

From Perception to Action: The Role of Auditory Input in Shaping Vocal Communication and Social Behaviors in Birds

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Abstract

Acoustic communication signals are typically generated to influence the behavior of conspecific receivers. In songbirds, for instance, such cues are routinely used by males to influence the behavior of females and rival males. There is remarkable diversity in vocalizations across songbird species, and the mechanisms of vocal production have been studied extensively, yet there has been comparatively little emphasis on how the receiver perceives those signals and uses that information to direct subsequent actions. Here, we emphasize the receiver as an active participant in the communication process. The roles of sender and receiver can alternate between individuals, resulting in an emergent feedback loop that governs the behavior of both. We describe three lines of research that are beginning to reveal the neural

mechanisms that underlie the reciprocal exchange of information in communication. These lines of research focus on the perception of the repertoire of songbird vocalizations, evaluation of vocalizations in mate choice, and the coordination of duet singing.

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Introduction

Songbirds are specialists in vocal communication that have been intensively studied in relation to how an individual acquires and produces complex, learned songs [Catchpole and Slater, 2008]. At its core, however, vocal communication requires the exchange of information between at least two individuals – a sender and a receiver.

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The sender invests in the production of acoustic cues that are broadcast into the environment. The receiver and potentially other individuals detect and respond to those sounds [Searcy and Marler, 1981]. Conspecific receivers often respond by producing their own signals that may in turn influence the behavior of the original sender. In this way, information flows in both directions during bouts of communication, forming a dynamic loop in which participants exchange information and influence each other's behavior [Todt and Naguib, 2000; Benichov et al., 2016; Okobi et al., 2019].

This exchange of information is particularly challenging to study because it requires experimenters to collect data from each participant simultaneously while both are engaged in the process of communication. Decades of studies using songbirds have been remarkably productive, providing unprecedented insights into the neurophysiological mechanisms used in song imitation and production [reviewed in Mooney et al., 2008]. These studies, however, commonly ignore the contributions of receivers, which provide critical sensory feedback. In the same way that deafening a bird blocks autogenous auditory feedback that is necessary for song imitation [Konishi, 1965], removal of receivers blocks social feedback that is necessary for the full expression of communication behaviors. In the absence of a receiver, information exchange cannot occur. In that context, the dynamic loop between partners is broken, preventing researchers from understanding the behaviorally relevant mechanisms that underlie the full repertoire of behaviors used in vocal communication.

Exciting studies in songbirds have begun to uncover how communication signals are perceived by receivers and used to shape behavioral sequences. These studies not only refute the idea that nearby conspecifics are passive receivers of communication signals, but also begin to reveal the neural mechanisms that regulate the flow of information between individuals. Here, we describe 3 areas of research that focus on the roles of receivers in vocal communication in songbirds. First, recent experiments reveal the information conveyed by songbird vocalizations, and how this information is decoded by the nervous system. Second, studies of female mate choice have provided new insights into how sensory information can shape motor behavior. Finally, studies of duet singing in which females and males alternate song production show how vocal information is used in the moment-to-moment control of singing.

Perception of Information in Vocal Communication Signals

Male and female songbirds use vocalizations to convey information to conspecific receivers. This can include messages about the state of the sender or environmental conditions [Marler, 2004; Elie and Theunissen, 2019b] and information about who is producing the vocalization [Slabbekoorn and Smith, 2002; Vignal et al., 2004; Levretero et al., 2009; Ligout et al., 2016]. All these pieces of information are encoded in the acoustic features of vocalizations. The behavioral and neural challenge of receivers is to detect and interpret information contained in these acoustic signals in order to choose and produce an appropriate behavioral response. This step of acoustic information decoding is repeatedly occurring in each participant of a communication process as they alternate their role between receiver and emitter. The correct detection and interpretation of information is crucial for maintaining the dynamic loop between partners.

The behavioral responses of receivers can reveal the messages contained in each vocalization. For example, Zann [1996] identified the vocal repertoire of zebra finches (*Taeniopygia guttata*) by associating specific behaviors of both senders and receivers with the production or hearing of acoustically distinct vocalizations [Elie and Theunissen, 2016, 2019b]. The vocal repertoire of zebra finches includes a dozen categories that are used to communicate information about distinct social and environmental features. For instance, courtship song is used as an advertisement signal to attract a mate, whereas begging calls are used to signal hunger. Categories of vocalization constitute the vocabulary of a given species [Marler, 1956].

