

What songbirds teach us about learning

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Bird fanciers have known for centuries that songbirds learn their songs. This learning has striking parallels to speech acquisition: like humans, birds must hear the sounds of adults during a sensitive period, and must hear their own voice while learning to vocalize. With the discovery and investigation of discrete brain structures required for singing, songbirds are now providing insights into neural mechanisms of learning. Aided by a wealth of behavioural observations and species diversity, studies in songbirds are addressing such basic issues in neuroscience as perceptual and sensorimotor learning, developmental regulation of plasticity, and the control and function of adult neurogenesis.

The study of birdsong exemplifies a neuroethological approach to understanding brain function, in which a detailed knowledge of naturally occurring behaviours can inform and guide the search for underlying neural mechanisms. Songbirds also illustrate the neuroethological tenet that 'specialist' animals can provide revealing examples of basic processes shared by less specialized animals. For example, songbirds display complex perceptual learning, in which experience interacts with inborn predispositions to learn. They engage in sophisticated motor skill learning, guided by performance-based feedback. Their capacity for song learning is restricted to a sensitive period in development, the timing of which depends on experience as well as hormones, and varies between species. To subserve vocal learning, songbirds have evolved a discrete set of brain structures, which include specializations of widely conserved vertebrate circuitry, such as basal ganglia networks. The structures involved in song learning and production have also revealed some of the most compelling examples of adult neurogenesis and its regulation. Finally, the properties of song learning make it a model not only for general sensory and motor learning, but also for human speech learning, providing one of the few model systems for the human capacity to acquire vocal behaviour.

In this highly selective review of birdsong learning, we begin by outlining some behavioural observations. We then describe what can be inferred about nervous system function from these observations, as well as what has been learned about how the brain solves these behaviourally defined tasks. In some cases, inroads have been made into understanding how the nervous system carries out components of the behavioural repertoire; in most, however, our understanding remains incomplete. Nevertheless, songbirds provide a system where observation of naturally occurring

behaviours has delineated a series of questions of general relevance to learning, in a context where it is highly tractable to elucidate neural mechanisms.

Behavioural basis of vocal learning

The importance of hearing

The scientific study of birdsong began in the late 1950s, with Thorpe¹ and Marler². They showed that birds, taken from the wild as eggs or nestlings and tutored with songs of unrelated adults of the same species (conspecifics), ultimately produce songs that resemble the tutor songs (Fig. 1a–c). In contrast, birds raised in acoustic isolation from conspecific males produce very abnormal 'isolate' songs (Fig. 1d). Moreover, some songbirds, like humans, have learned, geographically restricted 'dialects'². These results illustrate that hearing the sounds of others during an early 'sensory learning' period (Fig. 2) is essential to normal learning.

Songbirds must also be able to hear themselves in order to learn to vocalize normally. If birds are deafened after exposure to the songs of others, but before they begin practising their vocalizations during 'sensorimotor learning' (Fig. 2), they develop highly abnormal songs that show no evidence of learning³. However, the tutor no longer needs to be heard during this rehearsal phase. These behavioural results suggest that during the sensory phase of learning, young birds form an internal representation of song to which they are exposed — a song 'template'. Later, during the sensorimotor phase, birds use auditory feedback to compare their developing vocalizations with the template, and guide their song modification using this comparison^{3,4}.



Birdsong and human speech

Speech and song are both complex acoustical signals (Fig. 1), and numerous features of song learning show striking parallels to human speech development⁵. Most important, humans, like songbirds, depend critically on hearing both themselves and

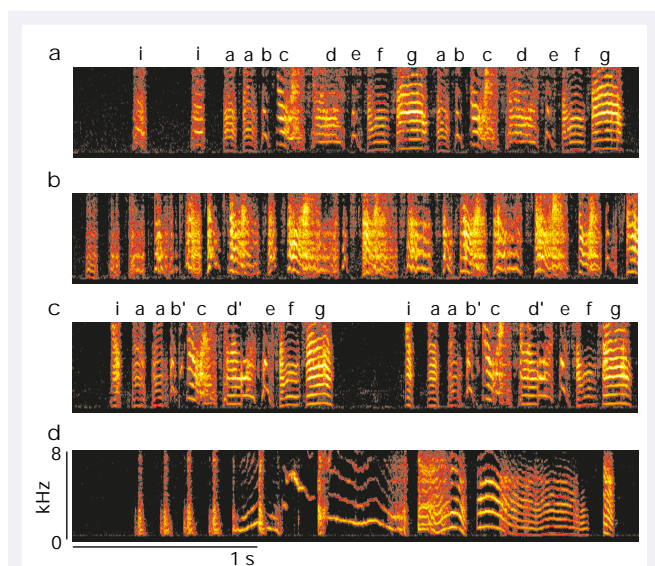


Figure 1 Birdsongs consist of ordered, often highly stereotyped strings of sounds separated by brief silent intervals. Sound energy is plotted as a function of frequency and time. Syllables are indicated by letters, and form a repeated 'motif'. **a**, Adult zebra finch song. **b**, Song of a zebra finch, tutored by the bird in **a**, at an early stage of sensorimotor learning. **c**, Song of the same bird close to song 'crystallization'. Note the similarities between this bird's song and that of its tutor. **d**, Song of a zebra finch raised in acoustic isolation. Note the overall simplicity of this song, but its general similarity of structure to other zebra finch songs.

others for normal learning. The need for experience of the sounds of other individuals is evident in the culturally transmitted languages and dialects of humans, as well as in the abnormal vocalizations of children raised without exposure to speech. The importance of auditory feedback is revealed by the profound deterioration of speech that occurs if children become deaf early or even late in childhood⁶.

