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Auditory–vocal mirroring in songbirds

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Mirror neurons are theorized to serve as a neural substrate for spoken language in humans, but the existence and functions of auditory–vocal mirror neurons in the human brain remain largely matters of speculation. Songbirds resemble humans in their capacity for vocal learning and depend on their learned songs to facilitate courtship and individual recognition. Recent neurophysiological studies have detected putative auditory–vocal mirror neurons in a sensorimotor region of the songbird's brain that plays an important role in expressive and receptive aspects of vocal communication. This review discusses the auditory and motor-related properties of these cells, considers their potential role on song learning and communication in relation to classical studies of birdsong, and points to the circuit and developmental mechanisms that may give rise to auditory–vocal mirroring in the songbird's brain.

1. Introduction

Since their discovery in the monkey frontal cortex almost three decades ago, 'mirror neurons' that are active both when an individual observes and executes a specific movement have been advanced as a substrate for imitative learning, including for skills that form the basis of communicative behaviours, such as spoken language [1–10]. Beyond a role in skill learning, their capacity to encode both sensory and motor aspects of complex sequential behaviours would appear to predispose mirror neurons to function as a critical cellular interface for switching rapidly and efficiently back and forth between receptive and expressive modes of communication. Indeed, both motor theories of speech perception and forward models of speech learning invoke a congruent sensory-motor interface that could be served by auditory–vocal mirror neurons [11–14].

Despite the postulated importance of mirror neurons to learned vocal communication, whether and how mirror neurons operate to facilitate vocal learning, perception and production in the human brain remains largely speculative. Moreover, a detailed understanding of neural mechanisms for learned vocal communication will depend not only on studies in humans, but also on integrated physiological, anatomical and behavioural studies that are only practical in suitable animal models. Few such models exist: although human speech undoubtedly evolved from the vocalizations of our animal ancestors, vocal learning is a uniquely human trait among extant primates and a rarely encountered trait in only a few other vertebrate taxa, including cetaceans, echolocating bats and songbirds. As discussed here, studies of auditory–vocal sensorimotor neurons in songbirds provide compelling evidence that mirror neurons are engaged in vocal learning, perception and production.

Birdsong shares numerous traits with human speech: both are complex sequential vocal behaviours learned by imitation; and both serve an essential communication function, facilitating individual recognition, courtship and group cohesion [15–20]. Furthermore, songbirds and humans are both specialized for low-frequency hearing and display similar auditory perceptual capabilities, including a capacity for categorical perception of learned vocalizations [21–23]. And despite the evolutionary distance separating songbirds and humans, birdsong and speech exhibit strong developmental and neural parallels, including juvenile critical periods for auditory and vocal motor learning, a developmental progression from fragmentary babbling vocalizations to more complex, sequential and stereotyped vocal patterns, and specialized sensorimotor circuits that play an essential role in vocal learning, production and perception [15,17,19,24].

