The search for a neural basis of communication: Learning, memory, perception and performance of vocal signals

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Abstract

Brain mechanisms for communication must establish a correspondence between sensory perception and motor performance of individual signals. A class of neurons in the swamp sparrow forebrain is well suited for that task. Recordings from awake and freely behaving birds reveal that those cells express categorical auditory responses to changes in note duration, a learned feature of their songs, and the neural response boundary accurately predicts the perceptual boundary measured in field studies. Extremely precise auditory activity of those cells represents not only songs in the adult repertoire but also songs of others and tutor songs, including those imitated only very few times or perhaps not at all during development. Furthermore, recordings during singing reveal that these cells also express a temporally precise auditory-vocal correspondence, and limits on auditory responses to extremely challenging tutor songs may contribute to the emergence of a novel form of song syntax. Therefore, these forebrain neurons provide a mechanism through which sensory perception may influence motor performance to enable imitation. These cells constitute the projection from a premotor cortical-like area into the avian striatum (HVCX neurons), and data from humans implicate analogous or homologous areas in perception and performance of the sounds used in speech.

Introduction

Vocal communication is a primary mechanism through which humans share information between individuals and across generations. Because of that central role in our culture, the question of how the brain enables us to communicate has been the topic of much inquiry. Especially interesting in that regard is the fact that the signals we use in vocal communication are learned through experience (Doupe and Kuhl, 1999), and we encounter evidence of that experience-based learning in nearly every conversation that we have. Even a casual listener can easily detect the features of regional dialects, such as those from New England or the American South, and those dialectical features persist because they are learned anew and thus preserved by each generation. In the imitative process through which we acquire speech, the neural networks that underlie vocal communication must enable us to accomplish two fundamental tasks. First, we must perceive the signals performed by others. That cognitive ability is essential to acquire those signals when we are very young, and it is equally important later in life as we engage in interactive conversations. Second, we must learn to perform our own versions of the sounds we use in spoken communication. In that process, we rely on feedback-dependent trial and error to eventually develop high-quality imitations of the sounds we hear performed by others (Doupe and Kuhl, 1999). At the heart of that imitative process lies a linkage between perception and performance, and how the brain forges that link has been the topic of lively discussion (Iacoboni *et al.*, 1999; Rizzolatti

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et al., 2001; Iacoboni *et al.*, 2005). Here I will discuss recent results that shed new light on how that linkage may occur. Those data, collected using a songbird model of human speech, reveal a pathway through which the brain encodes perception of the songs performed by others and links that perception to a representation of the bird's own vocalizations (Prather *et al.*, 2008; Prather *et al.*, 2009).

In addition to reviewing the evidence for that possible basis of imitative learning, I will also discuss features of auditory processing in that pathway that may influence additional aspects of vocal communication, such as identifying individuals based on their vocalizations or shaping the syntax in which sounds are produced. Specifically, activity in those cells represents not only the sounds that compose the bird's vocal repertoire but also features of past auditory and vocal experience (Prather *et al.*, 2010). Through that neural representation of experience, auditory processing through those cells is thought to facilitate rapid and reliable perception of dialectical features and perhaps even individual identity based on the details of sounds produced by others. Additional data reveal that those cells are limited in their ability to encode the features of songs that approach or surpass species-typical performance limits, and it is thought that this limit may influence perception and the emergence of novel forms of vocal syntax (Prather *et al.*, 2012). The studies that revealed the characteristics of these cells, performed as part of a vibrant collaboration with Rich Mooney, Steve Nowicki, Susan Peters and Rindy Anderson, reveal the power of the songbird model to provide detailed insight into the relation between vocal communication and the structure and function of underlying neural circuitry.

Songbirds Are an Excellent Model for Understanding the Neural Basis of Vocal Communication

Several characteristics recommend songbirds as ideal subjects for understanding the neural basis of vocal communication. First, they are one of the few animals to communicate using learned vocalizations. The sounds used in speech are also learned vocalizations, but across species vocal learning is quite rare. Vocal learning is defined as the ability to modify vocal signals as a result of experience, most easily recognized as imitating the sounds that others produce (Jarvis, 2004). Songbirds learn their songs by imitating the songs they hear performed by others in a feedback-dependent process that is strikingly similar to how humans acquire speech (Doupe and Kuhl, 1999; Mooney *et al.*, 2008). Even though vocal learning appears to have evolved independently in birds and humans (Feenders *et al.*, 2008), the brain must overcome similar challenges in each case. Therefore, songbirds provide an excellent model in which to study the neural basis of how an organism learns to imitate the sounds used in vocal communication.