The capacity for such hearing-dependent vocal learning is not widespread⁵. Apart from humans, no primates have been shown to learn their complex vocalizations. Among the rest of the mammals, only cetaceans (whales and dolphins) and some bats show evidence of vocal learning. In contrast, the vocal behaviour of the many thousands of songbird species, as well as of parrots and hummingbirds, provides a rich source of possible models for human speech learning.

Some aspects of birdsong are clearly not analogous to human speech. Although birdsong is used for communication, it does not seem to be 'language' in the sense of conveying complex meaning. What it shares with speech is the learned sensorimotor control of an elaborate vocal system. The strikingly similar requirements for this vocal learning in songbirds and humans suggest that there may be related neural mechanisms, even in brain areas that are not homologous.

Neural substrates for vocal behaviour

The behavioural studies of vocal learning indicate that there must be neural circuitry for a variety of processes, in particular (1) producing the motor commands that give rise to the complex sounds of song; (2) perceptual learning of sounds, including the memorization of the tutor song; and (3) evaluating auditory feedback relative to the internal template, and generating signals that can guide consequent modification of vocal motor output. The likely locations for these processes are a set of brain structures known as the 'song system' (Fig. 3), outlined below.

The motor pathway

Song, like speech, requires the coordinated control of vocal and respiratory musculature^{7,8}. Evidence suggests that the 'motor pathway'

of the song system (Fig. 3) generates and coordinates the patterned breathing and vocal muscle activity necessary for song production. Lesions of either of the two main nuclei of this pathway, the HVC (abbreviation used as proper name) and the robust nucleus of the archistriatum (RA), result in abnormal songs or muteness⁹, and neurophysiological activity in HVC and RA is correlated with song production^{10,11}. There is evidence for a motor hierarchy: HVC encodes higher-level song structure than does RA¹², and microstimulation in HVC causes interruption of singing and restarting of the song, whereas the same stimulation in RA disrupts only the structure of syllables without altering song patterning¹³.

Auditory areas and mechanisms

A network of forebrain auditory areas (Fig. 3) radiating from Field L, which is analogous to primary auditory cortex of mammals, is the likely source of auditory inputs to the song system^{14,15}. These high-level auditory regions may also be sites of some of the specialized operations critical to song learning. In addition, the song system itself contains some of the most complex sensory neurons known, which respond selectively to the sound of the bird's own song^{16–18} (see below).

The anterior forebrain pathway and basal ganglia function

The anterior forebrain pathway (AFP) indirectly connects the motor nuclei HVC and RA^{9,19,20} (Fig. 3). Anatomical, physiological and behavioural evidence supports the identification of this pathway as a specialized basal ganglia thalamo-'cortical' loop^{19,20}. In contrast to the song motor pathway, the AFP seems to contribute minimally to the production of stable adult song^{9,21}. However, lesions of the AFP during song learning prevent birds from developing normal adult songs^{21–23}, consistent with a function in sensory or sensorimotor learning (see below). The combination of a specialized basal ganglia circuit and a stereotyped motor output may make the AFP a particularly tractable system for revealing principles of basal ganglia function in motor learning.

Sensory learning

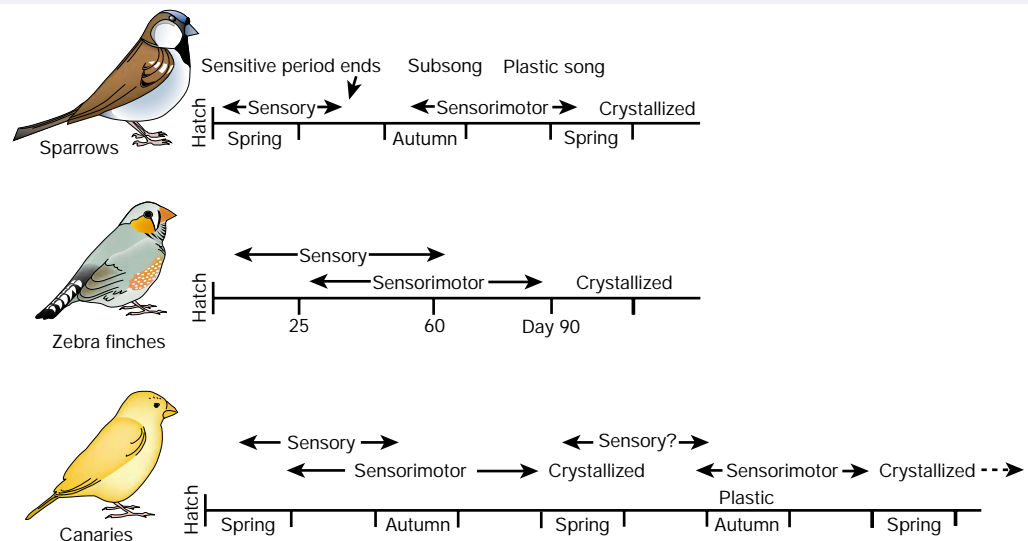
Nature versus nurture

The brain of a young songbird is not a clean slate. Without previous song exposure, young birds show greater changes in heart rate and more begging calls in response to conspecific songs than to songs of other species (heterospecific songs)^{24,25}. Moreover, although young birds are capable of copying heterospecific song, especially if it is the only model available, they will preferentially learn conspecific songs when given a choice²⁶. Finally, although birds raised in acoustic isolation sing much less complex songs than tutored birds, their songs contain some species-specific structure^{2,4} (Fig. 1d). Because most of this structure is absent in birds deafened before sensorimotor learning^{3,4}, isolate songs seem not to be pre-specified motor programs, but rather involve some sensory recognition, perhaps with respect to an 'innate template'. These behavioural studies indicate that there must be genetically determined circuitry for innate species-specific song recognition and learning.