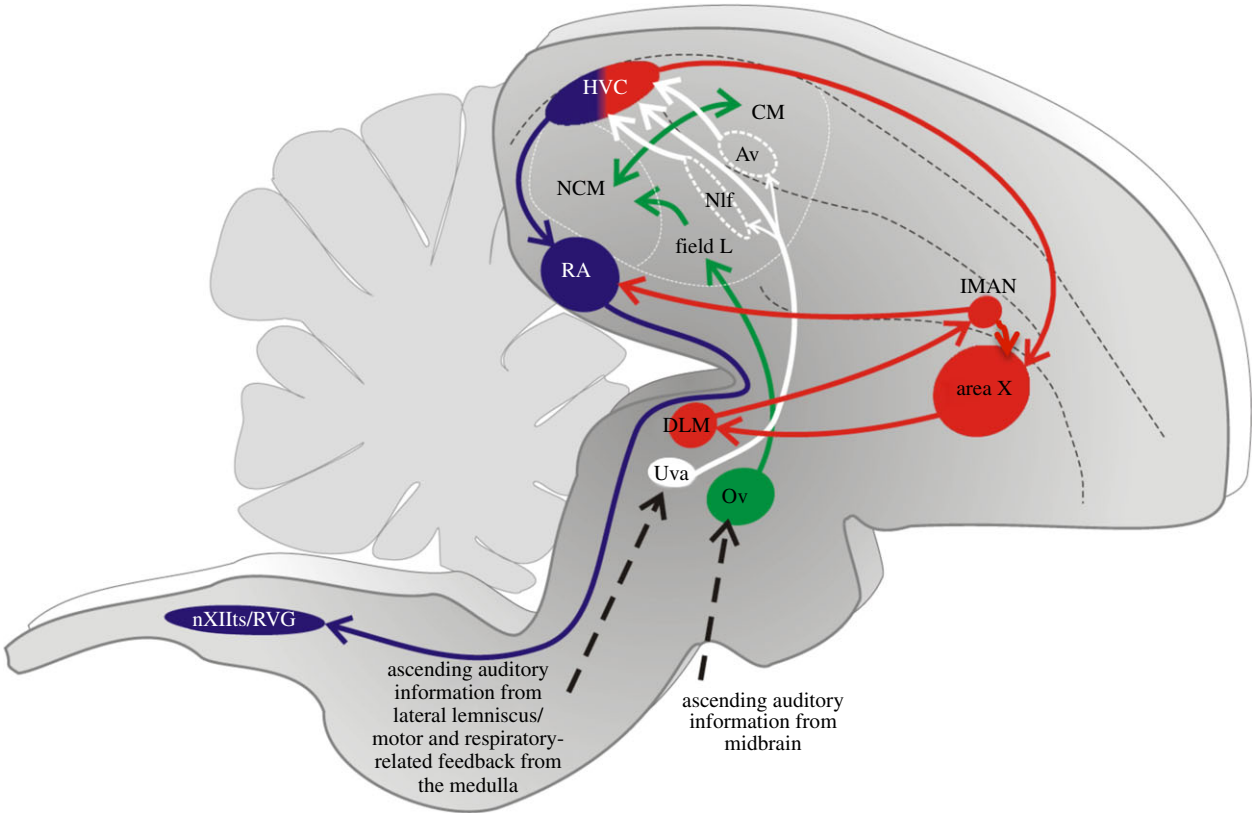

Figure 1. A schematic of the song system emphasizing HVC and its connections. This parasagittal view of the songbird brain shows the SMP (blue) and AFP (red), the ascending auditory pathways (green) and the auditory inputs to HVC (white). At the microscopic level, HVC_X and HVC_{RA} cells are randomly intermingled within HVC. Av, nucleus avalanche; CM, caudal mesopallium; DLM, medial part of the dorsolateral thalamic nucleus; HVC, abbreviation used as proper name; LMAN, lateral magnocellular nucleus of the anterior nidopallium; NCM, caudomedial nidopallium; Nlf, nucleus interface; OV, nucleus ovoidalis; RA, robust nucleus of the arcopallium; Uva, nucleus uvaeformis; VRG, ventral respiratory group; nXIIts, tracheosyringeal division of the hypoglossal nucleus.

The song system (figure 1) refers to a distributed network of forebrain and brainstem nuclei that distinguishes the songbird's brain from the brains of other birds that only produce innate, unlearned vocalizations [19,20,25]. The song system is commonly divided into two functionally distinct pathways, a song motor pathway (SMP) that plays an essential role in singing and an anterior forebrain pathway (AFP) that shares strong similarities to mammalian cortical-basal ganglia loops. While AFP lesions do not prevent singing, lesions made in the AFP of juvenile zebra finches interfere with their ability to accurately copy a tutor song, whereas AFP lesions made in adults prevent audition-dependent vocal plasticity and the more subtle modulation of song variability that occurs when a female is nearby [26,27]. Thus, the SMP and the AFP have motor roles in adult singing, and it is speculated that coordination of activity in these two pathways plays an integral role in song learning [28].

Notably, both of these pathways receive input from distinct pools of projection neurons that are intermingled in the nucleus HVC [29,30], which is located on the dorsal aspect of the caudal telencephalon and occupies a functional position at or near the apex of a sensorimotor hierarchy for song [25,31,32]. By rough analogy to the human brain, HVC can be likened to Broca's area (vocal premotor cortex in primates), containing one projection neuron type (HVC_{RA}) that innervates the song motor nucleus RA (an analogue of the vocal motor representation in the primary motor cortex) in the SMP and another projection neuron type (HVC_X) that provides input to a striatopallidal structure (area X) in the AFP. Beyond their similar anatomical locations in the vocal motor hierarchy, HVC and Broca's area share comparable functional roles in the generation of learned vocalizations: similar to Broca's aphasics, adult songbirds with HVC lesions cannot sing, although they continue to produce innate vocalizations, such as alarm calls, and also produce simpler vocalizations that resemble the babbling vocalizations produced by juvenile songbirds at the earliest stages of song learning (i.e. subsong) [25,33]. Furthermore, chronic recordings made in singing birds indicate that both HVC_{RA} and HVC_X cells fire in temporally precise bursts during singing [34–38], and both focal cooling and microstimulation experiments point to HVC as a core component of the neural machinery for the temporal patterning of song [32,39].

2. Sensorimotor roles for HVC and the phenomenon of auditory–vocal mirroring

Interestingly, songbirds with HVC lesions also show deficits in the ability to recognize the songs of other birds of their own species [40] or to learn new contingencies to these songs [41], suggesting that HVC serves auditory as well as premotor functions. Consistent with this idea, some of the earliest electrophysiological recordings made from HVC in awake songbirds found that certain HVC neurons could be excited by auditory presentation (i.e. playback) of the bird's own song (BOS) [42]. Subsequent recordings in a variety of anaesthetized songbird species, including sparrows and zebra finches, detected HVC auditory neurons that were highly tuned to temporal and spectral features in the BOS but that could also respond to other acoustically similar

