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Birdsong: **Can an old bird change his tune?**

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The stereotyped courtship songs of 'age-limited' songbirds, which learn their songs during a specific early period of their lives, were once thought immutable, but recent studies suggest that their maintenance may actually rely on subtle cues provided by auditory feedback.

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The song of a male songbird is the polished product of a vocal learning process which, like human speech, happens early in life, occurs in stages and requires auditory guidance. One apparent difference between birdsong and speech is that the adult song of certain songbird species is unaltered by deafening whereas, without hearing, speech degrades. Birdsong and human speech may be more alike than previously thought, however, as recent evidence [1–4] suggests that adult birds use auditory feedback to adjust their song when what they hear is not what they expect.

Song and speech learning both begin with an early perceptual phase. During a sensitive period known as sensory acquisition, a young male songbird must listen to and memorize the song of an adult male of his own species in order to grow up to produce a 'good' song — one that is sexually attractive to females — as an adult. Sensory acquisition is followed by sensorimotor learning — a song rehearsal period that begins with 'subsong', which is reminiscent of human infant babbling, followed by 'plastic' song, when the juvenile bird matches his own song with the memorized model.

The neural processes likely to underlie the sensorimotor learning of song production include a 'comparator' that uses auditory feedback to detect differences between the bird's own song and the memorized model, and a resulting error signal that can alter the vocal output to improve the match. This process culminates at sexual maturity when the previously variable song becomes stereotyped, or 'crystallized', such that each song bout consists of identical motifs, or phrases, which are constructed from the same orderly sequence of single or multi-note syllables. In those songbird species referred to as 'age-limited learners', such as the white-crowned sparrow, song learning is restricted to this initial period in life, after which no new notes are learned.

In a now classic study, Konishi [5] deafened juvenile white-crowned sparrows singing plastic song, or adult birds singing crystallized song, and showed that sensorimotor learning during the plastic-song period relies on auditory feedback, whereas adult song does not. In apparent distinction to human speech, these and other findings lead to the hypothesis that, once song is perfected, a central pattern-generating program is established that is read out by the motor system like a tape, independent of auditory feedback. Early hints that continued audition is actually important to the song of adult birds began to emerge when more age-limited learners were studied, and in some, such as the zebra finch [2] and Bengalese finch [3,4], previously crystallized songs degraded after deafening.

These findings suggested that audition, which during development enables a bird to compare its own song to a memorized model, is also important in adults. However, the main effect of audition in adulthood appears to be to maintain, rather than to change song. Deafening might not be the best way to demonstrate such a maintenance role, as it permanently removes auditory signals from which comparisons can be made and thus may not provide the correct 'currency' for any comparator, or may be so dramatic as to diminish or shut down any error correction system. Finally, because it is irreversible, deafening is an experimental one-way street of no return.

Now, Leonardo and Konishi [1] have ingeniously challenged the zebra finch's auditory and vocal-motor system to reveal its mature workings by perturbing the sounds that an adult bird hears when he sings. Leonardo developed a computer-controlled system which is triggered by the bird's song to broadcast recorded excerpts of that song that are slightly delayed so as to overlap with the bird's own vocalization. Thus, the bird hears something unusual whenever he sings — a garbled combination of his own song and the excerpts. Two great strengths of this approach are that the procedure is non-invasive and reversible, which allowed the authors to test whether any changes in song would reverse when the computer-generated sounds were stopped.

Exposure to this novel auditory feedback caused four of five adult zebra finches to dramatically alter their previously crystallized songs. Changes occurred in both the overall organization of song as well as in the spectral structure of individual syllables. In one protocol, birds were exposed to artificial feedback which varied in when and what portion of song was superimposed on the bird's voice.

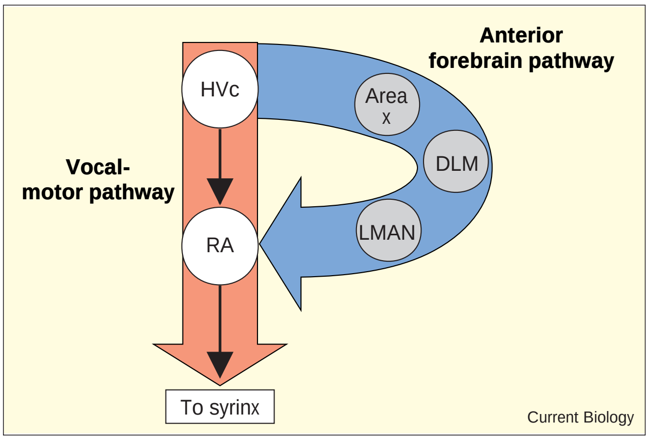
Within about six weeks in this environment, birds altered their songs in a manner reminiscent of changes observed sixteen weeks after deafening [2], the most dramatic change being the production of stuttered notes. Additionally, differences in syllable order occurred between motifs, in striking contrast to the stereotyped motifs of control adults. Altering auditory feedback may have caused song to change more quickly than observed after deafening as, in a second protocol, the targeted syllable of one bird decrystallized within a week from a tonal sound into a distorted harmonic stack.

Remarkably, upon cessation of the playback protocols, songs returned to their pre-experimental forms in about ten weeks. Thus, vocal plasticity can occur in the song of adult age-limited learners, but a number of features of the plasticity suggest that this capacity for change operates conservatively in adults. Firstly, changes in song are not apparent unless auditory feedback is perturbed. Secondly, alterations take place with a time-course that is much slower than for other learned behaviors, such as fear conditioning and spatial learning. And finally, even when adult song changes, some memory of the original version is maintained, as the song returns to its original state when the abnormal auditory feedback is stopped.

