

# Birdsong: models and mechanisms

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Recent studies have provided important information concerning the neural signals that subserve vocal learning in songbirds: advanced signal processing techniques are beginning to clarify the behavioral trajectories followed by developing birds; single-unit physiology in behaving animals is providing important clues about sensory and motor representations during learning; *in vitro* whole-cell recordings are revealing patterns of synaptic communication; and experimental alterations in song behavior have advanced our understanding of specific structure–function relationships. The construction of theoretical and computational models will be crucial in integrating such disparate experimental results.

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## Abbreviations

<b>AMPA</b>	$\alpha$ -amino-3-hydroxy-5-methyl-4-isoxazole propionate receptor
<b>DLM</b>	dorsolateral nucleus of the medial thalamus
<b>EDL</b>	error-driven learning
<b>Hvc</b>	nucleus Hvc of the song system, acronym used as a proper name
<b>IMAN</b>	lateral portion of the magnocellular nucleus of the anterior neostriatum
<b>NMDAR</b>	<i>N</i> -methyl-D-aspartate receptor
<b>RA</b>	robust nucleus of the archistriatum
<b>RL</b>	reinforcement learning

## Introduction

Song learning in birds has emerged as an important model system for studying how complex problems in motor learning and sensorimotor integration are solved at the level of cells and circuits. Songbirds learn to sing by memorizing the song of an adult ‘tutor’. The tutor song serves as a template for evaluating auditory feedback from the juvenile’s own vocalizations, and the results of this evaluation are used to improve the quality of the developing bird’s song [1] (Figure 1). A key issue in song learning is where, when and how the results of this comparison are used to adjust neural circuits for song production (Figure 2).

Here, we briefly review recent experimental results and their relationship to basic models of song learning in the zebra finch (*Taenopygia guttata*), concentrating on the functional role of the lateral portion of the magnocellular nucleus of the anterior neostriatum (IMAN).

## Selective and instructive models of song learning

Although deafening experiments strongly support the template description of auditory feedback shown in Figure 1, the neural mechanisms underlying sensorimotor plasticity remain a mystery. For example, template information may act in a selective or instructive manner to guide song learning [2]. In a selective model, song learning results from the overproduction of innately encoded song elements or syllables, followed by a ‘selecting out’ of elements belonging to the tutor song. In instructive learning, the template information is used to drive the motor pathway beyond innately encoded behaviors toward the reproduction of the tutor song.

Recently, Tchernichovski *et al.* [3,4\*\*] investigated this distinction in a longitudinal study of the development of vocal behavior in zebra finches first exposed to tutor song at 40 days of age. Tutor exposure resulted in a sudden increase in the diversity of song features produced, and vocalizations became rapidly more structured and stable; however, accurate imitation of the entire tutor song occurred only gradually (according to the measure of advanced signal processing developed in [5\*]). Detailed acoustic analysis revealed that several syllables can emerge from very similar syllable prototypes. Moreover, some prototype sounds that were similar to tutor syllables, but that occurred out of order with regard to tutor sequence, were abandoned rather than being translocated to the correct temporal location. Although more complete analyses are needed, these results are consistent with instructive mechanisms and argue against the selection of pre-encoded song elements. But genetic factors may set species-specific predispositions towards both sensory and motor aspects of song [2,6], and may enable rapid acquisition of species-specific song [3].

