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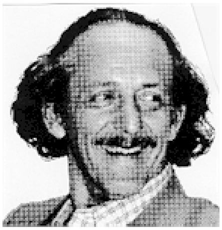

Current Comments

Birdsongs and Avian Linguistics—There's More to Them Than Meets the Ears

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The melodic singing of birds is a pleasure that most people enjoy. Perhaps you live in the country and welcome the robin's song as the first herald of spring. Or maybe you live in a city apartment filled with the singing of a canary. I remember hearing a canary sing for the first time at my grandmother's house. I've been fascinated and thrilled ever since to hear birdsongs. As a onetime student of linguistics, I was doubly intrigued when I learned from Peter Marler, Rockefeller University, New York, that avian "linguistics" has become quite a sophisticated area of research.

The songs of birds have been appreciated since Paleolithic times.[1,2] Cave paintings of open-beaked birds suggest that our early ancestors were impressed by avian vocalizations. Literary references to birdsongs occur in Dante's *Divine Comedy*, where different songs of various bird species symbolize paradise or hell.[2] John Locke was one of the first authors to write about the acquisition of birdsongs. In his seventeenth-century work, *An Essay Concerning Human Understanding*, Locke stated that birds learn their tunes through perception and memorization.[3] Immanuel Kant noted in 1803 that house sparrows do not instinctively know their song, but must learn it.[4]

But the scientific study of birdsongs is largely a twentieth-century development. Today, we know that not all birds sing. Most use simple calls to communicate. These calls are innate, or hereditary, and usually provide basic information about danger, food, or mating.[5,6] Some birds, however, have developed far more complex sound patterns, or songs, in addition to simple calls. These birds are considered to be true songbirds, or oscines.[7]

Oscines belong to the largest order of birds, the Passeriformes. Passeriformes, known as perching birds, include over half of all bird species.[7] The oscines are characterized by the seven sets of syringeal muscles they use to produce sounds.[8] These muscles control a bird's voice box, or syrinx, which is similar to the human larynx[9] in that both are used to produce sound. However, the songbird syrinx plays a more active role in sound production. For example, the human larynx produces monotonous sounds, which the mouth and throat then refine into speech. In songbirds the syrinx not only produces sound, but also determines the patterns that these sound vibrations will take.[10] Most birds have only two sets of syringeal muscles.[8] But the songbirds have developed five additional sets of muscles, greatly enhancing their ability to create complex patterns of vocal sound.

Songbirds may have a distinct evolutionary advantage over birds that cannot sing.[11,12] According to M.C. Baker, Colorado State University, songbirds seem to show greater speciation—the number of species within a taxonomic family. For example, there are currently 84 families of birds that don't sing. These nonsinging families are differentiated into 3,518 species. Songbirds have only 36 different families, but they are divided into 3,990 species. Thus, there is an average of 111 different species for every songbird family, compared to only 42 species per nonsinging bird family.[11] The capacity to learn songs seems to have promoted a greater rate of adaptive radiation into new environmental settings.

How birds acquire songs varies among species, but some general rules apply. Usually, only male birds sing.[5] Their songs are always conspecific—that is, birds sing only the songs of their own species.[6] Masukazu Konishi, California Institute of Technology, was one of the first to discover that songbirds must *hear* these conspecific songs if they are to develop normal singing patterns.[13] And this has to occur during the "critical period"[6,14] in a songbird's life, usually before it is a year old. If the bird is deafened during this time, or kept from hearing the voices of its own species, it will never learn to sing normally.[13]

What controls the critical period is not clear, but in some songbirds it coincides with male sexual development. Fernando Nottebohm, Rockefeller University, castrated a young male chaffinch before it learned to sing. Even when the bird was two years old, it still hadn't developed the ability to sing. But the bird developed normal vocal patterns after receiving injections of testosterone, a male sex hormone, and hearing normal chaffinch songs.[14]

Other research indicates that the song learning process may also depend on an innate "template."[13] The template is a genetically programmed song model against which a songbird compares what it hears. The model contains basic information about conspecific song syllables to prevent a songbird from learning syllables belonging to other bird species.[12] After the critical period in birdsong learning, the bird does not begin to sing for several months.[15,16] Researchers suggest that the bird now reinforces and remembers only those sounds matching the template. That is, the template restricts the syllables the bird learns to those that satisfy the requirements for correct song development within its species.[12]

The first stage of singing is called subsong,[12,17] when the songbird first applies its syrinx to the task of reproducing the intricate melodies of song. In the 1800s, Charles Darwin compared this subsong stage to the babbling of human infants.[18,19] During this, and the subsequent plastic song stage, the songbird makes more sounds than it will use as an adult. In fact, up to four times as many syllable types as are eventually needed may be produced.[16] But due to the template, this overabundance of syllables is quickly refined to include only correct song notes.

