Allison Doupe

(1954–2014)

Neuroscientist and psychiatrist who linked birdsong and human speech.

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In this era of interdisciplinary science, there is a common phrase: much is known but in different heads. Occasionally, multiple disciplines come together in one remarkable head.

Allison Doupe, a systems neuroscientist, avian biologist and clinical psychiatrist, brought together many perspectives to give us a new understanding of birdsong and, ultimately, of human speech. Straddling the bird laboratory and the clinic, she discovered the principles by which birds learn their songs, and used these insights to propose the neural basis for learning various motor skills, including speech, in humans.

Doupe, who died of cancer on 24 October, grew up in Montreal, Canada, where she attended French-speaking schools. After graduating from McGill University in Montreal, she moved to Harvard University in Cambridge, Massachusetts, where she simultaneously earned a PhD in neurobiology and an MD from the medical school. Doupe continued to pursue both science and medicine on the west coast. She trained in psychiatry at the University of California, Los Angeles, and then completed a five-year postdoctoral fellowship at the California Institute of Technology in Pasadena with avian neurobiologist Mark Konishi. It was this fellowship that got her hooked on birdsong.

In the late 1980s, avian neurobiology was an exciting discipline. Studies, including those in which researchers recorded from, or lesioned, different parts of a bird's brain, had revealed most of the major structures involved in producing and learning songs. The production of song was governed by well-defined clusters of neurons innervating the vocal muscles. Song learning relied on a complex network of specialized forebrain areas, including auditory and motor-control centres that form a sensory-motor circuit. Neurobiologists knew that birdsong was learned during a crucial period early in life through imitating, usually a parent.

Doupe was intrigued by the parallels between birdsong and human speech. Unlike many other taxa, birds and humans rely on imitative learning as well as auditory feedback to develop normal communication skills. In a now-classic 1999 *Annual Review of Neuroscience* paper with linguist Patricia Kuhl, Doupe laid out for the human-speech research community the mechanistic questions that had been explored in birdsong (A. J. Doupe and P. K. Kuhl *Ann. Rev. Neurosci.* **22,** 567–631; 1999). This paper framed the study of both avian and human communication for the next decade.

One problem that needed solving was how infant humans and juvenile birds match what they hear from adults with the sounds that they produce as they begin to vocalize. As a postdoctoral fellow, Doupe became intrigued by the auditory template hypothesis: when young birds hear adults sing, they form an auditory memory of the sounds they hear, even though they are as yet unable to reproduce them. Birds, like humans, practise until the sounds they produce match the auditory template in their brain.

By recording the activity of individual neurons, Doupe found that the adult song was represented within the young bird's sensorimotor pathway, now called the anterior forebrain pathway. In this network, she also discovered neurons that selectively responded to the bird's own song, but not the song of an adult tutor. Doupe and her students suggested that whenever young birds practised their songs, the electrical signals sent to the motor pathway were compared with a parallel discharge sent through the song-learning pathway, where the template adult song was stored. This 'efference copy' model, although still theoretical, has proved useful for understanding brain activity during learning, including the acquisition of human speech.

Doupe's birdsong research, along with her clinical experience, ultimately led her to questions about the role of social context. She and her students demonstrated how the anterior forebrain system in songbirds generates the variation in performance needed for birds to improve their song during practice sessions, yet allows the birds to sing stereotyped renditions in the presence of a potential mate. This work established the birdsong system as a model for understanding many aspects of sensorimotor control and its development in humans, including the importance of generating variation to allow learning. Many have compared the anterior forebrain pathway in songbirds to the cortico-basal ganglia system in humans — the region involved in the learning of skills that become habitual, such as driving, typing and walking.

In life, as in her science, Allison was passionate about development and learning. Her devotion to her twin sons, now ten, like her dedication to her many students, postdocs and patients, was legendary. Her work will continue under the guidance of her extended scientific family, including her husband and collaborator, Michael Brainard. But for all of us who learned the importance of tutoring from working with her, her absence will make our work a little less perfect. ■

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