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Neural correlates of learned song in the avian forebrain: simultaneous representation of self and others

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Songbirds are extraordinary vocalists and sensitive listeners, singing to communicate identity, engage other birds in acoustical combat, and attract mates. These processes involve auditory plasticity in that birds rapidly learn to discriminate novel from familiar songs. Songbirds also are one of the few non-human animals that use auditory feedback to learn their vocalizations, thus auditory–vocal interactions are likely to be important to vocal learning. Recent advances strengthen the connection between song recognition and processing of birdsong in the auditory telencephalon. New insights also have emerged into the mechanisms underlying the ‘gating’ of auditory responses and the emergence of highly selective responses, two processes that could facilitate auditory feedback important to song learning.

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Abbreviations

BOS	bird's own song
cM	caudal mesopallium
cmM	medial cM
IEG	immediate early gene
NCM	caudomedial nidopallium
NE	norepinephrine
NIf	interfacial nucleus of the nidopallium
RA	robust nucleus of the arcopallium

Introduction

A vast amount of animal communication involves facial and vocal signals, two examples of remarkably complex natural stimuli. Indeed, this stimulus complexity raises formidable obstacles to and opportunities for understanding how the brain represents natural objects. Although acoustically complex, animal vocalizations such as bird-song afford an unparalleled opportunity to explore the sensory processing of natural objects, because vocaliza-

tions are stereotyped sounds constrained by obvious behavioral functions.

Birdsong is a mellifluous vocalization that evolved under strong sexual selection pressure: in most songbirds females select a mate on the basis of his song [1]. Because songbirds of the suborder Oscini learn their songs, sexual selection has triggered an arms race in brain areas important to song learning, song perception and song production [2,3]. The importance of birdsong to intraspecific communication and the robust neural substrates for song make oscine songbirds an unusually attractive model system in which auditory processing of complex natural acoustical objects can be explored.

In this review, we provide a brief introduction to song behavior and its neurobiological underpinnings. Then we focus on recent advances that strengthen the connection between song recognition and processing of birdsong in the auditory telencephalon. We also discuss how, in a song pre-motor nucleus that receives input from the auditory telencephalon, auditory responses are dynamically modulated as a function of the bird's state and how synaptic mechanisms contribute to the emergence of highly selective song representations. These various new findings provide insights into the neural coding of communication sounds, and promise to generate a cellular framework for understanding how the brain represents complex natural stimuli.