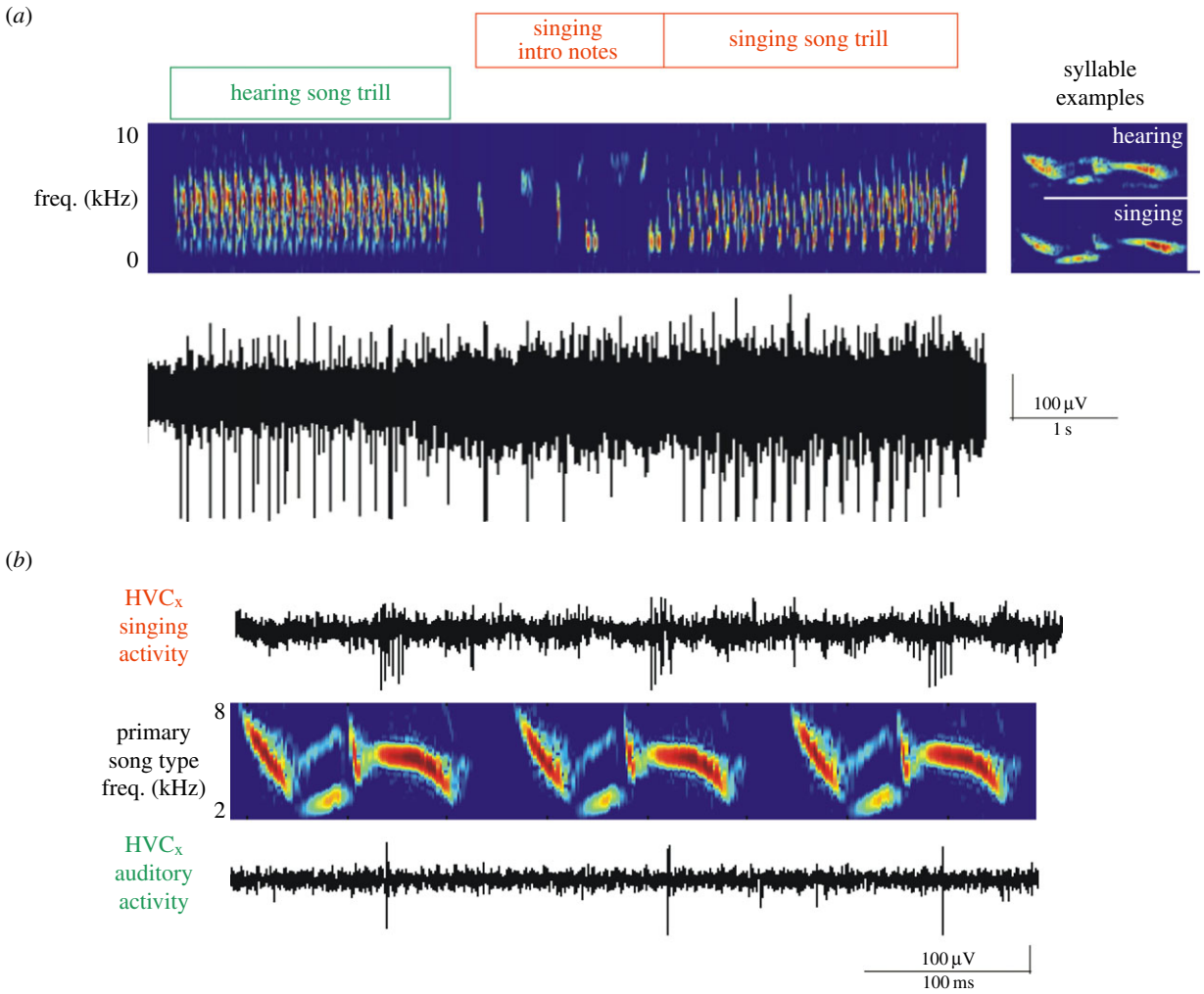

Figure 2. Chronic extracellular recordings from freely singing swamp sparrows reveal auditory–vocal mirroring in HVC_X cells. (*a*) Action potential activity (bottom trace) of an HVC_X cell as it listens to its song, which consists of a trilled syllable (top inset at right) played through a nearby speaker (green box over sonogram) and as it transitions to singing the same trilled syllable (red box over sonogram and bottom inset at right). (*b*) An expanded view of the action potential activity of this cell during hearing (bottom trace) and singing (top trace) three repeated syllables in the song (sonogram shown in the middle). Adapted from Prather *et al*. [38].

songs of conspecific birds, including the tutor song on which the BOS was modelled [38,43–51]. In fact, in anaesthetized zebra finches, BOS playback is sufficient to excite neurons in all nuclei in the song system downstream of HVC, including the motor neurons and nerves that innervate the vocal organ, and reversible inactivation and functional connectivity studies indicate that HVC is the source of this widespread auditory responsiveness [52–56].

Although the detection of neural activity in HVC during singing and BOS playback are suggestive of auditory–vocal mirror neurons, the earliest studies of singing and auditory-related activity in the HVC of freely behaving birds used multiunit methods and thus could not resolve whether the same neurons were active during singing and song playback. Subsequent single unit studies in freely behaving swamp sparrows (*Melospiza georgiana*) and Bengalese finches (*Lonchura striata* var. *domestica*) that used antidromic stimulation methods to distinguish HVC_X from HVC_{RA} cells established that only HVC_X cells exhibit auditory activity during quiet wakefulness and also revealed that about a third of HVC_X cells are active both during singing and BOS playback (figure 2*a*) [35,38]. Remarkably, this subset of HVC_X neurons discharge action potentials at exactly the same time in the song phrase, regardless of whether the bird is singing or listening to its song through a speaker (figures 2*a*,*b* and 3*b*). One explanation for this behaviour is that these cells respond to auditory feedback during singing and to similar auditory cues when the BOS is played through a speaker. However, the singing-related activity of these cells is unperturbed by acoustic manipulations that disrupt auditory feedback, suggesting that HVC_X cells switch from auditory to purely motor-related activity as the bird transitions from listening to singing [38,57]. Therefore, HVC_X cells display a temporally precise form of auditory–vocal mirroring that could be well suited to facilitate song learning and perception.