Besides the information on the state and needs of the sender, vocalizations also carry information about the identity of the sender. Behavioral tests of auditory discrimination in adult male and female zebra finches revealed that both sexes only need acoustic cues of vocalizations to discriminate individuals, irrespective of the category of vocalization that is produced [Elie and Theunissen, 2018]. By leveraging a database of thousands of zebra finch vocalizations that included the context of production and the identity of the signaler, Elie and Theunissen [2016, 2018] could characterize both the acoustic properties that distinguish categories of vocalizations and the acoustic parameters that distinguish different senders. Thus, within a zebra finch vocalization, there is sufficient acoustic information for the male and female receivers to perceive not only the category of vo-

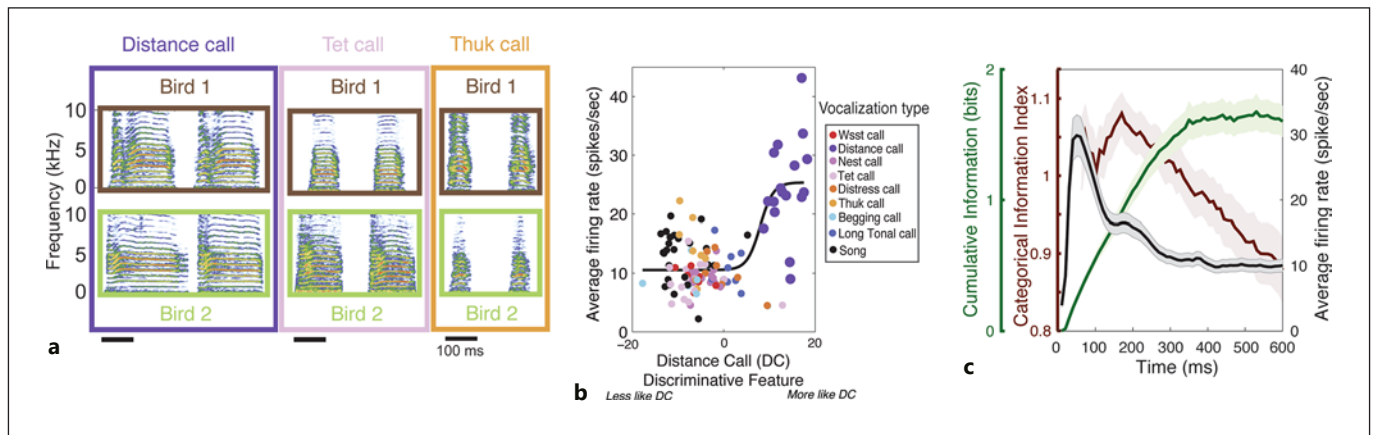


Fig. 1. Auditory forebrain neurons in zebra finches classify vocalizations into natural categories corresponding to the species repertoire. **a** Spectrograms of zebra finch vocalizations illustrating the variability within and across three categories of vocalizations (distance call [DC], tet call, and thuk call) performed by different birds [Elie and Theunissen, 2016, 2018]. **b** This auditory forebrain neuron responded categorically to DC versus other categories of vocalizations [Elie and Theunissen, 2015]. Each dot represents the average firing rate of this cell in response to each rendition that was presented, and those data are plotted against the spectrotemporal feature that was most effective in acoustic discrimination of DC

from all other categories of vocalization. Colors indicate different categories of vocalizations. These data are fit by a sigmoid function (black line), and the transition from low to high firing rate responses indicates the categorical nature of auditory processing in this cell. **c** The time-varying mean firing rate of forebrain neurons (black), cumulative information (green), and categorical information index (red) are shown following the onset of each vocalization (lines and shading indicate means \pm SE). During sound perception, neural information about the vocalization increases over time (green trace), while categorical responsiveness peaks between 100 and 200 ms (red trace) [Elie and Theunissen, 2019a, b].

calization, but also the identity of the sender (Fig. 1a). Interestingly, the sender's identity is communicated not by the individual "voice" that would result from the biophysics of the vocal tract but rather from the unique vocal gestures of senders (e.g., time-varying pitch) [Elie and Theunissen, 2018].

The population of neurons that mediate the categorization of vocalizations are found in the avian auditory cortex. Approximately half of the hundreds of auditory neurons sampled in Field L, caudolateral and caudomedial mesopallium (CLM and CMM), and caudomedial nidopallium (NCM) encoded information about the category of vocalization in the time-varying pattern of action potentials [Elie and Theunissen, 2015]. Some of these neurons had highly selective responses to only one category of vocalization. These neurons were also "invariant" to the acoustic differences found between birds in that category (Fig. 1b) [Elie and Theunissen, 2015]. In other words, acoustic variations within that same category of vocalization did not result in variations in the neural responses. Therefore, these neurons have "categorical responses": they are both selective for a specific category and invariant to the individual-specific acoustic differences within that category.

