

Chapter 3

New Insights into the Avian Song System and Neuronal Control of Learned Vocalizations



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Abstract The songbird brain contains a network of structures that are specialized for imitative vocal learning. Over the past few years, many new insights have emerged about the structure and function of that system. Among those insights are understanding how specific pathways contribute to specific aspects of vocal behavior, such as control of the acoustic properties of the vocalizations, control of the sequence in which those sounds are produced, and production of calls as well as songs. New research also has indicated that sites outside of the canonical vocal communication system play key roles in the learning, perception, and performance of the sounds used in vocal communication. This chapter details many of those insights and advocates for an expanded perspective on the vocal communication system as a set of interconnected nuclei that are specialized for the production of not only songs but also multiple types of learned signals used in vocal communication. In addition, several new experimental tools and approaches are highlighted that will allow deeper investigations into fundamental questions about the neural basis of learned vocal communication.

Keywords Auditory · Canary · Cortex · Finch · Learned vocal communication · Songbird · Sparrow · Striatum

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3.1 Introduction

Knowledge of the songbird vocal communication system is expanding at an increasing pace. With the advent of new experimental tools and the insights gained from these tools, studies of songbird neurobiology open the door to even broader questions. For example, how does the brain serialize individual actions into behaviorally meaningful sequences? How does the brain compute and employ error signals to refine subsequent behaviors? How does the nervous system store and recall memories to guide behavioral performance? The results and perspectives that are highlighted here make it clear that neurobiological research using songbirds holds the promise of yielding answers to these and other questions regarding the sensorimotor mechanisms that underlie learned behaviors.

3.2 Historical Perspective

3.2.1 *The Canonical Song System*

The songs performed by thousands of songbird species are learned behaviors that require juvenile auditory experience and ongoing auditory feedback to master and maintain the song. Beginning with the discovery that the songbird brain contains a network of discrete sites and circuits (Fig. 3.1) dedicated to song perception and

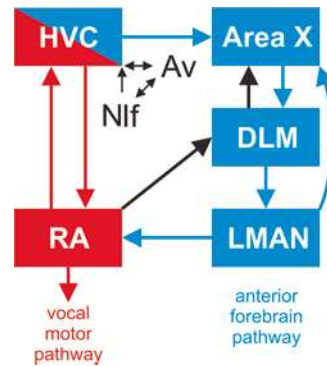


Fig. 3.1 Components of the song system. When the song system was first described, a role for five sites arranged into two interconnected pathways was highlighted (*red*, vocal motor pathway; *blue*, anterior forebrain pathway). In the years since those seminal experiments, additional connections between those sites have been found (additional connections are represented using *black arrows*), and new sites have also been identified as important contributors to song learning and maintenance (additional sites are represented using *black letters*). *Area X*, vocal portion of the avian basal ganglia; *Av*, avalanche; *DLM*, dorsolateral nucleus of the medial thalamus; *HVC*, sensorimotor cortical nucleus; *LMAN*, lateral magnocellular nucleus of the anterior nidopallium; *Nif*, nucleus interfaccialis; *RA*, robust nucleus of the arcopallium

Table 3.1 Abbreviations

| | |
|-------------------|--|
| AFP | anterior forebrain pathway |
| Av | Avalanche, a ventral region in CM |
| CM | caudal mesopallium |
| CMM | caudomedial mesopallium |
| DLM | medial portion of the dorsolateral thalamic nucleus |
| Field L | primary auditory cortex |
| HVC | used as proper name for vocal motor nucleus in the nidopallium |
| HVC _{Av} | HVC cells that project to Av |
| HVC _{RA} | HVC cells that project to RA |
| HVC _X | HVC cells that project to Area X |
| LMAN | lateral magnocellular nucleus of the anterior nidopallium |
| NCM | caudal medial nidopallium |
| NIf | nucleus interfascialis of the nidopallium |
| RA | robust nucleus of the arcopallium |
| UVA | nucleus uvulaeformis |
| VMP | vocal motor pathway |

performance (Nottebohm et al. 1976), researchers have sought to understand how this *song system* enables imitative learning. That seminal experiment, and many studies that followed, revealed five interconnected brain sites that are closely associated with song performance: the sensorimotor cortical nucleus HVC (used as a proper name for the vocal motor nucleus in the nidopallium all abbreviations appear in Table 3.1), the motor cortical nucleus RA (robust nucleus of the arcopallium), and specialized regions of anterior forebrain (lateral magnocellular nucleus of the anterior nidopallium, LMAN), the basal ganglia (Area X) and the thalamus (dorsolateral nucleus of the medial thalamus, DLM) (Reiner et al. 2004; Mooney et al. 2008). Among those sites, HVC plays an especially important role because injury to HVC is associated with deficits in both song performance (Nottebohm et al. 1976) and song perception (Brenowitz 1991; Gentner et al. 2000) and because the activity of HVC neurons plays a central role in song learning (Roberts et al. 2012; Roberts et al. 2017). Consistent with a key role for HVC in learned vocal imitation, HVC activity encodes sensory and motor information about song performance (Katz and Gurney 1981; McCasland and Konishi 1981). Furthermore, HVC is the origin of two pathways (Fig. 3.1): the *vocal motor pathway* (VMP) through the motor cortical nucleus RA, and the *anterior forebrain pathway* (AFP) through the basal ganglia Area X. Both of these pathways play key roles in vocal learning (see Sakata and Yazaki-Sugiyama, Chap. 2; Leblois and Perkel, Chap. 4).

3.2.2 Composition of the Song System and Functions of Specific Components

The VMP includes axonal projections from cell bodies in HVC to the motor nucleus RA (Fig. 3.2). Lesions to either HVC or RA result in vocal deficits such as “permanent and complete elimination of the audible components of song” (Nottebohm et al. 1976). Through these projections from HVC to RA and from RA to targets downstream, the VMP exercises control over brainstem motor neurons that control the muscles of the vocal organ and the associated respiratory structures (Schmidt and Wild 2014; Wild and Botelho 2015). The HVC neurons that project to RA (HVC_{RA} cells) are active during singing in a cascade of activity from one neuron to the next (Hahnloser et al. 2002; Lynch et al. 2016). Focally cooling HVC neurons disrupted the kinetics of HVC activity and resulted in the slowing of song performance (Long and Fee 2008; Andalman et al. 2011); whereas, focally warming HVC had the opposite effect (Long and Fee 2008). This led researchers to suspect that temporal features may be primarily controlled by forebrain circuits including HVC, but some aspects of song timing may be controlled by sites outside of HVC and the VMP (considered further in Sect. 3.3.4).

