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Why Search for Mirror Neurons in Songbirds?

Imitation is an essential engine for propagating human culture, enabling people to transmit art, music, speech, and language from one generation to the next. The young child's ability to vocally imitate the speech of parents and peers is arguably one of the most essential forms of learning for human societies, because it provides the foundation for spoken language (Locke, 1993). The sensorimotor interactions that underlie human speech learning and communication remain poorly understood. An emerging idea is that sensorimotor neurons selectively active during both the execution and observation of specific gestures (i.e., mirror neurons) could play an important role in the learning, perception, and production of speech and language (Iacoboni et al., 2005; Kohler et al., 2002; Rizzolatti, 2005; Rizzolatti & Arbib, 1999, 1998; Rizzolatti & Craighero, 2004). Explicitly testing this idea is impractical, and consequently whether mirror neurons are important to human speech and language remains a matter of substantial debate. In this context, an important goal is to develop a suitable animal model in which to search for auditory-vocal mirror neurons and explore how they function to enable learned vocal communication.

Songbirds afford two great advantages in attaining this goal. First, they are one of the few nonhuman animals to communicate using learned vocalizations. Indeed, despite the fundamental importance of speech learning to human societies, and the widespread use of vocal communication by other animals, vocal learning in nonhuman species is quite rare. Importantly, studies in nonhuman primates have failed to uncover evidence of vocal learning. Oscine songbirds (order: Passeriformes) culturally transmit their courtship songs from one generation to the next, providing an experimentally tractable system in which to study mechanisms of vocal imitation and learned vocal communication (Doupe & Kuhl, 1999; Marler, 1970; Marler & Tamura, 1964). Moreover, both songbirds and humans learn to produce a complex and temporally precise sequence of vocal gestures using auditory signals originating from tonotopically organized hair cells of the inner ear. Therefore, even though

vocal learning in birds and humans evolved independently, the brains of juvenile songbirds and humans must accomplish highly similar and challenging sensorimotor transformations. The second great advantage of using songbirds to search for auditory-vocal mirror neurons is that the neuronal circuitry for singing and song learning, known as the song system, is well described and amenable to cellular- and synaptic-level analysis (Dutar, Vu, & Perkel, 1998; Farries & Perkel, 2000; Mooney, 2000, 1992; Mooney & Prather, 2005; Nottebohm, Kelley, & Paton, 1982; Nottebohm, Stokes, & Leonard, 1976). Importantly, the advent of miniaturized recording technologies has enabled experimentalists to analyze the behavior of anatomically identified song system neurons in singing and listening birds (Fee & Leonardo, 2001; Hahnloser, Kozhevnikov, & Fee, 2002; Leonardo & Fee, 2005; Yu & Margoliash, 1996). These features render the songbird an exceptional organism in which to search for auditory-vocal mirror neurons, to explore their involvement in learned vocal communication, and to analyze the synaptic and circuit mechanisms that give rise to their complex sensorimotor properties.

Such an undertaking can be informed by the realization that mirror neurons for learned vocal communication are predicted to display three key features. First, individual mirror neurons should display a systematic auditory-vocal correspondence. Second, their auditory properties should be tightly linked to vocal perception. Third, they should be strategically located to influence learned vocal communication. Following a brief introduction to song learning and the song system, this chapter discusses recent advances that identify song system neurons displaying all three of these features. Consideration is then given to how the activity of auditory-vocal mirror neurons is likely to be harnessed for vocal learning and communication and how synaptic and experiential mechanisms give rise to this auditory vocal correspondence.

Song Learning and Song as a Communication Signal

Songbirds learn to sing during a juvenile sensitive period comprising two distinct phases—sensory learning and sensorimotor learning—both of which depend on auditory experience (Mooney, Prather, & Roberts, 2008). During sensory learning, a young bird listens to and memorizes one or more tutor songs, usually those of the male parent or a nearby adult male of the same species (Immelmann, 1969; Marler & Peters, 1982b, 1982c, 1987, 1988). One consequence of this auditory imprinting process is that geographically separate populations of songbirds of the same species display regional dialects, similar to the different regional dialects of human speech (Marler & Tamura, 1964; Thorpe, 1958). During the ensuing phase of sensorimotor learning, the pupil relies on auditory feedback to match its song to the memorized model, which is often referred to as the song "template." Sensorimotor learning begins with "subsong," which resembles infant babbling in its rambling and poorly

structured quality, and advances to "plastic" song, which though more structured than plastic song, is still highly variable from one song bout to the next (Immelmann, 1969; Konishi, 1965; Marler & Peters, 1982a, 1982c; Marler & Waser, 1977; Price, 1979). During the plastic song phase of sensorimotor learning, song also exhibits slower adaptive changes, rendering it increasingly similar to the memorized tutor song. Sensorimotor learning terminates in song crystallization, a developmental process wherein the song becomes highly stereotyped and usually much less dependent on auditory feedback (Konishi, 1965; Lombardino & Nottebohm, 2000).

