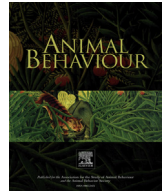




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Overproduction and attrition: the fates of songs memorized during song learning in songbirds

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Most songbirds learn their songs through imitation. However, what a male sings as an adult is not necessarily a complete inventory of what he memorized at some earlier point in time: songbirds commonly memorize more material than they eventually sing as adults. Work with swamp sparrows, *Melospiza georgiana*, first confirmed that males rehearse many of the song models to which they are exposed during the sensory phase of song acquisition but subsequently include only a subset of those rehearsed songs in their adult repertoire. This process of overproduction and selective attrition has since been demonstrated in other species as well. More recently, the persistent memory of tutor songs rehearsed but not included in the adult repertoire has been demonstrated at the neural level. Furthermore, memories of song models heard during the sensory phase of acquisition but never detected during rehearsal in the sensorimotor phase also may persist into adulthood. Here we review behavioural and neural studies of overproduction and attrition in song learning. We discuss factors that may trigger the persistence of some models and the rejection of others in an individual's repertoire and possible functional consequences of this phenomenon. Data from human speech research indicates that humans also may unconsciously retain memories of features of languages heard early in life but never spoken.

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Some adult motor patterns and sensory predispositions are established early in life during a sensitive period in which the developing organism is particularly responsive to certain stimuli that lead to lasting changes in neural, embryological, physiological and behavioural processes (Hensch, 2004; Knudsen, 2004; Marler, 1987). A classic example comes from the work of Konrad Lorenz (1937), who demonstrated that irreversible social bonds are formed in some bird species when newly hatched young first encounter an individual of the same or a different species, or even an inanimate object. Another example is the development of binocular vision, in which neural connections available at birth are either lost or modified depending on the nature of visual stimuli experienced at an early age (Hubel & Wiesel, 1970). Yet another example comes from first language acquisition in humans, which occurs almost effortlessly at a very young age (Kuhl, 2004), with deprivation of exposure during early years resulting in abnormal language competence (Fromkin, Krashen, Curtiss, Rigler, & Rigler, 1974; Newport, 1990).

In some cases, the effects of stimuli experienced during an early sensitive period are not apparent until much later in life. Young birds cross-fostered as nestlings by another species can show a preference as adults to mate with members of the foster species (Immelmann, 1972; Lorenz, 1937). Juvenile barn owls, *Tyto alba*, that experience abnormal auditory spatial associations can better adjust to similar abnormalities as adults than those raised without the abnormal association (Knudsen, 1998). Prelingual children who have lost hearing, but who experienced oral and aural input before that loss, improve at a faster rate with a cochlear implant than children with no such experience (Tong, Busby, & Clark, 1988).

Songbirds typically memorize conspecific songs during an early sensitive period but may not attempt to produce these songs until many months later (Catchpole & Slater, 2008). One noteworthy aspect of this juvenile learning is that often more songs are learned than are expressed in adulthood. This phenomenon, termed overproduction and selective attrition, was first documented in detail by Marler and Peters (1981, 1982a) in the swamp sparrow, *Melospiza georgiana*. Since this early work, further work on swamp sparrows and other species has demonstrated the generality of this phenomenon and provided insight into its functional significance.

We here review the early acquisition of models and their eventual fate in the song-learning process. We first provide an

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overview of song learning, overproduction and selective attrition, using laboratory studies of the swamp sparrow as a reference point. We then review studies of overproduction and selective attrition in a variety of songbirds that suggest possible functional consequences of this common phenomenon, with field studies in particular providing insight into its potential significance for the functions of song. We also review evidence, both behavioural and neural, supporting the idea that memories of songs heard during the sensitive period persist even if those songs are no longer produced; that is, that the brain stores some song memories through adulthood regardless of whether those songs are retained in the adult's repertoire, perhaps even if those songs were never rehearsed during development. Finally, given the well-established parallels between birdsong development and human speech acquisition (Doupe & Kuhl, 1999; Marler, 1970a, 1970b; Soha & Peters, 2015), we discuss recent evidence suggesting that early language experience leads to similar persistent memories of language features.

SONG LEARNING, OVERPRODUCTION AND SELECTIVE ATTRITION IN SWAMP SPARROWS

Swamp sparrows, and almost all songbirds studied to date, learn to sing through imitation (Beecher & Brenowitz, 2005; Catchpole & Slater, 2008; Kroodsma & Baylis, 1982). When young swamp sparrow males are raised in isolation in the laboratory having no experience with their species-typical song, they do eventually develop songs, but these songs are abnormal in most respects (Marler & Sherman, 1985). A typical swamp sparrow song is composed of the same multinoted syllable repeated 10–20 times in a trill (Fig. 1a). So-called 'isolate songs' are composed of syllables having fewer notes, contain fewer notes per song overall, the duration of these notes and the intervals between them are of longer duration and songs are produced with more segmentation than wild-type songs (Marler & Sherman, 1985). By contrast, songs of swamp sparrow males exposed to recordings of species-typical song models in the laboratory are often precise copies of those models (Marler & Peters, 1977; Fig. 1).

