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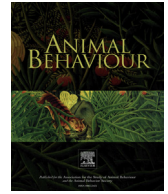
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Overproduction and attrition: the fates of songs memorized during song learning in songbirds

Susan Peters[*], Stephen Nowicki

Department of Biology, Duke University, Durham, NC, U.S.A.

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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

* Correspondence: S. Peters, Department of Biology, Duke University, Box 90338, Durham, NC 27708, U.S.A.
E-mail address: speters@duke.edu (S. Peters).

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 though 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
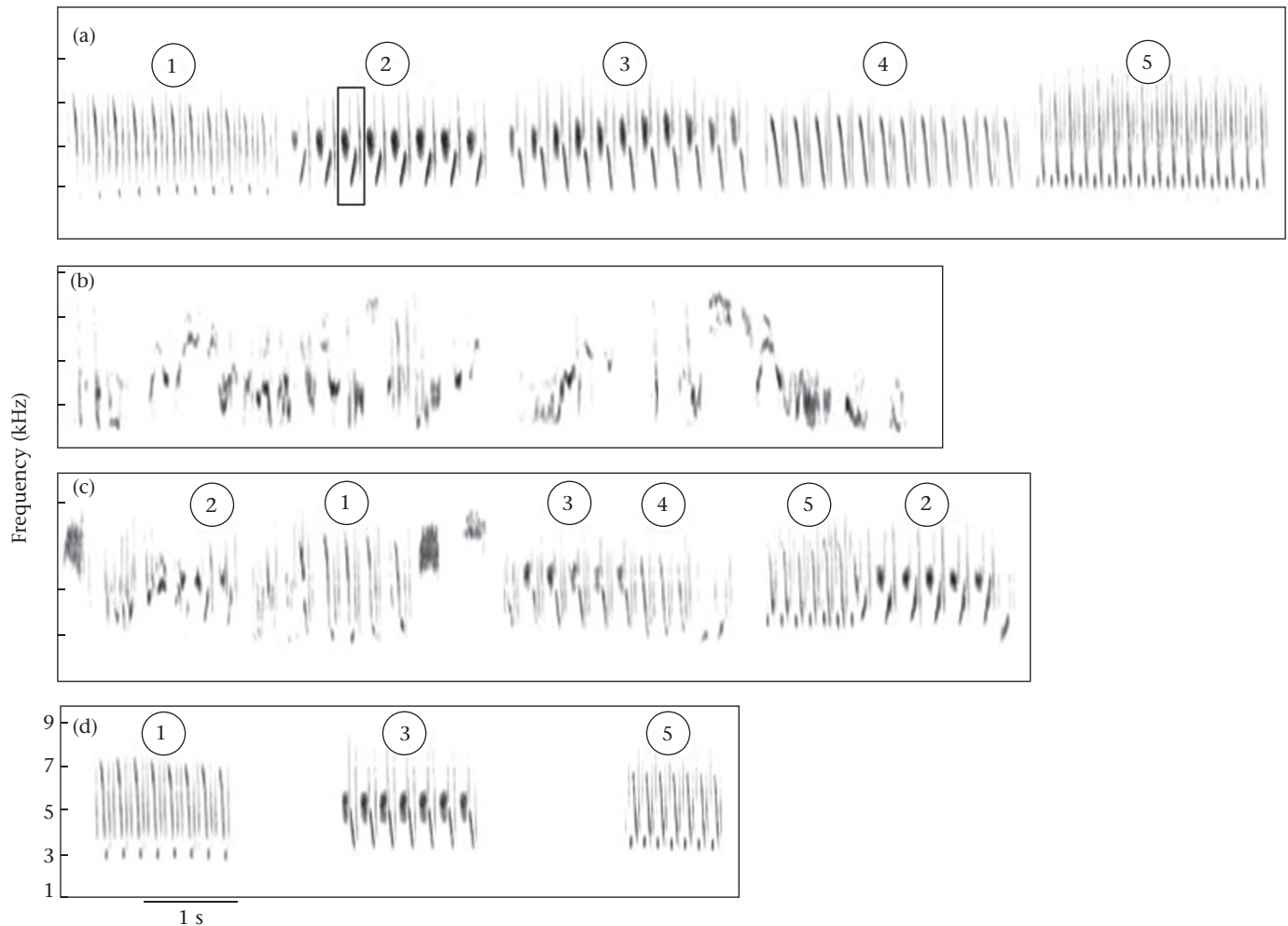
Figure 1. Overproduction and selective attrition in swamp sparrow song development. (a) A subset of five tutor songs labelled 1–5 played to a swamp sparrow male during his sensory phase. The box in tutor song 2 indicates one syllable, composed of four notes; swamp sparrow song types typically comprise a single syllable repeated in a continuous trill, so 'syllable type' is synonymous with 'song type' when referring to adult swamp sparrow song. (b)–(d) Examples from the song development of one swamp sparrow male: (b) subsong; (c) plastic song demonstrating overproduction, defined as rehearsal during plastic song of more song material than is eventually included in the adult's song repertoire; in this case rehearsal of all five tutor songs is evident; (d) crystallized song demonstrating selective attrition: two of the tutor songs rehearsed in plastic song were discarded, and three were crystallized. Specifically, copies of models 2 and 4 were present during the plastic song phase, but were absent from the bird's final repertoire. This winnowing of syllable types prior to crystallization of the final repertoire is the process of selective attrition.