A second advantageous characteristic of songbirds is that they possess a network of brain sites that are dedicated to song learning, performance and perception (reviewed in Mooney *et al.*, 2008). That network, collectively known as the song system, is the anatomical basis through which the telencephalon exerts its control over vocalization, a connection that is a hallmark of birdsong and speech but is absent in the neural circuitry of most of other animal vocalizations (Kroodsma and Konishi, 1991; Wild, 2004). Within the song system, the nucleus HVC (abbreviation used as a proper noun) has been the focus of extensive research by us and others. HVC is the origin of two major pathways: a song motor pathway (SMP) that is essential for song production (Nottebohm *et al.*, 1976; Simpson and Vicario, 1990), and an anterior forebrain pathway (AFP) that has been implicated in song perception and plasticity (Scharff and Nottebohm, 1991; Olveczky *et al.*, 2005). The first step in the AFP is the projection from HVC to Area X, the avian homolog of the human striatum (Person *et al.*, 2008), and that HVC_X projection is the focus of the studies described here. The development of techniques to record from the song system in freely behaving birds has enabled us to sample HVC_X cells and other cells to explore the link between neural activity and the performance and perception of vocal signals.

Neural Representations of Signal Perception

To investigate the link between neural activity and song perception, we turned to swamp sparrows (*Melospiza georgiana*). Like humans, swamp sparrows perceive categorical differences between some of the sounds they use in vocal communication (Nelson and Marler, 1989). Armed with that knowledge and the insight that HVC_X cells have been implicated in song perception (Scharff *et al.*, 1998; Gentner *et al.*, 2000), we investigated whether categorical perception was evident in the activity of individual HVC_X cells. We found that individual HVC_X neurons express categorical auditory responses to songs containing notes of different durations, and the categorical boundary evident in the activity of individual neurons predicts the boundary evident in song perception (Prather *et al.*, 2009). It remains unknown whether activity related to perception emerges first in these cells, or whether they are reporting the emergence of such activity at presynaptic locations. Nonetheless, HVC_X cells are a locus where activity related to the perception of vocal signals is represented in the activity of individual neurons.

Important in light of a possible role for these cells in communication, HVC_X neurons are sensitive to detailed song features of both self-produced songs and songs produced by other individuals. Specifically, individual cells are sensitive to specific acoustic features, such as individual note transitions, and HVC_X cells respond to songs containing those features regardless of the identity of the singer (Prather *et al.*, 2008). Therefore, these cells provide a substrate for perception of the signals used in vocal communication. Additional studies also reveal a possible role for activity of HVC neurons (not identified as HVC_X but almost certainly including those cells) in additional complex features of song perception. For example, HVC cells in young birds are selective for the “tutor song” that served as the model for the bird’s own vocalizations (Volman, 1996; Nick and Konishi, 2005). Furthermore, our results reveal that HVC neurons may facilitate recognition of native dialects or perhaps even specific individuals. Specifically, HVC responses to songs heard or rehearsed only during juvenile development can persist in the adult, and responses to developmentally relevant songs are commonly as strong as or stronger than responses to anything in the adult repertoire (Prather *et al.*, 2010). Together, these results reveal that neurons in HVC, especially HVC_X cells, are active in association with complex, socially relevant features of song perception. A fascinating future direction will be to extend these studies of song perception beyond the male song system to include female songbirds. Females do not sing, but their skill in song perception is as good as or better than that of males (Brenowitz, 1991) and they use that perception to guide their selection of a mate from among many suitors. A few research groups have begun to discern the neural basis of female song perception (e.g., MacDougall-Shackleton *et al.*, 1998; Woolley and Doupe, 2008; Menardy *et al.*, 2012), and we look forward to future recordings of male and female birds as they are engaged in the performance and perception of signals in real-time communication.

Linking Perception to Vocal Performance

Our studies of swamp sparrows in the field and in the laboratory reveal that they countersing in response to song from another bird. That natural territorial behavior provides an excellent context in which to discover how the brain establishes a correspondence between song perception to motor representations of song. In the laboratory, we played birds their own songs through a speaker and recorded the activity associated with that sensory perception and the subsequent production of either that same song or another in the bird’s repertoire. Importantly, all of the HVC_X neurons that expressed categorical auditory responses were also active when the bird sang (Prather *et al.*, 2008; Prather *et al.*, 2009). Individual HVC_X neurons were selectively active in association with one song type in the bird's vocal repertoire, and the identity of that song varies across cells such that all elements of the repertoire are represented in the population. Consistent with a role in linking auditory perception and vocal motor performance, individual cells were active in association with a specific song both when it is heard and when it is sung (Prather *et al.*, 2008). Just as each cell was selectively active in response to specific songs, selectivity was also observed when the bird sang. Invariably, the song type represented in the auditory domain was also represented when the bird sang. Tests using transient distortion of auditory feedback indicated that this activity during singing was a motor-related signal as opposed to the bird simply hearing itself sing (Prather *et al.*, 2008). Therefore, individual HVC_X neurons in the swamp sparrow brain express precise representations of both auditory perception and song performance. Thus, HVC_X neurons may provide a mechanism through which sensory perception is linked to motor performance to enable imitation. Notably, we also found an identical sensorimotor correspondence in Bengalese finches (*Lonchura striata domestica*) (Prather *et al.*, 2008; Fujimoto *et al.*, 2011). Bengalese finches and swamp sparrows are of distant phylogenetic relation, and the presence of a precise sensorimotor correspondence in both species suggests that this link between sensory and motor activity is a fundamental feature of how the nervous system has overcome the challenge of vocal learning.