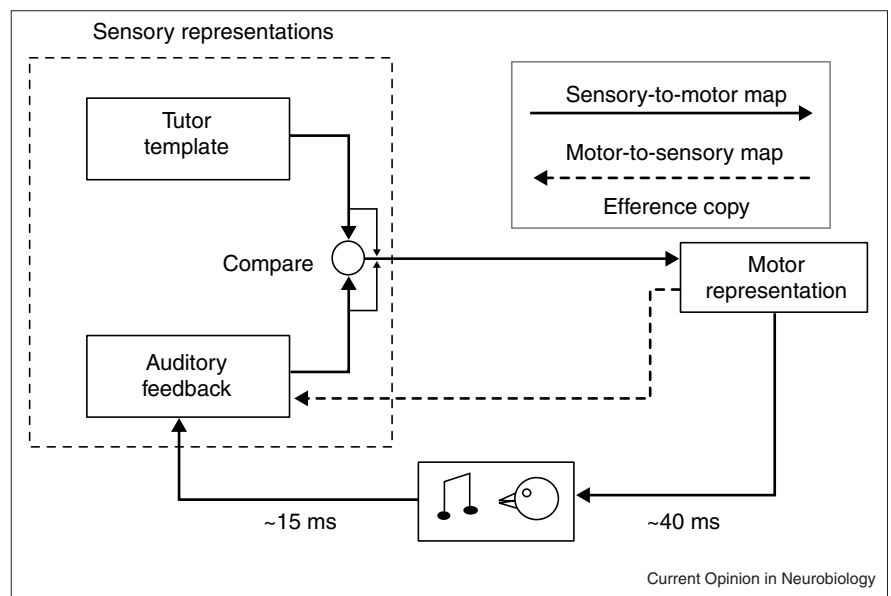
The instructive/selective distinction is closely related to the distinction between error-driven learning (EDL) and reinforcement learning (RL) strategies for song development. In EDL, song-related feedback is compared to the template, and resultant mismatches produce an ‘error signal’ that actively drives the motor system toward the tutor song. Thus, EDL is one form of instructive learning.

In RL, variability in song production results in a range of vocalizations and template comparison results in a graded evaluation of the degree of match to the tutor. This evaluation is sent nonspecifically to neurons in the motor pathway and is used to reinforce motor patterns that give a better match to the template. For example, a good match may act as a ‘gate’ for Hebbian plasticity, reinforcing connections between neurons that are co-active during tutor-like vocalizations [7,8\*\*].

Even though RL acts by selectively reinforcing appropriate patterns of motor behavior, it need not rely on the

Figure 1

Diagram showing the sensorimotor phase of song learning. In most models, auditory feedback from a juvenile bird's own song is compared with a previously memorized song or 'template.' In an EDL strategy, this comparison results in an error signal that actively drives the motor pathway toward reproduction of the tutor song. This strategy relies on a feature-based sensory-to-motor mapping so that errors computed in sensory coordinates can drive motor changes. In an RL strategy, comparison results in a graded evaluation of the overall match to the tutor that is used to reinforce motor patterns that give a better match to the template. Transmission of this nonspecific reinforcement signal does not require a detailed mapping from sensory representations onto the corresponding motor representations. Thin arrows indicate template and/or auditory feedback representations may affect motor activity directly without being explicitly compared. Any learning strategy must deal with the fact that auditory feedback is delayed (by 55 [= 40 + 15] ms or more) relative to the motor signal. A motor-to-sensory 'efference copy' transformation (dashed arrow) may be



important for reducing this delay, transforming motor signals into a prediction of the expected auditory feedback. Recent experiments by Dave and Margoliash [29\*\*]

strongly support the existence of a sensory-to-motor mapping that includes a predictive component. The functional significance of a sensory-to-motor prediction is unclear.

overproduction of innately encoded song elements. In particular, RL mechanisms can take advantage of small random variations in vocal output to continuously morph individual song elements toward the tutor song. Therefore, although the Tchernikovski *et al.* [4\*\*] results argue against overproduction and selection during zebra finch song development, they do not rule out RL.

### IMAN output as a comparison signal

Many experiments suggest that the projection from IMAN to the premotor robust nucleus of the archistriatum (RA) carries a signal related to template comparison. Most strikingly, lesions of IMAN in juvenile birds severely disrupt song learning, whereas lesions in adults have at most subtle effects on song production [9–11]. Experimental manipulations reveal, however, that IMAN lesions can affect song behavior in adults: IMAN lesions prevent both song plasticity that is normally associated with damage to the vocal nerve and delayed learning from a tutor in isolate-reared birds [12,13]. Moreover, the slow degradation of vocal production normally produced by deafening in adult birds [14] is prevented by lesioning IMAN [15\*]. Interestingly, the severity of deafening-induced song degradation is dependent on age [16,17], paralleling the effects of deafening in humans [18].

These results from IMAN lesioning are easily interpretable within the EDL framework: first, deafening results in a mismatch between aberrant auditory feedback and the template; second, the resulting error signal actively alters RA circuitry; last, IMAN lesions interrupt the error signal and hence prevent changes in song output [15\*].