of occurrence of a syllable does not necessarily predict whether it will be crystallized (e.g. Figure 1 in Marler & Peters, 1981; Marler & Peters, 1982d). Over the whole course of plastic song, however, swamp sparrow males sing imitations of syllables destined to be crystallized significantly more often than those that are discarded (Marler & Peters, 1982c).

Swamp sparrow singing behaviour is seasonal, as for most temperate zone songbirds (Brenowitz, 2004), and song more or less ceases during the winter. The following spring, when singing resumes, males go through a plastic song phase before recrystallizing their adult songs. This second round of plastic song is shorter than the first, and fewer syllables are rehearsed, but as in the previous plastic song stage, they are sung in a variable, less stereotyped manner (Marler & Peters, 1982c). Swamp sparrow male song repertoires remain the same from year to year (Marler & Pickert, 1984), and during the early spring period of plastic song that precedes a male's second breeding season, Marler and Peters (1982c) identified not only syllables included in previously crystallized adult songs but also syllables that had been previously overproduced and lost during the first year of song development. At the beginning of their second breeding season, white-crowned sparrows,

Zonotrichia leucophrys, exhibit re-expression of multiple song types memorized as juveniles, but as in swamp sparrows, individuals recrystallize the same songs from year to year (Hough, Nelson, & Volman, 2000). Thus it appears that the memory of sounds rehearsed only during plastic song in the first year are maintained and can reappear during plastic song in subsequent years even though they are never included in the adult repertoire.

FUNCTIONAL CONSEQUENCES OF OVERPRODUCTION AND SELECTIVE ATTRITION

Overproduction and selective attrition have been described in several species including nightingales (Hultsch, 1991), canaries, *Serinus canaria* (Mundinger, 1995), chaffinches, *Fringilla coelebs* (Thorpe, 1958a, 1958b), white-crowned sparrows (Dewolfe, Baptista, & Petrinovich, 1989; Nelson, 2000), song sparrows (Nordby, Campbell, & Beecher, 2007), field sparrows, *Spizella pusilla* (Nelson, 1992), chipping sparrows, *Spizella passerina* (Liu & Kroodsma, 1999), red-winged blackbirds, *Agelaius phoeniceus* (Marler, Mundinger, Waser, & Lutjen, 1972), and chestnut-sided warblers, *Setophagia pennsylvanica* (Byers & Kroodsma, 1992). The

extent of attrition of rehearsed material from plastic to crystallized song ranges from less than 10% (as in nightingales) to near 80% (as in swamp sparrows) and may be negatively correlated with adult repertoire size (Hultsch & Todt, 2004).

Marler and Peters (1989) suggested that one functional consequence of selective attrition may be the rejection of heterospecific song material that a male has inadvertently memorized (Table 1). To investigate this possibility, they combined data from a series of swamp sparrow song-learning experiments in which males had been trained with approximately equal numbers of swamp sparrow and song sparrow trills. During plastic song, the males sang imitations of swamp sparrow syllables significantly more than expected based on the proportions of song material with which they were trained, although these birds did rehearse some heterospecific material. Through selective attrition, they subsequently discarded significantly more song sparrow than swamp sparrow syllables. Because these were laboratory-reared birds raised in social isolation, the most parsimonious explanation for selective attrition in this case is that an auditory template system guided the rejection of this heterospecific material (Marler & Peters, 1977) (see also Soha, 2017). As in swamp sparrows, selective attrition in other species can lead to the elimination of unsuitable material, such as heterospecific song memorized by chaffinches (Thorpe, 1958a, 1958b), or syllables of poor copy quality as occurs in nightingales (Hultsch, 1991).

