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ARTICLES

Bird song learning in an eavesdropping context

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Bird song learning is a major model system for the study of learning with many parallels to human language development. In this experiment we examined a critical but poorly understood aspect of song learning: its social context. We compared how much young song sparrows, *Melospiza melodia*, learned from two kinds of adult 'song tutors': one with whom the subject interacted vocally, and one whom the subject only overheard singing with another young bird. We found that although subjects learned from both song models, they learned more than twice as many songs from the overheard tutor. These results provide the first evidence that young birds choose their songs by eavesdropping on interactions, and in some cases may learn more by eavesdropping than by direct interaction.

Keywords: eavesdropping; *Melospiza melodia*; passerine; social learning; song acoustics; song learning; song repertoire; song sparrow; vocal communication

The use of elaborate vocalizations, or song, in intraspecific communication is common in a wide variety of animal groups (Searcy & Andersson 1986). In the oscine passerines (songbirds), song has the additional, intriguing aspect, found in only a few animal taxa: it is learned, with much of that learning occurring early in life. Song learning in songbirds has many parallels with human language learning and has become a leading model system for studying the neurobiology of learning (Marler 1970a; Doupe & Kuhl 1999; Tchernichovski et al. 2001; Williams 2004; Brenowitz & Beecher 2005; Gardner et al. 2005). We examined an additional and only recently appreciated parallel between human language learning and bird song learning: the key role of social factors in vocal development. That social factors are important in songbird vocal development is now widely accepted (Catchpole & Slater 1995; West & King 1996; Snowdon & Hausberger 1997; Goldstein et al. 2003; Beecher & Burt 2004), but how precisely they contribute to song learning is poorly understood (Nelson 1997).

We examined two hypotheses concerning the role of singing interactions in song learning. The 'direct interaction' hypothesis is suggested by laboratory experiments showing that birds learn songs more readily from a nearby singing bird than from tape-recorded song played to them over a loudspeaker. Direct interaction is the predominant model for human language learning, and is usually conceptualized as the parent tutoring the infant (Goldstein et al. 2003). This hypothesis is also contained in the selective attrition theory of Nelson & Marler (1994). This theory focuses on the selective nature of song learning, that is, that a young bird hears and memorizes many more songs during his song-learning period than he will keep for his final song repertoire. The bird must therefore choose which particular songs he will retain for his final repertoire. Nelson & Marler proposed that song learning has two phases. In the first phase, occurring during the bird's natal summer, song learning is primarily a process of listening to and memorizing songs sung by adult birds. In the second phase, occurring during the next spring when the young bird attempts to establish his territory, the bird 'selects' the songs that he will retain for his final repertoire. Nelson & Marler described this later phase as a 'selective attrition' phase, because the learning consists of the bird pruning his repertoire of memorized songs, keeping some, dropping others. They also described it as a phase of 'action-based' learning, because they supposed that the learning is shaped by countersinging interactions that the young bird has with

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his new territorial neighbours. Specifically, they suggested that the young bird attempts to match the songs of his new neighbours ('matched countersinging') and eventually pares his song repertoire down to those songs that are the best matches to his neighbours' songs (Nelson 1992).

A second hypothesis concerning the role of social interaction in song learning is the 'social eavesdropping' hypothesis. 'Social eavesdropping' is defined as extracting information from a signalling interaction between other individuals (Peake 2005). We have hypothesized a possible role for eavesdropping in vocal learning (Beecher & Burt 2004) by extrapolation from recent field experiments indicating that birds eavesdrop in other contexts involving song. These studies have shown that adult songbirds eavesdrop on singing interactions of neighbourhood males and subsequently make decisions about whom to challenge or whom to mate with on the basis of information that they have extracted concerning status relationships of the singing males (Otter et al. 1999; Peake et al. 2001; Mennill et al. 2002; Naguib et al. 2004). Thus, it is plausible that young males might use the same kind of information to make tutor- and song-selection decisions in the song-learning process. Another relevant perspective is Pepperberg's (1985) 'social modelling' theory that vocal learning depends on the young bird observing communication interactions between individuals who have mastered the communication system.