Plastic song rapidly evolves into mature singing,[12] when individual conspecific syllables are put into patterns.[17] In most songbirds, the template doesn't contain complete information about how to arrange the syllables into patterns. Marler found evidence to support this in experiments with young song sparrows.[6] The sparrows were exposed during the critical period to tapes of syllables produced by song sparrows and swamp sparrows. The syllables were artificially arranged in different patterns, both correct and incorrect. When full song developed months later, the song sparrows learned the correct song sparrow songs made up of song sparrow syllables. But they also learned the incorrect songs composed of swamp sparrow syllables.[6,20,21] That is, the genetically inherited template didn't prevent the song sparrow from learning inappropriate songs.

When it comes time to arrange syllables into a meaningful structure, a conspecific model may be followed, but the young song sparrow doesn't need to hear adult song sparrows singing in order to compose the basic syntax of the songs of its species.[12] Even a deaf song sparrow can arrange a song more or less correctly despite the abnormal "buzzy" quality of its notes. Learned notes and syllables are usually combined with inherited traits by the time most songbirds are a year old.[22]

As a bird's singing matures, even more complicated learning can be detected. For example, adult birds can vary songs in individual ways without losing their species identity. These individual variations are known as repertoires. The number of different variations a songbird uses ranges from two to several thousand. For example, the redwing blackbird sings about six different song variations[23] while the brown thrasher may know as many as 2,000.[24]

Repertoires develop when the song is being learned. Researchers suggest that repertoires enhance a songbird's ability to settle in a territory and defend it.[25,26] A songbird develops its repertoire at the same time it is looking for its first territory. Experiments show that songbirds have an easier time settling in territories if they know a variety of different songs. If a songbird can draw from a large repertoire, it will be better able to match the song of a potential neighbor. It can then move into the territory without resistance.[23,27,28] In fact, some species of songbirds learn their repertoires from future neighbors.[27,29]

But repertoires are also used to defend a territory.[23] John R. Krebs, Edward Grey Institute of Field Ornithology, Oxford, England, states that a songbird may use its repertoire to defend a large territory all by itself. This is known as the "Beau Geste" hypothesis. By frequently changing song types, a songbird might fool invaders into thinking that the territory is crowded and unsuitable for new settlement. The Beau Geste strategy would be most effective if the songbird changed its perch while singing. Also, densely vegetated areas with low visibility could enhance the deception that many different birds are singing. The Beau Geste theory takes its name from a book about a soldier who single-handedly defended a fort by propping up his fallen comrades around its parapets—the attackers were fooled into thinking the fort was well protected.[30]

But potential mates, as well as enemies, might be fooled by the Beau Geste strategy. To prevent this, male and female songbirds within a territory learn dialects.[5] Dialects are recognizable similarities in birdsong repertoires.[12,31,32] Nottebohm[31] suggested that certain species of songbirds mate preferentially with birds of their own dialects. This hypothesis is confirmed by Baker.[33,34] Also, female songbirds recognize the dialects of their mates even though females do not normally sing.[13,33]

Dialects may be learned when a bird is young and still living in the area where it was born.[5,31] Not all birds acquire dialects.[35] Those that do may live in areas where specialized adaptations are needed for survival.[31] Thus, a songbird might be guided back to the area for which it is best adapted through dialect recognition.[5,32] This is still a controversial subject among birdsong researchers. Young songbirds can also learn dialects of other territories. This ability is useful when, for example, a young songbird is diverted from its migratory route. The bird can settle and breed in the new territory by learning a novel dialect.[12,34]

P.F. Jenkins, University of Auckland, New Zealand, suggests that some species of birds may actually prefer to mate with birds *outside* their dialect. Saddleback songbirds, for example, are very stable populations that tend to stay in one territory for several generations. The risk of excessive inbreeding among saddlebacks is particularly high. As a result, saddlebacks use dialect recognition to avoid breeding with their kin too often.[36] Thus, dialects are specialized consequences of vocal learning that ensure the best possible mating combinations within a species.

Incidentally, the existence of dialects is what first led Marler, one of today's top birdsong experts, to become interested in birdsongs. Marler appreciated the complexities of birdsongs while carrying out botanical studies in England. He observed that chaffinches used distinct dialects that marked them as inhabitants of a specific geographical location. This aroused his curiosity about how and why such differences exist. As a result, he redirected his career to zoology, and the study of birdsong acquisition.[37,38] Much of the research used in this essay grew out of Marler's work over the past 30 years.

