grasslands by adding a diverse mixture of native species without knowing which are likely to facilitate invaders and which will enhance habitat for natives.

Competing pressures

Ecologists widely recognize and applaud the research by Bertness and his colleagues, but many question whether facilitation really is as important as competition or predation is. First in line with such questions is Paine himself. He praises Bertness's experimental work, but he questions his intense focus on habitat-forming species. "If you want to call that facilitation, fair enough, but it's boring," Paine says. "His [Bertness's] current hobbyhorse … is much less studied and much less understood and much less experimentally tractable than the one that has made me famous—but not rich."

Paine argues that keystone interactions are actually the most important kind of positive interaction. *Pisaster*, by preying on the enemies of sessile invertebrates, facilitates those invertebrates. "When you add it, it's like hitting the system with a ball-peen hammer," says Paine. In the kelp-forest example, Paine says that sea otters, not urchins, are the keystone. Otters eat urchins, which is what allows kelp to thrive and facilitate other species.

Bertness's own research in fact underscores the importance of keystone species, Paine claims. In a study published online on 29 July 2002 by the *Proceedings of the National Academy of Sciences*, Bertness and student Brian Silliman attribute the decline of salt-marsh cordgrass in parts of the southeastern United States to herbivory by snails, which are plentiful because humans have overfished snail-eaters such as the blue crab. Paine calls this a clear example where a keystone species, the blue crab, is more important than the so-called foundation species, cordgrass.

"I agree that our blue-crab work is a spectacular example of a keystone," Bertness says. But "strong keystone species effects are almost always associated with predators controlling important foundation species."

To an outsider, the debate may seem like semantic wrangling, and some ecologists are inclined to agree. "I personally think the whole idea of positive versus negative interactions is not intellectually productive," says Clive Jones of the Institute of Ecosystem Studies in Millbrook, New York. The struggle over which is more important "comes from a very strong desire: physics envy." Ecologists would like to predict what happens in an ecosystem based on very simple data, he says, and Bertness and company may just be swapping the obsession with competition for an obsession with facilitation. Ecologists should focus on the conditions that foster positive and negative interactions, not on deciding which predominates, he says.

Shahid Naeem of the University of Washington, Seattle, a veteran of a war of words over diversity in ecology (*Science*, 25 August 2000, p. 1282), says he is also bemused by the argument. One group focuses on the keystone species and the type of diversity it promotes, the other on foundation species and another type of diversity, he says: "But that's simply changing what you think of as diversity. … It serves us poorly to have people championing one cause over another." In other words, strong words are no substitute for strong science.

That may be one of the few points of agreement in this fractious discipline: Only creative, rigorous experiments can decide the outcome. "If you ask me if it's worth doing experiments [on facilitation], the answer almost certainly is 'yes,' " Paine says. But ask him if he knows how they will turn out, and he answers, "I don't have the faintest idea."

–BEN SHOUSE

Ben Shouse is a writer in Santa Cruz, California.

Neuroscience

Singing in the Brain

Researchers flocked here in December 2002 for the first international conference devoted to birdsong. New findings presented at the meeting shed light on the neural circuits that coordinate the intricate movements needed to create song

NEW YORK CITY—Songbirds have long captivated certain humans. The English composer George Henschel, for instance, reportedly kept a highly trained bullfinch that sang "God Save the Queen." Henschel was intrigued when an untrained canary kept in an adjoining room picked up the tune and finished it off properly whenever the bullfinch paused too long in midmelody.

In recent decades, the fascination with songbirds has hatched a remarkably productive niche in neuroscience. By studying how male birds learn and produce their song (females generally listen and judge; see sidebar, p. 648), researchers have gleaned insights into the neural mechanisms of learning and motor control. Birdsong researchers were the first to discover that—contrary to decades-old dogma—new neurons can be born in the adult brain (*Science*, 3 January, p. 32). They've also revealed many mechanisms by which sex hormones set up differences between the brains of males and females during development.

Despite all this interest, birdsong researchers had never come together for a conference of their own until last month, when 200-plus scientists from around the world gathered for a soggy few days at Hunter College in Manhattan. It felt something like a family reunion. The grand patriarchs of the field were there, including Peter Marler, whose work with sparrows in the 1950s pioneered the scientific study of birdsong; nearly all in attendance could trace their academic lineage to him. "It's like being at your wedding," one researcher said. "Everyone you ever wanted to see in the whole world is there, but you only get to see them for 5 minutes."

