

Birdsong and Vocal Learning during Development

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Glossary

Imitation – A song that is a good copy of a tutor song.

Improvisation – A song that resembles a tutor song, but which is substantially different in certain respects.

Invention – A song which cannot be traced to a tutor song.

Sensitive period – A relatively short period early in life when the bird is receptive to song memorization.

Sensorimotor phase – The phase during which the bird sings and tries to match its output to earlier-memorized songs; follows or overlaps the sensory phase.

Sensory phase – The phase of song learning during which the bird memorizes tutor song.

Song – A relatively complex vocalization used in interactions with males and/or female conspecifics. A single song (or strophe) is usually relatively short (usually 2–4 s) and is separated by a longer period of silence before the next song. In some cases, birds sing more continuously and individual songs can be quite long (e.g., 20 s or more in sedge warblers).

Song crystallization – A developmental phase in songbirds in which there is a transition in song from poorly structured vocal material (subsong or plastic song) to stereotyped, well-structured song patterns that are typical of adult birds.

Song learning program – The genetic-developmental program thought to underlie song learning in a species (or a race or population of a species).

Song repertoire – Defined in terms of song types or elements. Most birds form song elements into stable song types, but others (e.g., sedge warblers) improvise songs from their repertoire of song elements.

Bird Song as a Model System

Songbirds (oscine passerines) are one of the few animal groups in which individuals learn their vocal signals. Vocal learning has been found so far only in the humans, two other mammalian groups (cetaceans and bats), and two other avian groups (parrots and hummingbirds). Although other animal groups capable of vocal learning will probably be discovered in the coming years, vocal learning is clearly the exception in the animal kingdom: in most animals, individuals develop perfectly normal

species-typical vocal signals without having to hear models of these signals. Among vocal learners, songbirds stand out because of their complex vocal repertoires. Some songbirds show extraordinary powers of vocal mimicry, far exceeding human capabilities.

In the 1970s, it was discovered that songbirds possess a distinctive set of neural circuits dedicated to their vocal communication system. Research has since attempted to parse out the roles of different parts of the system in the perception, production, memorization, and learning of vocal signals. The bird song system has become a major model system in neurobiology in part because of its potential to provide insights into the neural mechanisms of learning and memory. The discovery of neurogenesis within the adult songbird song system, the first unambiguous demonstration of neurogenesis within the adult vertebrate central nervous system, was a key element in the establishment of the bird song system as a model system in neurobiology.

Parallels between Bird Song Learning and Human Language Learning

Yet another reason for the interest in the bird song system as a general model system is the number of parallels between vocal learning by songbirds and language learning by humans. These parallels were first pointed out by Peter Marler in a seminal 1970 paper. Six of these parallels are included here, with an additional parallel – social context – which will be discussed further in the section titled “Comparative differences in song bird learning.”

1. In both songbirds and humans, the vocal communication signals are learned.
2. This learning takes place during a sensitive period that begins soon after birth or hatching and concludes some-time later. There is some uncertainty as to when and how completely the sensitive period closes in humans, but it is generally accepted that second-language learning, unless started early in life, is considerably more difficult than first-language learning. The sensitive period for songbirds depends on the species, and is discussed in the section titled “Comparative differences in song bird learning.”
3. Dedicated neural systems underlie the perception, memorization, learning, analysis, and production of the vocal signals.

4. The sensory-memorization phase precedes the production phase. For example, infants understand more than they can say. Some songbirds do not even begin to practice vocalizing until they have memorized all the songs they will sing.
5. Related to the previous point, there is a babbling or subsong phase in which the individual practices vocalizing. The vocalizer presumably matches these productions to the models that were memorized earlier. The signals are refined until they ultimately reach the adult level.
6. Auditory feedback is essential for vocal learning, at least until the normal vocal repertoire has crystallized. Although deafening after this period can cause degradation of vocal signaling, auditory feedback after crystallization is generally less critical for maintenance of the vocal repertoire.
7. Vocal learning is inherently a social process.

Vocal Learning is a Social Process

The fact that people around the globe learn different languages is of course sufficient evidence that language is learned. The additional hypothesis that language must be learned in a social context seems self-evident. On the rare occasions that an individual has been isolated from human contact during development, language is inevitably deficient, but this of course is just one of the myriad clinical problems shown by such individuals. Extrapolation of this isolation test to songbirds is sometimes referred to as a Kaspar Hauser experiment, named after one such unfortunate human (although the story is partly apocryphal). Most songbirds when isolated from the sights and sounds of other birds from hatching until maturity develop abnormal songs (some exceptions are discussed below). Presentation of tape-recorded song to the isolated bird is often sufficient, however, for the bird to develop normal species song. It is this last fact that led many investigators to overlook this importance of social context for bird song learning.