Constraints on Auditory Processing May Contribute to the Emergence of Novel Syntax

HVC neurons and their contributions to perception may shape not only real-time communication but also juvenile development and eventually the emergence of new forms of vocal syntax. In another study of swamp sparrows, we recorded the activity of HVC_X neurons in response to songs with artificially accelerated trill rates. Previous studies of swamp sparrows had revealed that they fail to accurately imitate songs with highly accelerated trills, instead singing brief and rapid trills interrupted by silent gaps (Podos, 1996). Because the portions of the song that were reproduced in those cases were imitated with accurate reproduction of phonological features, that gap-filled "broken syntax" was initially proposed to arise from vocal-motor limitations. We considered whether limitations in the processing of sensory signals could also contribute to broken syntax. In adult swamp sparrows that sang songs with normal syntax, HVC_X neurons exhibited precise responses to each song element (syllables in a trill) when they were presented at a natural rate, however those cells failed to response to each element when syllables were presented at an accelerated trill rate (Prather *et al.*, 2012). Gaps in the responses of HVC_X neurons became larger with increasing trill rate, and cells responded to only about half of all song elements at the trill rates where broken syntax emerges. This "flickering" auditory representation in animals that are not themselves performing broken syntax reveals a central constraint on the sensory processing of rapid trills. Because HVC_X neurons are also implicated in both song learning and perception, these sensory constraints may influence perception such that broken syntax may constitute accurate imitation of an inaccurately encoded song model. The impaired ability of HVC_X neurons to faithfully follow accelerated trills may point to a central constraint on the sensorimotor activity of these neurons that could further interfere with motor aspects of imitation. Considered together with the studies described in previous sections, these results suggest a mechanism by which the properties of HVC_X neurons may influence not only song perception and performance but also the evolution of vocal syntax.

Value of Avian Studies for Understanding the Neural Basis of Human Vocal Communication

Recent findings reveal important parallels between the processing of vocal communication signals in songbirds and mammals. Specifically, brain structures that participate in auditory processing and vocal performance in songbirds are analogous and in some cases homologous to corresponding mammalian brain structures. HVC is analogous to human premotor cortical areas, and the vocal motor pathway emerging from HVC projects to the avian analog of human vocal motor cortex (nucleus RA, robust nucleus of the arcopallium) (Reiner *et al.*, 2004; Wild, 2004). In an entirely separate pathway emerging from HVC (reviewed in Mooney *et al.*, 2008), the HVC_X neurons described here project into the avian homolog of human striatum (Area X) (Person *et al.*, 2008). HVC_X cells are the first step in a pathway that courses from premotor cortical cells (HVC), to the striatum (Area X), through a song-dedicated region of the thalamus, to additional forebrain premotor cortical areas, and finally to the vocal motor cortex (nucleus RA). Thus, HVC_X cells are part of a cortico-striatal-thalamo-cortical loop that is dedicated to the learning, performance and perception of the signals that songbirds use in vocal communication. Such loops are also a prominent feature of the human brain (Seger, 2009), and injuries to premotor cortical sites or striatal sites have been implicated in disordered speech, especially in disordered sequencing of speech such as that which occurs in stuttering (Fox *et al.*, 1996; Alm, 2004). Those data point to cortico-striatal projections as important contributors to the sequencing of the individual sounds that compose speech, however the complexity of information encoded in that activity of human cortico-striatal-thalamo-cortical loops makes it extremely challenging to discern how activity at a specific site is related to specific facets of vocal behavior. In contrast to that complexity, the loop that originates from HVC_X cells is dedicated to vocal behavior. This dedicated behavioral context and the parallels between human and avian brain structures provides a tractable opportunity to discover how activity at specific sites is related to specific facets of vocal communication. In support of that idea, studies of one species of songbird (Bengalese finches) have revealed that HVC_X activity is a neural correlate of the sequence in which notes are produced to compose song (Fujimoto *et al.*, 2011), and lesions in the striatum immediately downstream of HVC_X cells induces repetition of individual song notes (Kobayashi *et al.*, 2001). Therefore, songbirds hold the promise of revealing the circuits and cellular mechanisms that underlie vocal sequencing, guiding the development of targeted therapies for disordered speech. These findings and others support our hope that results obtained in songbirds will yield mechanistic insight to guide understanding of the neural basis of human vocal communication.

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