Presentations covered everything from genetics to behavior to theories on song evolution. One area in particular, though, that has taken wing of late is research on the motor-control circuits in the songbird brain. New work has revised the view of how birdsong is produced and may yield clues about how the brain generates other

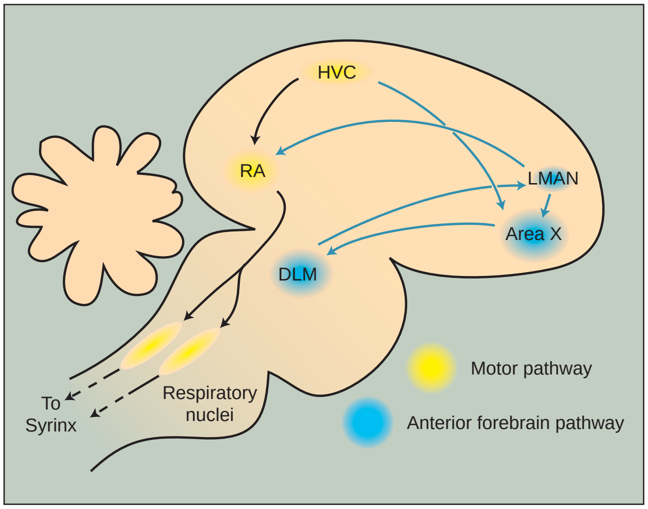
Prepare to be serenaded. Male zebra finches are some of birdsong researchers' favorite subjects.

CREDIT: VIREO

types of sequenced behavior. Researchers also have found that a song-learning pathway in the bird brain has remarkable similarities to a crucial motor-control circuit in mammals, a finding that could lead to insights into brain evolution.

Unraveling the song

For years, researchers have suspected that a hierarchical chain of command exists in the songbird brain. According to one popular scenario, neurons in brain regions at the top of the chain serve as the conductor, issuing bursts of electrical activity like flicks of a baton to dictate the overall organization of the song. Neurons in mid-level areas, like the musicians, handle the details of which note gets played when—in this case, by sending commands to the bottom level, the brainstem regions that control the muscles that open and close the bird's vocal organ, the syrinx.



Birdsong blueprint. One pathway in the songbird brain produces song (black arrows); another is critical for song learning (blue arrows).

ILLUSTRATION: ADAPTED FROM ALLISON DOUPE/UCSF

In zebra finches, the lab rats of birdsong research, songs consist of roughly 20 syllables, each of which is a fixed sequence of several notes. Previous work by Albert Yu and Daniel Margoliash of the University of Chicago demonstrated that neurons in a forebrain area called the robust nucleus of the archistriatum, or RA, fire bursts of activity just before a particular note is sung (*Science*, 27 September 1996, p. 1871). Neurons in another forebrain area, known simply as HVC, fire rapidly throughout the song and modulate their firing rate according to which syllable is about to be sung, Yu and Margoliash found. This suggested that HVC is the maestro, RA the musician.

But recent work from the lab of Michale Fee at Bell Laboratories in Murray Hill, New Jersey, presents a different view. Only a subset of HVC neurons sends signals to RA. Fee, reasoning that these so-called HVC$_{(RA)}$ neurons are likely the ones most directly involved in song production, improved his recording setup to zero in on these cells—something other researchers had been unable to do.

Unlike the highly active HVC neurons described by Yu and Margoliash, the HVC$_{(RA)}$ neurons are fairly quiet, firing no more than a single burst during a song motif, a sequence of syllables that lasts about a second. The neurons' timing, however, is remarkably precise: Each one fires at a particular point in a motif each time it is sung.

Simultaneous recordings from HVC and RA neurons confirmed that the message is getting through. Bursts from HVC$_{(RA)}$ neurons elicited bursts in RA, but RA stopped firing when a drug silenced HVC neurons. These findings, which Fee and colleagues Richard Hahnloser and Alex Kozhevnikov reported in fall 2002 in *Nature*, suggest that HVC$_{(RA)}$ neurons are indeed sending commands to RA—but they're not, as Yu and Margoliash concluded, ordering RA to play a particular syllable. Rather, the HVC$_{(RA)}$ neurons act something like the bouncing ball on the screen of a karaoke machine, keeping track of time and telling RA what to do from moment to moment.