Our previous field and seminatural laboratory studies with song sparrows, *Melospiza melodia*, have suggested that interactive singing is a critical stimulus for song learning (Nordby et al. 1999, 2000, 2001), but we could not determine whether young birds learned primarily via direct interaction with the tutor or from eavesdropping on other singing interactions. Thus, we designed the present experiment to compare learning that results from direct interaction of the subject with an adult singer ('interactive tutor') and learning that results from the subject overhearing or eavesdropping on similar interactions between another young bird and a singing adult ('overheard tutor'). We use the term 'tutor' or 'tutor song' to denote the source of (the model for) a particular song that the young bird has learned, regardless of whether the tutor song was produced by a tape recorder, a computer or a particular bird.

METHODS

Subjects

We brought eight young song sparrows in from the field near Seattle, Washington at about 3–4 days posthatching (hatch dates ranged from 2 May to 27 May 2004). The birds were hand-reared to independence at approximately 30 days using the hand-rearing protocol described in Nordby et al. (2000). Throughout the study, a Seattle photoperiod appropriate for the given date was maintained for all birds. Birds were released at the capture site after the experiment.

Experimental Design

Song tutoring occurred in two stages (Fig. 1). During the first 2 months of their lives, all the subjects received song tutoring from four adult males (Phase 1). Following a 5-month hiatus in which they heard no song, subjects were then exposed to two of the original tutors for an additional 3 months (Phase 2, early spring). The design is based on previous observations, in the field and in the laboratory, that a song sparrow is more likely to retain for his adult repertoire a song that he heard in his natal summer if he is exposed to it again the following spring (Nordby et al. 1999, 2001). Thus, we expected the birds to learn more from the two tutors present during both Phase 1 and 2 than from the two tutors present only in Phase 1. The experimental manipulation was that one of the two late tutors became a subject's interactive tutor, while the other became the subject's overheard tutor (i.e. it was overheard interacting with another subject). Thus, the key question was whether, at the end of Phase 2 when the subject's song repertoire crystallized, the subject would learn (retain) more songs from his interactive tutor or his overheard tutor.

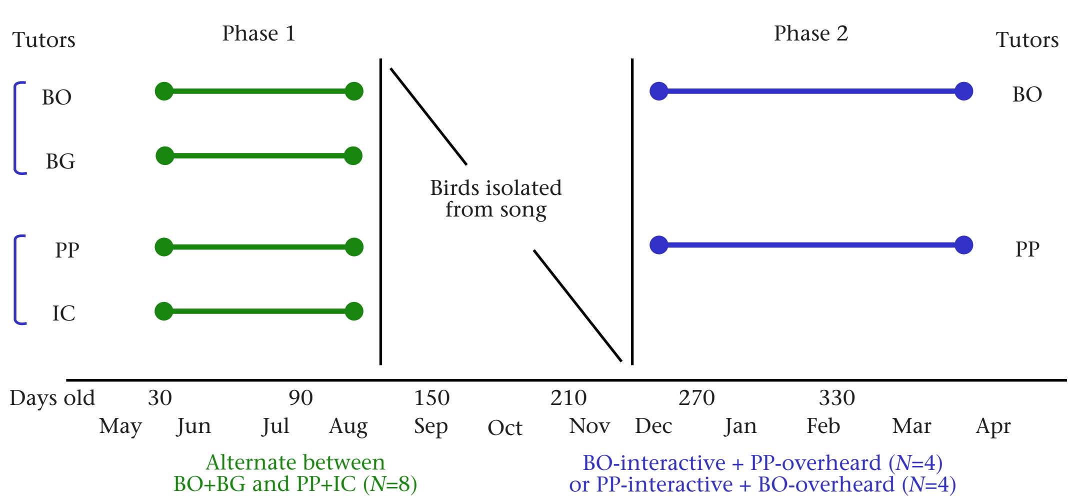

Figure 1. In Phase 1, young song sparrows as a group were exposed to two pairs of tutors; the group was moved from the room housing tutors BO and BG to the room housing tutors PP and IC every fourth day. In Phase 2, individual subjects interacted with one of the four tutors from Phase 1 and overheard interactions between another tutor–subject pair (see Fig. 2).

