



Learning to Sing

Probing Nature versus Nurture with the Songbird

The phrase “nature and nurture” is a convenient jingle of words, for it separates under two distinct heads the innumerable elements of which personality is composed.

Francis Galton, 1874

From Philosophy to Science

Before the dawn of scientific methodology, the discussion of inherited and learned traits, or nature versus nurture, was restricted to the armchair speculation of philosophers. However, enter Charles Darwin in the 1800s, public discourse regarding natural selection, survival of the fittest, and interaction between genes and environment commenced.

Darwin’s grandson Francis Galton, 19th century geography, coined the phrase “nature versus nurture.” In 1874, Galton wrote *English Men of Science: Their Nature and Nurture*. He may have borrowed the phrase from Shakespeare’s *The Tempest*, in which Prospero insults Caliban by exclaiming “A devil, a born devil, on whose nature nurture can never stick.” Thus, the question of nature and nurture, how a human being’s identity—personality, behavior, and morphology—is determined, has been a subject of public discourse for quite some time.

With advances in technology, neurobiologists and animal behaviorists have begun probing the means by which genetic and environmental factors shape our behavior. Using animal models, scientists can link neural processes with behavior. Perhaps surprisingly, the songbird, for example the common Australian zebra finch, is the perfect animal model in which to explore the nature versus nurture conundrum. Current songbird research elucidates the genetic and environmental factors that influence

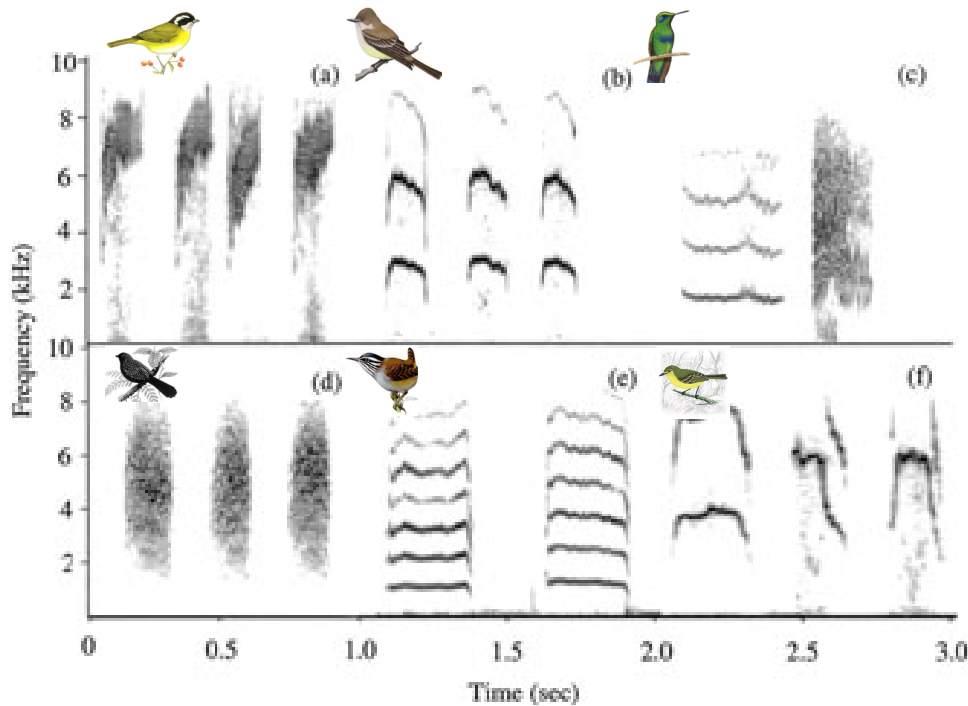
song learning. In doing so, researchers hope to uncover the degree to which singing behavior is determined by innate and learned traits—or nature and nurture.

In the following, we will investigate the neural processes and structures involved in song learning. Then we will consider current research that elucidates the factors—both innate and learned—influencing singing behavior.

Learning to Sing

When a toddler learns to speak, he or she may undergo a period of babbling prior to the pronunciation of his or her first word. Babbling reflects a motor process that accompanies his or her development of verbal comprehension. In the young male songbird, similar processes of vocal production and comprehension occur such that singing may be developed and used to attract potential mates.

After the male zebra finch is born, he learns to sing in two phases: sensory acquisition and sensorimotor learning. During sensory acquisition (20-55 days post-hatching), the finch listens to and memorizes his tutor’s (elder of the same species) song. During sensorimotor learning (45-90 days post-hatching), the zebra finch begins to babble, or produce a *subsong*. This subsong evolves into a plastic song in which elements of the tutor’s song begin to appear. The *plastic song* modulates until it matches that of the tutor and other birds of the



Each bird species has its own song. These sonograms, or digital representations of bird songs, illustrate characteristic songs of 6 distinct songbird species: (a) Sooty-capped Bush-Tanager, (b) Black-capped Flycatcher, (c) Green Violet-ear, (d) Gray-breasted Wood-wren, (e) Streak-breasted Treehunter and (f) Yellowish Flycatcher.