A number of studies suggest that another functional consequence of overproduction and attrition is to enable males to fine-tune their songs to be more effective in their interactions with other males by matching the song types of territorial neighbours (Table 1). For example, male field sparrows often sing more than one song type when settling on a new territory in their first spring. After interacting vocally with neighbouring males, first-year males retain the song that most resembles their most actively singing neighbour (Nelson, 1992). Likewise, song sharing in western populations of song sparrows has been shown to be advantageous for territory tenure (Beecher, Campbell, & Nordby, 2000). Yearling song sparrows settling on new territories overproduce and then drop songs during the crystallization process. Those songs that are dropped from the repertoire are shared by significantly fewer neighbours, and dropped songs are also poorer matches to neighbour songs (Nordby et al., 2007).

Overproduction and selective attrition also have been studied in the context of song dialect maintenance, which affects the efficacy of both male–male and male–female signalling (Table 1). Male Puget Sound white-crowned sparrows typically have one song type in their adult repertoire and form large vocal dialect populations along the Pacific Northwest coast (Baptista, 1977). In a contact zone between two dialects at the mouth of the Columbia River, about 40% of the new territory occupants sang songs from two different dialects upon arrival in April from their wintering grounds and then subsequently discarded one of these over the next few days or weeks (Nelson, 2000). Eighty-eight per cent of these males kept as their adult song the dialect sung by the majority of their neighbours, and no male added a new dialect after arrival. New arrivals that overproduced were significantly more likely to match their neighbour's dialect than males that did not overproduce (Nelson, 2000).

Another functional consequence of overproduction and attrition may be to facilitate a male's ability to selectively produce songs that are more effective in the context of female assessment (Table 1). One possible example comes from work on brown-headed cowbirds, *Molothrus ater*, in which it has been shown that young males respond to subtle visual signals such as wing movements and beak gapes produced by females (King, West, & Goldstein, 2005; Smith, King, & West, 2000; West & King, 1988). In particular, female cowbirds produce infrequent wing strokes simultaneously with the male's production of specific songs at the onset of their first breeding season. Males respond by retaining song material that elicited the female response. Furthermore, songs that prompt wing strokes are more effective in stimulating copulation solicitation displays than songs that do not provoke wing strokes (West & King, 1988).

Swamp sparrows provide a second possible example. Because of motor constraints associated with how fast the repeated syllables of a song can be produced (Hoese, Podos, Boetticher, & Nowicki, 2000; Nowicki, Westneat, & Hoese, 1992), some swamp sparrow songs are more challenging to perform than others (Podos, 1996, 1997), and female swamp sparrows have been shown to prefer songs that are relatively more difficult to produce (Ballentine, Hyman, & Nowicki, 2004). When young swamp sparrow males were trained with song models composed of syllables produced at abnormally rapid trill rates, they rehearsed these syllables during the sensorimotor phase, indicating that these models were memorized during the sensory phase (Podos, Peters, & Nowicki, 2004). However, copies of rapid trill models that were retained in crystallized song were rehearsed at a significantly slower rate than the model trill rate, while those that were rehearsed and lost through selective attrition were more similar to the accelerated trill rate of their respective model (Podos et al., 2004). This finding suggests that selective attrition in swamp sparrows may allow individuals to target which model songs they crystallize based on their ability to perform those songs.

A final hypothesis for the functional significance of overproduction and attrition in song suggests that persistent memories of songs rehearsed but never crystallized may serve to facilitate a male's ability to recognize or assess songs of other males in the

Table 1
Possible functional consequences of overproduction and selective attrition in song learning

Process	Functional consequence
Selective attrition	
Elimination of nonsuitable song material	Males discard nonconspecific material as well as poor model copies
Selective production	
Production of song types that are particularly effective in male–male signalling	Males retain song types that match neighbour song types
Production of song types that conform to the local dialect	Males retain song types that match the neighbourhood dialect, which could facilitate both male–male and male–female signalling
Production of song types that are particularly effective in female assessment and mate choice	Males retain songs for which females indicate a preference, such as songs that a male is able to produce well, either as quality of copy, or in performance of the song, or other characteristics
Overproduction	
Enhanced recognition of local song types that are not part of an individual's repertoire	The persistent memories of models heard but not crystallized may augment recognition and assessment of local population songs

population even when a male does not include those songs in his own crystallized repertoire (Table 1; Prather et al., 2010). Testing this idea in the field will be difficult, of course, but laboratory studies in which birds raised with known models are tested using both behavioural and neural measures of perception may lend insight into this idea.