Before considering how HVC auditory–vocal mirror neurons might function to facilitate song learning and communication, it is notable that auditory responses can be detected in the HVC of female songbirds that typically do not sing [58,59], and HVC lesions in female songbirds impair their ability to discriminate appropriately between conspecific and heterospecific songs [40,60], indicating that HVC's auditory function, at least in females, may not be a simple consequence of singing. Furthermore, the auditory responses of HVC cells in adult male zebra finches are strongly state-dependent, only emerging during sleep or under anaesthesia [61–64]. Songbird neurobiologists use zebra finches for experimental subjects because of their

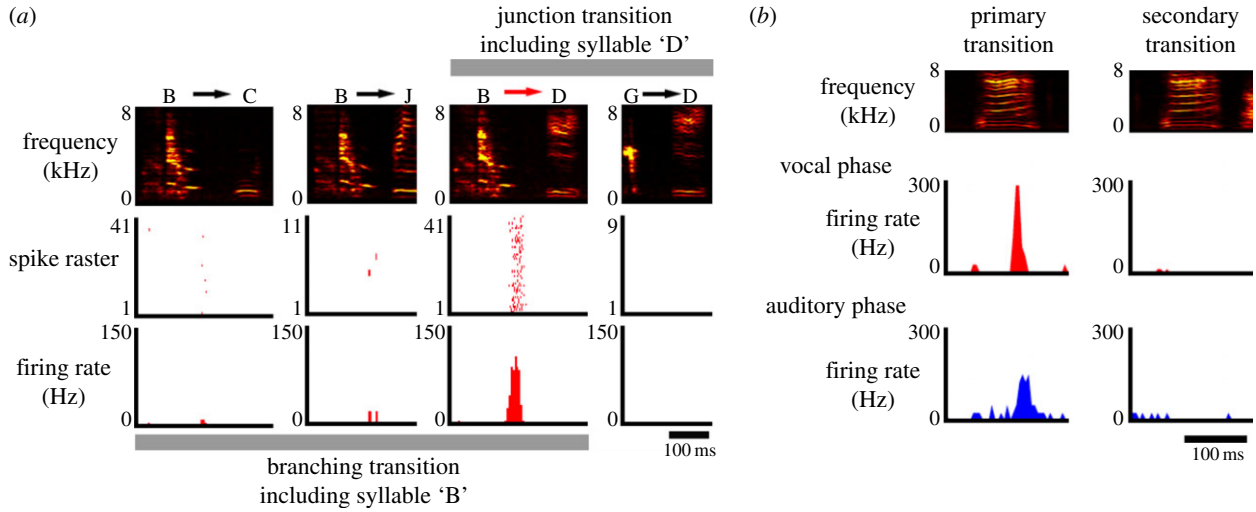

Figure 3. Auditory–vocal mirror neurons can display similar selectivity for specific syllable transitions during motor and auditory phases. (*a*) Extracellular recordings from an HVC_X cell in the Bengalese finch reveals that singing-related action potential activity occurs during the transition from syllable B to D, but not during other syllable–syllable transitions involving either syllable B or D. (*b*) The selective firing for a primary syllable–syllable transition exhibited during singing (i.e. the vocal phase) is maintained during auditory playback of various syllable transitions (auditory phase). Adapted from Fujimoto *et al*. [35].

suitable captive breeding habits, with the consequence that there has been some uncertainty as to whether auditory–vocal mirroring is a common feature of HVC_X cells across species. Recent experiments from our own laboratory have used longitudinal recordings across the sleep–wake boundary to establish that precise auditory–vocal mirroring also is a trait of HVC_X cells in male zebra finches [57]. Thus, although the auditory responses of HVC_X cells are more tightly regulated by behavioural state in zebra finches than in swamp sparrows and Bengalese finches, auditory–vocal mirroring appears to be a common trait of this cell type in a wide variety of songbird species.

3. Role in production

A prevailing view is that HVC sits atop the song motor hierarchy and plays an integral role in encoding temporal aspects of song [65]. Although HVC lesions abolish singing, indicating a critical role in song production, and HVC_{RA} cells are thought to form a synfire chain that generates a precise timing signal for song patterning [34,36,39], whether and how HVC_X cells contribute to these processes is unclear. Notably, HVC_X axons form synapses on other neurons in HVC and on striatopallidal neurons, but not on song premotor neurons in RA [30,66] (by analogy to mammalian cortical circuitry, HVC_X cells resemble cortical pyramidal neurons that extend axons to the basal ganglia but not to the pyramidal tract). While lesions made downstream of HVC in the AFP of adult songbirds do not prevent singing, they can render the song less variable [67,68]. Therefore, while a prevailing view is that HVC_X cells are not essential to song production, whether these cells may play a more nuanced role in singing has not been rigorously tested and remains plausible.

A more direct attempt to test whether HVC_X cells are necessary to singing used retrogradely transported chlorin-e_6-coated latex microspheres from area X to facilitate the targeted laser ablation of HVC_X cells [69]. This manipulation not only had no effect on song, but also killed only slightly more than half of the HVC_X cell population. Therefore, a subtler role for HVC_X cells in song motor control cannot be excluded, mediated perhaps by their long-range projections to area X or by the excitatory synapses that their local collaterals make on HVC_{RA} cells and HVC interneurons [66]. In the former scenario, the singing-related activity of HVC_X cells could influence to what extent the AFP contributes to performance variability and action selection, two prominent functions that have been ascribed to mammalian cortico-basal ganglia pathways. In the latter case, HVC_X cell activity could either directly or indirectly alter the timing or magnitude of HVC_{RA} firing patterns during singing, which are thought to shape song's temporal features through a synfire mechanism local to HVC [34,36,39,65].