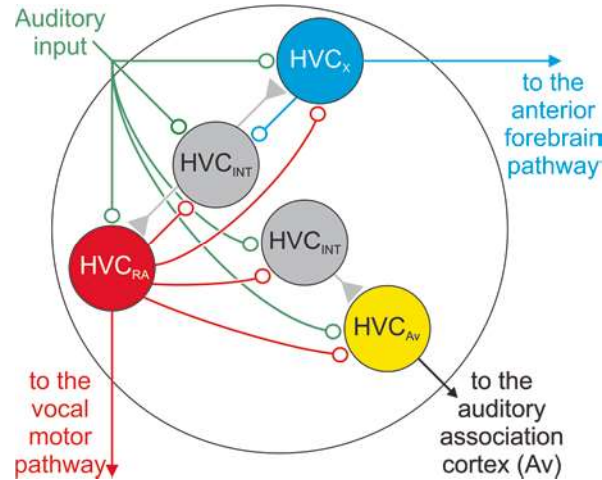


Fig. 3.2 The vocal motor pathway and anterior forebrain pathway emerge from the HVC microcircuit. Three types of neurons that project their axons to sites outside of HVC and at least two classes of locally projecting interneurons (gray HVC_{INT}) are arranged in a local HVC microcircuit that gives rise to three pathways: a projection to the vocal motor nucleus RA (red HVC_{RA} cells), a projection to the avian basal ganglia nucleus Area X (blue HVC_X cells), and a projection to the auditory association cortical area Avalanche (Av; yellow HVC_{Av} cells). As noted in Figs. 3.1 and 3.3, this local HVC microcircuit is interconnected with many other sensory and motor sites to enable feedback-dependent imitative vocal learning. See Table 3.1 for all abbreviations. (adapted from Prather 2013)

The motor nucleus RA integrates input from HVC and from another pathway into which HVC neurons project, the AFP (Fig. 3.1). The AFP begins with projection neurons from HVC to the specialized basal ganglia nucleus Area X (HVC_X cells). Area X neurons project to the thalamic nucleus DLM, which projects to the cortical nucleus LMAN, which in turn projects onto the VMP at the level of RA and projects back to Area X (Fig. 3.1). The relative influence of HVC versus LMAN on the activity of RA neurons varies over the course of development: LMAN has the dominant influence during early development, and HVC affects RA far more strongly in the adult state (Aronov et al. 2008; Oveczky et al. 2011). In contrast to the VMP, experimental lesions within the AFP did not prevent birds from singing. Instead, lesioning in AFP impaired a bird's ability to imitate tutor songs and prevented motor exploration for trial-and-error learning. For example, lesions of either LMAN or Area X in zebra finches (*Taeniopygia guttata*) had little or no effect on the production of stereotyped song by adult birds but prevented normal song development in juvenile birds (Sohrabji et al. 1990; Scharff and Nottebohm 1991). Those results suggested that Area X and its projections within the AFP may be important for either learning or improving the bird's imitation of a tutor song through vocal practice. Support for that idea also comes from the observations that exposure to tutor song for as little as one day was sufficient to enhance vocal learning significantly and to stabilize dendritic spines on HVC_X neurons (Roberts et al. 2010; Chen et al. 2016). These data highlight HVC_X neurons as central mechanisms through which experience can influence vocal performance.

Area X neurons project to the thalamic nucleus DLM, and DLM neurons are entrained to their inputs from Area X with very high precision (Goldberg et al. 2012). Furthermore, lesions in DLM largely abolished the normal variation present in the babbling of young birds and caused a dramatic increase in song stereotypy (Goldberg and Fee 2011). While much remains to be explored regarding the function of DLM neurons, those data suggest that DLM also plays a key role in the variation in vocal behavior that occurs during song learning.

DLM neurons project to the cortical nucleus LMAN, and normal activity in LMAN is essential for vocal learning (Bottjer et al. 1984). LMAN neurons that project to RA are thought to introduce variation into the performance of song features that are controlled by activity in HVC and RA, as variance of these features was vastly decreased when the output of the AFP was inactivated (Oveczky et al. 2005). In addition, blocking the output of the AFP during tutoring prevented the gradual improvement in imitation that normally occurs during song learning (Charlesworth et al. 2012; Ali et al. 2013). Thus, both the AFP and the VMP exert their influences on vocal control through their projections onto the motor cortical nucleus RA, and it is through these pathways that the song system controls song learning and performance.

Historically, experience-dependent vocal learning has been most closely related to the five structures within the VMP and AFP (Fig. 3.1). However, those brain areas are interconnected with other sites that are also responsive to auditory stimuli and are active during vocal performance. The following sections highlight advances in

knowledge of how sites in the VMP and AFP function and how they may work in concert with additional sites to form the neural basis of learned vocal communication.

3.3 New Insights Into the Function of Sites in the Canonical Song System

3.3.1 *Role of HVC in Imitative Learning*

Across the population of HVC cells, different projection neurons respond to different portions of the adult song, providing a spatially intermingled representation of the vocal repertoire (Peh et al. 2015). In addition to that sensory representation, some neurons can represent both the adult song and tutor songs that the bird heard only during juvenile development (Prather et al. 2010; Moseley et al. 2017). While those cells respond to both a tutor song and the bird's imitation of that model (Moseley et al. 2017), the co-representation is not simply a result of acoustic similarity between those song types because the strength of auditory response is not predicted by the degree of acoustic similarity between the tutor song and the bird's copy (Prather et al. 2010; Moseley et al. 2017). Intriguingly, the prevalence of these co-responsive cells, termed *bridge cells*, is directly related to the bird's accuracy of imitative learning: birds that possess greater numbers of bridge cells also achieve better learning outcomes (Moseley et al. 2017). These data provide mechanistic insight into how HVC may contribute to imitative vocal learning. Auditory-responsive cells are located throughout HVC, cells that represent different portions of the vocal repertoire are spatially intermingled, and the number of cells that are co-responsive to both the bird's own song and tutor song is correlated with the accuracy of imitative learning (see Sakata and Yazaki-Sugiyama, Chap. 2).

