Songs in Flight

Pursuing Learning in Songbirds

Learning

There are many kinds of birds—some walk, some swim, and of course there are the ones that fly. Some of them have nice songs. That was the sum of my knowledge about the biology, behavior, or evolution of birds as I entered my last year of graduate school. I had been studying neural plasticity in rats, because they were the primary animal system in which to study neurobiology. Neural plasticity is the capacity of neurons—particularly synapses between neurons—to modify their form in order to alter their function in response to experiences (learning).

To Study Learning—In Birds!

In November of that year, I was attending the Society for Neuroscience Meeting and went to a plenary talk by Fernando Nottebohm of Rockefeller University. He spoke to 1,200 neuroscientists about his recent discovery that a small number of clearly delineated brain regions appeared to be dedicated to song production in canaries. He had found that these regions were bigger in males than females and bigger in spring than in fall, parallel to differences in singing. Young male canaries learn how to sing from adult males. Nottebohm also found that these brain areas could not be found in species like pigeons or chickens that do not learn their vocalizations.

"It would be wonderful to study learning in an animal like that!" I gushed to one of my professors with whom I was sitting. She replied that Nottebohm was a friend and asked if I wanted to meet him. After a dozen others had spoken to Nottebohm, she introduced me, and again I spoke of how exciting his presentation had been to me. He responded politely and asked what I did. When I told him that I measured anatomical changes in synapses, he also became excited and said that was exactly what he next wanted to do in birds. Within a short time, we had arranged for me to work as a postdoc with him, and I have been doing research on synaptic plasticity in birds ever since.

Learning at Cornell

In my initial research at Cornell, my students and I studied how hormonal changes would affect song-related brain areas. Males and females differ greatly in hormone levels in the circulation, and the levels of these hormones are much higher in spring than in other seasons. We were able to show that these qualities are associated with huge differences in the composition of particular groups of synapses. From the beginning, we included a naturalistic component in the research—not only

Photos in this article: Frank DiMeo unless otherwise noted demonstrating a phenomenon in the laboratory, but also carrying out parallel experiments on wild birds to see whether our observation was a feature of artificial lab constraints or part of the true biology of birds. Paying attention to natural behaviors as exhibited in naturalistic contexts is an approach that is prominent in biological research at Cornell and is relatively rare elsewhere. It has fostered learning about ecology and about evolutionary selection—disciplines to which I had little exposure before coming to Cornell—which continue to be a source of intellectual growth.

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Learning at Oxford

I spent my first sabbatical working with John Krebs at Oxford University, learning statistical procedures for comparing brain anatomy among species. We used these procedures to show a relation between the volume of one song-related brain area and how much song learning was typically shown by the species—this area is huge in nightingales that learn elaborate songs, for example, and small in house sparrows that do not. In Krebs' lab, I also observed elegant experiments on spatial learning in chickadee species. He had found that some of these species hide hundreds of food items and remember the locations for at least several weeks and that in these species, the hippocampus is larger than in related species that do not hide food items. Chickadee food caching is a wonderful form of learning to study. It is rapid, easily observable, natural, and occurs repeatedly throughout adult life; it also appears to be carried out by a brain component that has a similar role in mammals.

Song Learning

On returning to Cornell, my students and I shifted focus toward studying features in the brain specifically related to learning. We carried out experiments on song learning and added experiments on spatial learning in black-capped chickadees. Dave Airey, Ph.D. '00, found that individual birds differ in how much song they learn—and these individual differences in behavior correlate with the volume of the brain area that organizes song production. Furthermore, he found that differences between males in the size of this brain structure are heritable—if it is large in an adult male, it will tend to be large in his sons, and vice versa. Christine Lauay, Ph.D. '03, and Rob Komorowski '03 raised birds so that they never heard a song—and so had nothing to learn from—and found substantially fewer synapses in this brain region in adulthood. These results together suggest that genes help to determine a male's capacity for song learning and that, with rearing in a good (song) environment, he can build synapses that use this capacity.

What about the Females

As we were doing these experiments, we thought about how song learning and song expression are used by birds in real life. We realized that we had only been paying attention to half the story—males sing to females. In many species, a female will choose to mate with the male she encounters who has the most elaborate song. Logically, for her to make such assessments, she must be at least as good as a male in learning about song. Yet I, along with most of the other scientists studying neurobiology of song, had paid very little attention to females. This oversight is quite common in neurobiology for most research issues, except those closely tied to endocrinology.

We recently completed our first series of experiments exploring the nature of song learning in females. Lauay and Nicki Gerlach '03 found that females raised without hearing song are still attracted to song, but cannot discriminate between good and bad songs. Lauay and Komorowski then showed that such females have far fewer synapses in an associative brain area. Postdoc Michelle Tomaszycki and Sara Blaine '05 found that anesthetizing this specific brain area in an adult female does not impair her interest in interacting with a male, but leaves her unable to remember the interaction when she meets him again. We are currently eager to find out whether this is due to impaired auditory memory or to a general deficit in integrating and retaining social information.

And Then There Are the Chickadees

After seeing Krebs' beautiful experiments at Oxford on spatial memory in British chickadees, my students and I began to study Ithaca chickadees. Tom Smulders, Ph.D. '98, found that the hippocampus in local chickadees takes up more of the brain and has more nerve cells in the fall, when birds are busy hiding seeds for winter, than it does in other seasons. Graduate student Bernard Tarr and Mubdiul Imtiaz '06 recently found that simply taking a chickadee out of the wild and bringing it into the lab causes the hippocampus to shrink over the next few weeks.