Sensitive periods for sensory learning of song

Numerous forms of learning are subject to 'sensitive' or 'critical' periods during which experience is crucial in shaping nervous system function. One well known sensitive period is that for human speech; after early adolescence, it is difficult to learn to produce the sounds of a new language with the competence of a native speaker⁵. Many songbird species have a similar sensitive period (Fig. 2). For instance, recorded tutor songs presented to a white-crowned sparrow after 100 days of age do not appear in the bird's adult song. Similarly, white-crowned sparrows raised in isolation to 100 days of age and subsequently exposed to taped tutors still produce abnormal isolate songs as adults^{2,4}. For songbirds (and perhaps for humans as well), it seems that it is the capacity for sensory learning that declines with age (see ref. 5 for a review).

Figure 2 Timelines for song learning. **a**, In many seasonal species, such as the white-crowned sparrow, the sensory and sensorimotor phases of learning can be separated in time. The initial vocalizations, or 'subsinging', produced by young birds are variable and generic across individuals, akin to the babbling of human infants. Subsong gradually evolves into 'plastic song', which remains highly variable from one rendition to the next, but also begins to incorporate some recognizable elements of tutor songs. Plastic song is progressively refined until the bird 'crystallizes' its stable adult song. **b**, Zebra finches develop rapidly, and their two phases of learning overlap extensively. **c**, 'Open learners', such as canaries, can continue or recapitulate the initial learning process as adults.



The sensory exposure required for tutor song memorization can be surprisingly short. Nightingales can almost fully reproduce tapes of 60 songs that they have heard only once a day for 20 days²⁷, and zebra finches can learn well with less than a minute of tutor song exposure per day²⁸. In this respect, sensory learning of song resembles 'imprinting', in which animals very rapidly and irreversibly learn to recognize an animal or object of critical behavioural relevance.

Closure of the sensitive period is affected by experience

The sensitive period for song learning does not have a strict age limit. Rather, experience itself is centrally involved in closing the sensitive period. For instance, songbirds tutored with only heterospecific songs can incorporate new songs from their own species at a time when birds raised with conspecifics will no longer learn^{1,29}. For some species, even more deprivation, such as raising birds in complete isolation, can result in adults that will still incorporate new song elements^{29,30}. Thus, a lack of normal experience leaves the brain open to be shaped by the appropriate input for longer than usual. In most cases, however, plasticity seems not to last indefinitely, even in the absence of experience. Presumably, circuits poised to be shaped by activity-dependent events ultimately stabilize in some state, even if driven only by spontaneous activity.

Attentional or motivational factors also influence the timing of the sensitive period. Birds will learn from live, countersinging tutors for longer than they learn from taped tutors^{31,32}. Hormonal factors may be important as well, as manipulations that delay the onset of singing and decrease testosterone levels seem to extend the sensitive period^{1,33}.

Auditory neurons shaped by song experience

We do not yet know where and how in the brain the memory of the tutor song is stored during the process of sensory learning, nor how this memory is accessed during the evaluation of auditory feedback that guides vocal practice. However, the use of behaviourally relevant auditory stimuli has revealed neurons that clearly have been shaped by the individual bird's unique auditory experience during song learning. These 'song-selective' neurons, which are found throughout the adult male song system, respond more strongly to the sound of the bird's own song (BOS), and in some cases to the tutor song, than to other equally complex auditory stimuli, such as conspecific songs or BOS played in reverse or out of order¹⁶⁻¹⁸ (Fig. 4).

Although song-selective neurons reflect the individual bird's experience, it is not clear which aspects of that experience are

responsible for generating selectivity. In principle, these neurons might be shaped by the tutor song during sensory learning and/or by feedback of BOS during sensorimotor learning. The former possibility is especially intriguing; if tutor song selectivity arises during sensory learning, then this selectivity itself may be a manifestation of the tutor song memory. Moreover, such tutor-tuned neurons could participate directly in the subsequent evaluation of auditory feedback during sensorimotor learning: as a bird practises his song, auditory feedback from those variants that more closely resemble the tutor's song would be differentially effective in activating tutor-selective neurons. Hence, the degree of activation of these neurons during vocal practice could signal the degree of success in the young bird's attempts to mimic the tutor song.

This simple scenario, in which sensory learning generates tutor-selective neurons that can then guide feedback evaluation, faces a serious challenge. Developmental studies suggest that robust song selectivity does not emerge during sensory learning, but instead arises in parallel with the bird's own motor production. Moreover, the emerging song selectivity is characterized by greater response to BOS than to the tutor song, or by similarly strong responses to both these songs^{18,34,35}. These observations are consistent with the possibility that the critical experience that shapes song selectivity is exposure to feedback of BOS. The tutor song responses observed could arise simply because of similarity between the bird's learned song and the tutor song to which it was exposed; neurons tuned to BOS would tend to respond well to the acoustically similar tutor song (Fig. 4c).