The adult male's crystallized song is a highly effective communication signal that serves to attract mates and defend territory from other males. Both of these functions engage the adult songbird's acute auditory perceptual abilities, which psychophysical studies suggest are on par with those of humans (Dooling, 1978). Sensitive perceptual abilities enable a breeding male to detect subtle acoustical features distinguishing songs of familiar neighbors from those of intruders, thus enabling him to more efficiently defend his territory. When a breeding male hears an intruder's song, one way he responds is by singing (Hyman, 2003). During this antiphonal behavior, known as countersinging, the male's role rapidly switches from receiver to sender. Notably, such a dual role also is required of humans when they engage in vocal dialog, necessitating rapid switching between sensory and motor representations of the vocalization. It has been widely hypothesized that this dual role could be facilitated by mirror neurons that display a systematic sensorimotor correspondence, although auditory-vocal mirror neurons have not been described in primates or other mammals. Countersinging in birds thus affords a highly relevant communication context in which to search for auditory-vocal mirror neurons.

The Song System

Like human speech, and in contrast to most other vertebrate vocalizations, birdsong reflects the executive influence of the telencephalon on vocal and respiratory activity (for a review of brainstem and peripheral song mechanisms, see Wild, 2004; Mooney et al., 2008). The songbird's brain is distinguished by a network of nuclei, referred to collectively as the song system, that controls singing through the muscles of the syrinx (i.e., the bird's vocal organ) and respiration (Nottebohm et al., 1982, 1976). The song system comprises two major pathways—a song motor pathway and an anterior forebrain pathway.

The song motor pathway (SMP) generates precise motor signals necessary for song production and includes the telencephalic nuclei HVC and RA and the brainstem nucleus XIIts. Specifically, individual HVCRA neurons burst in a temporally sparse manner during singing and function as a population to generate a precise timing signal integrated via convergent and divergent synaptic connections HVCRA axons make with RA neurons, which then transmit activity to the brainstem vocal

network (Hahnloser et al., 2002; Leonardo & Fee, 2005). The anterior forebrain pathway (AFP) is necessary to acute song variability and slower forms of vocal plasticity, and comprises an indirect pathway from HVC to RA that includes Area X, DLM, and LMAN (Bottjer et al., 1984; Nottebohm et al., 1982; Okuhata & Saito, 1987; Olveczky, Andalman, & Fee, 2005; Scharff & Nottebohm, 1991). Our current understanding is that song variability depends on the activity of LMAN synapses on RA song premotor neurons. These synapses, which lie adjacent to those from HVCRA neurons, evoke NMDA receptor mediated synaptic currents that are thought to induce variability in the timing signals emanating from HVC (Canady, Burd, DeVoogd, & Nottebohm, 1988; Kao, Doupe, & Brainard, 2005; Kao, Wright, & Doupe, 2008; Mooney, 1992; Olveczky et al., 2005). Notably, LMAN activity is necessary for auditory feedback perturbations, such as deafening or exposure to distorted auditory feedback (DAF), to trigger increased song variability and plasticity (Brainard & Doupe, 2000; Williams & Mehta, 1999). Thus, it is likely that the AFP receives feedback-related information, even though the singing-related activity of LMAN neurons appears to be insensitive to acute feedback perturbations (Hessler & Doupe, 1999; Leonardo, 2004).

A noteworthy organizational feature of the song system is that the SMP and AFP receive song-related input from two different populations of projection neurons located in the telencephalic song nucleus HVC (these two different cell types are referred to as HVCRA and HVCX cells, based on their projections; HVC also contains several different classes of interneurons) (Hahnloser et al., 2002; Kozhevnikov & Fee, 2007; Prather, Peters, Nowicki, & Mooney, 2008). Although HVC receives input from other brain areas, including the telencephalic nucleus NIf and the thalamic nucleus Uva, HVC appears to be the highest site in the song system containing an explicit song motor representation. Notably, NIf neurons resemble HVC neurons in that both display time-locked activity during singing (McCasland, 1987). However, unlike HVC lesions, which permanently block singing, NIf lesions only transiently disrupt song (Cardin, Raksin, & Schmidt, 2005). In contrast, although Uva lesions can permanently disrupt song, Uva neurons do not display activity locked to song features (Coleman & Vu, 2005; Williams & Vicario, 1993).