BEHAVIOURAL AND NEUROLOGICAL EVIDENCE FOR PERSISTENT MEMORIES OF SONG

Evidence that a male songbird has memorized a song typically comes from the male's own reproduction of that song, either in his adult repertoire or in passing during plastic song. But it is possible that birds retain memories of songs to which they are exposed during their sensory phase even if they never attempt to produce those songs. Behavioural evidence for this possibility comes from interactive playbacks with nightingales (Geberzahn, Hultsch, & Todt, 2002). Nightingale males were tutored with different song types arranged in different song groups, and their song development was recorded to document tutor models that were heard but never imitated, as well as models that were rehearsed and either discarded or retained and crystallized. Researchers visually inspected an average of 971 plastic song patterns per male, along with an average of 1034 crystallized song patterns per male. Adult males respond to playback of tutor songs heard during their sensory phase either by song type matching (singing their own rendition of the playback song type) or by song group matching (singing an imitation of a model that had been presented in the same group of models during training). Geberzahn and colleagues presented adult males with playbacks comprising four different stimulus categories: novel songs that were never previously heard, models that were heard in the sensory phase but never detected during the sensorimotor phase, models that had been rehearsed and then discarded, and those retained in each bird's crystallized repertoire. Males typically sang both song type matches and song group matches to tutor models they imitated in their crystallized song, as well as to models they had rehearsed in plastic song but discarded. Males also responded to playback of songs they had been tutored with but had not imitated. Intriguingly, males not only sang group matches to these, but they also sang song type matches — imitations that had not been detected before during song development. Importantly, males did not song type match to novel songs, indicating that they were not merely learning de novo then singing matches to songs they had been tutored with earlier but did not imitate. There was no significant difference between song type matching to models rehearsed but discarded and to those never rehearsed, indicating that the memories of those models were equally accessible (Geberzahn et al., 2002). Thus, a lack of rehearsal during song development does not necessarily indicate that a song was not memorized.

Recent neurophysiological work on swamp sparrows also suggests that songs lost during selective attrition, and even songs that are heard during the sensitive period but never produced, can be retained as persistent memories in the bird's brain. Prather et al. (2010) recorded neural responses in the song system nucleus HVC, a specialized region where motor and sensory representations of song both exist (Margoliash, 1986; McCasland & Konishi, 1981; Prather, Peters, Nowicki, & Mooney, 2008). An HVC neuron in a swamp sparrow brain will respond robustly and selectively to the bird's own song and furthermore, the same neuron may respond to more than one crystallized song type (Mooney, Hoese, & Nowicki, 2001).

Prather et al. (2010) first trained six swamp sparrow males with conspecific songs during their sensory phase and then recorded their song development extensively from subsong through crystallized song to document as completely as possible which of the tutor

models were rehearsed during plastic song and, of those, which were eventually crystallized. As expected, these males exhibited overproduction and attrition and sang more syllables during plastic song than they crystallized. Prather and colleagues then recorded neural responses from a total of 20 cells in HVC to multiple stimuli, including the male's entire crystallized repertoire, a subset of the tutor models he heard during the sensory phase representing syllables rehearsed during plastic song and those not rehearsed, and novel conspecific songs (i.e. songs the bird had never before heard).

As expected, HVC neurons responded vigorously to multiple stimuli, but each neuron also showed selectivity in its response. A typical cell responded to multiple song types in a bird's crystallized repertoire but consistently responded most strongly to one of those types (termed the 'strongest crystallized song type'); another neuron from the same bird might favour a different crystallized song type. These same neurons also responded to tutor models, including models that were imitated and crystallized, those that were rehearsed in plastic song but never crystallized, and even tutor models heard during the sensory phase but with no evidence of ever having been rehearsed (see Figures 4C and 5A–C in Prather et al., 2010). Novel songs never elicited a stronger response than the strongest crystallized song type (Prather et al., 2010). Surprisingly, however, some of these neurons gave a stronger response to tutor model songs. In fact, 70% of the cells responded more strongly to tutor models than to the strongest crystallized song type. Notably, in 64% of the cells that responded more strongly to tutor models, the tutor model that evoked the response was not a model for the strongest crystallized song type, or of any song type retained in the birds' adult repertoire. Most of these tutor models had been rehearsed during plastic song, although they were not the most commonly rehearsed. Intriguingly, some responses were to tutor models for which there were never any documented imitations at all in the bird's singing history, thus demonstrating that HVC neurons can respond to models even when imitations of those models were sung only transiently, or possibly not at all.

