NEUROSCIENCE

Singing in the Brain

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"Birds' song tradition appears to be the truest in the world." –Kant (*1*)

It might come as a surprise to some, but the ability to reproduce vocalizations is rare in nature. All birds and mammals can probably memorize new sounds and may learn to respond appropriately to them, but very few species also produce sounds they have previously memorized. Among the 9700 known species of extant birds, three groups (songbirds, parrots, and hummingbirds), comprising roughly 5200 species, have such vocal learning abilities. Among mammals, only four taxa (humans, cetaceans, bats, and elephants) learn their vocalizations, and humans are by far the most sophisticated vocal learners. In order to produce normal, species-typical vocalizations, a vocal learner needs to hear a conspecific; learning to produce the appropriate sound is directed by auditory feedback control of the learner's voice.

Only vocal learners have developed a special neuronal circuit in the brain devoted to learning and producing vocalizations. These brain regions have not yet been investigated in mammals other than primates. However, the song-control areas of avian brains have received considerable attention from neuroscientists. *Neuroscience of Birdsong* provides a fascinating, thorough (though not complete) overview of their findings, which have been made possible by increasingly sophisticated technology. The introductory section, an easy read even for non-experts, covers song learning, discusses parallels between birdsong and speech, and briefly outlines the relations between avian and mammalian brains. In five thematic sections (each with its own lucid and incisive introduction), contributors provide sometimes very detailed summaries of such topics as lower and higher auditory perception, song acquisition and memory formation, neurogenesis, song recognition, central sensory processing, sensorimotor control, the role of hormones in modulating song behavior, neuronal plasticity, and genomic mechanisms. A final section, "On a Personal Note," offers insights into ground-breaking discoveries and fast-paced development of birdsong research through a biographical sketch of the field's founder, William H. Thorpe, and personal recollections by his student Peter Marler and Marler's students Masakazu Konishi and Fernando Nottebohm.

Neuroscience of Birdsong

H. Philip Zeigler and Peter Marler, Eds.

Cambridge University Press, Cambridge, 2008. 568 pp. $160, £80. ISBN 9780521869157.

As to be expected and as the editors readily admit in the preface, some topics had to be cut short. Nonetheless, the limited attention given to evolutionary aspects of birdsong research is particularly unfortunate, in view of the often-expressed interest in songbirds as models for human speech. Findings in the past decade have shown that avian cognitive abilities are surprisingly sophisticated, in some cases arguably on a par with those of primates. Birds solve complex problems using similar brain regions to mammals, although the bird brain lacks the laminar structure that characterizes the mammalian brain. An international consortium of neuroscientists has revised the nomenclature of the avian brain in order to correct outdated views and misunderstandings intrinsic in the classic terminology. Their results (*2*) highlight the analogies between the avian and mammalian (including human) brain. Including more recent descriptions of the striking similarities between the organization of the song-system circuit and the human vocal control system would have enhanced the relevance of avian studies for neuroscience as a whole.

Also absent is recent work that may be of particular interest for comparisons with humans. For example, noninvasive, in vivo studies of songbird brains by high-resolution magnetic resonance imaging now enable us to disentangle relations among brain circuitry, neural activity, and behavior. The behavior of an individual can be related to changes in its neuronal substrate after having experienced (sometimes repeatedly) different environments or social contexts.

In spite of these absences, *Neuroscience of Birdsong* offers senior students an excellent in-depth introduction to, and provides specialists an insightful summary of current knowledge about, song learning and production in birds. The volume will reward anyone interested in the neurobiology and mechanisms underlying vocal communication.

Well-studied singer: white-crowned sparrow, *Zonotrichia leucophrys*.

We are still only beginning to address the neuroscience of communication. For example, birds use other acoustic signals besides vocalizations. Songs or calls may be accompanied or even replaced by instrumental sounds (e.g., the wing-flapping of the flappet lark, *Mirafra rufocinnamomea*). The neural substrates of such sounds remain unexplored. In addition, singing in many birds (like speaking in humans) is only the vocal part of a composite audiovisual communication, and these complementary bodily gestures have yet to be tackled by neuroscientists.

Similarly, we are only beginning to explore birdsong as the nearest known nonhuman analogy to our language. Women are better than men at spelling and grammar as well as verbal recall tasks, although both sexes have about the same vocabulary. Sex differences in human brain anatomy have been long known; now data on sex differences in the neurocognition of language are slowly accumulating as a result of neuroimaging studies. Dueting male and female dark-backed weavers, *Ploceus bicolor*, produce similar song repertoires of similar complexity, yet they have different-sized brain areas and different complex network properties (*3*). Through comparison with human data, models of dueting avian species may help unravel the mystery of how different brains can achieve the same vocal performances.

Contrasting studies of birdsong and monkey calls, Marler acknowledges, "The neurobiology of the song system, so productive for the study of learning, has told us virtually nothing about the meaning of vocal signals." Yet with great faith and undiminished enthusiasm, he notes, "There are endless new frontiers in the neuroscience of vocal behavior still awaiting our attention."

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