The essential role for hearing in song learning indicates that auditory information must influence the song motor network. Indeed, HVC has emerged as the earliest site where auditory information is integrated with explicit song motor commands. Auditory presentation of the bird's own song (BOS) strongly excites neurons in both the SMP and the AFP, and these auditory responses depend on input from HVC (Doupe & Konishi, 1991; Roy & Mooney, 2009; Vicario & Yohay, 1993). On the one hand, studies in the zebra finch, a semidomesticated songbird widely used for songbird neurobiology, reveal that these responses are most reliably detected when the bird is either sleeping or lightly anesthetized (Cardin & Schmidt, 2003; Dave, Yu, &

Margoliash, 1998; Schmidt & Konishi, 1998). However, recordings made in several other freely behaving songbird species show that auditory responses can be expressed in HVC during periods of quiet wakefulness, consistent with their serving a role in learned vocal communication (McCasland & Konishi, 1981; Prather, Nowicki, Anderson, Peters, & Mooney, 2009; Prather et al., 2008). Moreover, auditory responses in HVC, as well as other parts of the song system, are highly selective for the bird's own song (i.e., the BOS) (Doupe & Konishi, 1991; Margoliash, 1983, 1986; Theunissen et al., 2004; Theunissen & Doupe, 1998). Selectivity for the BOS develops in parallel with sensorimotor learning, indicating an effect of auditory feedback and hinting at a functional linkage by which auditory information could influence vocal learning (Doupe, 1997; Volman, 1993). Nonetheless, efforts to detect real-time feedback signals in either HVC or the AFP have been largely fruitless (Hessler & Doupe, 1999; Kozhevnikov & Fee, 2007; Leonardo, 2004; Prather et al., 2008) (for a possible exception, see Sakata, Hampton, & Brainard, 2008; this issue also is treated in more detail in the following section). Beyond a potential role in vocal learning, auditory responsive neurons in the song system are likely to serve a role in song perception, because lesions made either in HVC or the AFP can impair the bird's ability to recognize conspecific songs (Brenowitz, 1991; Gentner, Hulse, Bentley, & Ball, 2000; Scharff, Nottebohm, & Cynx, 1998). Taken together, these findings advance HVC as a fruitful site to explore how auditory and vocal motor information is integrated to enable learned vocal communication.

Coda: Parallels between Songbird and Human Brains

For the uninitiated, song system anatomy can appear relatively arcane and challenging to relate to mammalian brain architecture. In this light, it may be useful to draw several anatomical parallels, even though vocal learning evolved independently in birds and humans. First, executive influence of the cortex on human speech is exerted by Broca's area and the regions of the lateral motor cortex that indirectly control the various muscles important to phonation, including those of the larynx, tongue, orofacial region, and respiratory system (Burns & Fahy, 2010; Simonyan & Horwitz, 2011). In songbirds, this executive influence is exerted by projections from the telencephalic nucleus HVC to the caudal telencephalic nucleus RA, and thence to vocal motor neurons and respiratory premotor neurons in the medulla. With reference to human cortical organization, RA projection neurons can be analogized to layer V pyramidal neurons in the face motor cortex, while HVC can be viewed as an analog of the supragranular layers of the face motor cortex or Broca's area.

A second parallel is that the songbird's AFP displays organizational features strongly similar to mammalian cortical-basal ganglia pathways: Area X contains local neurons with properties highly similar to medium spiny neurons in the mammalian striatum and output neurons that make inhibitory synapses onto thalamic

neurons, much like mammalian pallidal neurons (Doupe, Perkel, Reiner, & Stern, 2005; Farries, 2001). Although the exact role of cortical-basal ganglia pathways in human vocal communication is not well understood, both hypo- and hyperkinetic basal ganglia disorders can disrupt speech (Martnez-Sanchez, 2010; Velasco Garcia, Cobeta, Martin, Alonso-Navarro, & Jimenez-Jimenez, 2011). Furthermore, mutations of a forkhead transcription factor (FoxP2) that is highly expressed in the human striatum leads to orofacial dyspraxias and impaired speech learning (Lai, Fisher, Hurst, Vargha-Khadem, & Monaco, 2001; Lai, Gerrelli, Monaco, Fisher, & Copp, 2003; MacDermot et al., 2005). Interestingly, expression of the avian homolog of FoxP2 is enriched in Area X of songbirds (Teramitsu, Kudo, London, Geschwind, & White, 2004), and knockdown of its expression in Area X in juvenile male zebra finches degrades the quality of song imitation (Haesler et al., 2007; White, Fisher, Geschwind, Scharff, & Holy, 2006).