These categorical responses occur between 100 and 200 ms after the onset of the auditory stimulus [Elie and Theunissen, 2019a]. Specifically, measures of the invariance of neural responses within the categories of vocalization peak in this time period (categorical information, Fig. 1c). These data suggest that perceptual categorization regarding the type of vocalization may emerge within 200 ms. Nevertheless, neural information regarding all aspects of the vocalizations (e.g., the quality, identity of, and distance to the sender) continues to increase throughout the duration of the stimuli (Fig. 1c). Therefore, while perceptual categorization of a vocalization may emerge rather early during the processing of an auditory stimulus (within 200 ms), additional information such as the quality or identity of the sender may continue to emerge throughout the duration of vocalizations. These time latencies are on the same temporal scale as behavioral reaction times between pair-bonded zebra finches that are calling back to each other with distance calls [Ma et al., 2017]. Therefore, these patterns of neural information in the avian auditory cortex are likely the neural correlates of the detection and interpretation of the behavioral information encoded in the acoustic features of vocalizations.

These results reveal that populations of auditory fore-brain neurons categorize sounds into classes that correspond to the types of vocalization constituting the repertoire of a bird species. How this activity relates to the control of behavioral responses is poorly understood. However, one can speculate that categorical mechanisms could facilitate the choice of the correct behavioral response by associating the typical response classes to specific call categories (e.g., calling back to a perceived contact call). Other pieces of information decoded from the vocalization, such as the identity of the emitter, could then gate the response (e.g., if the calling bird is/is not the mate, authorize/block the typical response of calling back). Future experiments should examine how the perception of different categories of vocalization triggers the production of an adapted vocal response as participants alternate their roles in the closed-loop context of vocal communication. For example, zebra finch partners produce duets of soft calls around their nest, and there is a categorical difference in calling behavior depending on the bird's position outside or inside the nest [Elie et al., 2010]. Characterizing the dramatic shift in neural activity that must occur in these two contexts will provide insights into the mechanisms for both perception and vocal control.

Female Evaluation of Song Quality in Mate Choice

In many species of songbirds, males use their songs as an advertisement signal to attract and court potential mates. Female receivers are skilled in detecting features of song that indicate the singer's identity and the quality of that song as a courtship signal [Catchpole and Slater, 2008]. In behavioral tests of female song preferences, song is sufficient to evoke behavioral indicators of mate choice (e.g., calls and copulatory postures). In this way, females act as both receivers and senders of communication signals [Dunning et al., 2014; Nagle et al., 2002]. In Bengalese finches (*Lonchura striata*), females vary in the songs that they find most attractive, but individual females are consistent in their song preferences across time and tests [Dunning et al., 2014]. Despite differences in female preferences for specific songs, some songs are nevertheless more attractive than others [Dunning et al., 2014]. These data reveal that female preference for specific males is closely related to the properties of songs performed by those males, and some songs contain features that make them broadly attractive to females of the same species.

Comparative studies have revealed a range of features that make songs attractive to females. Females of different species prefer different features, but a theme that emerges across studies is that females prefer behaviors that are more challenging to produce. For example, females of many species agree that "more is better." They prefer songs of greater amplitude [Ritschard et al., 2010] and duration [Eens et al., 1991; Wasserman and Cigliano, 1991; Kempnaers et al., 1997], and they prefer males who sing greater numbers of songs per minute [Gottlander, 1987; Alatalo et al., 1990; Collins et al. 1994]. In other species, female preferences are more closely related to qualitative song features. Female canaries prefer specific note types called "sexy syllables" [Vallet and Kreutzer, 1995, 1998], and female swamp sparrows prefer songs that contain challenging combinations of notes with large frequency bandwidths that are trilled rapidly [Ballentine et al., 2004].

