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SONG SPARROWS LEARN FROM LIMITED EXPOSURE TO SONG MODELS¹

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In many songbirds, song learning is characterized by a distinct separation between an early "sensitive phase" when an individual hears and is thought to acquire song models, and a later "sensorimotor phase" when the bird practices and reproduces the songs it has learned (Marler and Peters 1982, Slater 1983, Marler 1991). This separation demonstrates that birds store song models in memory before using them as prototypes for motor output. Here we address the question of how much exposure to song is necessary to allow acquisition, storage and retrieval from memory of particular models in the Song Sparrow, *Melospiza melodia*.

Laboratory song learning experiments typically ex-

pose test subjects to hundreds or even thousands of repetitions of tape-recorded song models over the course of training. This extensive exposure is presumed to maximize an individual's opportunity to copy song material (e.g., Kroodsma and Pickert 1984, Marler and Peters 1987). Acquisition from limited exposure to training songs has also been reported, however. A Whitecrowned Sparrow (Zonotrichia leucophrys) exposed to 120 repetitions of a song type over 20 days reproduced a good copy of that model (Petrinovitch 1985). Each of three European Blackbirds (Turdus merula) learned one song motif from a range of 12-50 presentations on a single day (Thielcke-Poltz and Thielcke 1960). The most impressive cases reported of learning from limited exposure involve the Nightingale (Luscinia megarhynchos). Four of five males faithfully copied a string of 12 song types presented once per day for 15 days. One male from another group that heard a string of 21 song types presented twice per day for five days acquired 90% of that string (Hultsch and Todt 1989a). In another experiment, one male learned an entire string

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	Model type	No. song types heard	No. presentations per song type	No. males learning	No. song types copied
Group A	Conspecific	6	1,680	2	3
	Conspecific	12	420	2	3
	Heterospecific	9	30	_	
Group B	Heterospecific	6	1,680	_	_
	Heterospecific	12	420	_	_
	Conspecific	9	30	2	2

TABLE 1. Amounts of exposure to and learning from tape recorded song models by Group A (5 birds) and Group B (4 birds).

of 60 song types presented once per day for only 20 days (Hultsch and Todt 1989b).

The Song Sparrow has been used extensively in both field and laboratory studies involving song recognition and perception (e.g., Peters et al. 1980, Searcy and Marler 1981, Searcy et al. 1981, Okanoya and Dooling 1988) and function (e.g., Searcy et al. 1985, Hiebert et al. 1989). This species has also been the subject of much song learning research (e.g., Kroodsma 1977; Marler and Peters 1987, 1988; Nowicki et al. 1992). We here present data showing that Song Sparrows are capable of learning from 30 repetitions of a song type heard in a single 5-min bout.

METHODS

We hand-reared nine Song Sparrow males. These birds hatched between 10–16 May 1987 and were collected between 4–9 days of age from five different nests. They were raised in their nest groups, out of auditory contact with adult birds, until training began at about 50 days of age (x = 49.6, SD = 1.88). At this time, we individually housed the birds in sound isolation chambers.

We trained birds with songs recorded in the field from adult territorial male Song Sparrows and Swamp Sparrows (M. georgiana). Each song type was unique and there was no overlap between song sparrow and swamp sparrow phonology. Training songs were broadcast through loudspeakers in the isolation chambers. All training song types were presented in five min bouts at a rate of one song per 10 sec (30 songs/bout). Bouts were arranged randomly on the tape and a session of nine bouts of different song types was presented twice per day (once in the morning and once in the afternoon). Most were heard for one-week or four-week periods but one set of song types was heard on one day only.

Five males (Group A) were exposed to a total of 18 Song Sparrow song types over the four week long training period. Six of these song types were heard during all four weeks (1,680 presentations per song type). Twelve other song types were heard, three each week, for only one week (420 presentations per song type). On one morning in the first week (average age = 55.4 days), Group A was exposed to one bout each of nine Swamp Sparrow song types. There were 30 presentations of each of these song types which were heard at no other time. Thus, Group A was exposed primarily to conspecific song except for 30 presentations each of nine heterospecific song types (Table 1). Four birds (Group B) heard almost entirely Swamp Sparrow song types during their training period. Again, they heard six song types for four weeks and another 12 for one week each throughout the training period. On one morning of the first week (average age = 55.8days), Group B heard one bout each of nine Song Sparrow song types. Each of these was heard on one day only, for 5 min, with 30 consecutive repetitions. Thus, over the entire training period Group B was exposed primarily to heterospecific song except for 30 presentations each of nine conspecific song types (Table 1).