A third parallel is that speech and birdsong demand exquisite interactions between auditory and vocal systems. In humans, clinical evidence points to connections between the tertiary auditory cortex (i.e., Wernicke's area) and speech motor areas (i.e., Broca's area) as a fundamental substrate for these auditory-vocal interactions (Catani & Mesulam, 2008; Geschwind, 1970). In songbirds, emerging functional and anatomical evidence strongly suggests that connections from secondary regions of the auditory telencephalon (i.e., CM) to HVC are the substrate for these interactions (Bauer et al., 2008; Roy & Mooney, 2009).

Although these parallels should not be taken too literally, they do raise the possibility that vocal learning in birds and humans depends on similar brain mechanisms. Furthermore, they reinforce the notion that auditory-vocal integration necessary to learned vocal communication can be explored at the cellular and synaptic level in the songbird's HVC. Finally, from a practical standpoint, the segregated projections from different HVC projection neuron types to RA and Area X afford experimentalists the possibility of distinguishing vocal motor signals from related signals conveyed to basal ganglia pathways (Hahnloser et al., 2002; Kozhevnikov & Fee, 2007; Mooney, 2000; Prather et al., 2008). This distinction may be harder to make when recording from cortical neurons in vocalizing mammals.

Auditory-Vocal Mirror Neurons in Songbirds

Armed with this perspective, and in collaboration with Stephen Nowicki and Susan Peters, two experts in songbird behavior, we explored the auditory and vocal motor representations of identified HVC neurons. This effort built on a longstanding collaboration between our labs to explore neural representations of song in the swamp sparrow, and the results of this research provided the first evidence of auditory-vocal mirror neurons for learned vocal communication (Prather et al., 2009, 2008).

### Neural Recordings in Countersinging Swamp Sparrows

Swamp sparrows exhibit two traits conducive to systematically examining the auditory and vocal properties of song system neurons. First, a captive male swamp sparrow will, at least occasionally, sing in response to hearing its own songs or the songs of other swamp sparrows played through an audio speaker. In the laboratory, countersinging in response to a bird's own songs enables a neurophysiologist to rapidly assess the auditory and singing-related representations of one and the same behavior by individual neurons. Second, male swamp sparrows typically sing several different song types, each of which consists of a highly stereotyped multinote syllable repeated 10 to 20 times in a continuous trill. Thus, recording a neuron's activity during a single bout of countersinging can be sufficient to characterize its behavior during the sensory presentation and motor performance of many iterations of a vocal gesture. Moreover, because an individual has several song types and because countersinging can be triggered by playback of the bird's own songs, a bird that hears one of its song types will sometimes sing the same song type (i.e., matched countersinging) and at other times sing another (nonmatched countersinging). These symmetrical and asymmetrical forms of countersinging allow the extent of any sensorimotor correspondence to be more fully probed.

These facets of swamp sparrow singing behavior are very informative, but recording associated neural activity is especially challenging, because a countersinging bird responding to a perceived intruder is in a highly aroused state. A miniature motorized microdrive developed by Michale Fee provided two significant advantages in this regard. First, it is sufficiently lightweight (~1.25 g) for a swamp sparrow to easily carry on its head as it hops and flies around its cage (Fee & Leonardo, 2001). Second, because this drive permits several extracellular electrodes to be precisely positioned under remote control, individual neurons can be isolated without handling the bird. Together, these features enable microdrive recordings of individual neurons as unperturbed birds engage in singing and other naturalistic behaviors.