While the importance of social contact is obvious for language learning in humans, the early studies of song learning in songbirds explicitly excluded social factors. They did so for both theoretical and experimental reasons. The original theoretical conception of song learning was derived from the classical ethological concept of imprinting, translated into the song-learning context by Thorpe, and then fully developed in the experiments of Marler and his colleagues. By analogy to the classical imprinting studies, it was supposed that the key stimuli for song learning would be very basic, processed by species-specific filtering mechanisms and that learning would occur during an early sensitive period. This view provided the rationale for the 'tape tutor' experiment, in

which all aspects of the species- and population-typical song-learning context were removed, the bird being isolated shortly after hatching and hearing song only through a loudspeaker in an isolation chamber. Besides fitting the theoretical view, the tape-tutor experiment also unquestionably provided more experimental control than would be possible were actual birds the song tutors. In a classic series of tape-tutor experiments, Marler showed that to develop normal song, a white-crowned sparrow male must hear conspecific song during an early sensitive period (roughly the second month of life); the bird will reject heterospecific song heard during this period, as well as conspecific song heard after the sensitive period.

Workers in the field became aware of the importance of social factors in song learning, however, with the discovery that birds learned more readily from live tutors than from tape-recorded song. Moreover, some of the rules of song learning derived from tape-tutor studies appeared to bend, if not break, when the song tutors were actual birds. For example, whereas tape-tutor studies had indicated that the sensitive period for white-crowned sparrow song learning closes at approximately 50 days, and that heterospecific songs are uniformly rejected, Baptista and Petrinovich showed that if a young white-crowned sparrow was exposed to a tape tutor through 50 days and thereafter exposed to a live tutor, the young bird would learn the song of the live tutor, and in some cases would do so even if he were a heterospecific tutor.

Field studies also provided a major impetus to the study of social factors. Although field studies cannot provide the experimental control of a laboratory study, they naturally bring into focus the social variables that are controlled out of laboratory experiments. To the question of when song learning occurs, field studies added the questions of where and from whom, and have given a new context for the questions of how many, which ones, and how accurately? Researchers doing the first field studies on song learning noted that learning appeared to occur later than indicated by the classical tape-tutor studies, post- rather than pre-dispersal, so that birds wound up learning songs not from their father and birds in the natal area, but from birds in the area where they would breed, often their neighbors of their first breeding season.

Despite the problems raised by field studies and by experiments with social tutors, the basic findings of the classical tape-tutor experiments have not yet been firmly contradicted in any species. In particular, although the sensitive period for song learning may extend much further into the first year for some species than was originally thought, for no species does it appear to be true that song learning is equally possible or equally likely at all points during the bird's life. Moreover, even if a powerful heterospecific social tutor can overcome it, the preference for conspecific song found in tape-tutor

experiments, at least for some species, does suggest some form of tuning for conspecific song. Nevertheless, comparative studies of songbird species have revealed an amazing diversity in song-learning patterns, both between species and between different populations of the same species, and this diversity should warn us not to take any particular pattern of song learning, for example, that shown by white-crowned sparrows, as typical or fundamental. We return to this point in the section titled 'Comparative differences in song bird learning'

What are the Social Variables in Song Learning?

Despite the recognition that social factors are critical in song learning, there is little understanding in the field of exactly how social variables shape song learning. The numerous comparisons of live versus tape tutors that have been made are usually indirect and often made across different studies. As researchers have pointed out, it is not at all clear what precise aspects of social stimulation influence song development, and indeed even whether the effects are 'truly social.'

The difference between results derived from tape-tutor and live-tutor experiments can be viewed from another purely theoretical angle. The tape-tutor and live-tutor paradigms implicitly suggest different models of the song-learning process. The tape-tutor paradigm implies that song learning is essentially a process of overhearing or simple eavesdropping on a singing adult. In contrast, the typical live tutor setup – with the young bird stationed close to a singing adult bird – implies that the fundamental process involves direct interaction of the older bird (song tutor) with the young bird. However, both experimental setups are potentially unnatural: we do not know whether in nature the young bird learns from a song tutor singing solo and out of sight (as implied by the tape-tutor design), from a song tutor who is up close and interactive (as implied by the typical live-tutor design), or, perhaps, in some other way altogether.

A theory developed by Nelson and Marler combines the 'simple eavesdropping' and 'direct interaction' models of song learning by proposing that the first process describes the early phase of song learning, while the second process describes the later phase of song learning. According to this theory, in the first phase of song learning, the young bird memorizes many songs during the natal summer, many more songs than he will ultimately keep for his final repertoire. In the second, action-based phase of song learning, typically occurring early in the following spring, the bird counter-sings with his new neighbors as he tries to establish a territory, and selects from his earlier-memorized songs those that best match the songs of the birds he is now interacting with. Thus, the

Nelson–Marler theory incorporates the implicit models of both the tape-tutor and live-tutor paradigms: the early, memorization phase of song learning follows the simple eavesdropping model, while the later action-based phase conforms to the direct interaction model.