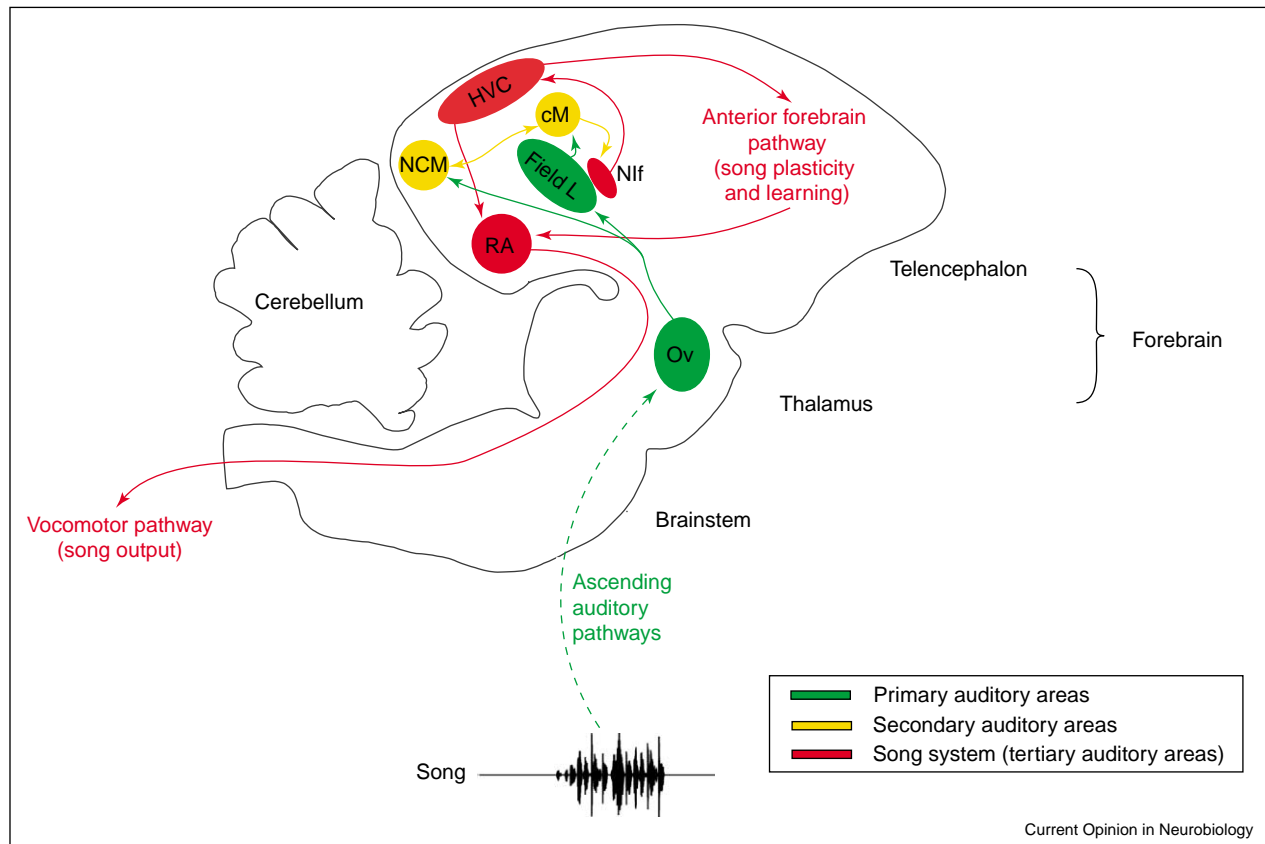
Song behavior

Song learning in juveniles comprises both sensory and sensorimotor learning phases: birds first memorize a conspecific tutor song, which they then vocally mimic by using auditory feedback. Juvenile songbirds sing variable or ‘plastic’ songs that become stereotyped or ‘crystallized’ at sexual maturity [4]. Crystallized songs attract females and elicit aggressive responses from other males, whereas plastic songs typically elicit less interest from adults of either sex. Analyzing auditory processing of song in the adult is therefore pertinent to the functions of song communication. Furthermore, many adult songbirds use auditory feedback to maintain stable songs [5], and thus analyzing auditory–vocal integration in the adult is relevant to song maintenance.

Neural substrates of song processing

Two interconnected subsystems in the songbird's telencephalon are important to auditory processing involved in sensory and motor song plasticity (Figure 1). One

Figure 1



The songbird song system is a specialized network of brain nuclei that are involved in singing and song learning. Not all song system nuclei (red) are shown; only the HVC, the robust nucleus of the arcopallium (RA) and the interfacial nucleus of the nidopallium (Nif) are included here. Arrows indicate synaptic projections between nuclei. The song system is present only in oscine songbirds and receives auditory input from secondary auditory regions (yellow): the caudal mesopallium (cM) and caudomedial nidopallium (NCM). In turn, secondary auditory regions receive input from primary auditory areas (green): the nucleus ovoidalis (Ov) and Field L. Primary and secondary auditory regions are present both in oscine songbirds and in songbirds lacking a song system (including oscine females in which the song system is present but substantially atrophied).

subsystem comprises primary and secondary regions of the auditory telencephalon, including the thalamorecipient zone Field L (which is analogous to mammalian primary auditory cortex), as well as secondary auditory areas, including the caudomedial portion of the nidopallium (NCM; formerly known as the caudomedial part of the neostriatum) and the caudal portion of the mesopallium (cM; designated cHV until the advent of the recently revised nomenclature of Reiner *et al.* [6]).