This may sound like a subtle difference, but Fee believes it has important implications for how birds learn to produce their song. This happens as a male compares his own song to a memorized version of his tutor's song. Because HVC represents time in a "sparse" way—each neuron is active only once per motif—if a bird needs to fix an error at a certain time in the song, it needs to tweak just the handful of HVC neurons active at that time, or about 1% of the total population, according to Fee's calculations. "It simplifies the learning process," he says. Fee's team presented computer-modeling data that support this idea. The researchers found that the less active the HVC$_{(RA)}$ neurons are, the more quickly learning can occur. For example, with simulated HVC$_{(RA)}$ neurons that fire once per song motif, learning takes half as long as with HVC$_{(RA)}$ neurons that fire twice per motif.

Sparse coding is an idea that's been floating around in the literature for some time, says Eric Vu, a neuroscientist at the Barrow Neurological Institute in Phoenix, Arizona, but the new findings are probably the best evidence yet that the brain actually uses such a system. And by suggesting that neurons can encode movement strictly in terms of time, the work adds an interesting twist to thinking on neural control of movement, which traditionally has focused on how neurons encode specific muscle contractions, Vu says.

Margoliash is also impressed by the work. "Without a doubt, they've significantly changed and improved our understanding of the system." But the case for sparse coding is not yet airtight, he says: "We don't yet know if all HVC$_{(RA)}$ neurons behave as Fee has described." Moreover, he says, although Fee's model suggests that much of the learning takes place in HVC, previous work has shown that RA circuits change during learning.

The brain's back roads

The direct route from HVC to RA is the song-production freeway. It conveys the neural signals needed to generate song, and if it's disrupted at any time in a bird's life, song breaks down. Another more circuitous path from HVC to RA veers off into the anterior forebrain. This pathway is not essential for song production per se, but disruptions to it in juvenile birds cause serious deficits in song learning.

Many researchers have been pecking away at this anterior forebrain pathway (AFP) in search of clues about the mechanisms of song learning. At the conference, several reported on their latest attempts to puzzle out its role in song learning. Although the picture is still somewhat fuzzy, one thing is coming into focus: The circuitry seen in songbirds is not unique.

David Perkel of the University of Washington, Seattle, presented evidence that the AFP is wired up much like the mammalian basal ganglia. This is the network of brain nuclei that goes haywire in Parkinson's disease; it plays a key role in controlling movement and has been implicated in learning skilled movements. Anatomical experiments in the 1970s suggested a gross similarity between certain regions of the avian forebrain and the basal ganglia, but Perkel is the first person to describe the circuit in songbirds in cell-by-cell detail, says Harvey Karten, a neuroscientist at the University of California, San Diego.

A main thrust of Perkel's recent work has been demystifying a neural black box in the AFP—a region aptly named Area X. He has found that Area X contains two classes of neurons that have remarkable similarities to components of the mammalian basal ganglia. One group of Area X neurons resembles neurons in the striatum; the other resembles those in the pallidum. Perkel has mapped out the connections of these neurons, described their electrical properties in detail, identified the neurotransmitters they release and respond to—and found that all of these properties are comparable to those of neurons in corresponding parts of the mam-

How to Please a Persnickety Female

A great deal of research has been done on how the male songbird learns and produces his song, but scant attention has been paid to his feathered muse. Males sing to woo females, but researchers aren't sure what lady birds listen for in a song and why.

At the recent Hunter College birdsong conference in New York City, Stephen Nowicki of Duke University in Durham, North Carolina, presented recent work that may help explain one preference common among female songbirds: a soft spot for the boy next door. Like people, songbirds have local dialects. And just as a New Jersey accent doesn't always knock 'em dead in, say, Mobile, Alabama, songs that don't adhere to the local dialect are a turnoff for female songbirds. Females, whether through inherited preference or a learned ability to recognize local songs, know what they're looking for.

The traditional explanation for this preference, Nowicki says, is that males with local-sounding songs are likely to come from a lineage that's been in the area for many generations. Thus they're likely to possess evolved traits that help them survive better in the local environment. A female looking for a mate would do well to secure some of the genes underlying these handy traits for her offspring, the thinking went.


Choosy. Female song sparrows listen for faithful songs.