Individual HVCX Cells Display an Auditory-Vocal Correspondence

Using this lightweight drive to record from antidromically identified HVC cells in adult male swamp sparrows, we found that HVCX cells display a precise auditory-vocal correspondence (Prather et al., 2008). When the sparrow passively listened to songs played through a speaker, an individual HVCX cell responded to only one song type in the bird's repertoire, with different HVCX cells responding to different song types (interestingly, HVCRA neurons in the awake sparrow were unresponsive to song playback, even though they respond to BOS playback in anesthetized sparrows (Mooney et al., 2001)). The highly phasic responses of HVCX neurons occurred reliably at a precise time in each syllable and depended on a specific sequence of notes in the effective syllable (Figure 19.1A). Neural recordings
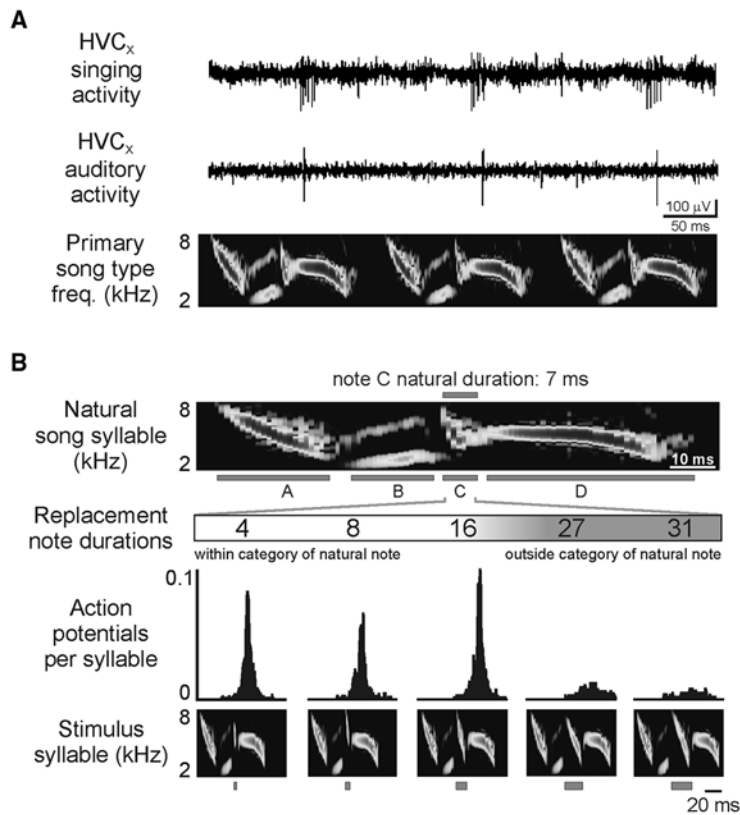
Figure 19.1
HVCX neurons in the adult swamp sparrow display a precise auditory-vocal correspondence, and their auditory properties are tightly linked to song perception (Prather et al. 2008, 2009). (a) HVCX cells are phasically active during the presentation or production of one song type in the bird's repertoire, and the syllable-locked timing of that activity is nearly identical when the bird sings (top panel) or listens to playback (middle panel) of that song type (bottom spectrogram). (b) The same cell was also tested for its responses to song playbacks in which the duration of one note in each syllable had been changed systematically (note C in the top spectrogram; replacement note durations indicated in second panel). The neuron responded strongly to songs with replacement notes shorter than 20 ms, but responded very weakly to songs with longer replacement notes (histograms in third row). Field experiments confirmed that the neural response boundary predicts a categorical perceptual boundary for note duration (Prather et al., 2009). Neural data in each panel were collected from the same neuron in a freely behaving adult male swamp sparrow.

made during matched and nonmatched bouts of countersinging also revealed that individual HVCX neurons displayed the most robust singing-related activity for the song type that evoked an auditory response in the playback condition. Even more remarkably, these neurons displayed almost identical patterns of activity when the bird sang that song type, firing at exactly the same time in the effective syllable as when the bird was quietly listening to the song played through a speaker.

Additional experiments by others and us have also confirmed the presence of an HVCX sensorimotor correspondence in the Bengalese finch (Fujimoto, Hasegawa, & Watanabe, 2011; Prather et al., 2008). This conservation across distantly related species suggests that colocalization of sensory and motor activity in HVCX cells may play an important role in shaping how vocal signals are perceived and performed. Specifically, HVCX neurons in adult male Bengalese finches are active in association with not only individual song syllables but also the specific transitions between consecutive syllables (Fujimoto et al., 2011). Taking advantage of the natural variance of Bengalese finch song sequence (Okanoya, 2004), those experiments reveal that HVCX activity encodes specific behavioral sequences from among many possible trajectories. The demonstration of an auditory-vocal correspondence in the same neurons that encode specific features of vocal sequence provides a potential mechanism through which auditory perception of vocal patterns may guide the generation of motor commands to imitate those patterns (Fujimoto et al., 2011). An important future goal will be to record the activity of HVCX cells in young finches and sparrows to determine the extent to which the patterns observed in adults are also evident during juvenile imitative learning.