A third model, the social eavesdropping model, suggests an alternative way in which social interaction might affect song learning. The central idea is that the young bird learns by eavesdropping, not on solo singing, but on singing interactions between two or more birds. Recent field experiments on songbirds have shown that males base their decisions on whom to challenge and females their decisions on whom to mate with on information about the dominance relationship of the singing males, information which they extract when eavesdropping on singing interactions. The social eavesdropping hypothesis proposes that young birds too may use information they extract from singing interactions they overhear to decide which songs to learn or retain. The relative dominance status of the two birds might be one important dimension. This idea is similar to the social modeling theory, as developed by Pepperberg, which suggests that observation by the young bird of communication interactions between individuals who have mastered the communication system may be critical for vocal learning.

There is a second unique type of information a young bird could extract from the interactive singing (counter-singing) of two adults that he could not extract from solo singing of these same birds: contextual information relating to singing rules concerning the appropriate replies to particular songs in particular contexts. We take for granted that humans have to learn the rules of language, but animal communication systems – although simple compared to human language – do have their complexities, and do follow fairly intricate rules. In the study of bird song learning, the focus has always been on the learning of particular songs rather than the learning of how to use them, but the two processes may be intertwined. This is the case for human language learning of course. Although the attention in studies of human language learning has been focused on direct interaction, especially between parent and infant, it is necessarily the case that the infant can potentially learn much more about grammar and the rules of language by eavesdropping on conversations among older individuals.

Some evidence suggests that songbirds may preferentially learn by eavesdropping on singing interactions of other birds. In an experiment on young song sparrows (*Melospiza melodia*) using live tutors, Beecher and colleagues compared two types of song tutoring: that resulting from direct interaction with the song tutor, and that resulting from social eavesdropping, that is, overhearing the singing interactions of other birds. Subjects were exposed to the songs of four tutors during the early memorization phase (phase 1) of song learning and to

just two of them again in the later action-based learning phase (phase 2). Of the two tutors returning in phase 2 one became a subject's interactive tutor, while the other became the subject's overheard tutor, that is, was overheard interacting with another, yoked subject. Subjects learned (retained) more songs from their overheard tutor than their interactive tutor (about twice as many on average). This result is consistent with the social eavesdropping hypothesis, and not the direct interaction hypothesis.

In a totally different approach to the problem in the same species, Templeton and colleagues examined the response of juvenile male song sparrows in the field to simulated adult song contests and solo singing. Songs were presented from two speakers separated by 10 m and 50 m from the bird. Juveniles were more likely to move toward the speaker, approaching closer and more quickly, during the simulated singing interactions between the two birds than during solo song or control playback trials (solo song sparrow and heterospecific song, in fact, were equally unattractive to the birds). These results suggest that juvenile song sparrows are especially interested in eavesdropping song contests and that these types of social interactions may be particularly powerful tutoring events for song learning.

Comparative Differences in Song Bird Learning

The prevalent model of song learning is based on the classic studies of Marler on the white-crowned sparrow (*Zonotrichia leucophrys*). During the sensory or memorization phase, the young bird must hear tutor song, and during the sensorimotor phase, it attempts to match its vocal output to the songs memorized earlier. Learning can be demonstrated by isolating the bird during the sensory phase, or by deafening it just before the sensorimotor phase; both typically produce a bird that sings abnormal song. Since isolation and deafening are extreme manipulations, and because their outcomes are generally considered to be obvious, song learning is usually demonstrated instead by showing that the bird develops songs closely resembling the songs it was tutored on; this method is unambiguous so long as song learning takes the form of simple imitation (copying) of tutor songs (but as we will see, it does not always do so).

Despite the uniformity suggested by the outline of song learning just given, it has been long known that songbird species show many variations on this theme. However, in fact, the diversity of oscine song-learning programs is more extreme than is generally appreciated, and varies along at least the following five dimensions.

1. *When song is learned or how long the song repertoire is modified.* The period during which birds can learn songs ranges widely, from a brief sensitive period in the first few months of life (white-crowned sparrow), to the entire first year (chaffinch, *Fringilla coelebs*, indigo bunting) to throughout the lifetime (village indigobird, *Vidua chalybeata*, great tit, *Parus major*, pied flycatcher, *Ficedula hypoleuca*, willow warbler, *Phylloscopus trochilus*). Species in which birds add songs to their song repertoires after the first calendar year are referred to as open-ended learners, species in which they do not as closed-ended (or age-limited) learners. Although closed-ended learning has generally been the default assumption, in most cases there is no evidence to support this assumption: song-learning experiments typically are not extended beyond the first year, and longitudinal field data are rarely gathered. Thus, species assumed to be closed-ended learners might on closer inspection prove to be open-ended learners, as, for example, McGregor and Krebs discovered for great tits.