Because of this problem of acoustic similarity, and because the tutor song is only an indirect representation of what the bird has actually memorized, the relative strength of neural responses to BOS and tutor song in normal adults cannot unambiguously reveal which experiences have shaped song selectivity³⁵ (Fig. 4c). This problem has been partly addressed by studying birds that were prevented from producing a good copy of the tutor song by denervating the vocal apparatus. These birds produce very abnormal songs, without the usual acoustic similarity to tutor song. Song-selective neurons in these birds, at least in the AFP, develop sensitivity to the sound of the abnormal songs produced by the bird³⁵. This indicates that BOS shapes song-selective neurons during sensorimotor learning.

But some AFP neurons in birds with deafferented vocal organs are strongly responsive to the tutor song as well as to BOS, despite the acoustic differences between the two³⁵. Thus, some song-selective neurons seem to reflect independently both sensory and sensorimotor learning. Such joint selectivity for BOS and tutor song could be a

useful property for song learning, which involves comparing these two stimuli. There is as yet little evidence in the song system for the simpler idea of auditory neurons with strong suprathreshold selectivity to tutor song alone.

Neurons with responses to BOS playback in anaesthetized or sleeping animals do not always show these responses when birds are awake, indicating that the strength, and perhaps the nature, of auditory responses to sounds are 'gated' by the behavioural state of the bird^{36,37}. In other sensorimotor systems, for instance locomotion in mammals or flying in insects, sensory responses related to a behaviour are 'gated' by the motor activity that generates the behaviour³⁸. That is, responses are diminished unless the animal is also engaged in the behaviour. Similarly, for songbirds as for humans, auditory feedback of self is available only when the animal is actually vocalizing. Thus, anaesthesia or sleep may artificially open a gate that is normally operated by the act of singing. Ultimately, an understanding of the neural mechanisms for evaluation of auditory feedback of BOS is likely to require recording neural activity when that feedback is produced — that is, during singing.

Forebrain auditory areas and sensory responses

Complex stimulus selectivity is also found in some auditory forebrain regions that provide input to the song system^{15,39–41}. In particular, the high-level auditory areas (Fig. 3) known as the caudomedial neostriatum (NCM) and the caudal portion of the ventral hyperstriatum contain neurons that show more immediate early gene induction or neurophysiological activity in response to conspecific songs than to heterospecific songs^{39,40}. For the most part, responses within these regions, unlike those within the song system, do not seem to be restricted specifically to BOS or tutor song stimuli. Hence, these forebrain regions may contribute to a general processing of conspecific sounds. However, one recent study found that, within NCM, some auditory responses seem to reflect the individual bird's song-learning experience^{42,43}. It therefore remains possible that some of the sensory learning of song occurs within this network of auditory forebrain areas.

This conclusion seems especially plausible as many animals that are not vocal learners, including some birds, are nevertheless capable of perceptual learning. Perceptual learning, including that of tutor song, may rely on sensory processing pathways that are phylogenetically widespread. In contrast, the sensorimotor component of vocal learning, which has appeared only rarely, may have required the evolution of specialized vocal areas such as the song system.

Assessing the functional role of brain regions in sensory learning

Lesion studies are problematic for identifying brain regions that are specifically involved in the sensory phase of song learning. This is because the main assay for what a bird has memorized is the song that the bird ultimately produces; any song abnormalities arising from lesions are therefore difficult to attribute specifically to disruption of sensory learning, as opposed to disruption of subsequent sensorimotor learning or song production. One attempt to circumvent this problem in investigating the role of the AFP has been to reversibly inactivate the AFP nucleus LMAN (lateral magnocellular nucleus of the anterior neostriatum) during tutoring sessions, but not during song rehearsal⁴⁴. Song learning in these experimental birds is reduced relative to controls. However, the decrease is small, and the songs of treated birds are not isolate-like, as might be expected if song memorization were completely prevented. Nonetheless, this experiment provides perhaps the most direct evidence of involvement of a brain area in song memorization, and could be extended usefully to testing the role of other brain areas.

Another approach is to study the effects of lesions in purely perceptual tasks, where aspects of sensory learning can be measured independently of song production. Although such studies have not addressed the issue of memorization of tutor song, they have found that lesions of song nuclei, including HVC and LMAN,