Thus, a brain area responsible for behaviors that include aspects of cognition in humans remains plastic in adulthood: it is able to increase its processing capacity at times when demand increases, but is susceptible to atrophy under conditions of stress or lack of use. An obvious experiment would be to look for brain changes that might occur if we prevent chickadees from storing food items. It is surprisingly hard to do—they will hide items in cage crevices or the water dispenser if no other places are available.

We are beginning to isolate mechanisms within synapses of the hippocampus that must act for the bird to show normal spatial learning. For example, Michael Shiflett, Ph.D. '03, found that if we prevent synapses in the hippocampus from activating a particular receptor molecule (the NMDA receptor for N-methyl-D-aspartate), birds

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can remember a storage location for 15 minutes but not for three hours or longer. As previous observations in mammals have suggested, this receptor seems essential to initiating processes inside the neurons that strengthen these synapses, thereby forming a long-term memory.

As we were doing these experiments, Alex Rankin '02 read about a drug that could block the receptor molecule on synapses that happen to be stimulated by marijuana. He asked if we could try it; I did not know much about the receptor and was pessimistic about whether we would see any effect. After several meetings with Rankin, however, I agreed. He found a source for the drug, gave it to chickadees as they were learning where a mealworm was hidden, and tested them two days later. To my surprise, birds had better memories two days later during trials in which they had received this "anti-marijuana" in their hippocampuses than during trials in which they had received saline.

We then found that, if we gave birds additional information between the initial learning and the test (we let them discover that the original storage site did not have a worm but another one did), then birds treated with the drug appeared unable to modify their initial knowledge of the worm site, such that their overall memory was impaired. We suspect that these receptors may act like dials that indicate whether a new memory should be made strong or should be made flexible. We are currently beginning experiments to study further precisely where the receptors are and how they are used. This research focus began by brainstorming with a well-read, enterprising undergraduate student.

Undergraduates Excel in Bird Studies

A major part of what has made research fun and interesting at Cornell has been the outstanding undergraduates who have chosen to help with it. Undergraduates have participated in nearly all of the significant findings in my lab. They have contributed to the genesis and execution of findings and have become coauthors on the subsequent publications. In some cases these students have received further recognition for their contribution. Nicki Gerlach and Sara Blaine received national awards for their research, and other undergraduates were named Merrill Presidential scholars or Hughes scholars in part because of the research. Inevitably, some ideas for experiments do not work out. Even here, undergraduate assistance has been invaluable, because we could assume that the data were collected carefully and objectively, and therefore we could learn something about biology from the failure.

Exhilarating Insights

Equally exciting has been the stimulation and insight that my students and I have received from other Cornell faculty members. Research at Cornell in Ithaca is sometimes limited because of logistical difficulties in interacting with a medical school that is 200 miles away. However, this distance has also allowed us to think about biology in ways that are unusual at other major research universities. Many of our faculty study unconventional animals. Research in many labs is grounded in evolution and in ecology, and these points of view are readily understood and accepted across campus.

Stephen T. Emlen, Neurobiology and Behavior, can direct me to a particular bird species in Africa that may have evolved an unusual form of song learning. Sandra L. Vehrencamp, Lab of Ornithology, can join me in searching for brain mechanisms that distinguish singing for aggressive reasons and singing to find a mate. Andrew H. Bass (fish—sound) and Carl D. Hopkins (fish—electricity), Neurobiology and Behavior, and Robert E. Johnston (rodents—olfaction), Psychology, and I can look for deep similarities affecting communication in very different animal systems. The list goes on: ecology and behavior perspectives with Thomas Eisner and David W. Winkler, Ecology and Evolutionary Biology, Andre A. Dhondt, Lab of Ornithology, and Elizabeth Adkins-Regan, Psychology; evolutionary constraints with Barbara L. Finlay, Psychology; and insight into process and mechanism from the vertebrate genomics program. To keep us in touch with the big picture, we prize our interactions with nonscientists, such as Paul R. Hyams, History, and James R. McConkey, English Emeritus, who ask what it all means in words that all people can understand.

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Birds and Humans—And Understanding

Justifying the study of bird brains to granting agencies—or to distant relatives—can be very difficult! After all, the bird lineage diverged from that of mammals a very long time ago. And how could insight into brain mechanisms in birds ever cure a human condition? Many people inside as well as outside the neuroscience community assume, without deeply examining the idea, that data from rats or perhaps mice will be more relevant to us.

The research we do in my lab, however, reminds us again and again that important problems in animals' lives were solved a very long time ago, and the solutions have been carried along to all descendents, both birds and mammals. Knowing where you have been and how to get back, learning and remembering the identities of other members of your species, and choosing the best mate are basic skills that were valuable to the first vertebrates and continue to be essential to all of their descendents.

Birds readily exhibit instances of such learning without the use of shocks, odd mazes, or lever pressing. Using birds, we can study closely the behavioral adaptations that have evolved to solve these kinds of problems, and we can learn how their brains do it. To the extent that all vertebrates are working with similar brain tools or that bird solutions converge on human solutions, our findings will tell us about ourselves as well as the birds. I am fascinated with the biology of the natural world and find Cornell very supportive of good science on any creature. Although I still cannot identify any but the most obvious species of birds by sight—I continue to learn about them—I am amazed by what I do know. Hummingbirds, phoebes, and swallows enjoy the Ithaca winter by migrating to Central or South America, but return to the very same nest sites they left; nightingales can hear eight repetitions of a set of sounds at two months of age, and then reproduce it precisely months later; female warblers can survey a dozen males on a spring day and return to mate with the one that was singing 44 notes, as opposed to others singing only 35 to 40 notes. Learning about the neurobiology that permits and encodes this learning is exciting.

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FASCINATING !

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- Neural plasticity is the capacity of neurons—particularly synapses between neurons—to modify their form in order to alter their function in response to experiences (learning).
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