Whether or not birdsong learning is a linguistic achievement comparable to human communication is open to question.[12] But the learning processes involved in birdsong acquisition suggest a sophistication of brain function that was previously considered unique to human beings. Nottebohm's experiments on the brains of canaries indicate that certain brain functions are indeed common to birds and humans. For example, songbirds exhibit left hemispheric brain laterality for vocal control.[18,19] Hemispheric laterality refers to the concentration of control over motor or cognitive activities in one side of the brain. In canaries, the brain is connected to the syrinx by the hypoglossal nerve. If the left side of this nerve is severed, the canary loses its ability to sing. But if the right side is cut, no major impairment results.[19,39] This indicates that the left hemisphere of the canary's brain controls its vocal ability. Previously, only humans were thought to show left hemispheric laterality of speech control.[39]

Data also show that the right side of the canary's brain can compensate for any loss of vocal ability when the left hemisphere is damaged. That is, the very young canary can still sing even after the left side of its hypoglossal nerve is cut.[18,19,39] It is hoped that humans may also share the ability to redirect linguistic functions in the event of brain injury.[39] In fact, recent research indicates that women are capable of regaining speech within a year after suffering strokes that damage the brain.[40] Researchers believe that female brains are less lateralized than male brains. Thus, control for speech in women is not as concentrated in the left hemisphere as it is in men. Consequently, the right side of the female brain may be able to take over speech control in the event of injury to the left hemisphere.[40]

Additional evidence that the songbird brain is capable of new growth, as well as repair, comes out of research on the canary's repertoire.[19] Canaries learn new repertoires every year in early spring.[39,41] Measurements of male canary brains show that they are larger in spring and smaller in fall.[19,38,39] Researchers suggest that a canary's brain gets rid of old repertoires in the fall by shedding the tiny branching sections called dendrites.[39] Dendrites are nerves responsible for acquiring new knowledge.[19] By shedding old dendrites, the brain has more "room" to store its new repertoires acquired in the spring.[41]

The range of a canary's repertoire is also directly related to the size of the part of its brain involved in song control.[19,39] Nottebohm calls this the "library theory."[39] A large library may or may not have a lot of books. But a library with a lot of books must have a lot of shelves. And a library without much space can only hold so many books. In canaries, those with small song control centers have small repertoires. But birds with larger repertoires have larger song control centers.[39]

The size of song control centers is also correlated with gender. Male canaries with large repertoires have significantly larger song control centers than females. But even male canaries with limited repertoires have larger song control centers than females, because only males sing. When females are injected with male sex hormones, their song control centers become larger than those of normal females. This sexual difference in the amount of brain space devoted to a learned behavior was discovered in 1976 by Nottebohm and his colleague A.P. Arnold.[42]

There also is evidence of differences in human brains that are gender related. I mentioned earlier the differences in lateralization between human male and female brains. It is also known that the area of the brain that coordinates activity between the left and right hemispheres is shaped differently in males and females. The significance of this isn't yet known, but it seems to be related to the degree of lateralization in each sex's brains.[43]

Clearly, research on birdsong acquisition is relevant to biomedical researchers, especially neurologists and neuro-

Table 1: Core papers from the *SCI®* cluster on sexual dimorphism in vertebrate brains, and the number of times they were cited in 1981.

Total Citations in 1981	Bibliographic Data
29	**Arnold A P, Nottebohm F & Pfaff D W.** Hormone concentrating cells in vocal control and other areas of the brain of the zebra finch (*Poephila guttata*). *J. Comp. Neurol.* 165:487-511, 1976.
20	**Gorski R A, Gordon J H, Shryne J E & Southam A M.** Evidence for a morphological sex difference within the medial preoptic area of the rat brain. *Brain Res.* 148:333-46, 1978.
20	**Raisman G & Field P M.** Sexual dimorphism in the neuropil of the preoptic area of the rat and its dependence on neonatal androgen. *Brain Res.* 54:1-29, 1973.
16	**Nottebohm F & Arnold A P.** Sexual dimorphism in vocal control areas of the songbird brain. *Science* 194:211-3, 1976.

anatomists. The *ISI/BIOMED*™ data base identifies related research in a variety of disciplines through research front specialty searching. We located a 1981 *ISI/BIOMED* research front entitled "Studies of birdsongs," which includes articles by Baker, Marler, and Nottebohm in its core. These articles were cited by 33 articles published in 1981, which gives you an idea of how active birdsong research is.

Nottebohm's publications are also included in a cluster of research on sexual dimorphism in *Science Citation Index®* (*SCI®*). I've described ISI®'s clustering procedure in earlier essays.[44] Table 1 shows the four articles included in this cluster, and the number of times they were cited in 1981.

Not many of us would have thought that birdsongs are anything more than a pleasant and diverting sound. But these seemingly whimsical melodies are actually vocal cues for important events in the bird's world—staking out a territory, defending it, and mating. Birds learn and recognize the complex repertoires and dialects of their species-specific songs because they have surprisingly specialized brains. And we now know that the bird's brain is comparable to the human brain in organization and function. As we learn more about birdsongs, the insult of being called a "birdbrain" will lose its sting. Who knows—it may eventually become a compliment.

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