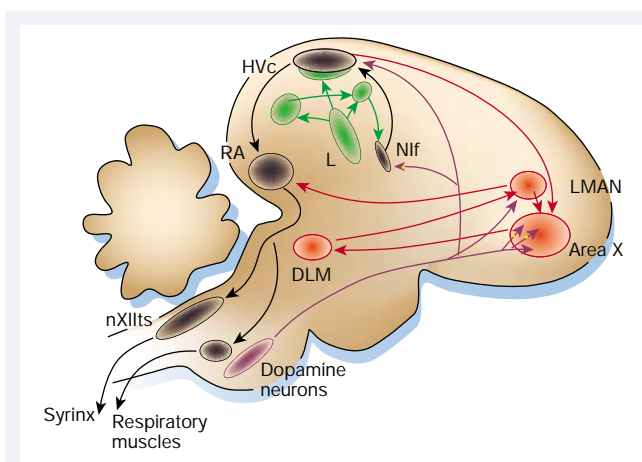


Figure 3 Neural substrates for learning: the song system. The motor pathway (black) is necessary for normal song production throughout life, and includes HVC (abbreviation used as proper name) and the robust nucleus of the archistriatum (RA)⁹. RA projects to the tracheosyringeal portion of the hypoglossal nucleus (nXlts), which controls the bird's vocal organ or syrinx, and to nuclei involved in control of respiration during song^{7–9}. Additional nuclei afferent to HVC, including the nucleus interfacialis (Nif), are likely to be part of the motor pathway, but their role is less clear. HVC sends a second projection to the anterior forebrain pathway (AFP, red). The AFP includes Area X, which is homologous to mammalian basal ganglia^{19,20}, the medial nucleus of the dorsolateral thalamus (DLM), and the lateral magnocellular nucleus of the anterior neostriatum (LMAN; a frontal cortex-like nucleus). LMAN sends a projection back into the motor pathway at the level of RA. Like basal ganglia in other vertebrates, Area X is the target of strong midbrain dopamine projections¹⁹; LMAN, HVC and Nif also receive dopamine inputs (purple). The Field L complex is the avian primary forebrain auditory area and projects to a complex network of higher auditory areas¹⁴ (green), including the caudomedial neostriatum and caudal portion of the ventral hyperstriatum (not labelled). Auditory inputs likely enter the song system at the level of Nif and possibly HVC¹⁵.

interfere with the performance of birds in tasks that require song memorization and discrimination^{45–47}.

Cellular and synaptic changes correlated with sensory learning

Tutor song memorization could be distributed across a number of brain areas, but because disruptions of the AFP affect learning, many studies have focused on this circuit in the search for neural mechanisms underlying the sensitive period for sensory learning⁴⁸. In zebra finches, the AFP and its connection to RA undergo numerous regressive changes by 60 days of age, when the sensitive period closes in this species. The synapses from LMAN to the motor pathway decrease in number when HVC innervates RA⁴⁹, and the initially coarse topographic projection from LMAN to RA undergoes refinement⁵⁰. Elimination of connections is also prominent within the AFP itself: LMAN neuron spine density decreases between 25 and 60 days of age⁵¹, and thalamic arbors in LMAN are pruned⁵². This is accompanied by decreased *N*-methyl-D-aspartate (NMDA) receptors in LMAN⁵³, faster NMDA currents at synapses from thalamus to LMAN³⁰, and loss of activity-dependent synaptic potentiation and depression at synapses within LMAN⁵⁴.

These regressive changes could potentially underlie an experience-dependent narrowing of song responsiveness as birds encode a particular tutor song memory. But in zebra finches, the period of sensory learning also overlaps with the onset of vigorous singing, sensorimotor rehearsal and refinement of auditory selectivity for BOS (Fig. 2), making it difficult to specifically attribute any changes to sensory learning. In addition, the song system is still developing during this time, such that many of the observed changes could reflect developmental events that are independent of learning. So far, only a small number of observations have been tested and found to