CREDIT: JOE MCDONALD/CORBIS

But recent research by Nowicki and William Searcy of the University of Miami pokes a hole in that notion. Captured female song sparrows, for instance, discriminate only against the songs of males who live 30 kilometers or more away from the females' native area, Searcy, Nowicki, and colleagues reported last year in *The American Naturalist*. But in the wild, they found, the average song sparrow never wanders more than 5 kilometers from home. This means that most females never hear the songs of foreigners. In practice, then, it seems that the preference for local dialect wouldn't be useful for helping females reject potentially maladapted interlopers. So why do females prefer homegrown songs?

Nowicki thinks that what females are really looking for is a perceptive, intelligent male—or more precisely, one who has the wherewithal to make a faithful copy of the local song type. Males who do this will tend to sound local, true, but more importantly from the females' perspective, they may also be revealing a few things about their vigor.

For instance, Nowicki hypothesized, if a young male doesn't get enough food at critical times during development, the song system in his brain might not get wired up the right way. Males blessed with good genes (and genetically well-endowed parents able to provide adequately for their offspring) would be less vulnerable to this nutritional stress and sing faithful copies of songs they heard when young.

To test the idea, Nowicki recruited two groups of song sparrows shortly after hatching. He gave birds in one group as much as they wanted to eat and gave the other group 70% of that amount for 2 weeks. As adults, the food-deprived birds had atrophied song structures in the brain and hadn't copied their tutor's song as well, averaging only 16 syllables copied, compared to 20 in well-fed birds, he reported at the conference.

Wild female song sparrows notice the effects of past nutritional stress, Nowicki's team has found. The birds solicit copulation less frequently in response to poorly learned songs. The stressed males were smaller and had weaker immune systems, Nowicki told those at the conference, suggesting that females were wise to give them the cold shoulder.

The nutritional-stress hypothesis makes a lot of sense, says Clive Catchpole of the University of London. Because birdsong is such an intricate behavior, it may be a sensitive indicator of a male's fitness. Producing a song is a difficult task for the brain, and any additional challenge—lack of food, infections, or other types of stress—is likely to take a toll, Catchpole says.

Indeed, his group reported at the conference that adding the stress hormone cortisol to the food of zebra finches causes them to drop a few syllables from their song. "It doesn't sound like much, but the females don't like it," Catchpole says. **–G.M.**

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malian basal ganglia. In a series of recent papers, he described these findings and argued that birdsong researchers might be able to extract valuable lessons from the literature on mammals, where the role of the basal ganglia in learning has been well studied.

More recent research presented at the conference suggests that even in birds, this network of neurons might not be dedicated exclusively to song learning. For example, Perkel's team reported that a similar circuit exists in chickens, for which no learned vocalizations have been documented. "I think it's reasonable to hypothesize that this is a generalized pathway for sensorimotor learning," Perkel says.

There may be an important lesson in these findings for students of brain evolution, says Karten: "If we could understand what the basal ganglia do in birdsong, that would be the first time we've understood the function of this ancient system in any nonmammalian vertebrate." In mammals, the basal ganglia are thought to control movement through their connections with the outer layer of the brain, the cerebral cortex. But in birds, which lack an obvious motor cortex, the original function of the basal ganglia may be easier to discern. After all, says Karten, "Were the basal ganglia just sitting around for 400 million years waiting for the motor cortex to evolve? Not likely!"

As the conference wound down, a roundtable discussion gave researchers a chance to voice their views on where the field was—and should be—headed. Many argued that songbird research needs to go genomic. Fledgling sequencing efforts at a half-dozen institutions have so far identified a total of about 75 zebra finch and canary genes, and the National Institutes of Health just awarded seven researchers $1.1 million over the next 3 years to help coordinate these efforts.

Others, including Marler, urged colleagues not to abandon the behavioral tradition in birdsong research in a rush to dissect its mechanisms with genetics and studies of neural firing patterns. Understanding behavior, he believes, will help researchers interpret the changes they see at the level of genes and circuits and help tie together different lines of investigation. "Let's not get so reductionist that we forget where it all began," Marler said.

But at a basic level, the conference attendees clearly do appreciate the behavior of their subjects. Applause followed whenever a researcher played a snippet of song in the course of a presentation, and the occasional slide of a handsome zebra finch in midsong was greeted by "oohs" and "aahs." Given the level of enthusiasm, it was hard to believe that this gathering was anything but the start of a tradition.

–GREG MILLER