Within the RL framework, it is difficult to see how the removal of a putative IMAN reinforcement signal could stabilize song; however, optimizing RL requires a balance between exploring motor space to find better solutions, and exploiting the improvements gained from past exploration [19]. It is possible that IMAN supports exploration in the motor pathway whenever there is a poor match between auditory feedback and the stored template. According to this hypothesis, the active role that IMAN plays during song development would decrease as the tutor song was copied. By causing a perceived mismatch between auditory feedback and the template, adult deafening would re-engage IMAN and actively destabilize the motor program, but IMAN lesions would prevent this destabilization. (For related ideas see [10,20–22].)

### Sensory-to-motor transformations

Although both EDL and RL can account for the behavioral and lesion data, a bright line distinction between these types of learning can be made at the circuit level. To drive specific changes in the motor pathway, EDL requires a feature-by-feature mapping between sensory and motor representations of song. In contrast, a nonspecific projection that signals the overall match to the template is sufficient for the graded evaluation used by RL.

According to the hypothesis that IMAN provides the error signal for EDL, the projection from IMAN to RA is a natural candidate for carrying out the required sensory-to-motor transformation. Consistent with this idea, the projection from IMAN to RA lacks a substantial degree of topographic

organization at the onset of song learning, but develops a refined pattern of connectivity during early stages of the sensitive period (between 20 and 35 days in normal but not deafened birds) [23–25]. These data support the notion that the IMAN–RA projection may be refined by specific learning, which is based on tutor song exposure or early vocal behavior, and may perhaps be the neural correlate of a sensory-to-motor mapping. Interestingly, this developmental pattern stands in contrast to the patterns of topographic organization within the anterior forebrain pathway, which are established at the onset of song learning and are not influenced by auditory deprivation [26\*,27].

The existence of a sensory-to-motor transformation, wherever its locus, raises the possibility that stored sensory representations might be used to drive motor circuits during song production, without being compared with auditory feedback from the bird's own song. In this direct template conversion strategy, auditory feedback is still required to learn and maintain the correspondence between sensory and motor representations. In a weaker form of template conversion, template information could be converted into a signal that biases motor output in the direction of the tutor song. This song could then be engrained within the motor circuit by continued motor practice [28\*].

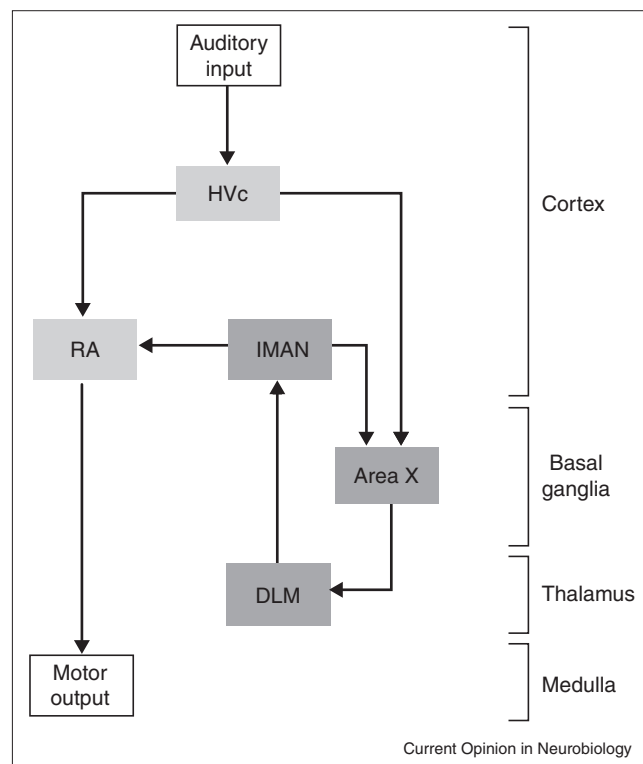
Recent experiments by Dave and Margoliash [29\*\*] demonstrate that a sensory-to-motor mapping does indeed exist. Using chronically implanted electrodes, they recorded activity of single neurons in RA. During singing, RA neurons produce bursts of action potentials, tightly timed to individual vocal gestures. When the bird is awake, RA does not respond to auditory stimulation. But when a bird is sleeping or drowsy, RA is responsive to auditory playback of the bird's own song, and, for a given neuron, the bursting pattern elicited by song playback is well matched to that displayed during singing. Intriguingly, 15% of the bursts recorded spontaneously during sleep also can be matched to patterns of premotor bursting.