Although it appears that female preference is variable across species, a closer inspection reveals features of male songs that are valued by females across different species. Consistent with the idea that females prefer especially challenging combinations, female Bengalese finches prefer songs that contain large frequency bandwidths that are performed at rapid tempos [Dunning and Prather, pers. commun.]. Interestingly, the "sexy syllables" preferred by female canaries consist of two notes that collectively span a large frequency bandwidth and are produced rapidly. If those same notes are separated by greater amounts of time, such that they are trilled at a slower rate, those syllables become much less attractive to females [Vallet et al., 1997]. Therefore, it appears that females pay close attention to spectrotemporal features of male song as a means of evaluating its quality as a courtship signal. In response to hearing songs that they find attractive, females often perform specific behavioral indicators of their preference, and those female responses can influence subsequent behaviors of males [West and King, 1988; Coleman et al. 2004]. Thus, female song evaluation and the associated indicators of preference can create a dynamic feedback loop between male senders and female receivers of courtship signals. These findings emphasize the importance of the link between perception of song features and the initiation of courtship behaviors that lie at the heart of female mate choice.

Curiosity regarding the neural basis of decision making has led researchers to investigate what brain sites and pathways underlie female evaluation of song quality and expression of mate preference. A series of studies in which specific brain sites were inactivated in females reveal that

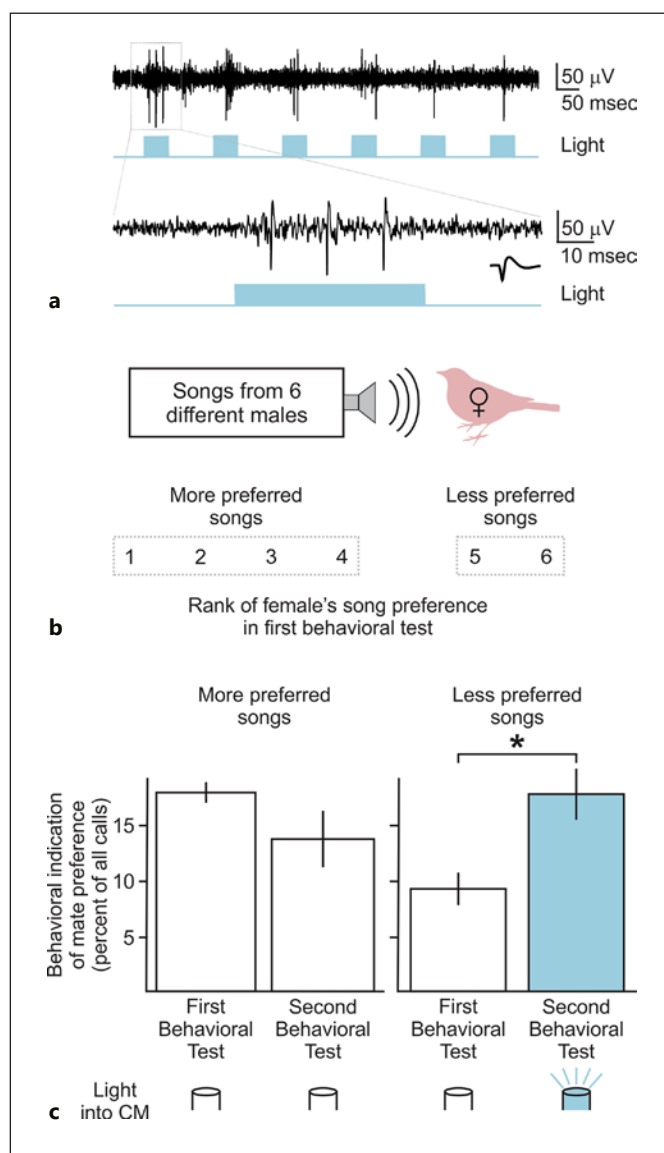
auditory cortical areas called CM (caudal mesopallium) and NC (caudal nidopallium) are critically involved in evaluation of song quality [reviewed in Murphy et al., 2019]. In studies of Bengalese finches, chemical lesions in CM and NC caused females to become less selective in their mate preferences [Lawley and Prather, pers. commun.]. That evidence of a link between activity in specific brain sites and the outcome of this decision making process led investigators to identify pathways through which auditory cortical areas might influence motor production of calls and copulatory displays.

Anatomical studies show that CM projects to the basal ganglia and cortex [Dunning et al., 2018]. These pathways may explain how CM can influence behavioral indicators of mate choice. For example, CM projects to the cortical area AIV (ventral portion of the intermediate arcopallium) [Mandelblat-Cerf et al., 2014; Dunning et al., 2018], which in turn projects to dopaminergic cells implicated in reward and behavioral motivation [Mandelblat-Cerf et al., 2014]. The disynaptic projection from CM to dopaminergic neurons in female birds could be the pathway through which activity in CM may influence song perception and motivation to engage in courtship behaviors. CM also projects to the vocal motor area RA (robust nucleus of the arcopallium) [Dunning et al., 2018], which in turn projects to vocal motor neurons in the brainstem [Fukushima and Aoki, 2000]. Activity in those motor neurons is both necessary and sufficient for female birds

to produce the calls that are elicited in association with mate choice and production of copulatory behaviors [Fukushima and Aoki, 2000].