3.3.2 *Activity of HVC During Singing*

HVC neurons are active when birds produce the sounds and the silences that compose their songs, and projection neurons generate brief bursts of action potentials at very precise points in the song (Hahnloser et al. 2002; Prather et al. 2008). Activity across the population of HVC projection neurons is nearly uniform in its distribution of activity throughout the syllables and gaps that compose song (Lynch et al. 2016). Rather than being tightly organized around specific motor gestures, as had been hypothesized (Amador et al. 2013), the activity of HVC_{RA} neurons appears to proceed in a way that is not directly coupled to specific movements. The population of HVC_{RA} neurons expresses a continuous cascade of activity

throughout the song (Lynch et al. 2016; Picardo et al. 2016): each syllable is driven by a population of HVC_{RA} neurons that is transiently active at each point in the song, and different populations drive different patterns of activity in the downstream motor pathway.

Several lines of evidence suggest that HVC generates the timing of individual song elements through neurons organized in a synaptic chain. Different mechanisms have been proposed through which that organization may be achieved (Hamaguchi et al. 2016; Galvis et al. 2017), but the common theme in those scenarios is the organization of neurons into chains of sequenced activity that direct song behavior. In these proposed synaptic chains, a population of HVC neurons acts like a clock producing a continuous series of “ticks” in which each tick leads to the activation of an ensemble of neurons in RA to produce the specific features that compose the corresponding portion of the song (Fee et al. 2004; Lynch et al. 2016). Some researchers have proposed that such chains may reside in HVC and control only timing (Long et al. 2010; Lynch et al. 2016). Others have proposed that multiple chains may exist in HVC and control both timing and sequencing (Galvis et al. 2017), and speculations have been mixed regarding the possible contributions of pathways that reside outside of HVC (Hamaguchi et al. 2016; Galvis et al. 2017). Additional research is necessary to more fully understand how these networks may give rise to the different phonology and syntax expressed by different songbird species, but the data suggest that circuits within HVC form part or all of a circuit that underlies the generation of song timing.

3.3.3 *Function of the Vocal Motor Pathway in Singing*

Within the VMP, manipulation of activity in HVC alters the temporal features of song, whereas manipulation in RA alters acoustic features. For example, altered androgen signaling in RA induced changes in the spectral properties of syllables but not their sequencing; however, similar manipulations in the upstream nucleus HVC induced changes in syllable sequencing but not acoustic features (Alward et al. 2017). In addition, pharmacological suppression of inhibition in RA produced robust and consistent increases in syllable pitch and amplitude; increasing inhibition in RA decreased syllable pitch and amplitude (Miller et al. 2017). Those results indicated that vocal performance is closely related to a precise balance of excitation and inhibition within the local network of RA. Additional experiments revealed that millisecond-scale changes in the activity of neurons in the VMP can result in changes in the output of the muscles used in respiration and control of the vocal organ (Srivastava et al. 2017). Even very subtle changes in the activation of those neurons and the associated muscles can result in song changes ranging from small differences in phonology to impairments of frequency modulation or elimination of certain syllables altogether (Sober et al., 2008; Mencia et al. 2017).

3.3.4 Neural Basis of Vocal Sequencing

Birdsong is like human language in that both skills require that individuals learn and apply syntactical rules. Acquisition of those skills can be quite challenging; for example, grammatical complexity is usually not fully mastered until at least seven years of age (Skeide and Friederici 2016). Similarly, the proper sequencing of individual sounds is essential to communication through song, and birds must learn the syntax of their songs just as they learn the phonology of individual notes (Prather et al. 2017; ten Cate 2018). In that process of learning vocal syntax, birds possess biological predispositions toward certain species-typical patterns, suggesting that neural or motor constraints may contribute to sequence-learning biases (James and Sakata 2017); however, those possible biases are not very restrictive since results from Bengalese finches (*Lonchura striata* var. *domestica*) revealed that birds can still express behavioral flexibility (Warren et al. 2012). This flexibility indicates that sequencing of the sounds that birds use in vocal communication does not reflect hardwired premotor circuitry. Instead, sequencing appears to be at least partially under active control.

Experimental manipulations revealed that activity in HVC plays a very significant role in shaping vocal sequence. Microlesions of the medial portion of HVC resulted in an increase in atypical syllable transitions in zebra finches (Basista et al. 2014). Similarly, cooling HVC in Bengalese finches altered not only the song tempo but also the probability that the bird would perform specific sequences (Zhang et al. 2017). Altered androgen signaling in HVC in canaries (*Serinus canaria*) also is associated with changes in syllable sequencing (Alward et al. 2017). In contrast, neither cooling nor altering the androgen signaling in the downstream motor area RA had any detectable effect on song syntax. Together, these studies make it clear that activity of neurons in HVC plays an important role in arranging individual vocal behaviors into behaviorally meaningful sequences.

HVC exerts its influence on vocal sequencing through activation of RA (VMP) and downstream motor neurons, but whether the AFP may also contribute to the control of vocal sequencing remains unclear. For example, lesions to the input of the AFP (Area X) abolished a zebra finch's ability to learn spectral features but left modification of temporal structure largely unchanged (Ali et al. 2013). In addition, lesions to the output of the AFP (LMAN) affected the spectral properties of Bengalese finch song syllables but not the sequence in which those syllables were produced (Hampton et al. 2009), suggesting that the AFP plays no role in vocal sequencing. In contrast, other authors found that pharmacological manipulations that increased the level of activity in LMAN (Hamaguchi and Mooney 2012) or the expression of specific genes in Area X (Tanaka et al. 2016) could induce sequence variability in adult zebra finches. Thus, findings have been inconsistent regarding the role of the AFP in sequencing, but they suggest the AFP plays little or no role in controlling that aspect of learned vocal behavior.