RESULTS AND DISCUSSION

Four of the five males in Group A learned from a total of six Song Sparrow song models. Half of these songs were learned from models that were heard for four weeks (1,680 presentations) and half from models that were heard for one week (420 presentations) (Table 1). None of the birds in Group A showed any evidence of learning from the one morning of exposure to Swamp Sparrow song.

Marler and Peters (1987) showed that exposure to 420 repetitions of conspecific song over one week is sufficient for learning in Song Sparrows in the laboratory. The present result confirms this, and shows that there is no preference for song types heard over the more extended exposure period. Although these birds heard twice as many song types for one week as they did for four weeks (Table 1), the difference in number of song types copied from these two lengths of exposure is not significant (Fisher Exact Probability, P = 0.28). Similarly, beyond a critical minimum amount, exposure does not influence tutor choice in Zebra Finches (*Taeniopygia guttata*) (Böhner 1983).

The four males in Group B did not learn from any Swamp Sparrow songs, even though they had far more extensive exposure to these heterospecific songs than did the males in Group A. In contrast, two of the males from Group B each learned from one Song Sparrow song type (Fig. 1) to which they had been exposed for only a single bout of 30 presentations on one day (Table 1). This limited exposure is the shortest period reported so far for successful song acquisition in an embezerine sparrow.

Two males from Group A and two males from Group B all happened to learn from the same Song Sparrow song model (Fig. 1). This allowed us to compare acquisition from extended exposure (Group A: 1,680 repetitions) versus limited exposure (Group B: 30 repe-



FIGURE 1. Sonagrams of training song (A) and copies of the first trill phrase by a bird with extended exposure (B) and one with limited exposure (C). The first syllable of the first trill phrase of the training song is indicated. Note that this particular training song included an unusually high proportion of harmonic overtones, which were also accurately copied by both birds (see Nowicki et al. 1992).

titions) with respect to the amount of a song that is copied and the accuracy of reproduction. All four males copied only the first trill from the song model, suggesting that extent of exposure did not influence completeness of copying. These incomplete imitations of a song model are not surprising because Song Sparrows tend to acquire fewer phrases from training models presented late in their sensitive phase. Marler and Peters (1987), for example, show that 60% of the acquisitions from models presented after 50 days with 420 or 2,520 repetitions consist of only one phrase. All four males produced the imitated phrase in a nearly identical fashion. Based on our visual assessment we could find no consistent differences among reproductions of the model song phrase. This suggests that, at least for this example, the extent of exposure did not influence either the completeness or the accuracy of imitation.

The birds in the present experiment were exposed to song relatively late in their sensitive phase for learning, as determined in previous laboratory studies of Song Sparrows (Marler and Peters 1987). It may be that, because they were deprived of song early in the sensitive phase, these birds were especially primed to learn conspecific song later, even from a limited exposure. Alternatively, a limited exposure earlier in the sensitive phase, when birds are known to learn best in the laboratory, might have resulted in an even more impressive demonstration of the ability to acquire songs heard only a few times. It is now well-known that social and other influences that a young bird normally encounters can affect the timing and nature of song learning in birds (Todt et al. 1979, Baptista and Petrinovitch 1984, Clayton 1987, Pepperberg 1988). It is likely that such factors also can influence the amount that a particular song must be heard in order for a bird to learn it. Nonetheless, our data demonstrate that Song Sparrows have the neural mechanisms necessary to capture the details of their own species' songs with only a few exposures to tape-recorded models.

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ANNUAL SURVIVAL OF BREEDING CASSIN'S AUKLETS IN THE QUEEN CHARLOTTE ISLANDS, BRITISH COLUMBIA¹

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Key words: Cassin's Auklet; Ptychoramphus aleuticus; survival rate.

Adult annual survival rate, which determines future life expectancy, is a basic demographic parameter fundamental to understanding population processes and life history strategies. Few estimates of adult survival are available for auks. Among populations breeding on the Pacific Ocean coasts, estimates are available only for the Cassin's Auklet *Ptychoramphus aleuticus* (Speich and Manuwal 1974) and Pigeon Guillemot *Cepphus columba* (Nelson 1991), both on the Farallon Islands, California and for the Ancient Murrelet *Synthliboramphus antiquus* on the Queen Charlotte Islands, British Columbia (Gaston 1990).

I report here the results of seven years of trapping breeding Cassin's Auklets at a colony in the Queen

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