Analyses of the singing-related activity of HVC_X activity reveal correlations with song features that are consistent with a premotor encoding role. In zebra finches, a single HVC_X cell fires brief action potential bursts several times during a single song phrase, the timing of which is temporally precise and invariant from one song bout to the next [37]. Correlational analyses revealed that the multiple bursts of a single cell precede similar song syllable features (i.e. either periods of sound or silence) in the song phrase by approximately 40 ms, consistent with a premotor activity signature [37]. These observations support a model in which HVC_X cells transmit precise timing information about song to the AFP and to other HVC cells during singing but cannot address whether this information is used for ongoing song motor control or serves other slower processes related to song learning and maintenance.

Zebra finches sing a single highly stereotyped song phrase comprising a linear sequence of syllables, with the result that a single syllable typically occurs in fixed context. This organization makes it difficult to determine whether the bursting activity of HVC_X cells correlates with specific syllables or syllable sequences regardless of context. By contrast, other songbird species, including swamp sparrows and Bengalese finches, sing multiple songs that are distinguished by different syllables or by different syllable–syllable transitions. Electrophysiological recordings in singing swamp sparrows and Bengalese finches indicate that bursting activity of HVC_X mirror neurons can correlate with specific syllables [35,38]. Furthermore,

recordings made in Bengalese finches, which often sing variable sequences of syllables, indicate that some HVC_X neurons can fire bursts in an all-or-none fashion for specific syllable–syllable transitions, or can display different levels of activity for different syllable–syllable transitions (figure 3*a*). Finally, HVC_X cells in Bengalese finches also can encode information about the initiation, evolution and termination of strings of repeated syllables [35]. Taken together, these observations indicate that the singing-related activity of HVC_X cells can encode syntactic information about song in a hierarchical fashion, spanning from the identity of individual syllables to the number of repeated syllables and the nature of inter-syllable transitions. Notably, these cells supply input to basal ganglia circuitry, which plays an important role in the initiation and termination of motor sequences, raising the possibility that HVC_X cell activity plays an important role in controlling song's syntactic features. In this light, an important goal of future experiments will be to systematically and selectively manipulate the activity of HVC_X cells, preferably through optogenetic methods, to determine whether their singing-related bursting activity can influence ongoing aspects of song production, including song syntax.

4. Role in perception and the effects of auditory experience

In monkeys and humans, the 'observation-related' activity of mirror neurons is speculated to facilitate understanding of another's actions by representing the corresponding sensations in the context of the observer's own action framework [8,10]. More broadly, motor circuits have been advanced as a substrate for perceptual processing of spoken language [13,14]. In this context, an important question is whether auditory–vocal mirror neurons in songbirds, which are embedded in a premotor nucleus critical for learned vocal control, are linked to song perception. Interestingly, lesions of HVC and in the AFP can interfere with the recognition of conspecific song [40,70,71], HVC_X cells are thought to be the sole source of auditory input to the AFP [53,72], and HVC_X cells can display highly selective auditory responses to specific features of the BOS, including individual notes and note sequences [38,44, 73–75]. Taken together, these observations implicate HVC_X cells in auditory processing important to song perception.

An analysis of HVC_X mirror neurons in swamp sparrows suggests how their auditory properties could contribute to song perception [44]. Swamp sparrows sing several distinct song types each comprising a monosyllabic trill, with each syllable composed of two to five acoustically distinct notes drawn from a pool of note types common to this species. Playback experiments in awake but non-singing sparrows reveal that individual HVC_X mirror neurons respond only to a single song type in the bird's repertoire, firing one or two action potentials very reliably at a precise time within the syllable [38,44]. Furthermore, reversing the order of the notes in the syllable of the effective song type is sufficient to attenuate or strongly abolish the cell's auditory response, indicating that they are selectively responsive to specific note combinations within an effective song type [38]. This sensitivity to specific note sequences, which also has been described for HVC neurons in other songbird species [46,76], requires a pronounced capacity for spectrotemporal integration [46,48,50,76]. Moreover, similar note sequences from the songs of other swamp sparrows also can evoke auditory responses from these cells, indicating that despite their remarkable selectivity, they are capable of encoding information about the songs of other birds and thus potentially suited to a role in song perception.

Swamp sparrows also provide a convenient platform for investigating neural correlates of song perception, as different breeding populations sing distinct dialects characterized by subtle differences in note morphology, including millisecond differences in the durations of specific note types [23,44]. Additionally, these subtle differences in note morphology, which are acquired through imitation, provide an acoustic basis by which individuals learn to recognize and distinguish birds from different breeding populations. Finally, behavioural studies have demonstrated that swamp sparrows perceptually group song notes that vary systematically in their absolute durations into distinct categories, similar to the manner in which humans group phonemes that vary continuously in voice onset times into two distinct perceptual categories [23,44]. A further similarity is that these categorical perceptual boundaries are not fixed in either humans or swamp sparrow populations but instead are determined by the individual's experience with a natal dialect [44]. Notably, swamp sparrow HVC_X mirror neurons respond categorically to changes in note duration in the effective song type, and the neural response boundary closely aligns with the categorical perceptual boundary evinced by sparrows that sing the same dialect, but not with the perceptual boundary of sparrows that sing another dialect (figure 4) [44]. Thus, the auditory response properties of individual HVC_X mirror neurons closely parallel the swamp sparrow's perceptual ability to distinguish subtle differences in vocal dialects, suggesting that these neurons could provide the neural substrate for categorical perception of learned vocalizations.