Studies of the neural basis of vocal sequencing have also suggested that circuits outside of the song system (but that feed into the song system) contribute to vocal

sequencing. For example, bilateral lesions of the thalamic nucleus uvaeformis (UVA) caused long-lasting song degradation (Coleman and Vu 2005). Those deficits can improve over time, but subtle changes in syllable sequencing can sometimes persist even after other parts of the song have recovered (Coleman and Vu 2005). The UVA receives synaptic drive from RA and projects to HVC (Coleman et al. 2007), suggesting that UVA could influence activity in the song system and thus play a role in shaping vocal sequencing. However, as in the previous consideration of a possible role for the AFP in vocal sequencing, studies of the effects of UVA have also yielded mixed results. For example, manipulating activity in UVA by focally cooling those neurons induced changes in the timing of individual elements but not in their sequence (Hamaguchi et al. 2016). Therefore, both of the pathways that emerge from HVC and are eventually recurrent onto vocal motor pathways (UVA and the AFP) may contribute to some features of vocal sequencing, but they apparently play a relatively minor role in that process.

In light of lingering uncertainty about the degree to which vocal sequencing is controlled by mechanisms residing in HVC and/or circuitry outside of HVC (that is recurrent onto the song system), it is especially interesting that the integrated control of phonology and vocal sequence may involve contributions from both HVC and the AFP. For birdsong and human speech, the fine phonological details of a specific vocalization can depend on the specific sequence in which that vocalization is embedded (Wohlgemuth et al. 2010; Bolhuis and Everaert 2013). In songbirds, the contributions of HVC and the AFP to this context specificity were realized through experiments in which presentations of song-contingent aversive stimuli were used to evoke changes in the properties of specific targeted syllables in Bengalese finch song (Tian and Brainard 2017). In songs of that species, a specific syllable can be performed as part of many different sequences (e.g., syllable A performed as part of $A \rightarrow B$ or $A \rightarrow C$ or $A \rightarrow D$). When aversive stimuli were delivered in association with one sequence context (e.g., stimuli delivered when syllable A was performed as part of $A \rightarrow B$), learned alterations of the properties of the targeted syllable could generalize across contexts (e.g., changes in A were also evident in $A \rightarrow C$ transitions). Moreover, this context-specific expression of contingent changes was strongly dependent on activity in the AFP (Tian and Brainard 2017). For example, following context-dependent changes to pitch (e.g., targeted changes to A in $A \rightarrow B$ that also caused nontargeted changes to A in $A \rightarrow C$), inactivation of LMAN caused larger changes to pitch for syllables in the targeted context ($A \rightarrow B$) than for the same syllable in the nontarget context ($A \rightarrow C$). The implications of those data from Bengalese finches are that the VMP may encode a relatively context-independent representation of a given syllable and that the AFP may provide a sequence-specific biasing signal to the motor pathway that enables the context-specific modulation of syllable features. The biasing signal may gradually modify the motor pathway representation such that the integrated control of spectral and sequential song features reflects a collaboration between mechanisms in the VMP and the AFP (Tian and Brainard 2017). An important goal of future research will be to continue to develop understanding of the neural mechanisms through which individual units of behavior (e.g., syllables) are learned and serialized into behaviorally relevant sequences (see Sect. 3.6).

3.3.5 *Expanding the Function of Neurons in the Song System*

In addition to songs, male songbirds also produce another form of learned vocalization: *calls*. Calls are typically shorter in duration and less complex in acoustic structure than syllables that compose song, and their relative simplicity initially led researchers to speculate that they are an innate behavior. However, behavioral studies have revealed that at least some aspects of call vocalizations are learned (Simpson and Vicario 1990).

Historically, relatively few studies have investigated the learning and performance of call vocalizations; instead, research has been focused primarily on songs because of their obvious dependence on sensory learning and ongoing auditory feedback (Mooney et al. 2008). However, researchers have become more interested in calls after the discovery that call performance is related to activity in the song system (see Elie and Theunissen, Chap. 7). For example, neural activity in the vocal motor nuclei HVC and RA is correlated with the production of calls by zebra finches (Hahnloser et al. 2002; Ter Maat et al. 2014), and blocking activity in song system structures reduces the precision of call timing and abolishes a bird's ability to avoid being "jammed" by predictable exogenous stimuli (Benichov et al. 2016). Additionally, lesions in HVC induced changes in call production in Bengalese finches (Murphy and Prather 2016; Urbano et al. 2016). Interneurons in HVC and HVC_x neurons that project into the AFP are active both when the bird performs a call and when the bird hears playback of those calls (Murphy and Prather 2016). Together, these findings reveal that the *song system* should be viewed as a set of interconnected nuclei that are not specialized just for song performance but are important for the production of multiple types of learned signals used in vocal communication.

3.4 An Expanded View of the Vocal Communication System

Originally, researchers thought that essential components of song learning (e.g., processing auditory feedback and comparing that information to a memorized song template to improve the quality of imitation) were functions of the canonical song system. These processes are now known to be associated with activity not only in those sites but also in additional areas of the songbird forebrain.

3.4.1 *Nucleus Interfacialis: An Interface Between Auditory and Vocal Motor Activity*

The nucleus interfacialis of the nidopallium (NIf) is part of a sensorimotor loop that connects auditory inputs to the VMP. The NIf is a major source of auditory input to HVC and is the primary driver of spontaneous activity in HVC neurons (Cardin and

Schmidt 2004; Coleman and Mooney 2004). Moreover, auditory activity in NIf plays a central role in how juvenile birds learn to imitate the sounds that they eventually include in their adult songs (Roberts et al. 2012; Lewandowski et al. 2013). In addition to being active in response to auditory stimuli, NIf neurons also are active during song production, with bursts of activity occurring prior to motor output (McCasland 1987; Lewandowski and Schmidt 2011). Singing-related activity in NIf is thought to play at least some role in how the brain sequences individual syllables to compose songs because bilateral lesions of NIf induced changes in song syntax in Bengalese finches but not in species like zebra finches that produce syntactically simpler songs (Hosino and Okanoya 2000; Cardin et al. 2005). However, experiments in zebra finches documented that transient inactivation (as opposed to permanent lesions) of NIf transformed their usual sequentially stereotyped songs into highly variable and unstructured vocalizations (Otchy et al. 2015; Piristine et al. 2016). These data suggest that the activity of NIf neurons may be an important component of the premotor activity underlying song performance but other components of the song system may eventually be able to compensate for its absence if NIf is permanently removed (see Pratt and Prather 2016).

