



Early song discrimination by nestling sparrows in the wild



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ARTICLE INFO

Article history:

Received 26 November 2013

Initial acceptance 27 January 2014

Final acceptance 27 February 2014

Published online

MS. number: A13-00980R

Keywords:

auditory template

birdsong

predisposition

species recognition

Zonotrichia

Songs play an important role in premating isolation in birds. However, when songs are learned, experience with both conspecific and heterospecific songs in early life could lead to the development of both mixed songs and mixed preferences. One way that such learning errors can be prevented is if birds can discriminate between songs of different species prior to learning and preferentially memorize conspecific songs. Prior captive studies have shown that white-crowned sparrows, *Zonotrichia leucophrys*, are able to discriminate songs early in the process of song memorization, after about 10 days since hatching. I studied early song discrimination in wild golden-crowned sparrows, *Zonotrichia atricapilla*, the sister species of white-crowned sparrow. The two species occur syntopically in the study population, and therefore sparrows were expected to selectively learn conspecific songs. Playbacks of songs elicited vocal responses from nestlings as young as 6 days old, and nestlings responded more to conspecific songs than to songs of the sympatric white-crowned sparrow subspecies. These results suggest that conspecific song templates exist at the onset of song memorization, and this could allow golden-crowned sparrows to learn the songs of their own species correctly despite syntopy with their sister species. I suggest that studying species recognition prior to learning could provide fresh insights into the evolution of reproductive isolation and song divergence.

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The production and recognition of species-specific signals is critical to the evolution of reproductive isolation (Coyne & Orr, 2004; Price, 2008). In many birds and other species, prior experiences affect both mating preferences and sexual display traits. Thus, learning plays an important role in the evolution and maintenance of divergent populations (Irwin & Price, 1999; Servedio, Sæther, & Sætre, 2009; Verzijden et al., 2012). Critically, the influence of learning on evolution (e.g. whether learning promotes or inhibits speciation) depends on whether mechanisms exist to ensure that learning is restricted to conspecific cues (Lachlan & Feldman, 2003; Lachlan & Servedio, 2004; Laland, 1994; Olofsson, Frame, & Servedio, 2011; Servedio et al., 2009). In the absence of mechanisms that restrict learning to conspecific cues, learning could lead to the breakdown of assortative mating through the acceptance of heterospecific mates (Grant & Grant, 1997) or convergence in courtship traits due to heterospecific copying (Sorjonen, 1986).

Selective learning has been intensively studied in the context of song learning in birds. In many species, the ability of birds to memorize songs is heightened during the period after fledging (i.e.

the 'sensitive period'), although the duration of this sensitive period can vary across species, populations and experimental protocols (Catchpole & Slater, 2008). During this period, young birds will typically hear the songs of many species that share the habitat. Thus, in order to produce species-typical songs later in life, young songbirds must avoid learning heterospecific songs. Because songs are often used for territoriality and courtship, birds learning mixed-species songs may be less successful in gaining mates, or may attract heterospecific mates (reviewed in Slabbekoorn & Smith, 2002). Females that do not sing in courtship also learn songs (Casey & Baker, 1992; Riebel, 2003), and selective learning may also be important for mate choice: those with mixed preferences may be more likely to choose heterospecific mates (e.g. Grant & Grant, 1997). Thus, overly permissive learning (i.e. learning both conspecific and heterospecific song) may be maladaptive because of sexual selection or selection against hybrids, and mechanisms to restrict learning to conspecific song elements are expected to evolve. Consistent with this prediction, laboratory studies have repeatedly shown that songbirds preferentially learn the songs of their own species over those of sympatric species (Braaten & Reynolds, 1999; Marler, 1970, 1990; Marler & Peters, 1977; Thorpe, 1958).

There are a few potential mechanisms that could promote selective song learning. Selective learning could be guided by song

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templates that allow naïve individuals to identify conspecific songs prior to learning (Marler, 1990); these song templates could be genetically inherited ('innate template': Marler, 1990) or acquired from fathers early on in life through sexual imprinting (ten Cate, Vos, & Mann, 1993). In addition, naïve individuals may be able to learn from conspecific tutors reliably through predictable patterns of social interactions (Baptista & Petrinovich, 1984). These general mechanisms are not mutually exclusive, and there is experimental evidence for the roles of both song templates and social interactions (Baptista & Petrinovich, 1984; Marler & Peters, 1977). A critical test for the song template model (either innate or acquired very early in life) is to show that young birds are able to discriminate between conspecific and heterospecific songs by the time they begin song memorization. In white-crowned sparrows, *Zonotrichia leucophrys*, experiments in captivity have shown that young fledglings (11–20 days old) preferentially respond to songs of conspecifics over those of sympatric heterospecifics (Nelson & Marler, 1993; Soha & Marler, 2001; Whaling, Solis, Doupe, Soha, & Marler, 1997). Because the sensitive period for song learning in this species is thought to occur after the young leave the nest around 10 days posthatch (Marler, 1970; Marler & Tamura, 1964; Nelson, Marler, & Palleroni, 1995), these results suggest that song templates exist prior to song memorization. Here, I adapt this behavioural assay for the field to investigate song discrimination prior to song memorization in the sister species of the white-crowned sparrow: the golden-crowned sparrow, *Zonotrichia atricapilla*.