The auditory mirroring of motor-related activity may also extend beyond simpler phonological features, to the syntactical level. At least some auditory–vocal mirror neurons in the Bengalese finch that fire differentially at alternative syllable–syllable transitions during singing also respond differently to these alternative transitions, indicating that transition selectivity is maintained across motor and auditory states (figure 3*b*) [35]. Because songbirds use both phonological and syntactical information to distinguish different songs, the auditory properties of mirror neurons in HVC are well suited to extract features that are important to song perception at multiple levels of acoustical complexity.

A remaining question is the extent to which the auditory activity of songbird mirror neurons is required for song recognition, including the discrimination of the songs of other conspecifics, which to the human ear can sound remarkably similar to one another. Interestingly, while most HVC_X neurons in anaesthetized songbirds display strong and selective auditory responses, less than half of HVC_X cells that display singing-related activity also respond to song playback during periods of quiet wakefulness [35,38,73,74]. Furthermore, studies in adult zebra finches reveal that auditory activity can only be detected in HVC_X and most other HVC cells when the animal is sedated, anaesthetized or asleep [57,62,63,77]. Indeed, auditory responses in the HVC of sedated zebra finches are strongly suppressed by arousing stimuli, such as a brief air puff delivered to the bird's chest [62]. These various findings point to the existence of a gating mechanism [78] that can control auditory drive to HVC_X cells as a function of arousal and,

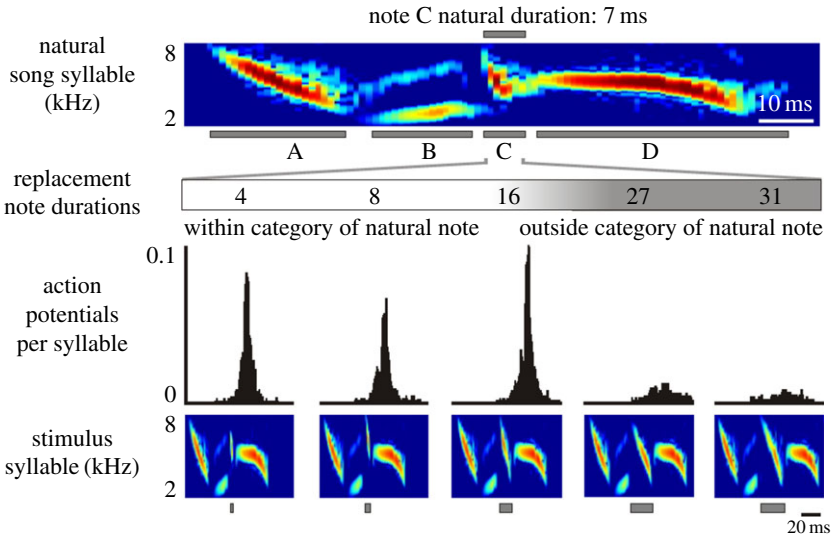

Figure 4. Categorical responsiveness of swamp sparrow mirror neurons to changes in note duration. Systematically varying the duration of the third note (note 'C') in the four-note syllable of the effective song type reveals that mirror neurons are sharply tuned to changes in note duration. Behavioural experiments (not shown) reveal that the neural response boundary parallels the perceptual response boundary for note duration in this breeding population of sparrows (approx. 20 ms) but differs from the categorical perceptual boundary (approx. 14 ms) in a separate breeding population of sparrows that sing a distinct song dialect. Adapted from Prather *et al*. [39].

presumably, in the service of attention. Thus, an important avenue for future research will be to determine whether the auditory activity of HVC_X cells, and thus auditory–vocal mirroring, is more widespread when the animal is performing demanding song recognition tasks.

5. Circuit and synaptic mechanisms underlying motor and sensory activity of auditory–vocal mirror neurons

A fundamental question in mirror neuron research is the nature of the functional circuitry and synaptic machinery that accounts for the complex sensory and motor properties of these cells. Are the sensorimotor properties of mirror neurons simply inherited from sensory and motor neurons in other brain regions, or do they instead arise through computations performed by the local circuit in which the mirror neuron is embedded? Such an understanding is important because it can shed light on the neural computations that facilitate imitation, perception and communication, and also because localizing where mirroring originates can inform the search for how experience shapes the underlying circuits to generate such a precise sensorimotor correspondence. Although this question is far from resolved in any system, the song system is highly amenable to a wide range of powerful methods, including intracellular and extracellular recordings in singing and anaesthetized birds, *in vitro* intracellular recordings, reversible inactivation, focal cooling, *in vivo* imaging, viral tracing and genetic manipulation of activity, that facilitate the detailed analysis of functional connectivity necessary to provide an answer. In fact, the product of several decades of research by a wide variety of groups has provided considerable insights into the circuit mechanisms that underlie the expression of singing-related and auditory-evoked activity of auditory–vocal mirror neurons.