Procedure

Song tutoring began on day 15 (15 May for the oldest birds), for 4 h per day until day 30, and thereafter throughout the daylight hours for another month. In Phase 1, subjects were taken to one of two rooms, each of which housed two adult song sparrows in separate cages, approximately 4 m apart. Because the young birds had not yet begun to sing at this age, we could expose them in groups; the only songs that they heard were from the two adult tutors in the room. Tutors BO and BG were in one room, and tutors PP and IC were in the other room. The tutors were territorial about their cages, and the two tutors in a room had frequent singing interactions. The subjects were rotated between the two rooms every fourth day. Young males began singing subsong after about day 60–70, so from the end of Phase 1 (which ranged from 30 June to 20 July for different-aged subjects) until the beginning of Phase 2 on 21 December, each subject was kept in a separate sound-insulated chamber. Thus, during this period the young birds could not hear one another or any of the adult tutors.

Song tutoring resumed in Phase 2 (21 December–31 March), but with only two of the original four tutors (BO and PP). We used a yoked-subject design in which on day 1, subject A was exposed to his interactive tutor (e.g. BO) and subject B overheard this interaction; on day 2, subject B was exposed to his interactive tutor (PP) and subject A overheard this interaction (Fig. 2). The cage of the interactive tutee was moved into a larger chamber (1.1 × 0.85 × 0.65 m) with the interactive tutor in a separate cage located 0.4 m away. For half of the subjects there was a black, opaque cloth between subject and tutor so that they could hear but not see one another. The next day this subject was placed in a similar chamber by himself where he could hear over a loudspeaker the singing of his yoked subject and the other late tutor. In the other 2 days of the 4-day cycle, the subject was returned to his home chamber and heard nothing (while other subjects cycled through the experiment).

The songs of the interactive tutor and tutee were recorded with a microphone and fed directly to a loudspeaker in the yoked chamber, the only modification being that the songs of the overheard subject, but not those of the overheard tutor, were reduced somewhat in amplitude. Thus, to the 'eavesdropping' subject, the overheard yoked subject would have sounded somewhat more distant than the overheard tutor. The microphone–loudspeaker connection was one-way (Fig. 2), so that the songs of the 'eavesdropping' subject could not be heard by the interacting tutor and subject in the yoked chamber.

Song Analysis

All songs of tutors and subjects were recorded and analysed. We measured the final song repertoire of each subject from the last 3 days of his singing at the end of March; in this species, a bird's song repertoire does not change after the bird is 10–11 months old (Nordby et al. 2002). We compared each subject's repertoire against the repertoires of the four tutors, and identified which tutor

