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The origins of vocal learning: New sounds, new circuits, new cells

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ABSTRACT

We do not know how vocal learning came to be, but it is such a salient trait in human evolution that many have tried to imagine it. In primates this is difficult because we are the only species known to possess this skill. Songbirds provide a richer and independent set of data. I use comparative data and ask broad questions: How does vocal learning emerge during ontogeny? In what contexts? What are its benefits? How did it evolve from unlearned vocal signals? How was brain anatomy altered to enable vocal learning? What is the relation of vocal learning to adult neurogenesis? No one has described yet a circuit or set of circuits that can master vocal learning, but this knowledge may soon be within reach. Moreover, as we uncover how birds encode their learned song, we may also come closer to understanding how we encode our thoughts.

1. Introduction

We write about — two stories: one about vocal learning and the pathways that support it, the other one about neuronal replacement in adult brain. The two stories come together in the song system of birds and are the topic of this article.

1.1. The learning of a song: behavior

Vocal learning is the ability to produce new sounds by reference to auditory feedback. This can be done by imitating an external model or by improvisation, as when we whistle a tune we made up in our mind. Humans are capable of vocal learning, the rest of the extant primates are not. In evolutionary terms, once vocal learning is in place, the first step has been taken towards the development of an open-ended system of sounds that can be used in communication and for the further development of language. Of course, the fossil record does not tell us when vocal learning first occurred or when human language got under way. We do not even know what it is about our brain, compared to that of chimpanzees, that makes us, but not them, capable of vocal learning. Vocal learning is not common in other mammals. There is circumstantial evidence of vocal imitation in humpback whales (Payne & McVay, 1971), porpoises (Reiss & McCowan, 1993; Richards, Wolz, & Herman, 1984; Tyack, 1986), killer whales (Foote, Griffin, Howitt, Larsson, & Miller, 2006; Yurk, Barrett-Lennard, Ford, & Matkin, 2002), harbor seals (Ralls, Fiorelli, & Gish, 1985), bats (Boughman, 1998), and even elephants (Poole, Tyack, Stoeger-Horwath, & Watwood, 2005), but the most numerous and well-documented examples come from birds, where it occurs in parrots, hummingbirds, and songbirds. If, as recently suggested, parrots (order Psittaciformes) and songbirds (order Passeriformes) share a common ancestor (Hackett et al., 2008), then vocal learning in birds may have evolved independently just twice. However, if this interpretation is accepted, then birds in the suboscine branch of the Passeriformes, which are not known to have vocal learning, would have surrendered this trait secondarily, and it is almost more parsimonious to assume that parrots and oscine songbirds developed the trait independently from each other. Research on avian vocal learning has focused mainly on oscine songbirds, a large group with some 4000 species oftentimes referred to as the “true songbirds”.

Speculation on how songbirds — or the common ancestor of songbirds and parrots — evolved vocal learning could be aided by observations of how vocal learning and its underlying circuitry develop in juveniles. This approach, based on the idea that ontogeny recapitulates phylogeny, is familiar to embryologists. For this effort

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to succeed in the context of vocal learning, it was necessary, first, to characterize the ontogeny of vocal learning, then to identify brain pathways involved with the acquisition and production of learned sounds. Neuronal replacement in adult brain was discovered while trying to understand how seasonal and hormonally driven changes in the size of song pathways came about. It was an exhilarating moment. After 100 years of a dogma that held that a lost neuron could never be replaced, there was now evidence that some kinds of neurons come and go and, in a very real sense, are as replaceable as the cells of our skin, gut, or liver. Each part of the story requires the others. Song learning without the underlying mechanisms is inexplicable; the anatomy of the song system without knowledge of the behavior it serves is uninteresting and irrelevant; neuronal replacement without a context of circuits and functions, is inscrutable. By their very nature, studies of vocal learning and of the song system of birds invite these various levels of observation. When brought together, they make for a good story. It is the story we would like to tell. It is too early to know how much of this story sheds insights on vocal learning in humans, but what we know about vocal learning in birds is bound to influence our thinking about this phenomenon in humans, and there are already reviews that point to parallels between the two systems (e.g. Doupe & Kuhl, 1999; Marler, 1970a).

What follows are descriptions of vocal learning in six songbirds: the chaffinch, white-crowned sparrow, zebra finch, swamp sparrow, chipping sparrow, and canary. In this description we use the term "syllable" to refer to a sound or complex of sounds that recur as a unit and that are preceded and followed by a discrete silent gap.