Similar to the manner in which mammalian motor cortex is recurrently connected to brainstem and basal ganglia structures, the songbird HVC is recurrently connected with downstream elements in the SMP and the AFP, as well as with neurons in the auditory telencephalon [79–85]. Thus, the functional properties of HVC mirror neurons must in some manner arise through complex and potentially reciprocal interactions with other brain regions. Nonetheless, a variety of evidence supports the idea that HVC is a site where a precise timing signal necessary for song motor patterning originates. Although one of HVC's major telencephalic afferents, NIf, contains neurons that may fire in a temporally precise manner during singing [86], completely ablating NIf disrupts singing for only a few days, after which the bird continues to sing normally [77,87]. And although lesions in a thalamic afferent to HVC, Uva, can permanently disrupt the song pattern [88], presumably by interfering with the bilateral coordination of HVC activity mediated through recurrent circuitry in which Uva is embedded, Uva neurons do not display singing-related activity that is precisely time-locked to the song [89]. Thus, HVC and more precisely HVC_{RA} cells are presumed to be the sites where an explicit, temporally precise code necessary for song motor control originates. The details of the synaptic machinery that generate this precise code are not well understood, but paired intracellular recordings reveal that HVC_{RA} and HVC_X cells form excitatory synapses on local interneurons, which in turn form inhibitory synapses on other HVC_{RA} and also HVC_X cells [66], reminiscent of half centre oscillatory circuitry known to drive rhythmical bursting activity in other pattern-generating circuits [90]. Furthermore, HVC_{RA} cells make direct excitatory and feed-forward inhibitory connections onto HVC_X cells [66], providing a circuit by which HVC_{RA} cells could transmit a copy of the premotor timing command through HVC_X cells to the AFP.

The remarkably selective auditory response properties of HVC neurons, including the sequence sensitivity of HVC_X cells, have motivated extensive studies of where and how such selectivity originates. Several of HVC's afferents contain auditory-responsive cells, and reversible inactivation studies implicate two of these—NIf and CM/Av—as the sources of much or all of the auditory drive to HVC [77,87,91,92].

Comparisons of auditory-evoked activity in these two afferents and HVC indicate that HVC_X cells are sites where highly phasic, BOS-selective responses arise. That is, although NIf and CM/Av contain neurons that are selective for temporal features of the BOS, these neurons fire in a more sustained fashion in response to BOS playback than do HVC_X cells [91,92]. Moreover, single and dual *in vivo* intracellular recordings from interneurons and HVC_X cells, as well as intracellular dialysis of HVC_X cells with blockers of inhibitory currents, show that the highly phasic and temporally precise action potential output of HVC_X cells arises through the sculpting effects of local inhibitory circuits acting on more sustained BOS-evoked excitatory drive originating from extrinsic sources [73,75,93]. Interactions between inhibitory and excitatory synapses are also implicated in the generation of note combination-sensitive responses of HVC_X cells [76,94]. Thus, two features of auditory–vocal mirror neurons, namely their temporally precise action potential responses to BOS playback and their sensitivity to specific note combinations, are likely to depend on local circuit interactions involving inhibitory interneurons.

Taken together, these studies shine the spotlight on HVC as the site where temporally precise premotor and auditory representations originate, while also delineating local circuitry that could account for the convergence and registration of these motor and sensory representations on individual HVC_X cells. Furthermore, because birdsong is learned through imitation, the synaptic and circuit mechanisms that result in this precise sensorimotor registration are likely to be influenced by auditory and motor experience acting on HVC during song development. The important role for inhibitory interneurons in transmitting signals from HVC_{RA} to HVC_X cells and for sculpting auditory responses in this latter cell type, as well as the key role assigned to inhibitory interneurons in regulating experience-dependent plasticity in other systems [95–98], suggest that inhibitory synapses onto HVC_X cells play an especially important role in the development and ongoing expression of auditory–vocal mirroring in the songbird's HVC.

6. Developmental origins of auditory–vocal mirroring

While HVC is a likely site where temporally precise auditory and vocal representations are generated and merged at a single-cell level, it is less clear exactly how this correspondence develops. Modelling studies suggest that if motor-related signals emanating from HVC_{RA} cells and auditory feedback signals from extrinsic auditory sources could be integrated by single HVC_X cells during singing, synaptic plasticity mechanisms that depend on the precise timing of pre- and postsynaptic spiking activity (i.e. spike-timing-dependent plasticity; STDP) could result in precise auditory–vocal mirroring [99]. Support for an effect of feedback on the auditory properties of HVC_X cells comes from the observation that BOS-selectivity in HVC and the AFP develops in parallel with the process of song imitation [43,100,101], and from the finding that exposing adult finches for prolonged periods to distorted auditory feedback can drive auditory retuning to the distorted BOS in both HVC and the AFP [53,87]. Perhaps most compellingly, *in vivo* multiphoton imaging reveals that deafening can destabilize and shrink dendritic spines on HVC_X but not HVC_{RA} cells, an effect that precedes and predicts the severity of subsequent song deterioration [102].

Despite evidence indicating that feedback shapes HVC auditory selectivity, a significant challenge to this STDP model is that the singing-related action potential activity of HVC_X cells is entirely insensitive to feedback perturbations [37,38]. Moreover, studies from our group using intracellular recordings in singing birds also reveal that the singing-related synaptic activity of HVC_X cells is unaltered by acute manipulations of auditory feedback [57]. Thus, how and when auditory feedback-related information impinges on HVC remains unclear. One possibility is that feedback signals are gated in a highly dynamic fashion as a function of behavioural and/or developmental state. In fact, HVC neurons in juvenile zebra finches appear to respond more readily to auditory stimulation during periods of quiet wakefulness than do HVC neurons in adults [61,103]. However, whether this developmental difference in responsiveness extends to feedback is unclear, and recordings made in the HVC of juvenile zebra finches have failed to detect changes in singing-related action potential activity in response to acute feedback perturbations [37]. Alternatively, processes of sensorimotor replay operating during sleep may play a role in organizing a mirror neuron network in HVC [104].