Another subsystem unique to oscine songbirds includes a network of brain nuclei specialized for singing and song learning (the 'song system' [7]). These areas are essential to learned vocal control but, similar to higher-level language areas in the human brain, are implicated in both sensory processing of song and song patterning [8,9]. Chief among these is the telencephalic nucleus HVC (used as a proper name), which receives indirect auditory input from the primary and secondary auditory areas [7]. The HVC

contains neurons with some of the most exclusive auditory responses yet to be characterized — they fire almost only in response to playback of the bird's own song (BOS) [10]. The function of these BOS-selective responses remains unclear, but their presence in a nucleus that is essential to song patterning has fueled speculation that they mediate song learning and maintenance.

Neural substrates for song recognition

Song recognition is important even in species that lack a song system and in female songbirds that do not sing. The auditory telencephalon is a prime site for neural processing important to song recognition, because it is present in both sexes of all bird species and it is activated in both sexes by conspecific song playback (e.g. see [11]). Recent evidence suggests that neurons in primary areas respond preferentially to conspecific songs over other sounds and that neurons in secondary areas develop response biases towards familiar songs.

Song attributes that drive responses in the auditory telencephalon

As expected of a system that has evolutionarily adapted to process behaviorally relevant sounds, Field L neurons show a strong response bias towards conspecific songs over even quite complex synthetic sounds. Grace *et al.* [12•] have shown that neurons in Field L and cM respond more strongly to conspecific songs than to synthetic sound ensembles designed to mimic the power spectra and amplitude modulation spectra of these natural songs. Interestingly, these neurons also respond preferentially to conspecific songs over BOS, suggesting that BOS selectivity emerges above Field L and cM.

A key issue is whether experience shapes the conspecific bias in Field L. In naive juvenile birds, which can imprint on conspecific tutor songs even in the absence of any social reinforcement, an innate bias could facilitate song recognition. Alternatively, conspecific response bias in Field L could arise through experience of other conspecifics, including the tutor, and thus could possibly constitute a tutor memory.

Another goal is to identify attributes absent in the artificial ensembles but present in natural songs that preferentially drive responses in the auditory telencephalon. The first statistical description of zebra finch song [13•] underscores that these songs, like other animal vocalizations but unlike environmental sounds, concentrate most power in low frequencies of temporal and spectral modulation (i.e. vocalists do not simultaneously trill rapidly and sweep through broad frequency ranges). Indeed, experiments using synthetic stimuli suggest that the modulation spectra of songs are even more salient than their frequency spectra in driving optimal responses of Field L neurons [12•].

Learned song recognition and response plasticity

An expectation of neurons involved in learned song discrimination is that their response properties should change as the bird learns to recognize a familiar song. Recent experiments in starlings — birds that produce songs comprising repeated, discrete multinote clusters (i.e. motifs) that are perceived as auditory objects — provide a compelling link between learned song recognition and response plasticity in the auditory telencephalon [14••]. In this case, the area of interest is the medial portion of cM (cmM), which receives auditory input from Field L and makes reciprocal connections with the NCM (Figure 1).

In adult starlings, cmM neurons are strongly biased in their responses towards familiar songs over novel songs after operant training using either of two task contingencies. Although birds in both task groups learned to discriminate familiar from novel songs equally well, the neuronal response distributions to familiar songs were

affected by the task contingency, suggesting that learning under different conditions influences the neural strategies used to recognize familiar songs. Furthermore, cmM neurons showed selectivity for the familiar songs — representing the first report of experience-dependent selectivity outside the song system [14••].

Selective cmM neurons were found to respond phasically to specific features, found only in a small subset of motifs, that could facilitate detection of the proportion of familiar motifs in a given song — an important cue for song recognition in starlings [15,16]. This region of the brain also seems to be strongly affected by the bird's past auditory experience, because less than half of the cmM neurons in wild-caught birds responded to any test songs, and no cmM neurons were selectively responsive to unfamiliar songs. Therefore, cmM neurons that become selective for familiar songs may be selected from a pool of neurons shaped by earlier auditory experience. This situation differs markedly from Field L, where most neurons respond to novel conspecific songs [17], and suggests that adult auditory experience can exert potent effects on the cmM network.