Discovery of these pathways led to speculation that activity in CM may be related to the production of calls as a behavioral indicator of mate preference. To test that idea, researchers used viral gene transfer to induce CM neurons to express transmembrane proteins (channelrhodopsin) that result in activation of cells in response to light stimuli, a technique known as optogenetics. Experimenters flashed brief pulses of light to induce phasic activity in CM neurons (Fig. 2a) [Dunning and Prather, pers. commun] and found that experimentally induced changes in CM activity can alter the preferences of a fe-

Fig. 2. Changing the activity of CM neurons in female birds induces changes in song evaluation and mate choice. **a** Optogenetic induction of light-sensitive channels in CM neurons (AAV9.CMV.hChR2.mCherry.WPRE.SV40, Penn Vector Core) enabled those cells to be activated by light. Electrophysiological recordings from CM (first and third rows) revealed that cells were consistently activated by pulses of blue light delivered directly to CM via fiber optic (second and fourth rows; 420 nm light, trains of 50-ms pulses at 6.66 Hz [Dunning and Prather, pers. commun.]). **b** Behavioral tests revealed each female bird's song preferences among the songs of 6 different conspecific males (following the methods of Dunning et al. [2014]). **c** In the first set of behavioral tests of each female's song preference, individuals were consistent in their preferences for songs they found more attractive (first column) or less attractive (third column). In the second test of preference, females were statistically unchanged in their preference when no light was present in CM (second column). When light was present in CM, however, females expressed significantly greater preference for songs they previously found unattractive (shaded fourth column; $p = 0.009$; $n = 4$ birds; means and SEs in each column; percentages are computed from all calls produced in response to all stimuli; light did not evoke obligate calling, indicating that optogenetic stimulation was not activating call-generating networks directly).



male for specific songs. The least preferred songs of individual females were identified prior to light stimulation of CM neurons (Fig. 2b; following the methods of Dunning et al. [2014]), providing a context in which to test the role of light activation in CM during behavioral report of song preference. When the female's least preferred songs were played without light stimulation in CM, the number of calls produced in response to those songs was relatively low (Fig. 2c). However, when that same stimulus was paired with light activation in CM, the number of calls was significantly increased by 92% (asterisk in Fig. 2c). These data reveal that increases in CM activity are associated with increased production of behavioral indicators of mate choice. CM neurons have multiple targets in the brain, including the basal ganglia and cortical areas, each of which may have different roles in shaping song preferences and behavioral indicators of a choice. Together, these results suggest that CM is an important hub in a neural network underlying the evaluation of sensory signals and the production of motor responses in the context of reciprocal communication. This optogenetic approach can be optimized to reveal the unique contribution of each pathway to this complex perceptual problem.

Role of Sensory Feedback in the Synchrony of Vocal Duets

In some species of songbirds, individuals coordinate the timing of their own sound production with that of a partner to produce vocal duets [Hall, 2009]. Vocal duets are defined as overlapping bouts of sounds produced by both partners of a mated pair [Farabaugh, 1982]. Many hypotheses have been proposed to explain the possible function of avian duetting [reviewed in Hall, 2004], including the joint resource defense hypothesis and the pair maintenance hypothesis [Voigt et al., 2006]. For example, simulated territorial intrusions increase the frequency of duet song production, suggesting that duet songs may be used as a form of territorial defense [Wingfield and Lewis, 1993]. In monogamous sparrow weavers, pairs invest considerable time and energy in learning and refining their duet performance, suggesting that duetting may be related to preservation of the pair bond [Lewis, 1982; Voigt et al., 2006].

Duetting behaviors differ across species, ranging from alternating vocalizations to complete synchrony [reviewed in Hall, 2009]. It is generally assumed that each participant in a duet regulates its behavior in relation to the behavior of its partner, resulting in an emer-

gent closed-loop control system. To address the influence of cues produced by the partner in the coordination of duet performances, we describe duetting behavior and neural activity in two songbird species: one that is native to South America and another that is native to Africa.

Duet Singing in Plain-Tailed Wrens

Plain-tailed wrens (*Pheugopedius euophrys*) are found in dense Chusquea bamboo in cloud forest habitats in Ecuador and are specialists in duet singing. During duets, female and male wrens rapidly alternate the production of syllables to generate precisely timed duets that often sound as if a single bird is singing (Fig. 3a) [Mann et al., 2006; Fortune et al., 2011]. The coordination of duet singing is of particular interest for understanding the neural mechanisms by which cues from other individuals, known as heterogenous feedback, modulate behavior.