These recordings demonstrated that HVCX cells display similar activity when they listen to or sing the same vocal gesture, but they do not resolve whether the singing-related activity is auditory or motor in nature. Indeed, an initially intriguing idea was that singing-related activity of HVCX neurons was a real-time auditory feedback signal. However, experiments employing DAF revealed that the singing-related activity in HVCX cells was unaffected by acutely disrupting auditory feedback (Kozhevnikov & Fee, 2007; Prather et al., 2008). Thus singing activity in HVCX cells appears to be motor-related, which can account for the singing-related signals that can be detected downstream in the AFP even in deafened birds (Hessler & Doupe, 1999). The ultimate source of this motor-related signal is likely to be the HVCRA cell population that directly and indirectly connects to HVCX cells through HVC's local synaptic network (Mooney & Prather 2005). Evidently, HVCX neurons receive a corollary discharge of the song motor signal precisely delayed by the local synaptic network to mimic the auditory signal evoked by the associated vocalization. Thus, HVCX cells exhibit one of the hallmarks of a mirror neuron: they display a systematic sensorimotor correspondence.

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Auditory Responses of HVCX Neurons Predict a Perceptual Boundary

One characteristic predicted of an auditory vocal mirror neuron is that its auditory properties should be tightly linked to the individual's vocal perception. As previously mentioned, lesions to HVC can impair a songbird's ability to distinguish conspecific songs, implicating auditory responsive HVC neurons in song perception. One hint that swamp sparrow HVCX neurons facilitate song perception is that they respond to other swamp sparrow songs containing note sequences similar to the requisite sequence in the effective song type from the bird's own repertoire (Prather et al., 2008). The ability of HVCX cells to respond to other birds' songs raises the possibility that they could facilitate song perception, and are not simply involved in the processing of self-generated vocalizations. However, establishing a tighter link to perception requires comparing neuronal and perceptual responses.

Fortunately, this comparison was simplified by an earlier field study that established that swamp sparrows perceive continuous changes in song note duration in an all-or-none, or categorical, manner (Nelson & Marler, 1989). This remarkable ability of the brain to group stimuli that vary in a continuous manner into discrete perceptual categories facilitates a wide range of communication behaviors, including human speech (Diehl et al., 2004). To begin to explore the link between HVC auditory-vocal mirror neurons and categorical perception, we measured how individual HVCX cells responded when the freely behaving sparrow heard variants of the effective song type in which the duration of a single note in each syllable of the trill had been systematically varied (Prather et al., 2009). Indeed, HVCX neurons respond categorically to changes in note duration, indicating that their activity is tightly linked to perception (Figure 19.1B).

One potential discrepancy was that this neuronal response boundary differed from the previously published perceptual boundary (Nelson & Marler, 1989). Notably, this perceptual boundary was measured in a New York sparrow population geographically distinct from the Pennsylvania population used in our neural recordings. Because different sparrow populations learn different song dialects (Balaban, 1988), one intriguing idea is that the perceptual boundary for note duration may be influenced by learning and thus may differ between these two populations. Indeed, a parallel set of field studies that we conducted confirmed that the Pennsylvania population's perceptual boundary differed from the New York population and agreed with the neural boundary we had measured in the lab setting (Prather et al., 2009). Thus, the perceptual boundary for note duration was accurately predicted by the auditory responses measured in HVCX neurons, including a subset from which it was possible to collect singing-related activity and document that they exhibited a systematic auditory-vocal correspondence. This tight link between auditory properties and song perception lends further support to the idea that HVCX neurons function as auditory-vocal mirror neurons.

Functions of Auditory-Vocal Mirror Neurons in Perception and Learning

As previously mentioned, one expectation is that auditory-vocal mirror neurons will populate brain regions where they can affect learned vocal communication. In the songbird, auditory vocal HVCX neurons occupy a pivotal position where they could influence receptive and expressive aspects of song communication. Their position in the sensorimotor hierarchy also could enable them to play an important role in song learning.

Functional Implications for Communication

A role for HVCX neurons in receptive aspects of vocal communication is strongly supported by the close parallel between their auditory response properties and the bird's categorical perceptual boundaries, as well as by the deleterious effects of HVC and AFP lesions on song recognition (Brenowitz, 1991; Gentner et al., 2000; Scharff et al., 1998). As theorized for mirror neurons generally, auditory-vocal mirror neurons could facilitate perception by enabling the listener to categorize the songs of other birds in reference to its own repertoire. Because a songbird learns its song repertoire, song perception mediated by HVC auditory-vocal mirror neurons should be strongly influenced by learning. Two features are consistent with this view. First, lesions in the AFP, to which HVC mirror neurons send their axons, disrupt a bird's ability to distinguish different conspecific songs, with the most substantial deficits for songs most like its own (Scharff et al., 1998). Second, auditory selectivity in HVC, as well in the AFP, is strongly influenced by the sensorimotor effects of singing (Doupe, 1997; Volman, 1993). The importance of self-experience is underscored by the finding that HVC and AFP neurons acquire BOS selectivity even in birds that are made to sing spectrally distorted songs by cutting the vocal nerve or partially blocking airflow through the syrinx (Roy & Mooney, 2007; Solis & Doupe, 1999). Although a perceptual mechanism dependent on self-experience may provide a highly narrow filter through which to recognize song, it may also enable a degree of sensitivity not readily achieved without explicit sensorimotor interactions. Additionally, some juvenile songbirds, including swamp sparrows, produce plastic songs from many (> 10) different tutors, but retain only a small subset of these songs in their crystallized repertoire (Marler & Peters, 1982a). One possibility is that overproduction followed by attrition permanently broadens the range of songs that can be discriminated through a sensitive filter dependent on sensorimotor experience of self-generated vocalization. If this model is correct, then HVC should contain a permanent record of transiently learned songs.