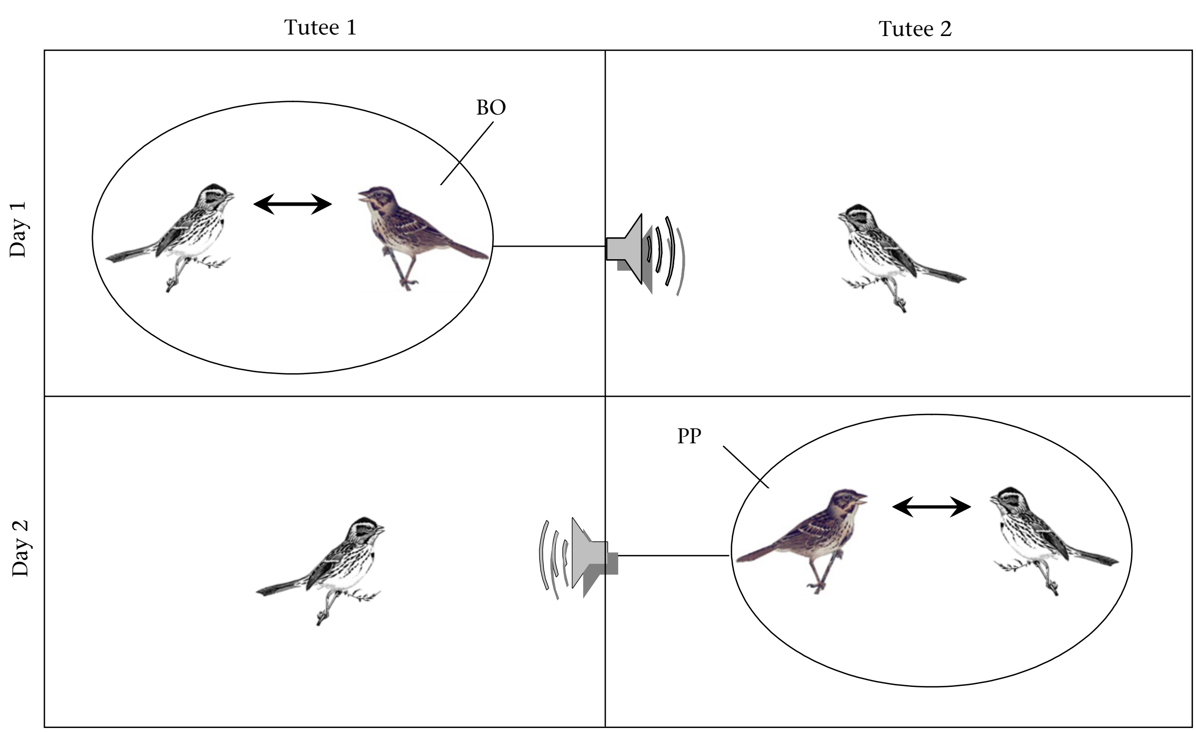

Figure 2. Schematic of yoked subject design. In Phase 2, a subject was exposed to one live tutor, the interactive tutor, on one day, and overheard another tutor–subject pair on a second day. For one-half of the subjects, the subject and interactive tutor were separated by a black cloth screen (not shown). On days 3 and 4 (not shown), the young bird was returned to his home cage in a closed chamber. Note that the diagram is not to scale and that the subject and interactive tutor were in their own separate cages within a larger sound-insulated chamber.

song type(s) were the likely model(s) for each subject's song type. Comparisons were made by three trained observers using methods described previously (Nordby et al. 1999, 2001, 2000).

The average repertoire size for the subjects was 8.5 songs, comparable to typical repertoire sizes of song sparrows in the field (Peters et al. 2000). Because we had chosen four adult song tutors for this experiment who had no song types in common (no 'shared' songs), we were able to unambiguously trace most of the subjects' learned songs to one of the four song tutors. We were able to identify a predominant tutor for 89% of these songs (i.e. 3/4 or more of the song's elements, notes, trills, buzzes, etc., were shared with one tutor song type). The remainder of the songs were hybrids composed of elements from multiple tutors' songs and/or contained unidentifiable elements and are considered 'unidentified' in the analysis below.

Statistical Analysis

We measured how many song types each subject learned or retained from each of the tutors, that is, from the interactive tutor (either BO or PP), the overheard tutor (PP or BO) and the two Phase 1-only tutors (BG and IC). We compared the number of songs each subject learned from their interactive tutor with how many they learned from the overheard tutor. To avoid assumptions about the underlying distribution, we tested the two-tailed hypothesis that subjects learned more from one type of tutor (interactive versus overheard) with a Monte Carlo simulation, 10 000 iterations (resampling statistics add-in for Excel, www.resample.com). With our counterbalanced design, each of the two late tutors was an interactive tutor for four subjects and an overheard tutor for four subjects; thus, if one tutor was more effective generally than the other, his effectiveness would have equal effect on both conditions.

RESULTS

We found that birds learned or retained more songs from the overheard tutor than from the interactive tutor, with 51% of the (identified) songs in their final repertoires from the overheard tutor versus 19% from the interactive tutor; the remaining 30% of their songs came from the two early-only tutors (Table 1, Fig. 3a). Focusing on songs learned from the two late-only tutors, birds learned 72% of these songs from the overheard tutor. Birds learned significantly more songs from their overheard tutor than from their interactive tutors (resampling, 10 000 iterations, $P = 0.008$). Our effect size d (mean difference divided by standard deviation) was 1.58, showing a 'large' effect (i.e. $d > 0.8$; Cohen 1988). The overheard tutor was preferred to the interactive tutor regardless of whether the interactive tutor could be seen (62% versus 14% for overheard versus interactive) or could not be seen because of the opaque barrier (41% versus 25%). Although, in general, tutor BO was more influential than tutor PP, our yoked-subject design separated the relative effectiveness of overheard and interactive tutors from the relative effectiveness of the particular tutors filling these roles: each tutor was more influential when he was in the role of overheard tutor than when he was directly interacting with a subject (Fig. 3b).