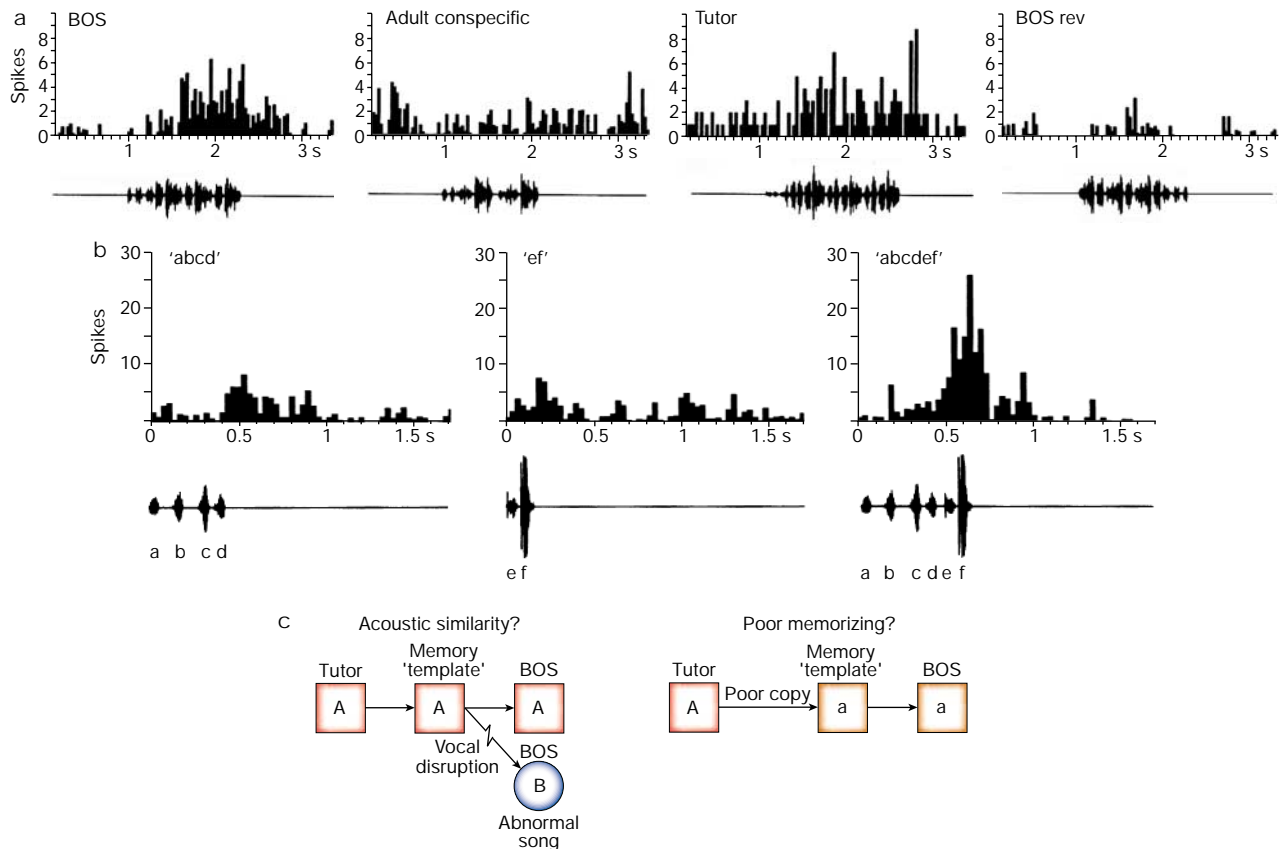


Figure 4 Song selectivity. **a**, Song-selective neurons respond better to the bird's own song (BOS), and in some cases the tutor song, than to equally complex conspecific songs. They also respond more strongly to the song in the forward order than to the same song reversed (BOS rev). **b**, Song-selective neurons are highly nonlinear, and in some cases 'combination sensitive'^{16–18}, responding better to a combination of sounds than to any of the sounds in isolation. Intracellular recordings have begun to address the cellular and synaptic mechanisms that must underlie such complex spectrally and temporally tuned responses to song^{99,100}, and raise the intriguing possibility that there are different representations of BOS in different classes of song-selective neurons¹⁰⁰.

c, If the bird both memorizes and reproduces the tutor song 'A' very faithfully, as in the left panel, the tutor song will be virtually identical to BOS. Neuronal responsiveness to these two songs will not distinguish which experience was primary in shaping the neurons. If, however, the bird memorizes poorly ('a') but copies the inaccurate template faithfully into its own song, as in the right panel, BOS will be the best reflection of what the bird actually stored in memory. Neuronal selectivity for BOS in this case will reflect what was memorized in response to tutor song exposure. Artificially altering the bird's song production (creating abnormal song 'B'³⁵) can eliminate similarity between BOS and tutor song, and help identify which of these stimuli shape the neural response.

correlate with learning rather than developmental age. For example, the elimination of spines normally seen in LMAN of zebra finches by day 60 does not occur in birds raised without tutors⁵¹, implying that spine loss in LMAN may be a cellular consequence of sensory experience and learning. In contrast, although isolation rearing enables late learning, it delays, but does not prevent, shortening of NMDA-receptor kinetics at thalamus–LMAN synapses³⁰. The ability of isolates to learn new songs clearly indicates that changes in NMDA-receptor kinetics, at least at thalamus–LMAN synapses, do not prevent song learning in the way that closure of the sensitive period does.

Sensorimotor learning

During sensorimotor song learning (Fig. 2), motor circuitry is gradually shaped by performance-based feedback to produce an adaptively modified behaviour. This feedback is critical throughout motor learning — at any point prior to crystallization, elimination of auditory feedback by deafening not only arrests the progression of sensorimotor learning, but also can lead to a rapid deterioration of song, including the loss of previously learned elements⁵⁵.

The AFP and sensorimotor learning

Because AFP lesions, like deafening, dramatically disrupt song development, this circuit may function in sensorimotor learning of

song. Studies of the AFP in adult birds provide several suggestions about what such a function might be. AFP lesions prevent a variety of changes to adult song that can otherwise be driven by manipulations of experience such as deafening or unilateral denervation of the vocal musculature^{56,57}. Because these manipulations create feedback of song that differs from what is expected, the effects of AFP lesions are consistent with the hypothesis that the AFP functions throughout life to evaluate auditory feedback of song with respect to the desired output, and to instruct changes in the motor pathway. Alternatively, or in addition, the AFP may act more permissively in motor pathway plasticity, enabling change without providing specific guidance. This is consistent with the known trophic role of the AFP in the survival, growth and innervation of RA neurons^{58,59}. Regardless of mechanism, the AFP seems to be crucial in both song learning and plasticity of adult song.

In adult birds, the AFP is active during singing^{60,61}, with premotor activity resembling that in the motor nucleus HVC. This suggests that AFP activity originates from HVC, and represents in part an 'efference copy' of the premotor signals sent to the motor output pathway. Efference copies of motor activity are common in sensorimotor systems, and may generate predictions about the expected sensory consequences of motor commands. Such an efference copy

of song motor activity in the AFP could be particularly useful during sensorimotor learning^{62,63}.

Song-selective neurons as motor neurons

Song-selective neurons not only respond to complex sensory signals, but also can be active during motor production^{61,63}. For instance, the same RA neurons that exhibit song-selective responses in sleeping birds are active during singing⁶³. There is a remarkable correspondence between these neurons' auditory responses to song and their premotor activity — playback of one set of syllables triggers an auditory response that resembles the premotor activity for the next syllable in the song. Thus the auditory response can be considered a prediction of the motor command for the following syllable. These results raise the possibility that song-selective neurons in both the motor pathway and the AFP are critically involved in linking sensory and motor representations in the song system^{62,63}.

