Zebra Finch male with two juveniles (c/o Michael Fee, MIT)

The Song System of Songbirds


The Song System of Songbirds

Evidence that song is learned


- Tape recorded song
- Reared birds in acoustic isolation and recorded “isolate” song which appears as adult.
  - Isolate songs were very simple; lack the complexity of normal song.
- Introduced ‘tutor songs’ and observed copying (learning from acoustic model).
- Observed that late tutoring does not reverse effects of isolation.
- Thus, birds learn their songs by listening, usually to their fathers; and song learning takes place during an early ‘critical period’.

Peter Marler, Mark Konishi, Fernando Nottebohm

White Crown Sparrow

**Isolate Song**

‘Isolate song’ is the song that develops in acoustic isolation from conspecifics. Usually similar in form to normal song in frequency, duration, tonal quality, simple note elements. Sometimes called “innate song”. But isolate song still develops with trial and error and improvement. A deafened bird develops song very differently. Isolate song is therefore learned.

Examples of isolate song from white crowned sparrows.

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**Selective Imitation**

Birds reared in isolation show innate preference for species-specific songs.

– given choice between conspecific and heterospecific (wcs tutored with 5 spp. songs copies only wcs song – Marler, 1970).

WCS’s will copy other species songs in no-choice tutoring.

Swamp sparrows copy songs that contain their own syllables, even if synthesized according to the temporal pattern of another species.

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**In the absence of auditory feedback, birds do not sing innate song**

Konishi: studied effects of deafening on song development of juncos, white crowned sparrows, grosbeaks

If deafening is performed after tutoring but before singing, the effect is profound.

If deafening is done as an adult it has no effect on song maintenance.

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**Song Development Phases**

- Sensory learning: birds listen to song of father (or other male) and memorize it. There is a critical period for learning. After this, tutoring has no influence on song production.
- Critical period can be extended by using live tutors, or even by having live females combined with tape tutors.

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**Differences in Stages for Song Development for 3 species**

- White-crowned sparrows (seasonal closed loops): Sensory learning ends in spring, critical period ends in fall. Critical period can be extended by using live tutors or even by having live females combined with tape tutors.
- Zebra finches (age-limited learners): Sensory learning ends in spring, critical period ends in fall. Critical period can be extended by using live tutors or even by having live females combined with tape tutors.
- Canary (open-ended learners): Sensory learning ends in spring, critical period ends in fall. Critical period can be extended by using live tutors or even by having live females combined with tape tutors.
Sensorimotor: bird starts to produce subsong (weak, unorganized, highly variable). Comparable to babbling in human infants.

Later, plastic song: has elements of normal song, recognizable tutor elements present. Plastic song uses many elements that are later discarded.

Crystallized Song: full song with little variation.

Song Template Hypothesis

During sensory phase, bird hears & memorizes father’s song.

During song development, bird starts to vocalize. Matches auditory feedback from its own song to the memorized template stored in brain.

Adjusts song output to match template if they differ.

Template is formed by:
- acoustic experience
- innate factors and preferences

Birdbrain

Lessons to:
RA, X, or HVc have serious effects on song production.

Sarah Botjer: lesions to LMAN disrupt song learning, but lesions in adults have no effect on song production.

Lesions to DLM and X also produce deficits in learning.

In canary (learn new songs as adult) lesions to LMAN cause progressive deterioration in song.

Anterior pathway: auditory feedback during song development.
Lesions to LMAN in zebra finches: single note songs that crystallize early.
Lesions to X: rambling, long songs, never stabilize.

Anterior pathway is also dramatically sexually dimorphic (especially X), and sensitive to steroid hormones.

Patterns of Neural Activity

During Song Production:
Electrophysiological recordings from single units in HVc and RA during singing show temporal relationships with sound output. Spikes precede sound output.

HVC activity seems to correlate with overall rhythm of entire song.

RA activity correlates with production of syllables.

Electrical stimulation in HVC may alter the rhythm of singing (phase advance?). Stimulation in RA causes syllable disruption.

During listening:
Forebrain nuclei neurons respond to acoustic input, and are song-selective.

LMAN: units are stimulated by BOS, not species-specific song, not by reversed song.

X: less selectivity to BOS.

LMAN thus has ability to listen to bird’s own song and compare it to template of song.
HVC neurons that project to RA
sparse code for short sequences of
song

HVC neurons that are intrinsic to HVC
inhibitory. Tonic firing during song.

RA neurons
abdominal muscles

From Fiete and Seung (2009)

From Fiete and Seung (2009)

In LMAN, units tend to respond selectively to Bird's Own Song (BOS)

Doupe & Solis, '97

15 different LMAN units show
selective responses to BOS,
compared to conspecifics or
reversed songs.

Zebra finch.
Doupe and Konishi (1991) PNAS

Is there stability in adult song?

Decrystallization of adult
birdsong by perturbation
of auditory feedback

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Department of Neural Science, Princeton University, Princeton, NJ 08544, USA

California Institute of Technology, Pasadena, California 91125, USA
During juvenile development, lesions to HVC has not effect on "babbling" or subsong (not yet crystalized).

In adults, lesions to HVC abolishes song.

A Specialized Forebrain Circuit for Vocal Babbling in the Juvenile Songbird
Dmitry Aronov, Aaron S. Andalman, Michale S. Fee. (2008). Science
Lessons from the study of birdsong

1) Birdsong offers an opportunity to study the neuronal circuits involved in a complex yet stereotyped behavior. Song is sometimes seen as a model for human speech.

2) Song has both an innate structure, and an essential learned component. Song learning takes place during an early critical period.

3) Song also requires practice and refinement during which hearing is essential. Studies of song are a premiere example of sensory motor integration.

4) The neural pathways for song are divided into two parts: a posterior pathway from forebrain to brainstem to syrinx involved in motor coordination and rhythm generation, and an anterior pathway involved in learning.

5) Our understanding of the function and mechanisms of vocal learning is incomplete. Lesion studies are still informative of the complex mechanisms involved in vocal learning.

References