Tutor song memories

A related issue is where tutor song experience exerts lasting effects in the juvenile's brain. In temperate songbird species, sensory and sensorimotor learning are separated by 8–10 months, indicating long-term storage of tutor song memories before vocal recall. In zebra finches, which are the preferred experimental models in most songbird laboratories because of their rapid generation times, the sensory and sensorimotor learning phases overlap. This compressed developmental timetable makes it unclear whether juveniles are capable of long-term storage. By raising naive zebra finches with Bengalese finch tutors (whose songs differ from those of zebra finches) for the first month after hatching, and then preventing the birds from hearing their own song by exposing them to constant loud noise, Funabiki and Konishi [18••] have shown that zebra finches store tutor songs over the long term.

Thus, long-term storage may be universal among songbirds, even among those that are rapid learners. A clue to where long-term memories of the tutor song are stored may lie in the observation that the amount of immediate early gene (IEG) expression evoked in the NCM of adult zebra finches by tutor song playback correlates with the number of song elements copied from the tutor [19]. Importantly, this tutor song-evoked IEG expression does not seem to depend on acoustical similarities to the BOS, consistent with an auditory memory [20]. A necessary goal of future studies will be to determine whether or not such changes in IEG expression are paralleled by the development of a response bias to the tutor song at the single neuron level.

Emergence of BOS selectivity

In contrast to neurons in the avian auditory telencephalon, neurons in the song system are most responsive to BOS [21]. Determining how BOS selectivity arises is of interest because experience-dependent mechanisms are necessarily involved and because neurons sensitive to self-generated vocalizations could mediate auditory feedback. Until recently, experimentalists surmised that BOS selectivity, quantified as a suprathreshold response bias towards forward BOS over either reverse BOS or other conspecific songs, was an emergent property of the HVC network, because Field L neurons are largely nonselective [17,21]. More recent evidence shows that BOS selectivity arises before the HVC, in its auditory afferent, the song nucleus NIf (M Coleman, R Mooney, unpublished; [17,22[•]]). Therefore, auditory experience may act at synapses in the NIf, or perhaps even earlier in the ascending auditory system, to shape BOS-selective responses over the course of development. This result redirects the search for the origins of BOS selectivity to the NIf, to areas anatomically interposed between Field L and the NIf, and to other auditory afferents to the NIf, possibly including the auditory thalamus.

Although BOS-selectivity does not arise in HVC, an enhancement of auditory selectivity does occur at this site. *In vivo* intracellular recordings reveal that BOS playback evokes more temporally sparse action potential responses in HVC and that NIf neurons fire to a wider range of auditory stimuli than do HVC neurons (M Coleman, R Mooney, unpublished). Blocking inhibition in individual HVC neurons augments firing evoked by BOS and other stimuli [23[•]], implicating local inhibition in sparse firing patterns. These results suggest that the HVC local circuit transforms a more broadly tuned auditory input from NIf, yielding a temporally sparse and more BOS-exclusive song representation in HVC.

Although the exact function of such sparse song representations remains unknown, several observations suggest that they could facilitate song learning and maintenance. First, similarly sparse firing patterns are shown by HVC projection neurons during singing [24], which may enable the auditory representation of the bird's song to be compared directly with the pre-motor activity signature giving rise to the sound. Second, higher-order sensory neurons in other systems fire sparsely [25–27], a pattern that is thought to simplify comparisons of the stimulus with relevant memories. Third, modeling studies indicate that, by limiting bursts from HVC pre-motor neurons to only once per song phrase, the pace of song learning can be maximized [28], because an error signal altering the activity of that neuron will modify only a single element in the song phrase. Ultimately, the generation of sparse song representations in HVC is likely to have important consequences for song behavior.