Each wren in a duet relies on sensory feedback from their partner to influence the features of its own vocal performance [Coleman and Fortune, 2018]. For example, the amplitude of syllables performed by the male can increase by more than 12 dB when he sings in a duet compared when he sings alone (Fig. 3a), but females do not change the amplitude of their vocalizations in a context-dependent manner [Fortune et al., 2011]. Furthermore, both male and female wrens adjust the timing of their vocalizations when delays of heterogenous acoustic cues are experimentally manipulated [Coleman and Fortune, 2018]. These findings demonstrate that heterogenous feedback, which defines the social context of singing, affects vocal motor output in both females and males, highlighting the value of studying each participant in the communication process and suggesting that males and females may have different strategies for maintaining their precisely coordinated behavior.

To understand how heterogenous cues may influence neurophysiological activity in the neural circuits that control singing, electrophysiological recordings were made from HVC, an area of the telencephalon that is necessary for song production [Nottebohm et al., 1976; McCasland, 1987]. HVC receives auditory input and is active during song production [reviewed in Mooney et al., 2008]. In anesthetized wrens, HVC neurons in both males and females respond to self-generated (autogenous) cues when those vocalizations are recorded and played back as sensory stimuli, but the nature of those auditory responses differs depending on social context [Fortune et al., 2011]. When autogenous cues are presented alone, as happens when the bird is singing by itself, HVC neurons