Manipulations of activity in other regions outside of the song system also influence the activity of NIf and its downstream targets in HVC. For example, microinjection of fadrozole into a secondary auditory area, the caudal medial nidopallium (NCM), to focally inhibit estradiol synthesis induced changes in the selectivity of auditory responses of neurons in NIf and HVC (Pawlish and Remage-Healey 2015; also see Remage-Healey, Chap. 6). Thus, NIf may also act as a conduit through which other regions outside of the canonical song system can affect the activity of neurons in HVC and its downstream pathways (Coleman and Mooney 2004; Bauer et al. 2008).

3.4.2 *The Auditory Lobule Is Essential for Imitative Vocal Learning*

Vocal learning and the function of the song system are intimately dependent on auditory processing: auditory input is a key component of imitative learning, and both juvenile learning and adult song maintenance are dependent on auditory feedback (Mooney et al. 2008; Murphy et al. 2017). In songbirds, auditory processing is closely linked not only to HVC and the AFP but also to primary and secondary regions that are analogous to auditory cortical regions in mammals (Jarvis et al. 2005; Wang et al. 2010). These auditory cortical sites in songbirds have been implicated in the formation, storage, and recall of tutor song memory (Prather and Mooney 2004; Prather 2013) and are interconnected with HVC (Fig. 3.3), forming a sensorimotor loop that links the auditory and vocal motor systems (Akutagawa and Konishi 2010; Lewandowski et al. 2013). Because of this functional implication in learning and the anatomical connection with other sensorimotor structures,

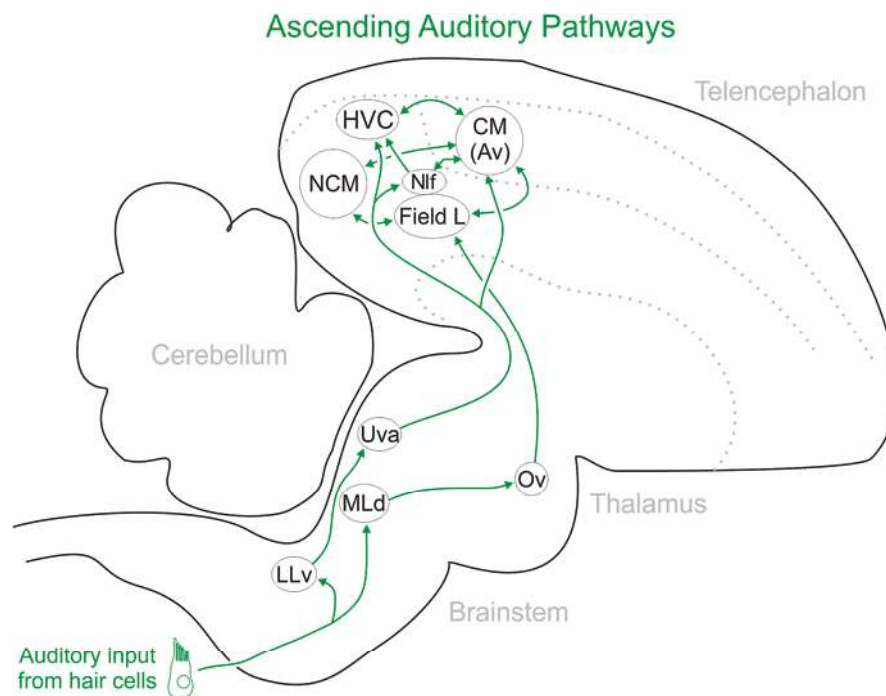


Fig. 3.3 Ascending pathways provide auditory input to the vocal communication system. The HVC and other elements in the canonical song system receive auditory input from hair cells of the inner ear along pathways that ascend in the songbird brain (see Elie and Theunissen, Chap. 7). Those sites play important roles in song learning and exert their effects by influencing activity in HVC and its downstream pathways. See Table 3.1 for all abbreviations. (adapted from Prather 2013)

auditory cortical structures outside of the canonical song system have become the focus of increasing amounts of research (see Sakata and Yazaki-Sugiyama, Chap. 2; Woolley and Woolley, Chap. 5).

The caudal mesopallium (CM) and the NCM are two such regions outside of the canonical song system that play important roles in the memorization and recall of tutor song (Gobes and Bolhuis 2007; London and Clayton 2008). These regions (described here as the auditory lobule) are advantageously positioned to serve such a role because they receive input from the primary auditory cortex (Field L; Fig. 3.3) and send projections to other forebrain sites including HVC (Bauer et al. 2008; Akutagawa and Konishi 2010). Experimental results have made it clear that these regions play a central role in the formation and retention of auditory memories and thus are essential for imitative vocal learning. For example, when cellular cascades are altered in the caudomedial mesopallium (CMM) and NCM during tutor sessions, juveniles produced poor copies of the tutor song (London and Clayton 2008; also see London, Chap. 8). Thus, the auditory cortical areas CMM and NCM are thought to contain the neural substrate for tutor song memory (Gobes and Bolhuis

2007; London and Clayton 2008). Moreover, these areas apparently act in concert with sites within the classically defined song system to shape vocal learning because impairment of song copying also occurred when activity in HVC was disrupted during tutor song exposure (Roberts et al. 2012) and because experience-dependent activity in CM influenced activity in HVC that guided vocal output (Bauer et al. 2008; Roberts et al. 2017).