These results support the idea that song neurons represent abstract 'features' of song using an encoding scheme that can be translated equally well into a sensory or motor representation. Under this 'sensory–motor correspondence hypothesis', auditory stimulation could engage premotor circuits used during singing. Consistent with this notion, song system auditory responses are highly selective, emerge during the period of sensorimotor learning, and are maximal for playback of the bird's own song (reviewed in [30,31]; see [32] for evidence of tutor song selectivity).

### Delays, predictions and motor-to-sensory transformations

It is likely to take 55 ms or more for the effects of premotor activity in RA to return in the form of auditory feedback (40 ms RA-to-motor output plus minimum auditory latencies of 15–20 ms [33–35]). Estimates of the total delay for signals passing through the anterior forebrain

Figure 2



A highly simplified diagram showing the principal circuits in zebra finch brain that control vocal learning and behavior. Hvc contains two separate populations of projection neurons: one sends axons to RA, and the other to Area X (the song-specific area of avian basal ganglia). The Hvc–RA pathway regulates production of 'already learned' songs in adult birds, and is assumed to be involved with song learning in juveniles. The anterior forebrain pathway includes the Hvc–Area-X–DLM–IMAN–RA pathway, and is necessary for normal song production in early stages of vocal learning, but is not on the main motor pathway for vocal behavior in older juvenile and adult birds. RA-projecting neurons in IMAN send axon collaterals to Area X, which creates a forebrain loop connecting Area X, DLM and IMAN. Several additional circuits and feedback loops are excluded for simplicity.

pathway are even longer (~100 ms). Processing complex acoustic features, or further processing related to template comparison, may increase these estimates significantly. These delays raise the issue of how template-driven changes are directed to the appropriate cells and synapses.

One possibility is that a copy of the motor activity is retained until the sensory information arrives. Potential sites where such 'corollary discharges' might be delayed include slow responses in the dorsolateral nucleus of the medial thalamus (DLM), which connects Area X and IMAN ([36]; see also [29\*\*]), the long feedback loop from RA to the song nucleus Hvc via the thalamus and medial portion of the magnocellular nucleus of the neostriatum (mMAN) [37], and the delayed onset of spiking in RA-projecting Hvc neurons [38].

A second possibility is to learn a motor-to-sensory mapping. Premotor activity can then be directly transformed into the

corresponding sensory representation, without waiting for the actual sensory signal to arrive. Troyer and Doupe [8\*\*] have proposed that such a motor-to-sensory ‘efference copy’ mapping develops in the connection between RA-projecting and Area-X-projecting neurons within HVC.

In their experiments comparing sensory and motor responses of RA neurons, Dave and Margoliash [29\*\*] provide direct evidence for a prediction signal. By aligning neural activity patterns relative to the acoustic representation of the bird’s own song, they calculated the latency between motor-related and sensory-related patterns of activity. The sensory-to-motor correspondence hypothesis (see above) predicts that this latency should be at least 55 ms: 40 ms for the motor latency from RA to singing, and 15 ms or more for the sensory latency to RA during song playback. Experimentally measured latencies activity fell in the range from 4 to 13 ms, which is significantly less than the predicted minimum of 55 ms and invalidates the sensory-to-motor correspondence hypothesis outlined above.

Instead, these results suggest that there is a mapping that ‘looks ahead’ at least 50 ms into the future. Dave and Margoliash [29\*\*] confirmed this prediction by replacing individual syllables with silence during song playback. Consistent with a ‘look ahead’ of 50 ms or more, sensory responses were most reduced during syllables that followed the deleted syllable with a latency of 0–3 syllables, and with the greatest reduction during the syllable subsequent to the deleted syllable. Although the sensory-to-motor prediction mapping described by Dave and Margoliash [29\*\*] may potentially relate to mechanisms compensating for feedback delay, its exact functional role remains to be elucidated.

From a mechanistic point of view, the ‘look ahead’ in the sensory-to-motor mapping follows naturally from principles of Hebbian learning. Consider a pair of representative neurons — one sensory and one motor — that are co-active at a particular time during singing. The sensory neuron is responding to an acoustic feature sung in the recent past, whereas the motor activity corresponds to a feature to be sung in the near future. Thus, Hebbian learning would act to connect neurons participating in sensory and motor representations separated by a look-ahead time equal to the sum of the sensory and motor latencies. If these connections are used to drive sensory responses during song playback, the look-ahead will compensate exactly for the expected feedback delay, leading to a 0 ms motor-to-sensory latency, close to the 4–13 ms latency measured by Dave and Margoliash [29\*\*].