1.2. The chaffinch, *Fringilla coelebs*

The study of song learning in the chaffinch was the first detailed account that used playbacks of taped song and sound spectrographic analysis to document vocal imitation in a songbird (Thorpe, 1958). Chaffinches show local song dialects, a phenomenon usually associated with vocal learning. Thorpe noted that before the onset of adult song, juveniles produce subsong, a soft, rambling set of vocalizations that he suggested was in the nature of "practice" and, quoting Charles Darwin's Descent of Man, akin to babbling in infants and lacking in communicatory significance (Thorpe & Pilcher, 1958). Chaffinch subsong incorporates sounds used earlier in the context of food begging (Nottebohm, 1972). Subsong is followed by "plastic" song. Plastic song is louder, more structured, and less variable than subsong; during plastic song one can recognize the song themes that the juvenile is striving to imitate and that will be used at sexual maturity. As plastic song becomes more and more like the model imitated, it also becomes much more stereotyped. At the end of plastic song change ceases and the song is said to have "crystallized". Crystallized song, Thorpe noted, is retained in future years. Thorpe also identified aspects of vocal learning that subsequent workers recognized as important. For example, chaffinches reared in acoustic isolation develop "isolate" song that is of the same duration and pitch as wild-type song but lacks the diversity and complexity of sounds found in nature. Thorpe noted, too, that while young chaffinches imitate the song of other chaffinches, even when this song is played over a speaker, they usually do not imitate the song of other songbirds, such as canaries, whose song is very different. Also, imitation of conspecific song was normally restricted to the juvenile period; exposure to new songs in adulthood did not result in imitation. Thorpe (1958) concluded that there was a bias for imitating conspecific song and that there was a sensitive period for song learning. However, if exposure to a tutor was withheld and first made available at 2 years of age, the model could still be imitated. In this case, then, vocal imitation is a self-terminating process (Nottebohm, 1969b; Thorpe, 1958). Later, this same observation was extended to zebra finches (Eales, 1985, 1987).

1.3. The white-crowned sparrow, *Zonotrichia capensis*

White-crowned sparrows are common in California's chaparral country. As in chaffinches, their song often differs between contiguous localities, giving rise to local dialects (Marler & Tamura, 1962). The suspicion that these dialects might result from imitation was supported when white-crowned sparrows reared out of earshot of conspecifics produced "isolate song," which differed markedly between individuals and differed also from the population dialect into which the birds had been born. However, when isolates heard wild-type song from their own species played over a speaker, they imitated that song, while playbacks of other species' song were ignored (Marler, 1970b; Marler & Tamura, 1964). As in chaffinches, the selective imitation of conspecific song suggests that the birds bring to the learning task a preference that might be motor and/or perceptual, and both such preferences or predispositions have been shown to occur (Marler & Sherman, 1983; Soha & Marler, 2000, 2001). Of course, something that looked like selective song imitation could also result if a bird had at its disposal all the programs for conspecific song and activated one of them upon hearing the corresponding playback. But the mechanism is probably not that simple. Thorpe (1958) and Marler (1970b) showed that mastery of an imitation can require several months of practice. Konishi (1965) showed that if, following playbacks of conspecific song the pupil were deafened, imitation failed to occur. Konishi inferred that therefore vocal learning consists of two steps: first the tutor song is laid down as an auditory memory; secondly vocal output is modified until the auditory feedback it generates matches the model. Such two-step learning has also been demonstrated in swamp sparrows, *Melospiza georgiana* (Marler & Peters, 1981a).

Early accounts of vocal learning in the white-crowned sparrow, conducted under laboratory conditions and using playbacks of recorded song, conclude that imitation occurred when the model song was presented 10–50 days after hatching; songs presented before 10 days or after 50 days were not imitated (Marler, 1970b). However, when white-crowned sparrow juveniles that had not heard adult song before were first exposed to a live tutor at 50 days of age, this model was imitated (Baptista & Petrinovich, 1984). We do not know what this tells us about when exposure to a live model has its maximal effect in the wild, but clearly under laboratory conditions a live tutor can be a more compelling model than recorded playbacks, and this alerts us to the importance that social variables might have in triggering imitation.

1.4. The zebra finch, *Taeniopygia guttata*

The vocal learning steps that culminate with imitation have been described in some detail in the Australian zebra finch. Young zebra finches master their learned song over a period of some 40 days, between post-hatching day 40, when they become independent from their parents, and 80, when they reach sexual maturity (Immelmann, 1969). At day 40 the young birds are in the *subsong* stage of vocal ontogeny. If a conspecific tutor song is presented at that time, the sounds of subsong start to undergo immediate modification in the direction of the tutor song. One can watch this change by recording at intervals after first presentation of the tutor song, and the trend is clear: over a period of days the sounds of the pupil become louder, less variable, and more like the sounds of the tutor song (Tchernichovski, Mitra, Lints, & Nottebohm, 2001). The path towards model mastery can, however, differ markedly between individuals. Some individuals spend the first few days after presentation of the model repeating rough approxima-