In support of the idea that activity in the auditory lobule may contribute to vocal learning, neurons in the CMM and NCM appear to be predisposed to respond to songs that birds go on to memorize and learn. For example, CMM and NCM neurons were most likely to respond to songs with species-typical characteristics such as song syntax and rhythmicity (Lampen et al. 2017; Mello et al. 1992). Furthermore, auditory-evoked gene expression in CMM can reflect the behavioral relevance of the sounds because responses to familiar songs were greater than responses to novel stimuli (Gentner et al. 2004; Terpstra et al. 2004). The highly selective auditory responses of auditory lobule neurons are evident even in female songbirds, indicating that selective responsiveness to behaviorally relevant stimuli is an auditory characteristic of the cells in CMM and NCM and does not require the co-expression of learned vocal behavior (Diez et al. 2017). Elsewhere in the songbird brain, data from HVC revealed that the amount of auditory evoked gene expression in HVC was positively correlated with the strength of song learning (Terpstra et al. 2004; Bolhuis et al. 2012). Together, these data suggest that neurons in the auditory lobule, HVC, or a combination of both locations contain the neural representation of a tutor song memory that is compared against ongoing vocalizations to guide the bird's vocal learning.

In addition to evidence from studies of gene expression, electrophysiological recordings also confirm that activity in CMM and NCM is closely related to auditory and social experience. Recordings of neural activity in developing birds revealed that by the time the bird begins to sing, small numbers of neurons are selectively responsive to tutor song, and those cells are distributed across several forebrain regions, including the auditory lobule and HVC (Adret et al. 2012). Among the cells in the auditory lobule, NCM neurons responded differently to songs that were novel versus songs that were at least familiar or perhaps even served as tutor songs (Thompson and Gentner 2010). These data suggest that learning is associated with neuronal responses in which behaviorally relevant stimuli elicit less robust activity in NCM neurons than irrelevant stimuli, providing a possible mechanism through which experience can be tied to learning (but see Adret et al. 2012 and also Yanagihara and Yazaki-Sugiyama 2016). Selective responsiveness was also evident in the activity of CMM neurons, where cells showed increased activity in response to songs that had been learned through operant conditioning than to novel songs (Gentner and Margoliash 2003). Neurons in CMM were more selective and encoded more information about song components than neurons in the lateral portion of CM (Jeanne et al. 2011; Calabrese and Woolley 2015).

Reminiscent of what has been described in HVC, activity in the auditory lobule also extends to calls as well as songs. Specifically, neurons in CMM and NCM were selectively responsive to calls from specific individuals, and some neurons in

those regions could use degraded spectral content to discriminate the distance across which that call travelled before reaching the receiver (Menardy et al. 2012; Mouterde et al. 2017). Those neurons may contribute to recognition of not only the location but also the identity of the source of a vocal signal. CMM and NCM are highly interconnected (Vates et al. 1996), and selectivity of auditory responses in each area is greater than that observed in the primary auditory cortex (Field L) (Meliza and Margoliash 2012). Thus, activity coursing through CMM or NCM may constitute different cortical processing streams that encode different yet complimentary features of the learned behaviors that birds use in vocal communication (Meliza et al. 2010).

3.4.3 A Subregion Within the Auditory Lobule Links Sensory and Motor Brain Sites

Within the CM portion of the auditory lobule resides a subpopulation of neurons that have been implicated as playing an especially important role in linking sensory and motor activity in vocal learning. That population of cells resides in the ventromedial portion of CM and is called nucleus Avalanche (Av). Like its surrounding auditory cortical regions, Av is activated by auditory stimuli (Jarvis and Nottebohm 1997), but in contrast to the connectivity of other portions of CM or NC, Av is reciprocally interconnected with HVC (Akutagawa and Konishi 2010; Roberts et al. 2017). The connection from HVC into Av provides a mechanism through which motor-related signals may be integrated with activity in the auditory system. Such a means of conveying information from the vocal production pathway to the auditory system has been theorized to facilitate vocal learning (e.g., Troyer and Doupe 2000), and HVC_{Av} neurons are well positioned within the HVC microcircuit to provide that link (Fig. 3.2). In support of a role for HVC_{Av} cells in vocal learning, ablation of those neurons in juvenile birds disrupted the bird's ability to imitate features of an adult tutor's song (Roberts et al. 2017). In addition, ablation of HVC_{Av} neurons in adult birds interfered with the bird's ability to adaptively modify the duration of vocal elements but did not affect the production of previously learned songs (Roberts et al. 2017). These data reveal that the connection between HVC and Av provides a link between motor and auditory pathways that is essential for vocal plasticity. Interestingly, some neurons in the region of CM where Av resides provide polysynaptic input to midbrain dopaminergic regions that are speculated to generate error signals to guide vocal plasticity in both juvenile and adult birds (Mandelblat-Cerf and Fee 2014; Dunning et al. 2018). One possibility is that information may flow from HVC into Av to be compared against auditory feedback, with the result of that comparison passed to dopaminergic areas and used to reinforce the behavior associated with that feedback (Roberts et al. 2017; Hisey et al. 2018). An important goal of future research will be to test that possibility and to further resolve the causal relation between activity in these pathways and juvenile learning and adult maintenance of the sounds used in vocal communication.

3.5 New Tools to Explore the Function of Neurons in the Vocal Communication System

In the past few years, a number of new and innovative ways have emerged to reveal the function of neural circuits in the songbird brain. For example, there have been significant advancements in methods for electrophysiological recordings from neurons in awake and freely behaving birds, methods of imaging activity across neuronal populations, and methods for stimulating specific pathways using optogenetic techniques. The development and adoption of new experimental tools has opened the door to addressing questions that were previously intractable. These tools have advanced the ways in which songbird neurobiologists can sample or selectively manipulate the activity of individual neurons or populations of cells in the appropriate behavioral context and, thus, continue to reveal the mechanisms and functions of neurons in the expanded song system.