2. *How many songs a bird learns.* In about 70% of songbird species studied, males sing multiple song types. These song repertoires range in size from small (e.g., chaffinch, great tit, swamp sparrow, *Melospiza georgiana*, all <5) to moderate (e.g., song sparrow, western meadowlark, *Sturnella neglecta*, 10 or so) to large (e.g., western marsh wren, *Cistothorus palustris*, common nightingale, *Luscinia megarhynchos*, >100) to huge (e.g., brown thrasher, *Toxostoma rufum*, >1000). Small- to moderate-sized repertoires are most common. Several experiments in which species (song sparrows vs. swamp sparrows) or subspecies (eastern vs. western marsh wrens) with different repertoire sizes were raised in a common environment established that differences in repertoire size in these cases were due to genetically based differences in the underlying song-learning programs.

3. *Copying fidelity.* Although imitation is the hallmark of bird song learning – typically it is the criterion by which song learning is assessed – birds do not always copy tutor songs precisely. In different species (and sometimes in different populations of a species), song-learners appear to vary along a continuum ranging from imitation (faithful copying of tutor song), to improvisation (variations on the tutor material) to invention (bird develops species-typical songs that bear no obvious relation to the tutor material, and which might or might not even require song tutoring).

4. *Role of early song experience.* Because bird song learning was first demonstrated by showing that songbirds raised in isolation develop abnormal song, there has been a tendency to assume that isolation-rearing will always have this effect, and hence isolation conditions are usually omitted from song learning experiments. However, isolation does not always produce abnormal song. Three recently discovered examples are the grey catbird, the

sedge warbler, and the canary: these birds generate large, normal song repertoires when raised in song-isolation conditions. These birds probably need to hear themselves sing in order to develop their normal repertoires (though this has not been tested), but it is still surprising that they can develop their large repertoires of good species songs without ever hearing external conspecific song models.

5. *Degree of canalization.* In white-crowned sparrows and several other species, birds copy tutor material only if it fits tightly constrained species-specific parameters, and in these cases song learning would be classified as environmentally canalized (*sensu* Waddington). Other species are less selective as to what material they will copy for their songs. For example, in a common-environment experiment on two closely related species, Marler and Peters found that when presented with the same tape-recorded regime of song sparrow and swamp sparrow songs, song sparrows will copy heterospecific as well as conspecific elements, but swamp sparrows will not. Other species are capable of copying virtually anything they hear, the best-known examples probably being brown thrashers, northern mockingbirds (*Mimus polyglottus*), marsh warblers (*Acrocephalus palustris*), Indian hill mynahs (*Gracula religiosa*), and superb lyrebirds (*Menura novaehollandiae*).

Conclusion

The study of bird song learning is only about 40 years old, and is still in its relative infancy. Nevertheless, it is a system that has a tremendous potential as a model system, given (1) our considerable knowledge of the neurobiology of the songbird vocal control system, (2) its many parallels with human language learning, and (3) our ability to investigate how the system functions in the both the lab and the field. A fourth potential advantage is simultaneously a significant problem: What do we do with the staggering diversity of song-learning programs observed in the songbird group (4000-plus species)? This diversity must give pause to any investigator who would consider

one particular songbird species – say the zebra finch (presently the most popular species in neurobiological studies) – as representing the songbird learning program. The field will need to address this problem and use this comparative variation as a research tool if we are to move into the next phase of this very fruitful research area.

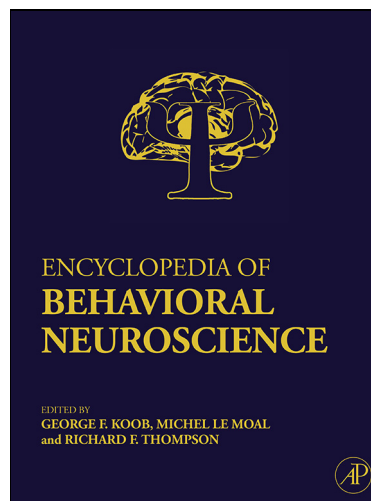
See also: Animal Models of Learning and Memory; Behavioral Development and Socialization; Developmental Neurogenesis; Evolutionary and Developmental Issues in Cognitive Neuroscience; Neurogenesis and Memory; Social Communication; Social Learning and Behavior Transmission.

Further Reading

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