Another idea is that mirroring is a consequence of supplying excitatory auditory drive to a strongly interconnected and thus highly resonant premotor circuitry. In this view, temporally precise bursting activity in HVC initially emerges in the form of premotor activity, rather than through auditory experience. Subsequently, as the juvenile sings its song many thousands of times over the course of song learning, synaptic connectivity in the premotor network would become deeply ingrained. Supplying excitatory drive to the premotor network, which could be achieved by activating auditory afferents to HVC, would trigger the network to recapitulate a premotor-like pattern of activity, resulting in mirroring. Although this idea deserves important consideration, it is insufficient by itself to account for the existence of selective auditory responses in the HVC of female songbirds that do not sing [58], or for the highly selective auditory responses in the adult male swamp sparrow HVC to tutor songs that are not maintained as copies in the bird's adult repertoire [45]. In fact, *in vivo* multiphoton imaging, electrophysiological, optogenetic and reversible inactivation experiments in juveniles indicate that HVC plays an essential role in helping to encode auditory experience of the tutor song [105,106]. These studies reveal that a naive juvenile's first auditory experience of a tutor song rapidly stabilizes and strengthens excitatory synapses on HVC_X and HVC_{RA} cells, a process that is paralleled by the emergence of pronounced, spontaneous bursting activity in both HVC and RA [106,107]. Therefore, early auditory experience of the tutor song and not simply singing-related premotor activity could be critical to the development of a precise auditory–vocal correspondence in HVC.

7. Mirror neurons in vocal learning and communication

In the absence of techniques for systematically manipulating the activity of specific neuron types in the HVC of freely behaving songbirds, the specific function of auditory–vocal

mirror neurons must remain a matter of conjecture. However, their remarkable sensorimotor properties and critical location in the sensorimotor hierarchy raise the possibility that they play important roles in song learning, perception and, in those species that sing multiple song types, the adaptive matching of songs to conspecific neighbours. An important near-term goal is the application of intersectional strategies to selectively express genetically encoded modulators of neural activity in HVC_X cells to test their roles in song learning, perception and communication.

One major function of HVC_X cells, including mirror neurons, appears to be to provide the AFP with a copy (i.e. corollary discharge) of the vocal motor commands issued by HVC. In fact, although the singing-related activity in the AFP persists in deafened birds [108], indicative of a motor origin, lesions placed in the AFP do not prevent singing [67], consistent with a corollary discharge signal. One idea is that HVC_X cells transmit corollary discharge signals to the striatopallidal circuitry that provides precise timing information about song, which in an error correction framework could facilitate the temporal assignment of variability signals used to adaptively modify song [28]. However, the auditory–vocal correspondence exhibited by some HVC_X cells also has the potential to function in a more sophisticated manner by providing a predictive estimate of the auditory feedback that will result from the corresponding premotor signal generated by HVC [38]. Indeed, it is speculated that such forward (i.e. motor to sensory) predictions are an integral ingredient for complex skill learning, including speech learning [11,12]. In both songbirds and humans, forward models could be compared with vocalization-related feedback to generate error signals that adaptively train the vocal motor network. This idea presumes that the comparison occurs downstream of HVC_X cells, either in the AFP or possibly in CM/Av, an auditory region that also receives input from HVC [79]. The absence of feedback sensitivity in the AFP makes the CM/Av region of special interest in this regard.

Auditory–vocal mirror neurons in HVC are likely to contribute to song recognition and also could play a subtler role in singing in birds with multiple song types by helping guide the selection of appropriate song types as determined by communicative context. As previously discussed, the close parallel between acoustic selectivity of mirror neurons and the bird's perceptual boundaries advance these cells as likely candidates for facilitating song recognition in the framework of the individual's own repertoire. In birds with multiple song types, such as swamp sparrows, male–male rivalries can involve a process of matched countersinging, where a resident male sings a song from its own repertoire that is most like that of its rival. Auditory–vocal mirror neurons could facilitate this vocal matching process: listening to the rival's song would activate mirror neurons in the resident that encode a similar song in the resident's repertoire; this auditory activity could then lead to the selective recruitment of premotor neurons encoding for that song. One possibility is that the mirror neurons function as premotor neurons; another possibility is that they recruit HVC_{RA} cells that encode the desired song type, either through local connections in HVC or long-range recurrent connections through the SMP or AFP.

8. Conclusion and future directions

Although still nascent, mirror neuron research in songbirds affords scientists the potential to understand how these fascinating cells contribute to the complex behavioural and perceptual skills necessary to learned vocal communication. Furthermore, it is likely that the synaptic and circuit basis for sensorimotor mirroring will be most readily explored in the songbird, an organism in which a variety of high-resolution recording and imaging methods are now practical, and in which the generation time is sufficiently rapid to facilitate ontological experiments that seek to determine how experience shapes the development of mirror neurons. Current evidence suggests that auditory and vocal experience act at the level of local circuitry in HVC to generate a precise form of auditory–vocal mirroring that is not evident in earlier stages of the sensorimotor hierarchy.

The recent application of viral genetic methods to label and manipulate the activity of HVC neurons holds the promise that the role of auditory–vocal mirror neurons in vocal learning and perception can be tested more directly. An important near-term goal will be to use intersectional viral strategies to limit expression of transgenes, such as channelrhodopsin or archaerhodopsin, to HVC_X cells and employ song-triggered optogenetic methods to disrupt their activity in song learning, production and recognition assays. Another important goal will be to map in greater detail the organization of the functional circuitry in which auditory–vocal mirror neurons are embedded, a process that can provide greater insight into the structure and function of the complex networks which can account for such remarkable sensorimotor properties. A reasonable goal over the next decade will be to understand at a synaptic and circuit level how the properties of mirror neurons are generated and how they contribute to imitative vocal learning, perception and communication.

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