Crystallization and selection of song

Studies of developing or 'plastic' song reveal that some bird species sing more sounds as juveniles than are ultimately preserved in their adult song. For example, birds exposed to multiple tutor songs may sing plastic songs that include virtually complete renditions of each tutor song, even though they will eventually sing only one of these⁶⁴. During sensorimotor learning, birds are thus not only learning how to produce previously memorized sounds, but are also selecting which of these acquired skills will ultimately be expressed. It is clear that external stimuli, including social interactions, are important in this process. For example, white-crowned sparrows singing multiple juvenile songs in the field crystallize the one that is most similar to songs of other birds in the vicinity, and this selection can be reproduced in the laboratory using song playback⁶⁴. Social influences on song crystallization are not only acoustic; male cowbirds will preferentially retain songs that prove effective in eliciting courtship displays from females⁶⁵.

How messages about song quality are conveyed to the song motor pathway is unknown. However, in adult birds, social context strongly modulates the level of activity within the AFP of the song system during song production^{66,67}. Similar modulation during the final stages of sensorimotor learning might have a role in song selection. Because reinforcement signals provided by social interactions can be non-acoustic, ascending dopaminergic projections from the midbrain ventral tegmental area could be involved (these are thought to have a highly conserved role in mediating effects of reward and reinforcement). In songbirds, dopaminergic pathways send a particularly dense projection to nuclei of the song system, especially Area X of the AFP^{19,20}, and are thus well situated to modulate song learning.

Regulation of sensorimotor plasticity

Although there is strong evidence for sensitive periods for the sensory phase of song learning, it is less straightforward to determine whether there is similar regulation of sensorimotor learning. The stability of adult song in many species raises the possibility that motor circuitry becomes 'crystallized' and unchangeable, although this could also reflect continued matching of song output to an unchanging sensory template. Pytte and Suthers⁶⁸ showed that transiently disrupting motor production with botulinum toxin in very young or adult birds has no lasting effects on song. However, if birds are prevented from vocalizing normally during the later stages of sensorimotor learning, just before or during song crystallization, song becomes permanently distorted⁶⁸. This pre-crystallization period may thus represent a motor sensitive period during which it is crucial that birds have normal opportunity for rehearsal.

More pronounced perturbations of the motor periphery make it clear that adult song production does not become completely refractory to the influence of experience. Crushing the nerve that innervates the syrinx⁶⁹, or interfering (reversibly) with the mechanics of syringeal movement⁷⁰ not only acutely disrupts song, but, unlike botulinum toxin, eventually leads to permanent elimination of song elements

and gross changes to the temporal pattern of song. Such changes must reflect alterations in the central motor pathway of adults.

It is not certain whether these disruptions of motor production are caused by damage to the motor periphery *per se*, or by the resulting abnormal auditory feedback (see ref. 71 for full discussion). Manipulations of auditory feedback that can be imposed without interfering with motor production, such as deafening or reversible disruption of auditory feedback, can also lead to deterioration of adult song^{55,72–75}. This indicates that there is not a complete loss of plasticity in the motor pathway even in response to a primarily sensory manipulation, and suggests that auditory feedback continues to exert an important influence on adult song.

The degree of song deterioration after hearing loss is much less severe in adulthood than in juveniles^{55,72}, and the effects of deafening continue to wane even after the apparent crystallization of adult song. For zebra finches, the consequences of deafening for adult song are much greater shortly after song crystallization than when birds are deafened progressively later over the ensuing months^{76,77}. Humans show a similar dependence on auditory feedback. In adults, speech gradually deteriorates after hearing loss, but exhibits progressively less deterioration as hearing loss occurs later over the second, third and fourth decades of life⁶. These findings suggest that for both birds and humans, even after sensorimotor learning seems to be complete, there is nevertheless a continuing, covert stabilization of adult vocalizations.

Sleep may be important in such consolidation of song, or in song learning more generally. During sleep, some of the spontaneous bursting of adult RA neurons is similar in its pattern to the activity of the same neurons during singing, and thus perhaps reflects 'replay' of activity that occurred during the day⁶³. Such replay could be involved in 'off-line' alteration or strengthening of connections in the neural network for song; this would be consistent with reports hypothesizing a role for sleep in learning and consolidation of memory⁷⁸.

Hormones and sensorimotor plasticity

Songbirds vary widely in the degree to which they can modify their song in adulthood. 'Closed-learners' like the zebra finch or white-crowned sparrow pass through a single period of song learning and then normally retain an essentially unchanging song throughout life. In contrast, 'open-learners', like canaries or starlings, initially pass through sensory and sensorimotor learning resulting in stable adult song, but then can continue to learn^{79,80} (Fig. 2). In canaries this occurs seasonally; after a winter period of song variability, they produce a stable song each spring into which new elements have been incorporated⁷⁹. Comparisons across species that have different capacities for learning, and within species at times when learning is differentially enabled, have the potential to reveal what factors regulate nervous system plasticity.

Steroid hormones may be one such factor. Sex steroids are well known to shape the development of the sexually dimorphic song system^{4,81,82}, but they also seem to influence learning more directly¹⁹. Testosterone levels rise during sensorimotor learning, in parallel with song crystallization; they are high in springtime, when song is stable, and low in late summer and autumn⁷⁹. Testosterone treatment can precipitate premature crystallization of abnormally simple song^{83,84}. Conversely, depletion of testosterone can delay or prevent crystallization of song^{85,86}. Testosterone causes numerous structural and electrophysiological changes in song system neurons^{19,87}, which could influence plasticity. Because steroid hormone receptors are particularly enriched in the song motor pathway and LMAN^{19,87}, testosterone could be acting directly at these sites. Alternatively, because androgens increase singing, the effects of testosterone on the song system could reflect the indirect consequences of increased motor performance⁸⁸.