Golden-crowned sparrows and white-crowned sparrows are sister species (Carson & Spicer, 2003; Weckstein, Zink, Blackwell-Rago, & Nelson, 2001; Zink & Blackwell, 1996) that share sympatric breeding ranges in western North America. While there are occasional reports of hybrids (Miller, 1940), the two species are not known to maintain any hybrid zones. These two species sing distinct songs, but they share some key features that are known to be important in song learning of white-crowned sparrows. For example, white-crowned sparrows preferentially learn songs that contain a whistle (Soha & Marler, 2000), a feature that is shared across the two species (Fig. 1). However, there is no evidence that individuals in sympatry sing mixed songs. The lack of mixed or heterospecific song as well as the establishment of reproductive isolation between these closely related species could be driven by the evolution of mechanisms to ensure selective learning. Here, I test the hypothesis that a song template exists before the period of song memorization in golden-crowned sparrows by determining whether they can discriminate between songs of conspecifics and

songs of sympatric white-crowned sparrows during the nestling stage.

METHODS

Study System

I studied golden-crowned sparrows at Hatcher Pass, Alaska, U.S.A. (61°46'N, 149°13'W) in June–July 2012. At this site, golden-crowned sparrows are syntopic (i.e. they co-occur in the same habitat) with the Gambel's subspecies of white-crowned sparrows (*Z. leucophrys gambelii*). Golden-crowned sparrows defend territories against conspecifics, but interspecific aggression is rare (Shizuka & Hudson, n.d.). The territories of the two species overlap considerably, and nestlings are likely to hear the songs of both conspecific and heterospecific neighbours. No mixed-species pairs have been detected at this population ($N = 60$ golden-crowned sparrow nests in 2012–2013).

Nests ($N = 11$ nests used for this study) were found during the incubation or nestling stages. Nests found during incubation were checked daily to determine the hatching date for each individual. Hatch date (day 0) was the first day that an individual was seen to have completely emerged from the egg (due to hatching asynchrony, some eggs hatched on the second day). For nests found during the nestling stage, I estimated hatching day using feather length (see below). Individual chicks were marked using nontoxic markers until day 6, at which point they were banded with U.S. Fish and Wildlife-issued leg bands.

Playback Stimuli

Song recordings were collected in the field using a solid state recorder (Marantz PMD-660, 16-bit depth, 48 kHz sampling rate) with a shotgun microphone (Sennheiser ME67). Playback stimuli were constructed using Raven Pro 1.3 (Cornell Lab of Ornithology, Ithaca, NY, U.S.A.), saved as a .wav file, and played back using an iPod Touch. Each 2 min track consisted of a single song repeated 12 times at 10 s intervals. Each track was high-pass filtered above 1 kHz and standardized for root-mean-squared amplitude. I prepared six playback tracks for each treatment, each consisting of a song from a different individual (see Supplementary Fig. S1). The conspecific and heterospecific playback tracks were presented as paired sets (e.g. stimulus 'a' was always matched with stimulus 'b' in Fig. S1), and each chick from the same brood listened to a different stimulus set. I used a balanced design so that each stimulus set was used roughly an equal number of times. All playback songs were recorded away from the experimental site. For white-crowned sparrows, songs were recorded from the Gambel's subspecies throughout its range in Alberta, British Columbia, Canada, and Alaska in 2011. For golden-crowned sparrows, all songs were the typical dialect in Alaska, recorded more than 100 km away from the study site in 2011.

Nestling Playback Protocol

Playback experiments were conducted on day 6 ($N = 4$), day 7 ($N = 8$) or day 8 ($N = 17$) after hatching. For the five nestlings with unknown hatch day, experiments were conducted when the length of the longest exposed primary feather corresponded with the average of chicks at 7 or 8 days old. Each nestling was placed individually in a portable pet carrier outside of the focal territory, and song stimuli were broadcast at standardized volume (~ 60 dB at 1 m) from a speaker (iHome Audio, iHM60) set directly outside the pet carrier. The speaker and pet carrier were partially covered with a tarp to reduce the volume of playback sound that could be

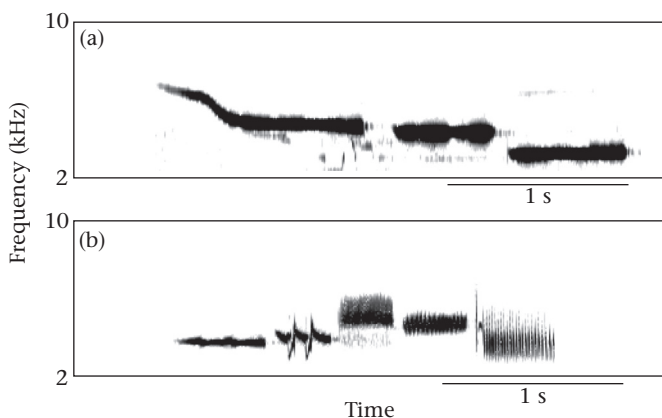


Figure 1. Spectrogram of songs of (a) golden-crowned sparrow and (b) Gambel's white-crowned sparrow.

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