated to a particular communication task; however, if multiple distinct behaviors rely on discrimination of similar signals, then we would expect the evolution of multifunctional neural systems in order to reduce redundant computations. In this latter case, behavioral differences based on sex, reproductive status, species, or social context require plasticity in the neural circuits underlying the social communication without unduly disrupting other important behaviors, such as feeding or avoiding predators (e.g. [44]). One hypothesis for how multifunctional neural systems overcome this challenge is that the sites of sensory–motor integration are particularly flexible loci for plasticity or evolution [50].

In this article, we review the system of acoustic communication in anurans to demonstrate variability in sensory–motor gating and to propose a general mechanism by which the modulation of sensory–motor gating may underlie context-dependent social behaviors in vertebrates. We propose that direct modulation of sensory or motor systems is likely to arise if dedicated sensory

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pathways exist, or if the sensory or motor systems do not contribute extensively to other essential tasks (Fig. 1a and b). In these situations, the animals could prevent behavioral responses to signals in inappropriate contexts by inhibiting the dedicated sensory or motor neural systems. Moreover, because active neurons consume more energy than resting neurons [5,55,56,79,80], the animals would save energy if they decreased neural activity throughout the relevant sensory or motor pathways by inhibiting early stages of those neural pathways. In contrast, we argue that context-dependent modulation of sensory–motor transformation is particularly likely to evolve in situations in which the sensory and motor systems are multifunctional (Fig. 1c). If a single sensory channel provides information necessary for other essential tasks, particularly predator detection and avoidance, then context-dependent shifts in the animal's sensitivity to the social communication signals would impair predator detection in some situations (as in [44]). We propose that, in this situation, modulation at the sensory–motor interface can resolve these tradeoffs to enable subtle tuning of social behavior to context while preserving other essential sensory–motor tasks.

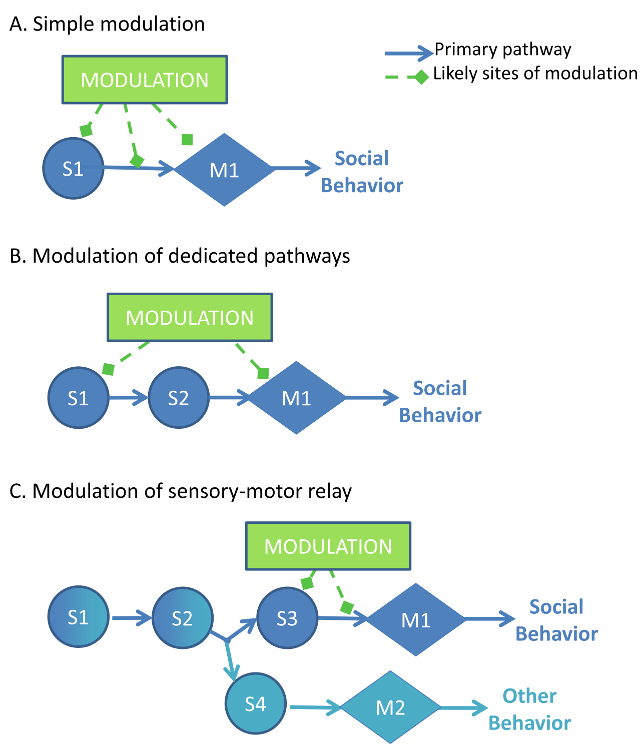


**Fig. 1.** Context dependence of stimulus-evoked behaviors arises from modulation of a sensory–motor transformation, whether the neural basis of the behavior is simple or complex. This modulation can include standard synaptic transmission from other sensory or integrative neurons that depolarize or hyperpolarize neurons, neuromodulatory inputs such as neuropeptides or monoamines, or hormonal modulation that modifies the activity of the simple circuit. (A) Even behaviors controlled by the simplest circuits involving one or a few sensory neurons (circle) contacting one or a few motor neurons (diamond) can be modulated by changing the responses of either the sensory neuron, the sensory–motor synapse, or the motor neuron to produce context dependence via the hormones or neuronal inputs that signal context (green rectangle). (B) If the important functions of sensory or motor paths are restricted to the focal behavior, then we predict that modulation will occur early in either the sensory or motor pathways. By reducing sensory or motor activity very early in the pathway during times in which the behavior is not necessary, the animal can eliminate unnecessary energetic costs of neural activity. (C) When sensory or motor neurons are involved in multiple behaviors important for survival or reproduction, modulation of the sensory–motor relay itself can enable appropriate context dependence of social behavior while preserving other essential functions. The context-dependent modulation can target either the specialized higher-order sensory neurons that trigger the motor output or the sensory–motor synapses. These examples are the focus of this paper. In vertebrate social communication, one neural system that is ideally situated to provide this contextual modulation is the social decision-making network.

## 2. Reproductive communication in anurans

Most frogs and toads rely heavily on acoustic communication for their reproductive behaviors, with male vocalizations mediating both male–male competition and female mate choice in a wide range of species. Anuran reproductive behaviors are amenable to investigation given the limited repertoire size and the robust behavioral responses of males (evoked calling) and females (phonotaxis) to playback in many focal species (reviewed in [41,77,90]). Moreover, the neural systems underlying acoustic social communication in anurans are well-studied (reviewed in [101,107]). Whereas much of the vocalization pathway is dedicated exclusively to acoustic communication, the auditory pathways underlying both male and female responses to sound likely contribute to acoustically-based predator avoidance [11,13], and the motor pathways that subserve phonotaxis should contribute to other locomotive tasks such as foraging. Thus, multifunctional neural systems likely underlie these acoustic social behaviors.

Moreover, both the intrasexual competition of males and the mate choice of females are highly variable. Not only are evolved genetic differences in calls and responses pervasive among populations and species, but the behavioral responses of individuals to conspecific signals are context-dependent. For example, sexes differ not only in the primary types of responses they display to conspecific signals (e.g. locomotive or vocal), but they also differ in the range of signals to which they respond [9–11]. Within an individual, reproductive behaviors vary depending on season, hormone levels, and reproductive state such that vocalizations of males and responsiveness of females are lower in the non-breeding season or when reproductive hormones are low (reviewed in [90,108,109]). Both sexes display extensive plasticity in their responses to signals based on acoustic social context (males: reviewed in [104]; females: examples include [1,7]), prior experience [8,15,21], and timing of visual cues [99]). Responses to social signals also depend on environmental features such as apparent predation risk [11,13], light levels [6,13,86], and ambient noise [93]. These many sources of variation in reproductive acoustic behaviors suggest that the sensory–motor systems underlying reproductive behaviors experience extensive modulation, despite the contributions of these same neural systems to other important behaviors affecting survival.

## 3. Neural bases of acoustic social responses

Responding to conspecific signals, whether via locomotive or evoked vocal responses, relies on auditory processing, auditory–motor integration, and motor systems. Recent reviews provide extensive information on anuran auditory and vocalization pathways [101,107]; we summarize the most relevant points here. Vertebrates share conserved hindbrain and midbrain auditory pathways, which are typified by the distributed processing of separate auditory streams within hierarchical processing stages. A series of brainstem nuclei respond to increasingly complex features of sounds, culminating in anurans in the torus semicircularis (torus), homolog of the inferior collicular in mammals. The laminar nucleus of the torus represents a major sensory–motor interface: it receives inputs from all earlier auditory stages and sends widespread projections to multimodal forebrain regions, to motor portions of the brainstem, as well as descending connections to other auditory regions. Auditory inputs from the laminar nucleus reach tegmental and hindbrain motor centers that regulate vocalization in males and general locomotion pattern generators that initiate