Auditory gating in the song system

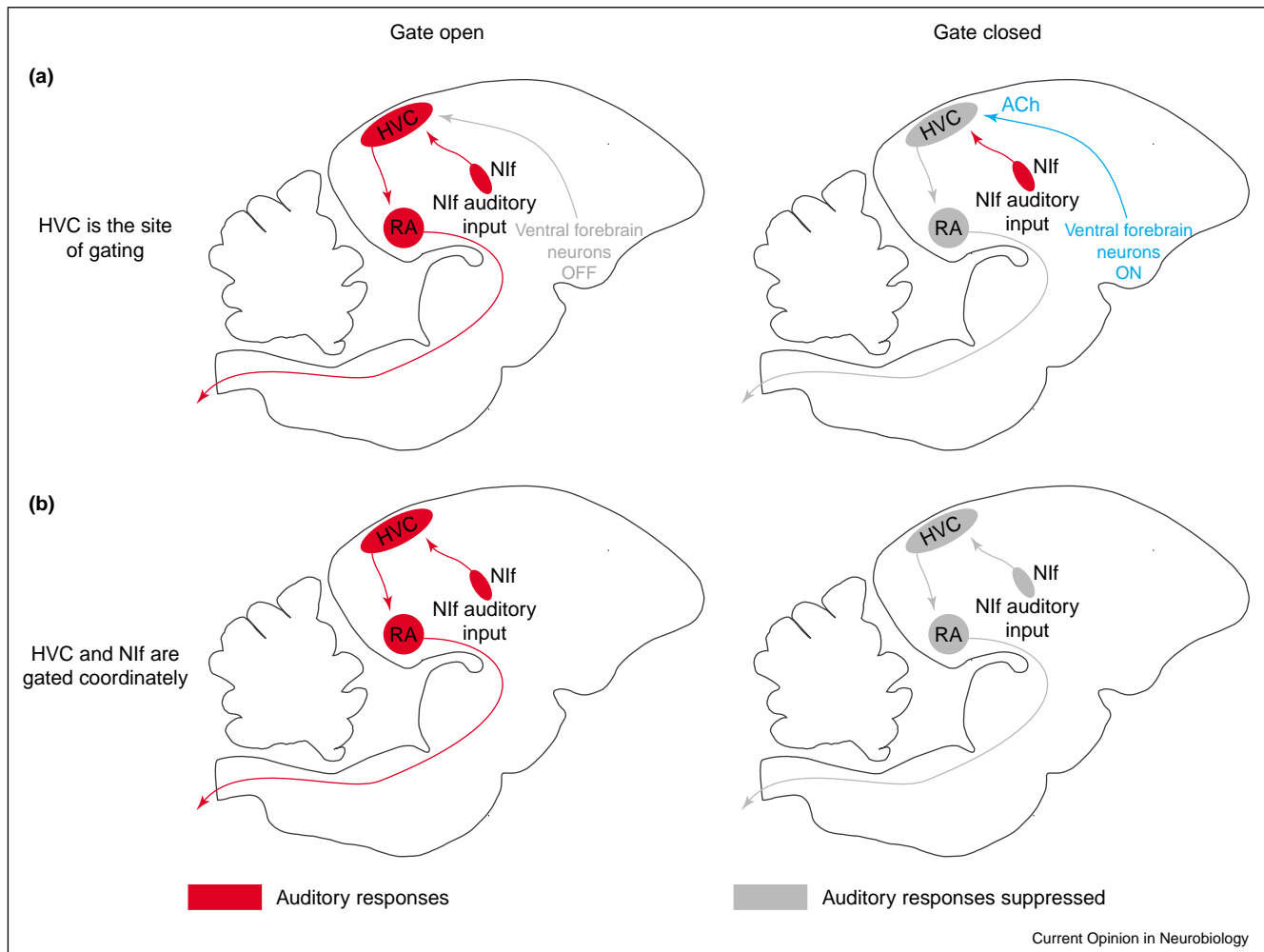
A remarkable feature of HVC auditory activity in adult male zebra finches is that BOS-evoked responses are highly robust under anesthesia or during sleep, but they diminish on waking [29,30]. Although the function of gating remains unknown, the absence of auditory response modulation in Field L [22[•],30,31] indicates that auditory signaling is carefully regulated only in the pre-motor areas, where it presumably acts to modify vocal output. One idea is that attention can open or close the gate, thereby dictating when audition-dependent vocal modification may occur. Gating may be especially important in adult songbirds in species such as the zebra finch that must sing stable songs to attract mates but that also rely on auditory feedback to maintain song stability.