3.5.1 *Recording Activity of Identified Neurons in Freely Behaving Birds*

The ability to sample neural activity while birds are freely behaving is essential to investigate the neural circuits that underlie behavioral performance. In the early years following the discovery of the canonical song system, researchers were able to record from awake and freely behaving birds, but it was challenging to identify individual neurons among a population of simultaneously recorded cells (McCasland 1987; Yu and Margoliash 1996). The development of a miniature, motorized microdrive and the use of antidromic stimulation techniques facilitated the sampling of extracellular activity from individual, type-identified neurons as birds were engaged in singing and song perception (Fee and Leonardo 2001; Hahnloser et al. 2002). Moreover, the implementation of intracellular recordings in awake, singing birds has enabled the detection not only of action potentials but also subthreshold influences on song control that were previously invisible in extracellular recordings (Long et al. 2010; Hamaguchi et al. 2014). Microdrive recording systems have been adapted to be extremely lightweight (less than 1 g in their motorized configuration) (Jovalekic et al. 2017) and have incorporated additional data collection systems, such as a compass and accelerometer (M. Fee, personal communication), and telemetered recording (e.g., Schregardus et al. 2006; Hasegawa et al. 2015). These technologies continue to advance, and they will provide increasingly high-resolution insights into the neural circuits and patterns of cellular activity that underlie learned vocal communication.

3.5.2 Optical and Electrophysiological Methods

Microelectrode arrays and the ability to record from individual neurons over long periods of time have increased our knowledge of how neural activity is related to the acquisition and refinement of song behavior. Using carbon nanofibers arranged in an electrode array, it is possible to record from neurons in HVC for as long as 107 days (Guitchounts et al. 2013). Using electrode arrays, it is possible to simultaneously record from tens or perhaps even hundreds of sites in the brain, providing an electrophysiological approach to recording the activity of many neurons at once in sites that are deeper than imaging techniques may be able to sample. Sampling from neurons over long durations can allow researchers to potentially record from an individual neuron as it matures through plastic song development to stereotyped adult song (Okubo et al. 2015). These types of techniques will be central to our future understanding of how experience shapes motor performance to enable vocal learning and maintenance.

Similar to microelectrode arrays, which can sample many neurons simultaneously, imaging techniques can also discern the activity of many neurons at one time during behavior (Picardo et al. 2016; Katlowitz et al. 2018). Microimaging of cells and calcium imaging of voltage fluctuations have enhanced the scope of what is possible in songbird research. For example, head-mounted microscopes can be used in concert with fluorescent indicators to monitor calcium concentrations in relatively superficial structures such as HVC, and these types of techniques can enable sampling from the same population of neurons in freely behaving birds over the course of several weeks (Liberti et al. 2017). As in the case of electrophysiological recordings, these techniques will continue to provide insight into how the perception and performance of vocal behaviors emerge from the activity of multiple neuronal populations.

3.5.3 Selectively Activating Neurons to Discern the Function of Specific Pathways

In addition to recording the activity of neuronal populations, the ability to selectively manipulate the activity in those cells is also a powerful tool to understand how specific circuits contribute to auditory perception and vocal learning. The creation of optogenetic techniques gave the entire field of neuroscience the ability to use light to selectively excite or inhibit neurons with very high spatial and temporal resolution (Deisseroth 2015). This technique has since been adapted for use in songbirds and is beginning to reveal the role of specific cells in juvenile song learning (Roberts et al. 2012; Hisey et al. 2018) and adult song plasticity (Hisey et al. 2018; Xiao et al. 2018). Together with automated methods of monitoring behavior, optogenetics can enable precise stimulation of individual pathways, thus forming a

behavior-dependent, closed-loop experimental paradigm to investigate the role of specific pathways in specific aspects of behavior (Tanaka et al. 2018; Xiao et al. 2018).

3.5.4 *Manipulating the Genetic Environment*

With the continued development of ways to understand and control the genetic environment in songbirds (Agate et al. 2009; Liu et al. 2015), genetic techniques will further enhance our ability to identify the neural structures and functions that underlie vocal control and learning. For example, songbird researchers can induce neurons in specific regions of the songbird brain to express human genes that are thought to play important roles in speech development and pathology (Abe et al. 2015; Tanaka et al. 2016). With those genes expressed in songbirds, researchers can begin to gain insight into the mechanisms through which those gene products may impact cellular function to affect vocal performance (Burkett et al. 2018; Lovell et al. 2018; but see Mueller et al. 2016).

Gene expression varies throughout song learning and development (Olson et al. 2015; Burkett et al. 2018; London, Chap. 8). Manipulating the expression of specific gene products in focal sites (e.g., FOXP2 expression in Area X) during developmental sensorimotor learning can induce incomplete and inaccurate imitations of the tutor song (Haesler et al. 2007) and affect adult song control (Murugan et al. 2013). Because songbirds acquire their songs in a pattern that is strikingly similar to how humans learn the sounds used in speech (Prather et al. 2017), additional studies investigating the role of genes (e.g., FOXP2) in vocal learning deficits can lead to translational applications to human mutations and pathologies. In addition to that clinical relevance, genetic manipulation in songbirds can also be used to discern the mechanisms that regulate the divergence of sexually dimorphic features during development (Zhao et al. 2018). These tools will help researchers continue to reveal not only how insights from songbirds can help to advance human health but also how comparative studies may provide a deeper understanding of how individual gene products and their interactions shape brain development and function (Konopka and Roberts 2016; Mets and Brainard 2018).

3.6 Important Questions and Next Steps

The songbird brain provides an excellent context in which to investigate the neural basis of learned vocal communication. With the advent of many new tools and the strength of the research that has come before, future studies will yield unprecedented insight into how the brain enables an organism to perceive, learn, memorize, recall, and perform a series of complex individual behaviors in a specific sequence.

Those broad themes can be reframed as a series of important questions, each of which are briefly considered in the following sections.

3.6.1 How Does the Brain Serialize Individual Behaviors Into Meaningful Sequences?

The sequencing of individual behavioral units into behaviorally meaningful sequences is integral to many forms of behavior, and that is especially evident in the sounds used in vocal communication. Just as the content of this sentence would be altered if the words or letters were shuffled in their sequence, song syntax would be disrupted if the sequences of notes or phrases were rearranged. That impact is also evident in the activity of individual neurons: neurons in the vocal communication system are more responsive to songs with notes played in their natural sequence (Lewicki 1996; Prather et al. 2008). Similarly, female responses to song are altered when the sequencing of song elements is manipulated: females respond most robustly to the song of their preferred male when his notes are sequenced in his natural order (Dunning and Prather, in preparation).