New neurons in adult brains

The song system has contributed greatly to our understanding of neuron generation in adulthood, again aided both by behavioural

knowledge and by the discrete circuit underlying song. The initial suggestion that new neurons were born in the adult mammalian brain⁸⁹ met with resistance. But in the early 1980s, while searching for possible mechanisms underlying seasonal changes in song and in the volume of the song control nucleus HVC, Goldman and Nottebohm⁹⁰ discovered striking amounts of adult neurogenesis in the songbird forebrain, including HVC. Because many new neurons were added to a well-defined circuit, Nottebohm and colleagues were able to provide compelling evidence for neurogenesis, including electron microscopy, retrograde neuronal labelling, and neurophysiological recordings from newly generated neurons^{91,92}. Only recently has it become more generally accepted that adult neurogenesis also occurs in mammalian brains⁹³.

Neurogenesis is regulated in adult songbirds (as it seems to be in mammals): not all brain areas receive new neurons, and not all neuronal types are readily generated anew in adulthood⁹². Although neurogenesis occurs in non-song learners and in many areas of the avian forebrain, including the hippocampus, studies within the well-delineated song system have facilitated recognition of the regulation of neurogenesis. For instance, HVC has two intermingled populations of long-range projection neurons, one projecting to the motor nucleus RA, and the other targeting the basal ganglia nucleus Area X (Fig. 3). Only RA-projecting neurons are born in adulthood⁹², and selective killing of these neurons in adult birds results in a peak of increased insertion of new neurons into HVC⁹⁴. In contrast, killing adult Area X-projecting neurons does not result in more neurogenesis. Newly generated neurons are produced when Area X-projecting neurons are killed in young birds, but the new neurons are all RA-projecting⁹⁴. Thus the birth or recruitment of neurons is sensitive to injury or vacancy signals from the brain, but not all neuron types can be generated with equal ease.

Many more neurons are born in adulthood than ultimately survive. However, studies in adult songbirds have also led to some of the best evidence for prolonged survival of new neurons, with newly generated RA-projecting neurons in HVC living for at least 8 months⁹¹. In addition, these neurons send long-range projections to their appropriate targets within pre-existing, myelinated adult circuits⁹¹. Understanding the molecular signals that allow this growth and targeting should inform the search for factors important for the migration and connection of neurons in adult mammalian brain and spinal cord.

In songbirds, the evidence that neurogenesis and neuronal recruitment is sensitive to experience and environmental cues is multifaceted and compelling. Recruitment of new neurons is clearly seasonally and hormonally regulated. There are large differences in the number of new neurons observed after injection of [³H]thymidine in the autumn compared with the spring, and treatment of birds with testosterone dramatically increases the insertion and/or survival of new neurons in HVC, without affecting the rate of neurogenesis in the ventricular zone^{95,96}. Eliminating auditory input by deafening animals also alters the number of new neurons in HVC⁹⁷, as does the act of singing⁸⁸.

Perhaps the most intriguing question regarding adult neurogenesis is whether newly generated neurons have an important function, especially in learning. In songbirds, the strong association between a stereotyped learned vocal behaviour and discrete brain areas should make it feasible to test whether there is a causal link between new neurons and song plasticity. Interestingly, there are peaks of neuron loss and replacement in canary HVC that correlate with seasonal periods of song instability and restabilization, respectively⁹². However, new neurons are also inserted in other seasonal species that do not change their songs⁹⁸. Thus, critical experiments remain to be done, to see whether eliminating neurogenesis prevents song learning or modification.

The observation that many birds that incorporate new neurons nonetheless have an unchanging adult song is of interest in its own right. Even the disruption of adult zebra finch song that is triggered

by ablation of RA-projecting neurons (and is followed by increased neuronal recruitment) is succeeded by gradual recovery of song to its pre-ablation state⁹⁴. Songbirds thus provide an example of a system where learned capacities and memories persist despite neural turnover. The mechanisms underlying such resilience to cell loss and replacement may be particularly relevant in the future as we attempt to repair the adult brain by inserting new neurons.

Future directions

This review highlights the richness of song learning behaviour, and the many questions of general relevance to learning and memory posed by behavioural studies. Much about the neural foundations of this behaviour remains unexplored, and we hope to have conveyed here the potential waiting to be tapped.

Songbirds have many experimental advantages, including their small size, relatively rapid development, and the ease both of altering their experience and of recording brain activity during behaviour. These features, together with the specialized brain areas for song, give this system the potential to elucidate neural mechanisms of learning from the systems down to the cellular and molecular levels.

It is a disadvantage, for molecular studies in particular, that birds do not possess the genetic tractability of animals such as mice and flies. However, the naturally occurring differences in learning between species effectively provide opportunities to study mechanisms of phenotypic variation. Moreover, new tools for 'non-genetic' animals are under development, and songbirds may prove to be relatively easy vertebrates to manipulate. Indeed, as additional organisms are selected for genome sequencing, we would be well served by targeting animals such as songbirds. Ultimately, if we are to address questions of complex natural behaviour including our own, we must tackle, at all levels of analysis, systems where evolution has resulted in elaborate, learned behavioural capacities and the corresponding neural mechanisms. □

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