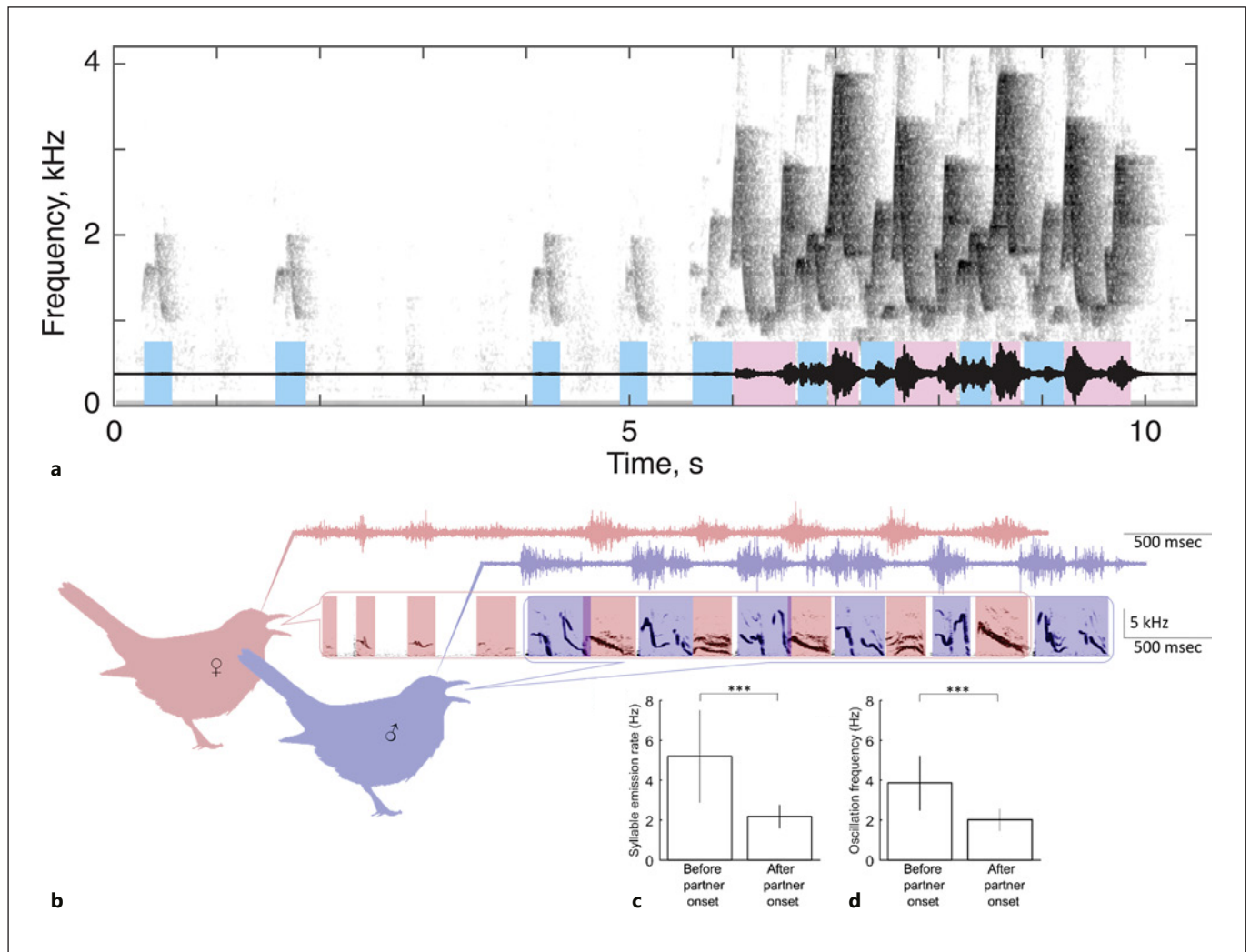


Fig. 3. Vocal performance is precisely coordinated between male and female singers in duetting species. **a** In this duet between a male and a female plain-tailed wren, the male sang low-amplitude solo syllables prior to the high-amplitude duet (spectrogram on top and oscillogram of voltage vs. time on bottom; male syllables = cyan bars; female syllables = magenta bars). **b** In this duet between a male and a female white-browed sparrow weaver, the female initiated the vocal performance as shown by the spectrogram of the combined male and female vocal activity (bottom

trace; male signals are shown in blue and female signals in red) [Hoffmann et al., 2019]. Simultaneously recorded traces of activity in male and female premotor nucleus HVC (top 2 traces) reveal that HVC activity in each participant is linked to the production of syllables [Hoffmann et al., 2019]. **c, d** Bar plots show the rate of syllable emission and the oscillation frequencies of multiunit neural activity in HVC before and after the partner joined the duet (means \pm SD; *** $p < 0.001$), respectively [Hoffmann et al., 2019].

in both males and females respond. However, when those same cues are presented along with corresponding heterogenous cues, as occurs during duet singing, neurons produce the strongest responses observed [Fortune et al., 2011]. Thus, in the context of the cooperative performance of duetting, both behavior and the corresponding neural activity are regulated by heterogenous cues performed by each partner in the duetting pair.

Duet Singing in White-Browed Sparrow Weavers

Male and female white-browed sparrow weavers (*Plocepasser mahali*) also produce tightly coordinated duet songs. This cooperatively breeding species of songbirds is native to eastern and southern Africa where it lives in mixed-sex groups. Individuals have repertoires of learned vocalizations comprising 40–90 different syllables [Collias and Collias, 1978; Lewis, 1982; Voigt et al., 2006]. As

in plain-tailed wrens, male and female sparrow weavers rapidly alternate their production of syllables to form their duets (Fig. 3b) [Hoffmann et al., 2019]. In most cases, males perform the first syllable and show less temporal variability in syllable production than females [Hoffmann et al., 2019]. Female sparrow weavers vocalize during the intervals between male syllables, but males sometimes start their next syllable before the female has completed her syllable, leading to overlap [Hoffmann et al., 2019]. These findings suggest that males establish the rhythm of the duet, with synchrony emerging as a result of females responding to male cues.

Despite this evidence, it is possible that each bird performs its own portion of the duet independent of ongoing signals from its partner. In this case, synchronization could emerge due to mutual responses to heterogeneous cues, but these performances would be vulnerable to disturbances. Alternatively, birds may modulate their singing on a syllable-by-syllable basis in response to heterogeneous cues. This strategy would lead to robust performance, but it would also be computationally demanding. Thus, it seems likely that duet control in songbirds may involve a blend of both of these strategies.

Sparrow weavers appear to use both mechanisms. The first vocalizations performed by the initiator of a sparrow weaver duet establish a rhythm and induce the other member of the pair to perform its vocalization (Fig. 3b), which demonstrates that each bird has an internal pattern for the production of vocal sequences. In turn, the response of the partner cues the original performer to modulate its rate of vocalization so that the pair engages in a coordinated vocal performance (Fig. 3b, c) [Hoffmann et al., 2019]. This indicates that the song rhythm generated by one member of a duetting pair can be adjusted to accommodate the patterning of the partner's vocalizations. This sensory-based tuning of motor performances seems to underlie the precisely coordinated behavior that defines duetting [Logue et al., 2008; Fortune et al., 2011; Templeton et al., 2013; Rivera-Cáceres, 2015].