As noted in Sect. 3.3.4, studies of how the songbird brain controls the phonology and sequencing of individual syllables have yielded varying results. Some findings have suggested that sequencing and phonology are encoded in separate pathways in the brain, while other data suggest that sequence and phonology are encoded through similar circuits. Additional studies incorporating a range of different techniques will be necessary to discern the amount of overlap in the circuits responsible for controlling the phonology and sequencing of individual song syllables. For example, researchers can take advantage of tools to alter singing-related auditory feedback by changing the pitch of that feedback, the timing of that information, or some combination of spectral and temporal changes (Sober and Brainard 2009; Wyatt et al. 2017). By altering different aspects of the feedback that a bird experiences during singing, researchers can induce different forms of adaptive changes in phonology or sequence, thus providing an experimental context that will be helpful in disambiguating the neural control of each of those aspects of learned song performance (Warren et al. 2012; Tian and Brainard 2017).

Insights gained from adult birds will be especially useful in guiding studies of juvenile birds undergoing song development. By comparing the patterns of neural activity detected in juvenile birds undergoing natural song variability (i.e., the *plastic song* phase of late development; Mooney et al. 2008) versus adult birds undergoing feedback-induced song variability, one can gain insight into the degree of similarity in neural substrates underlying these forms of vocal plasticity (Hisey et al. 2018).

3.6.2 How Does the Brain Compute and Use Error Signals to Refine Behavior?

The importance of auditory input is clear in the case of imitative vocal learning in juvenile birds, and auditory feedback continues to play a central role in the refinement of vocal behaviors and their maintenance throughout adulthood (Tschida and Mooney 2012; Murphy et al. 2017). These findings have led researchers to the following central questions: How does the brain compare current performance against a memorized model to guide the development and maintenance of vocal signals, and how does the brain compare motor commands against the associated auditory feedback to enable the refinement and maintenance of vocal behavior? By taking advantage of new tools, such as large-scale array recordings and imaging neural ensembles, songbird researchers will be able to continue resolving the neural circuits involved in the comparison of those signals. With the knowledge of how errors are computed and represented in specific patterns of neural activity, researchers will then be able to investigate the mechanisms through which error signals direct changes in the structures and functions of downstream motor pathways to enable adaptation (Gadagkar et al. 2016; Hisey et al. 2018). Insights into how errors are detected and encoded in the songbird brain will provide a search image for understanding how those processes also occur in the human brain, how sensorimotor interactions enable acquisition of new abilities, and how disruption of activity in those circuits may lead to the emergence of behavioral pathologies.

3.6.3 What Is the Neural Substrate for Learning and Memory?

Before a tutor song model can be recalled and used to guide the development of vocal imitation, a memory of that song must be formed and stored. A long-standing set of questions in the songbird field have been: Where is the memory of a tutor song stored, through what mechanisms and patterns of activity is that memory recalled, and how does that recalled memory act to shape subsequent vocal performances? Songbirds offer many natural behavioral advantages to address these questions. For example, in some species, the period of sensory learning (when the tutor song is committed to memory) is separated by many months from the period of sensorimotor learning (when the bird begins vocalizing and using feedback to refine its imitation of that model) (Mooney et al. 2008; Sakata and Woolley, Chap. 1). That natural pattern of vocal development provides a context in which to disambiguate the formation and storage of a memory versus the recall and use of that memory to guide ongoing behavior. In addition, some species sing a repertoire of song types that are acoustically distinct (Krebs and Kroodsma 1980), providing a context in which to identify how different tutor song models are represented as distinct engrams in the brain (Mooney et al. 2001; Prather et al. 2010). With the advent of new tools to enable researchers to record from individual neurons over extended periods of time, researchers may be able to monitor activity throughout juvenile development and

thus investigate the role of specific neurons in memory formation throughout sensory learning and memory recall during sensorimotor learning. Together, the experimental tractability of the songbird vocal communication system and the variety of investigations that are possible in that context highlight the value and broad relevance of songbird neurobiology for understanding the neural basis of learning and memory.

3.6.4 How Can Studying Songbirds Inform Understanding of the Human Brain?

Research has revealed that properties of the avian auditory cortex are more like those of mammalian neocortex than was previously appreciated. Specifically, a study revealed that neurons in a region of the chicken brain that corresponds to the mammalian auditory cortex (a complex including Field L and CM) are arranged in layers in which auditory neurons interact via radially arranged intrinsic connections (Wang et al. 2010). These layers do not correspond precisely to those that have been described in the mammalian neocortex, but they do reveal that defining characteristics of the neocortex are also present in the avian brain (Wild and Krutzfeldt 2010; Woolley and Woolley, Chap. 5).

Additional studies have also shown that, as in the human brain, lateralization of function occurs in the songbird brain (Long et al. 2016; Prather et al. 2017), and these findings may provide insights into the ways that factors such as fluency and early experience influence the neural substrate for language. For example, in birds that are sequentially tutored with two different songs, the pattern of lateralized dominance depends on the proficiency of learning from each tutor in each epoch of development (Olson et al. 2016). The greater the retention of song from their first tutor, the more right dominant the birds are when they are exposed to that song, which is indicated by greater EGR-1 expression in the right hemisphere than the left in response to song played through a speaker. The more the birds learned from their second tutor, the more left dominant they are when they are exposed to that song. Thus, song memories are preserved in a lateralized manner that is dependent on the proficiency of song learning (Olson et al. 2016). These similarities between features of songbird and human brains provide further motivation to use songbirds as an animal model in which to explore how auditory memories are stored, how they are recalled, and how that information is blended with ongoing sensory feedback to influence vocal motor activity.

3.7 Chapter Summary

Following the discovery of a neural network that is specialized for vocal learning in the songbird brain, researchers have sought to understand how that song system enables memorization of a tutor song model followed by comparison of that

memory against ongoing behavior to refine and maintain behavior. With the realization that some components of that network are analogous to cortical, striatal, and thalamic areas in the mammalian brain, birdsong research has the potential to help researchers understand not only how the nervous system enables experience-guided learning and memory but also how pathologies of the central nervous system afflict human cognition and behavior.

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