The timing and reversibility of alterations in adult song are reminiscent of the plasticity observed in auditory space maps in the barn owl's optic tectum, which shift to remain aligned with prism-induced abnormal visual cues, but then revert to their original state once normal vision is restored [6]. Both avian systems compare an ongoing state with a goal and use sensory-based signals to instruct subsequent modifications. While, in songbirds, the nature and location of the comparator remains elusive, recent progress has been made toward identifying sites that enable vocal plasticity and where error-generating signals could arise.

A great attraction of the songbird for studying mechanisms underlying learning is that song has an identified neurobiological substrate, much as there are identified brain regions controlling the perception and production of human language. The avian song circuit is divided into two anatomically and functionally distinct pathways (Figure 1). One portion, the vocal-motor pathway, connects telencephalic areas to syringeal and respiratory muscles used for singing, and drives song production throughout the bird's life. The second portion, known as the anterior forebrain pathway, is needed for sensorimotor learning, as lesions of brain nuclei in this pathway prior to crystallization result in aberrant song, but lesioning them after crystallization is without apparent effect. These findings have lead to the hypothesis that the anterior forebrain pathway is the locus of an instructional signal that guides the motor output of song during song development, but not beyond crystallization. As with auditory feedback, however, recent evidence suggests that the anterior forebrain pathway continues to be active in adults.

Figure 1



A schematic drawing of the avian song circuit. The vocal-motor pathway, required for song production, is shown in red and includes HVc and RA. RA directly innervates the motorneurons that control syrinx, the organ of song production. The anterior forebrain pathway, shown in blue, is implicated in song learning during development, and, now, in song maintenance in adults. It includes area X, the dorsolateral part of the medial thalamus (DLM), and the LMAN. LMAN projection neurons connect the anterior forebrain pathway with the vocal-motor pathway at RA. (Figure courtesy of John Spiro.)

The output of the anterior forebrain pathway is the lateral portion of the magnocellular nucleus of the anterior neostriatum (LMAN), which innervates the nucleus robustus of the archistriatum (RA), forging the link between the anterior forebrain pathway and the vocal-motor pathways. Recently, both electrophysiological and molecular studies have shown that the LMAN and the circuitry that feeds into it are selectively active even after crystallization: many adult LMAN neurons fire action potentials when the bird sings and when he hears his own song [7] — but not other auditory stimuli — and immediate-early genes and cell-signaling molecules are activated in the anterior forebrain pathway of adult animals by singing [8] and hearing song [9], respectively. These observations hint that LMAN is fulfilling a function that extends beyond crystallization. If, as recently revealed for auditory feedback, LMAN participates in adult song maintenance, the best way to demonstrate such a role is, similarly, to push the adult system into a state where it will attempt to compensate.

To test LMAN's adult role, Williams and Mehta [10] cut one of the nerves innervating the syrinx; this treatment initially disrupted syllable structure and then led to a slower period of song reorganization, where some syllables were dropped and others added. The LMAN was lesioned in certain birds prior to nerve section; remarkably, this prevented them from reorganizing their songs. In a related vein, LMAN lesions prevented the song degradation that otherwise occurs in adult Bengalese finches after deafening [7]. These findings indicate that LMAN is needed for the adult bird to change his song when what he hears is not what he expects. Thus, the LMAN permits experimentally-induced adult vocal plasticity, and lesioning LMAN removes the capacity for change, such that the song becomes truly immutable.

While the concept of neural plasticity implies change, and the idea that mature organisms retain a degree of neural and behavioral plasticity is not new, these studies of adult songbirds reveal that a mechanism which enables vocal *plasticity* may also serve to ensure the *maintenance* of stable song. If, beyond allowing plasticity, LMAN provides an error signal, then one expectation is that its activity should scale with perceived vocal error. Whether LMAN generates an error signal for song maintenance can now be explored using Leonardo and Konishi's protocol to exaggerate the signal, making it easier to detect. Even so, given the slow time-course of change induced by altered auditory feedback, one challenge will be to use chronic extracellular recordings to observe error signals as they shape song over these long time-courses.

But why would evolution preserve an error-correcting function which is only made manifest by experimental intervention? Is it merely to test the problem-solving skills of birdsong neurobiologists? The glaring fact remains that in zebra finches, once song is crystallized, removal of LMAN leads to no apparent change in song quality. One possibility is that crystallized song is not as stable as we think and LMAN lesions do subtly change song quality. Perhaps the hard dichotomy between plastic and crystallized song is more of a continuum, one along which even individual adult birds can travel. While studies have focused diligently on monitoring adult song following LMAN lesions, closer inspection of songs prior to lesioning might reveal that certain syllables do occur at very low frequency, only to vanish when LMAN is removed. Additionally, a bird syllable perceived by humans as identical before and after LMAN lesions may have lost subtle variations that can be distinguished by other songbirds, which could have consequences for the bird in its natural environment. There, low-level song variability may be important, depending on behavioral requirements. For example, it might behoove an age-limited learner to alter his song slightly in order to fit in to a new breeding territory. Thus, the LMAN may not simply be a developmental remnant in the adult, but serve a broader behavioral strategy that permits an old bird to learn new tricks.

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