As in the case of plain-tailed wrens, results of neurophysiological experiments in sparrow weavers point to the sensorimotor nucleus HVC as a site where the nervous system is blending external cues and internal patterns to establish the coordinated rhythm of duets. In awake, freely duetting sparrow weavers, the activity of neurons in HVC is exclusively motor and locked to each bird's own vocal production (Fig. 3b) [Hoffmann et al., 2019]. Neither the partner's vocalizations in actively duetting birds nor playback of duet songs in awake animals evoke auditory responses in HVC, indicating that activity of HVC

neurons does not directly encode auditory feedback [Hoffmann et al., 2019]. Although HVC neurons in this species do not produce action potentials in response to auditory stimuli, the motor-related activity of those cells is modulated in response to cues from the bird's partner. In HVC of the bird that initiates the duet, the onset of the partner's contribution induced a decrease in the rate at which bursts of multiunit activity are produced (Fig. 3c, d) [Hoffmann et al., 2019]. During the remainder of the duet, patterns of neural activity were synchronized, with the alternating roles of each member of the pair evident as a phase shift of 180° between the neuron activity in HVC of each participant (Fig. 3b) [Hoffmann et al., 2019].

Comparing the results in the two species of duetting birds is difficult. In the weaver birds, both participants are actively participating in the behavior, whereas HVC activity in the wrens was under anesthesia, changing the dynamics of the system. However, in both cases, HVC appears to play a critical role in the integration of auditory cues and vocal activity and thus the regulation of a closed-loop control system that spans two individuals and lies at the heart of coordinated duetting behavior.

Summary and Future Directions

Communication behaviors are typically produced with the intent of influencing the behavior of receivers, but communication is not a one-way street. In songbirds, the receiver is often not simply a passive recipient of communication signals, but rather an active participant that shapes the subsequent actions of the sender. This exchange of cues completes a feedback loop between individuals, and the mechanisms that underlie the control of communication are linked across participants. Understanding these linkages represents a significant scientific challenge requiring innovative approaches to divide the processes of communication into experimentally tractable components. This article describes a few of the approaches used by us and others to study the reciprocal transfer of information between participants.

Communication is dependent on complex social cues, providing an opportunity to investigate how the brain processes not only the acoustic signals used in communication but also the context in which those signals are produced. Context dependence is especially clear in the case of songbirds, as a male's songs are often accompanied by elaborate movements and intentional direction toward a specific female [Williams, 2001]. Such context dependence is also evident in the behaviors produced by other

species. In flies, for example, the patterning of acoustic songs performed by male senders varies across performances in a way that is closely related to ongoing visual experience [Coen and Murthy, 2016]. In these and many other forms of communication, the source of sensory feedback to the sender is often a response performed by the receiver. The results we have discussed here make it clear that it is imperative to study both participants if we are to understand the communication process. As new tools continue to become available to record the activity of neurons in not only one sender and one receiver, but also among groups of individuals as they are all interacting, new insights will continue to increase our understanding of how the brain enables the full spectrum of behaviors used in social communication.

In addition to the between-individual aspects of communication that we describe in this article, communication loops can also occur for single individuals. For example, echolocating animals, such as the oilbird (*Steatornis caripensis*), emit vocalizations for “self-communication.” They produce vocal signals and listen to the echoes of those signals reflected off of objects in their vicinity, and this auditory detection of spatial context in which they are vocalizing enables them to navigate in the absence of visual information [Brinklov et al., 2017]. During echolocation, it is the environment rather than a conspecific that conveys information about the sender’s context, and the sender modifies its subsequent signals based on that information. In both within-individual and between-individual behaviors, there is a critical role for context-dependent feedback. Together these results highlight the importance of studying feedback to reveal mechanisms for the control and coordination of complex behaviors.

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Statement of Ethics

The authors have no ethical conflicts to disclose.

Disclosure Statement

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Author Contributions

In studies of auditory perception of bird vocalizations, J.E.E. was involved in designing, conceiving, and performing the experiments, in analyzing and interpreting the data, and J.E.E. composed the text and figures. In studies of female song evaluation and mate choice, J.L.D. and J.F.P. designed the experiments, J.L.D. performed the experiments, and both analyzed the data and composed the text and figures. In the study of duetting in white-browed sparrow weavers, S.H. was involved in designing, conceiving, and performing the experiments, in analyzing and interpreting the data, and in composing the text and figures. In studies of duetting in wrens, E.S.F. and M.C. designed and performed the experiments, and both led the analysis and composition of text and figures.

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