Because a subject overheard two birds singing, he could have learned from the overheard yoked subject as well as from the overheard tutor. However, of the songs that subjects shared with their overheard tutor, they actually shared fewer of these songs with their overheard yoked subject (22%) than they did with the average unyoked subject (33%), whom they never overheard. This difference reflects the fact that the two subjects in a yoked pair tended to learn the songs of the opposite tutor (the one they overheard), whereas half of the unyoked subjects were in the same condition (overheard the same tutor) and thus showed the same general tutor preferences, and hence were more likely to share some songs by chance; chance shares are inevitable given that each subject is drawing his eight or so songs from the same limited pool of model songs: 40 songs from four tutors.

DISCUSSION

Our experiment was designed to pit a song tutor that interacted with the subject against an overheard tutor

Table 1. Number of songs learned from each tutor

Subject	Interactive tutor	Overheard tutor	Total songs	Interactive tutor (IT)	Overheard tutor (OT)	IT's early partner	OT's early partner
CC	PP	BO	9	0	7	0	2
HR	PP	BO	7	0	5	0	1
RC*	PP	BO	9	2	3	2	2
OR*	PP	BO	8	2	2	0	3
CB	BO	PP	10	4	3	2	0
TR	BO	PP	6	0	3	2	0
AP*	BO	PP	10	3	2	1	1
VR*	BO	PP	9	1	6	2	0
Mean number of songs learned			8.50	1.50	3.88	1.12	1.12
Mean proportion of songs learned (identified songs only)†				0.19	0.51	0.15	0.15

*The subject and the interactive tutor were separated by an opaque barrier (i.e. the subject could hear but not see the interactive tutor).
†Of the 68 songs learned, seven were not identified to tutor.