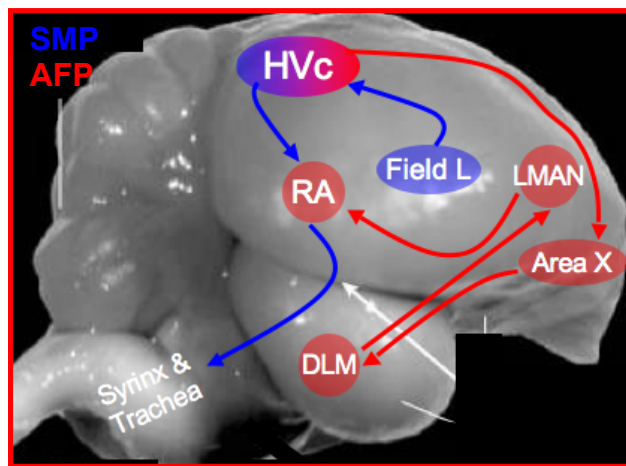
same species in its environment. At this point (~90 days post-hatching), the bird has developed a permanent, *crystallized song* reflecting the characteristic musical elements (pitch, rhythms, syllables, etc.) of its species. Thus, in the first 100 days post-hatching, referred to as the *sensitive period*, the male zebra finch develops a species-specific song.

All songbirds undergo a similar song-learning process, however, the timeline and order of sensorimotor and sensory acquisition may vary from one species to another. While there exists this general timeline involved in song learning, *how* is it that the songbird recognizes, understands, and responds to auditory stimuli?

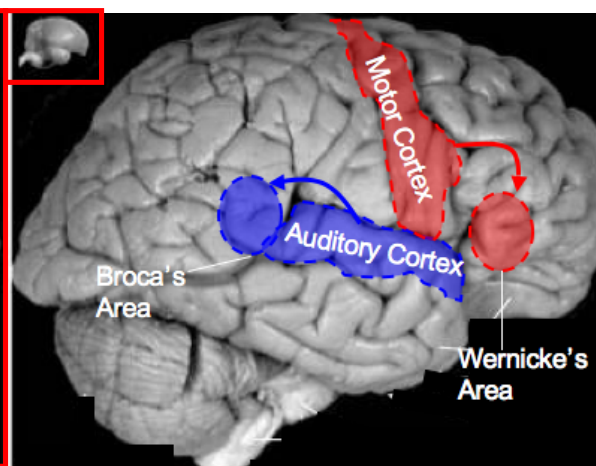
The zebra finch hears and produces sounds with neural structures that mirror those in the human brain. Let us first consider the process by which you, the human, hear and produce vocal sounds. Consider a typical conversation; you enter the kitchen and your mother asks you to set the table for dinner. Her request (an auditory stimulus) travels through your ear, into your brain via electrochemical signals passed from one neuron to another. You make sense of her words via the neural signals that propagate from the inner ear to an area on the superficial, or outer, cortex of the brain, called *Wernicke's area*. This signal then

makes its way to the auditory cortex, where it can be synthesized with additional auditory stimuli (the television program playing in the adjacent room, the clanking of pots and pans) and other sensory stimuli (the smell of turkey in the oven, the temperature of the room) in your environment. To generate a verbal response to her request, neurons in the primary motor cortex and *Broca's area* initiate speech production such that you can pleasantly respond "Sure, Mom, anything for you." While the neural pathways necessary for vocal comprehension and production are extensive and complicated, analogous neural structures are also found in the humble songbird.

The zebra finch brain is approximately the size of your thumb—much, much smaller than the human brain. Yet, it possesses structures that serve similar purposes in vocal learning, production, and perception, relative to those described in the human brain. When the songbird hears an auditory stimulus, for example, the song of a nearby bird, the neural signal propagates from the inner ear to *Field L*, where auditory signals are integrated similarly to the human auditory cortex. Yet, in the bird, there are two pathways in the brain that allow for the bird's acquisition and production of his song: First, the *song motor pathway* (SMP) sends input from Field L to the *HVC*. Then, the signal may be sent, via the *robust nucleus* (RA), to the



Songbird



Human

syrinx and trachea for production of a vocal response. Together, these SMP structures play a role in song production. Second, the *anterior forebrain pathway* (AFP), propagates signals from the HVC to *Area X*, involved in enforcing habits.

Then, the signal propagates through the *DLM* and *LMAN* to the RA, syrinx, and trachea, allowing for a vocal response. The AFP pathway is involved in both song acquisition and auditory-vocal feedback, such that the bird can learn his song and simultaneously compare it to that of its tutor.

The Innate Song

When, as by a miracle, the lovely butterfly bursts from the chrysalis full-winged and perfect...it has, for the most part, nothing to learn, because its little life flows from its organization lie melody from a music box.