EVIDENCE FROM SPEECH FOR PERSISTENT MEMORIES OF EARLY EXPOSURE TO VOCALIZATIONS

Marler (1970a, 1970b) first described a set of parallels between the learning and development of birdsong and human speech, similarities that have fuelled research into song learning for decades (see also: Bolhuis, Okanoya, & Scharff, 2010; Doupe & Kuhl, 1999; Jarvis, 2004; Soha & Peters, 2015). In their description of overproduction and selective attrition, Marler and Peters (1981, 1982a) noted that humans also make more sounds during infancy than are eventually included in their adult language and speculated that exposure to language helps narrow their phonological repertoire.

Considerable work has shown the influence of early experience on subsequent perception and production of speech sounds. Although human infants display an early perceptual ability to discriminate among phonemes of all languages (Eimas, Siquelan, Jusczyk, & Vigorito, 1971; Jusczyk, 1981), between 6 and 12 months of age they become increasingly attuned to the phonetic properties of their native language (Werker, Gilbert, Humphrey, & Tees, 1981). Non-native perception declines during this period as infants become better able to discriminate phonemes in their native language (Werker & Tees, 1984). Early experience also affects the development of speech production, of course. For example, differences in both vowel and consonant sounds can already be detected in the canonical babbling of infants between 5 and 10 months of age raised in different language environments (de Boysson-Bardies, Halle, Sagart, & Durand, 1989; Lee, Davis, & MacNeilage, 2010; Rvachew, Mattock, & Polka, 2006).

There also has been interest in the possibility that early childhood language memories can be retained even when exposure to that language is cut off. Internationally adopted children who have been exposed to one language for a brief time before immersion in a new language, have been the focus of fruitful research investigating the retention of first language exposure (Hyltenstam, Bylund, Abrahamsson, & Park, 2009). Evidence suggests that features of languages that are heard in early childhood but never or minimally produced have lasting effects on the ability to learn and produce these features later in life. For example, the retention of language properties as a result of early experience has been shown in the ability to develop more native-like accents when relearning a heritage language (Au, Knightly, Jun, & Oh, 2002). Furthermore, active recall attempts may enhance retrieval of a previously forgotten or unused birth language: recent research shows that international adoptees reacquire their birth language, even after long periods of disuse, at a more rapid rate than novel speakers (Oh, Jun, Knightly, & Au, 2003; Singh, Liederman, Mierzejewski, & Barnes, 2011).

Most recently, such effects have been documented even in neural responses to a language heard only briefly early in life (Pierce, Klein, Chen, Delcenserie, & Genesee, 2014). An intriguing paradigm for testing this effect is found in a comparison between tonal and nontonal languages. In tonal languages, such as Thai or Chinese, lexical tones are phonemic such that the same syllable has a different meaning depending on the tone applied. Brain activity in response to tonal information differs between individuals with and without experience with tonal languages (Zatorre & Gandour, 2008). Speakers of nontonal languages recruit right temporal regions for processing nonphonemically relevant tones like prosody and intonation, whereas speakers of tonal languages recruit left temporal regions for phonemically relevant tones (Gandour, Wong, & Hutchins, 1998; Hsieh, Gandour, Wong, & Hutchins, 2001). Taking advantage of this difference, Pierce et al. (2014) tested the responses of international adoptees from China who were brought into French-only speaking families at an average age of 12 months. Using fMRI (functional magnetic resonance imaging), the researchers demonstrated that as teenagers, both international adoptees and Chinese-French bilinguals recruited the same left temporal regions when processing lexical tones, while French monolinguals did not. In other words, the brain activation of the international adoptees precisely matched that of native Chinese speakers, despite the fact that internationally adopted children had no subsequent exposure to Chinese and no conscious recollection of that language (Pierce et al., 2014).

Thus, with similarity to what we have seen for the retention of vocal memories by the songbird brain, these data suggest that the human brain also retains language-related memories that are acquired early on, even though that information is apparently not relevant for the language that is subsequently mastered. The function of such persistent memories for speech perception and production is more speculative than it is for birdsong, but here again is another parallel between speech and song, building on comparisons Peter Marler first described over 40 years ago. Further research of overproduction, selective attrition and persistent memories in songbird development, both in the laboratory and the field, will undoubtedly uncover new insights into the functional consequences of these phenomena as well as implications for human speech.

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