### Multiple stages of learning

The models sketched above suggest that song learning may consist of multiple, possibly overlapping stages. An awareness of these different stages of learning, some of which may not have been identified, is crucial for interpreting changes in the neural substrate for song learning. For example, several studies have attempted to correlate

developmental changes in *N*-methyl-D-aspartate receptor (NMDAR)-mediated synaptic transmission with different phases of vocal learning.

The contribution of NMDARs is greater in juveniles than in adults at all synapses studied to date: NMDAR-mediated currents are much longer in juveniles [21,39,40], and the relative proportion of synaptic current attributable to NMDARs (compared with  $\alpha$ -amino-3-hydroxy-5-methyl-4-isoxazole propionate receptors [AMPA]) is also higher [40–42]. The increased contribution of NMDARs to DLM–IMAN synaptic transmission in juvenile birds is partly due to the fact that a large proportion of DLM–IMAN synapses contain only NMDARs and no functional AMPARs at 20 days (i.e. these are postsynaptically ‘silent’ synapses) [43]. This pattern suggests that enhanced NMDAR currents may provide a mechanism for modulating synaptic connectivity during song development [44].

Although the time course of these changes is not well known, it is clear that the transition to fast kinetics can occur during early phases of song learning [21,40] — that is, before the time of learning from a tutor, the loss in effectiveness of IMAN lesions, or the increased auditory selectivity of IMAN neurons. Social isolation of juvenile birds prolongs the sensitive period for learning from a tutor and delays the shortening of NMDAR currents at DLM–IMAN synapses [45,46]. But the transition to fast currents occurs by 65 days at these synapses in isolate birds, even though isolates exposed to tutors starting at 65 days learn new song syllables. These results leave open the possibility that long time course NMDAR currents may be necessary for early stages of vocal development, such as learning a basic sensorimotor map for the vocal system (see above), but not for later learning. If this is the case, then preventing birds from experiencing a period of long NMDAR-mediated synaptic currents during this early stage should disrupt song learning.

Consistent with this idea, premature increases in serum testosterone levels from 20 to 40 days of age cause precocious development of faster NMDAR currents at DLM–IMAN and IMAN–RA synapses and prevent normal vocal development [39,47]. Alternatively, social isolation may prolong the duration of NMDAR-mediated currents (or cause alternate changes) at other synapses. For example, synapses intrinsic to IMAN have a greater relative contribution from NMDARs than from AMPARs relative to DLM–IMAN synapses, and exhibit activity-dependent potentiation in juvenile but not adult birds [48,49]. These results suggest that DLM–IMAN synapses and synapses that are intrinsic to IMAN may have different roles during vocal development, and point to the intrinsic synapses as a potential substrate for late learning in social isolates.

### Multiple representations

Many of the models outlined here not only assume that there are several stages of learning, they also require the coordination of multiple representations of song. One

strategy for addressing the issue of coordination is to assign different aspects of learning to different sets of neurons. For example, intracellular recordings reveal that the responses of RA-projecting and Area-X-projecting HVC neurons alternate in time during song playback, suggesting a segregation of function [50\*].

Alternatively, different aspects of learning may be accomplished during different behavioral states (e.g. singing versus sleeping [29\*\*,52,53], or 'female-directed' versus 'undirected' song [54]). These behavioral states may be hormone dependent and/or controlled by strong projections from neuromodulatory subsystems to song nuclei [51].

More generally, circuits in addition to those discussed here, are likely to play significant roles during song learning, although the functional importance of these circuits is poorly understood. Computational models [7,8\*\*,28\*] will be important for integrating disparate experimental results, challenging previous interpretations, and driving further experimental investigations.

## Conclusions

Learning a complex behavior, such as birdsong, requires the orchestration of composite, distributed patterns of neural activity and plasticity. Advances in our ability to quantify the acoustic structure of song, combined with an increasing number of physiological investigations in singing birds, promise to yield a wealth of data concerning the neural mechanisms subserving song learning. The construction of detailed models will play a crucial role in extracting the principles learned from these studies and applying them to more general problems related to motor learning in mammals and humans.

## Acknowledgements

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