Douglas Alexander Spalding, 1875

In the 1950s, W. H. Thorpe, an ethologist at the University of Cambridge, discovered that isolating the songbird during its sensitive period results in the development of an abnormal *isolate song*. However, a predisposition for species-specific song characteristics was evidenced, as there were some species-specific features the isolated bird developed, despite not having been exposed to a tutor's song. Furthermore, exposing the bird to a tutor from a different species during the sensitive period lead to a song similar to its tutor, yet sung in the style of

the juvenile bird's species' song. Thus, it is clear that there is some innate mapping in the bird's brain that predisposes the bird to sing in a style reminiscent of his species.

What leads to the innate characteristics of bird songs? Researchers have begun cracking this enigmatic code via deducing the influence of various genes—hereditary molecular markers passed from one generation to the next. Exploring two genes: *FOXP2* in male and *zenk* in female songbirds has allowed researchers to elucidate the innate features of song learning and perception, respectively.

Current research has shown *FOXP2* to be involved in the planning and production of song. Investigation of this gene in the songbird was initiated in response to the identification of a mutation on the *FOXP2* gene in the human disorder *developmental verbal dyspraxia*. Thus, *FOXP2* plays a homologous role in birdsong to that which it plays in human speech development. Mutating or reducing the expression of *FOXP2* during the sensitive period disallows the bird from accurate replication of the tutor's song. Thus, this gene controls some aspects of species-specific song-learning, or the innate features of the birdsong.

On the other hand, the gene *zenk* plays a role in female's predisposed preference for her species-specific song. Genes like *FOXP2* and *zenk*, however, are certainly only small pieces of the puzzle; in 2008, the Songbird Neurogenomics

(SoNG) Initiative commenced with the hope of developing genomic tools and a strategy for probing gene expression in diverse songbird species and natural contexts. Future developments in technology may allow songbird researchers to determine the genetic basis for the innate features of the bird's song.

While there certainly exist innate features in birdsong—there are also features that are plastic and adaptable to the bird's environment throughout and after the sensitive period.

The Plastic Song

During and after the sensitive period, a bird's song changes in response to a variety of environmental factors. The extent to which a bird's song is adaptable, or *plastic*, is currently being investigated by numerous songbird laboratories. In this section, plastic changes in response to auditory experience, social interaction, and seasonal changes are discussed.

Current research suggests that neuronal connections in the song pathways are experience-dependent. The Bottjer lab at the University of Southern California is currently investigating the role of auditory experience in the formation of neural pathways in the zebra finch. Bottjer and colleagues disrupted song learning in juvenile birds by either deafening them or exposing them to loud random noise during the sensitive period. These disruptions affected neural connections from the LMAN to the RA in the AFP pathway, suggesting that this particular connection modulates in response auditory.



Jon Sakata (above) and his colleagues study how the brain changes in response to social influences on vocal learning and production on the Bengalese finch (right).



Additional research suggests that song system pathways adapt in response to social interactions between the bird and his tutor or other birds of the same species. The laboratory of Jon Sakata, at McGill University, is currently investigating how the song system pathways change in response to social influences. Sakata and colleagues determined that social context rapidly modulates the AFP pathway on vocal motor control. They observed two scenarios—one in which the bird was isolated and “practicing” his song, and another in which the bird was “performing” his song with the objective of attracting a female mate. They found that auditory-feedback was more influential when practicing than when performing. Thus, the Sakata lab has provided further evidence of song plasticity—how varying social contexts can *change* the song, via the AFP, later in life.

Lastly, seasonal changes also influence the size and activity of song system structures in seasonally breeding birds. Work has shown that changes in steroid hormone expression, like that of testosterone, mediate seasonal cell death. For example, the HVC decreases in size during non-breeding seasons, when testosterone levels are low. Other structures in the song system, e.g. the RA and Area X also decrease in size during non-breeding seasons. Thus, it seems that seasonal changes affect hormonal levels, like that of testosterone—and this plays an important role in influencing singing behavior; if testosterone levels are high, the bird will increase its singing behavior in pursuit of a female mate. This case illustrates an interesting environment-hormone interaction. Thus, hormones also play a role in plastic changes in the song system and resulting bird song after the sensitive period.

Integrating Nature and Nurture

In the songbird, there are a series of genetic *and* environmental factors that influence singing behavior. Inherited genes produce the innate features of birdsong, whereas a variety of environmental factors—auditory experience, social interaction, seasonal changes, play important roles in modulating singing behavior. This allows birds to adapt to their ever-changing surroundings in the wild.

Songbird research is fascinating in its own right. Yet, the analogous structures, processes, and behaviors in vocal production and learning across birds and humans prove songbird research to be exceptionally applicable as we strive to understand the nature versus nurture conundrum in the human condition.

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For Further Reading

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