Song learning occurs in two phases (Catchpole & Slater, 2008). During an early sensory phase, males listen to other individuals and memorize songs that they hear. The amount of song exposure necessary for learning can be very limited. For example, song sparrows, *Melospiza melodia*, are able to accurately copy a song phrase after hearing as few as 30 renditions of the model in 1 day (Peters, Marler, & Nowicki, 1992) while in nightingales, *Luscinia megarhynchos*, exposure to only 10 renditions results in accurate copies (Hultsch & Todt, 1989). Song production begins during the sensorimotor phase. At this time young males listen to their own song production and gradually modify their output to match the models that they have stored in memory, with the endpoint of this developmental process referred to as 'crystallization'. In some species, the sensory and sensorimotor phases leading to crystallized song are separated in time, although in other species these phases can overlap (Catchpole & Slater, 2008).

Marler and Peters (1988) determined the timing of song memorization of swamp sparrows under laboratory conditions by presenting different song types to males on a weekly basis, from the time they hatched until about 1 year of age. By matching the adult songs of the students to the models they heard, Marler and Peters determined that the sensory phase in swamp sparrows peaks very early, before 50 days of age, with very little song learning occurring after 140 days of age (Marler & Peters, 1988).

Sensitive periods can be flexible with factors such as life history or social interaction affecting its onset and duration (Knudsen, 2004; Marler, 1987). Laboratory studies show that song

deprivation early in life can extend or shift the sensitive period in some species (Nelson, 1997). The sensitive phase in swamp sparrows raised in the laboratory remains the same regardless of whether the birds are tutored with tape recordings or live tutors (Marler & Peters, 1988). This does not appear to be the case in song sparrows, however. Using tape-recorded songs in the laboratory, Marler and Peters (1987) found that the sensitive period for an eastern population of song sparrows peaks early, between 20 and 60 days of age, while exposure to live tutors extended the sensitive phase of young males beyond 140 days of age in a western population (Nordby, Campbell, & Beecher, 2001). Factors that may have contributed to this late learning include prolonged exposure to model songs, a possible predisposition for males from this population to learn songs when territories are established in the autumn, as well as the fact that individuals were able to vocally interact with their tutors (Nordby et al., 2001).

Marler and Peters (1982c) went on to document the timing of the sensorimotor phase and song development in swamp sparrows, by recording males weekly throughout their entire first year of life. As is true for a number of songbird species (Hultsch & Todt, 2004), some sporadic subsong occurred during the autumn, but continuous singing did not begin in earnest until the following early spring. A few male swamp sparrows sang subsong up until about 160 days of age but began singing in earnest at an average of 272 days of age, many months after the sensory phase peaks (Marler & Peters, 1982c). Following the general pattern observed in other songbirds (Catchpole & Slater, 2008; Konishi, 1985), swamp sparrow song develops through stages, progressing gradually to accurate copies of models heard during the sensory phase. The earliest stage of song production, called 'subsong', is often quiet and highly variable, with little or no repetition of sounds (Fig. 1b). Subsong contains little hint of what a bird heard during the sensory phase. It is during the next phase, 'plastic song', when the first attempts to produce songs memorized earlier can be detected. The first attempts at imitation do not occur until almost 8 months after the sensory phase peaks (Marler & Peters, 1982b), when parts of model songs can be recognized in plastic song although their production remains quite variable (Fig. 1c). As plastic song progresses, the young male's own vocalizations increasingly match the models to which he was exposed. Finally, the male's songs crystallize, after which songs remain stable for the remainder of the male's adult life (Fig. 1d).

Early studies of song learning tacitly assumed that the songs a male produces as an adult represent a complete record of what the male successfully memorized during the sensory phase (Marler & Peters, 1981). This assumption might seem especially valid for a species such as the swamp sparrow in which the songs a male crystallizes comprise his repertoire for the rest of his life. Some early anecdotes described songs detected in subsong or plastic song that did not appear in adult song (Poulsen, 1959; Thorpe, 1955), but it was the detailed spectrographic records of swamp sparrow song development documented by Marler and Peters (1981, 1982a) that revealed an unexpected result: young swamp sparrows often practise an abundant amount of material during plastic song that does not subsequently appear in their adult repertoires (Fig. 1c and d). This overproduction of song material is followed by attrition as development progresses: a typical swamp sparrow male sings an average of 12 and up to 19 different syllable types during plastic song but crystallizes only an average of three (Marler & Peters, 1981; Prather, Peters, Nowicki, & Mooney, 2010). Syllables sung in plastic song include imitations of models heard during the sensory phase and syllables not assignable to any model with confidence, with imitated syllables more likely to be retained through the attrition process than non-imitations (Marler & Peters, 1981). On any particular day when a bird is singing plastic song, the frequency

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