An important caveat is that state-dependent gating does not characterize HVC auditory activity in all songbirds. Early electrophysiological studies reported strong auditory activity in the HVC of waking canaries and white-crowned sparrows [32,33], two species lacking the high degree of sociality that is a somewhat peculiar trait of the zebra finch. Perhaps auditory gating is a special adaptation in zebra finches that carefully filters out song-evoked activity except when the bird is relatively isolated from other singers.

Recent studies of state-dependent auditory modulation in the zebra finch song system have led to a possible physiological mechanism and locus of the gate (Figure 2). Initial evidence placed the gate in the HVC, because infusing norepinephrine (NE) into the HVC, but not into the robust nucleus of the arcopallium (RA), suppresses auditory activity in the RA [34]. In this model, auditory activity in HVC neurons that project to the RA is directly or indirectly suppressed by neuromodulators, which close the gate. More recently, Shea and Margoliash [35^{••}] showed that stimulating ventral forebrain neurons that supply cholinergic input to the HVC also strongly suppresses auditory activity in the HVC and the RA, an effect that can be partly blocked by infusing cholinergic antagonists into the HVC. These recent experiments suggest that endogenously released acetylcholine from basal forebrain neurons is the gating molecule, but they do not resolve whether the effects of NE reflect a physiological role of endogenous NE. Auditory gating in song pre-motor areas thus seems to be under the control of neuromodulators, which are in turn influenced by arousal owing to social interactions with other birds.

Gating also occurs before the HVC, hinting that auditory gating occurs more globally. By intermittently arousing lightly sedated birds with brief air puffs, Cardin and Schmidt [22[•]] found that auditory responses are co-modulated in the NIf and the HVC. This result raises the

Figure 2



Proposed models of auditory information gating in the zebra finch song system. **(a)** In the first model, HVC is the site of gating. The putative mechanism at work in this model is that cholinergic input from the ventral forebrain suppresses auditory responses in HVC. It is possible to block this action by infusing cholinergic antagonists into HVC (Data taken from [35**]). **(b)** In the second model, there are three possible mechanisms for HVC and NIf to be gated coordinately. First, that NIf is the primary site of auditory gating, which indirectly silences HVC. Second, that HVC and NIf receive common auditory input that is modulated. Or third, that HVC and NIf receive common neuromodulatory input (Data taken from [22*]).

possibility that the primary site of modulation lies in the NIf, that these two areas receive a common input that undergoes modulation or that a similar neuromodulatory input acts to modulate auditory responsiveness at both sites in parallel.

The results of Shea and Margoliash [35**] suggest that at least part of the gate must be located in the HVC, and known anatomy supports either of the last two schemes. The thalamic nucleus Uva innervates both the NIf and the HVC, and the NIf and the HVC are densely innervated by cholinergic and other neuromodulatory inputs [36], raising the possibility that auditory activity is gated in parallel at these two sites. In addition, gating in the

HVC does not seem to involve all cell types equally, with at least one class of interneuron maintaining auditory responsiveness in the waking state [37].

As discussed in more detail in this issue by Hurley *et al.*, neuromodulators can dynamically reconfigure sensory as well as motor systems in a state-dependent manner. In the songbird, the selective reconfiguration of the HVC microcircuit by neuromodulators could have implications for both the generation of variable song patterns and auditory processing important to sensorimotor integration. Ultimately, future studies will need to use *in vivo* pharmacological manipulations to test the underlying assumption that gating is important to song learning

and/or maintenance, and to determine if the same circuits are dynamically reconfigured to produce and perceive different song patterns.

Conclusions

We have highlighted recent advances that strengthen the connection between song recognition and processing of birdsong in the auditory telencephalon and have provided a potential mechanism as well as a locus where auditory responses may be gated as a function of the animal's state. Taken together, these findings give rise to a possible neural substrate for the formation, storage and recall of auditory memories, as well as a mechanism by which the properties of that substrate may be regulated. These phenomena and mechanisms are probably important in integrating learning of the BOS and learned recognition of familiar versus novel songs of neighboring birds.

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