In support of that idea, we found that the adult HVC contains a persistent representation of juvenile experience (Prather et al., 2010). In a set of hand-reared swamp sparrows collected from the wild only a few days after hatching, we

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presented them with 21 different songs throughout their lives. In addition, we regularly sampled the vocal output of each bird throughout development and into adulthood. This record of the birds' lifetime of auditory and vocal experience revealed a subset of songs that were imitated during development but eliminated from the adult repertoire. The electrophysiological representation of those eliminated song types revealed that neurons in the adult HVC can be even more responsive to songs from the bird's developmental past than to any song in its adult repertoire. In addition, a small number of cells responded to tutor songs the bird heard during early development but for which no evidence of motor imitation was ever detected. Responses to song types that were heard but not imitated would have been nearly impossible to detect without a comprehensive knowledge of each bird's life history, and the ability of some HVC neurons to respond to song types not present in the adult repertoire could enable HVC to play a broader role in song recognition than would be possible if its neurons simply encoded the bird's current repertoire.

Auditory-vocal mirror neurons also could facilitate expressive aspects of vocal communication. More specifically, auditory activation of these neurons, which are embedded in the song motor network, could guide subsequent vocalization. In adult swamp sparrows, this process could enable a breeding male to select the song from its repertoire that most closely matches the song of a neighbor, resulting in matched countersinging. Young adult chipping sparrows (Liu & Nottebohm, 2007) and white-crowned sparrows in the late stages of plastic song also selectively crystallize songs in their repertoire most like those of nearby breeding males (Nelson & Marler, 1994), a developmental process of auditory-guided vocal matching that could be facilitated as well by auditory-vocal mirror neurons.

Functional Implications for Song Learning

Beyond serving a perceptual role in adult birds, auditory-vocal mirror neurons could also facilitate sensorimotor learning. An intriguing observation in support of this idea is that the auditory activity of individual HVCX neurons fails to accurately represent specific song features in a manner reminiscent of inaccurate imitation of those features (Prather, Peters, Nowicki, & Mooney 2012). Young swamp sparrows tutored with a trill that has been artificially accelerated well beyond species-typical norms sometimes produce brief bursts of accurately imitated syllables and trill rate that are separated by gaps of silence (Podos, 1996; Podos, Nowicki, & Peters, 1999). This "broken syntax" represents a major departure from the swamp sparrow's typical pattern of a continuous trill. In recordings of HVC auditory-vocal mirror neurons in adult swamp sparrows raised hearing tutor songs with normal trill rates, the auditory responses of HVCX neurons fail to follow highly accelerated trills, providing a possible sensory correlate of broken syntax. Although an individual cell can respond to some of the individual syllables in a highly accelerated trill, those responses are separated by gaps of several syllables' duration in which the HVCX

cell fails to respond (Prather, Peters, Nowicki, & Mooney, 2012). This parallel between features of HVCX auditory processing and imitative song learning suggests one way in which HVCX auditory-vocal mirror neurons could influence song learning. More precisely, if the auditory responses of HVCX neurons are used to guide motor learning, the failure of HVC neurons to faithfully encode accurate auditory representations of accelerated trills could result in the generation of broken syntax independent of any motor constraints.

Behavioral evidence suggests that sensorimotor learning depends on a neural comparator that detects differences between auditory feedback and the template, generating an error signal that adaptively modifies the song motor network to subsequently minimize these differences. Although the nature of any comparator circuit remains enigmatic, two features of plastic song—namely trial-and-error variations in performance and evaluation by auditory feedback—are reminiscent of reinforcement learning. A general feature of reinforcement learning algorithms is that they evaluate performance by comparing performance outcome to the predicted outcome. Realized in the context of sensorimotor learning, a neuron providing such a prediction might display motor-related singing activity that systematically corresponds to the auditory signal evoked by the associated vocal gesture.

The striking sensorimotor correspondence exhibited by HVCX neurons raises the possibility that the singing-related activity of HVCX cells provides a motor-based prediction of auditory feedback. In the context of a comparator circuit, combining this predictive signal with the actual feedback signal could be used to compute an error signal. Assuming that feedback insensitivity characterizes the entire HVCX cell population, these neurons could provide one of the inputs to the comparator. Based on current knowledge, this arrangement would localize the comparator to the AFP or to other HVC neurons, including interneurons and HVCRA cells (Mooney & Prather, 2005). Another possibility is that HVCX neurons are the sites of comparison, but singing-related corollary discharge overwhelms the feedback signal. This may be especially likely in the adult birds used as subjects in (Prather et al., 2009, 2008), because their crystallized songs are relatively insensitive to feedback perturbations. As noted previously, one important step will be to determine whether HVCX neurons display an auditory-vocal correspondence during sensorimotor learning. A second step will be to test whether juvenile HVCX neurons are sensitive to acute feedback perturbations, when song changes most rapidly in response to altered feedback signals.

Synaptic Mechanisms for Generating the Auditory-Vocal Correspondence

A major goal in systems neuroscience is to understand the mechanisms by which neuronal networks give rise to higher-order functions, including perception and complex behavior. In this regard, a distinct advantage afforded by the songbird is

that the neural networks that give rise to singing and song perception can be ana-lyzed with cellular and synaptic resolution. Specifically, studies in songbirds can begin to illuminate the synaptic and circuit mechanisms that produce the precise sensorimotor correspondence exhibited by HVCX neurons. Indeed, analysis of the HVC microcircuitry using both in vivo and in vitro intracellular methods already provides substantial insights into the synaptic mechanisms giving rise to the precise auditory-vocal correspondence in HVCX neurons.

Two sets of findings stemming from such analysis indicate that the systematic auditory-vocal correspondence in HVCX neurons is established by local circuit mechanisms in HVC. First, a synaptic substrate for conveying song-related motor activity from HVCRA cells to HVCX neurons has been identified using intracellular recordings from identified neurons in brain slices (Dutar, Petrozzino, Vu, Schmidt, & Perkel, 2000; Dutar et al., 1998; Mooney & Prather, 2005). Dual intracellular record-ings reveal that HVCRA cells are linked to HVCX cells via direct monosynaptic con-nections and disynaptic feedforward inhibitory projections (Mooney & Prather, 2005). This feedforward inhibitory linkage provides a plausible means by which corol-lary discharge transmitted to HVCX cells could be delayed so that it matches the timing of associated auditory feedback signals. Second, several observations stem-ming from in vivo intracellular recordings in HVC made in anesthetized birds indicate that the precise spike timing exhibited by HVCX cells depends on local inhibition. Intracellular recordings made from HVCX cells in both zebra finches and swamp sparrows reveal that BOS playback evokes strong membrane hyperpolarizations punctuated by highly phasic action potential bursts (Mooney, 2000; Mooney et al., 2001). These epochs of membrane hyperpolarization correlate closely with BOS-evoked firing in interneurons (Mooney, 2000; Rosen & Mooney, 2006), which make monosynaptic inhibitory connections onto HVCX cells (Mooney & Prather, 2005). Moreover, intracellular blockade of inhibitory input onto individual HVCX neurons shows that this inhibition is critical for regulating precisely when HVCX neurons fire action potentials in response to BOS playback (Rosen & Mooney, 2003). Finally, recordings made in either NIf or CM, both of which provide auditory input to HVC, fail to detect neurons that display either highly phasic BOS-evoked responses or a precise sensorimotor correspondence (Bauer et al., 2008; Coleman & Mooney, 2004).

Taken together, these various observations support the notion that the temporally precise sensorimotor correspondence exhibited by HVCX neurons is a product of local circuit mechanisms. These observations also raise the possibility that this precise correspondence is the product of an experience-dependent process wherein song-related corollary discharge emanating from HVCRA to HVCX neurons is "trained" by an auditory feedback signal (Troyer & Doupe, 2000). Of course, this raises the obvious question of the source of the training signal. In this light, a recent report that putative HVC interneurons in the Bengalese finch may respond to acute

feedback perturbations suggests a likely source (Sakata & Brainard, 2008). Indeed, an attractive idea is that feedback perturbations act to acutely modulate the activity of HVC interneurons, which then over a slower time course retrain the corollary discharge signal. If this process of retraining subsequently modulates AFP activity, it could enable auditory feedback perturbations to exert temporally specific effects on song performance.

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