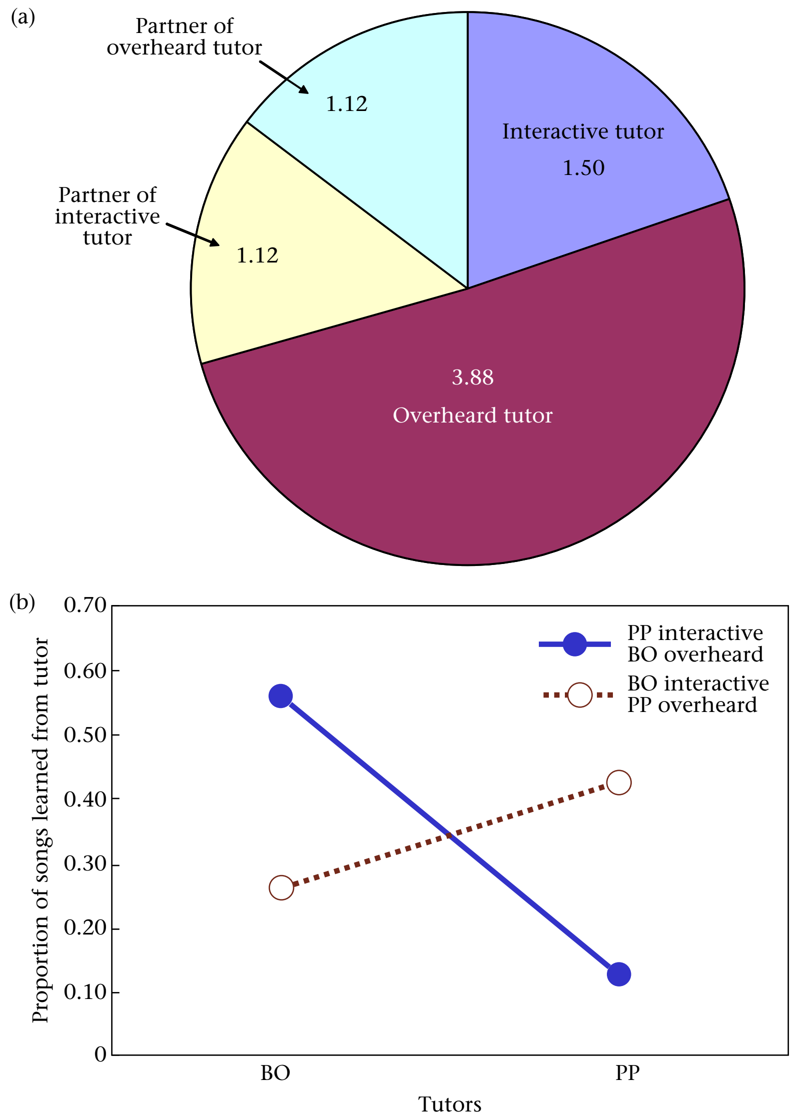

Figure 3. (a) Proportion of songs learned from all four tutors in their particular roles (Phase 2 interactive, Phase 2 overheard, Phase 1 partner of Phase 2 tutor). The pie diagram is appropriate because it shows that a bird's repertoire size is finite (8–9 songs in song sparrows) and that it selects some songs at the cost of other songs. (b) Relative effectiveness of Phase 2 tutors BO and PP in their two roles of interactive tutor and overheard tutor.

interacting with another young bird. Perhaps counterintuitively, we found that subjects learned more songs from the overheard tutor than from the interactive tutor. Our conclusion that overhearing was more potent than direct interaction in the present study requires three important caveats. First, this result reflects the particular conditions of this experiment and should not be casually extrapolated to field conditions. In particular, the 'up-close and personal' nature of the tutor vis-à-vis the subject may have been intimidating and/or may have convinced the subject that he could not invade this bird's territory, and thus, he directed his attention to the overheard, 'more distant' songs. Second, because we pitted the two learning contexts against one another, we can only say that overhearing was more critical to learning than direct interaction in these conditions, and not that direct interaction was unimportant or inhibitory. That the interactive tutor was not inhibitory is indicated by the finding that birds retained more songs for their final repertoire from the late interactive tutor than from the early-only noninteractive tutors (Fig. 3a). Finally, the results of this experiment will need to be replicated in a variety of different contexts, including, ideally, the field, and in a number of different species. It is possible that song learning may involve a mix of eavesdropping on interactions and direct interactions, and it will take many more studies to work out the relative roles and weightings of these two processes in song learning.

Our results may help to resolve a major controversy in the field of bird song learning concerning the role of social factors (Nelson 1997). The controversy grew out of the conflicting results of two different experimental paradigms and associated implicit assumptions about the role of social factors. In the classic 'tape tutor' paradigm, the method from which we have learned most of what we know about song learning, tape-recorded song is played to the young bird in his isolation chamber, thereby providing experimental control at the cost of social context (Marler 1970b). In the 'live tutor' paradigm, a live bird is the song tutor, thereby sacrificing experimental control in an effort to gain greater ecological validity. When pitted against one another, live tutors have generally been more effective than tape tutors (Casey & Baker 1993). Moreover, the rules of song learning may change when tape recorders are replaced with live tutors (Baptista & Petrinovich 1984; Catchpole & Slater 1995; Beecher & Brenowitz 2005), although this conclusion is itself controversial (Nelson 1998). Furthermore, the implicit assumptions generated by the two paradigms are different as well: the tape tutor paradigm implies that song learning is essentially a process of overhearing or eavesdropping on singing adults, whereas the live tutor paradigm implies that song learning is essentially a process of direct song tutoring of the young bird by an older bird. The latter assumption arises from the typical design of the live tutor experiment, in which a single adult male tutor is usually placed close to the young bird, like the interactive tutor in our experiment. The results of the present study confirm aspects of both of these seemingly contradictory assumptions: more song learning occurred by eavesdropping than by direct interaction when the two potential routes were pitted against one another, but nevertheless the learning that occurred via eavesdropping depended on its interactive context. Thus, social interaction is indeed critical for song learning, but it is the overheard interaction, not the one in which the bird directly participates, that is key.

It could be argued that social interaction per se was not critical to the effectiveness of the overheard tutor in the present experiment, that the overheard tutor might have been just as effective without the overheard yoked subject (or any other singing interactant). This argument would have to also assume that at the same time the interactive tutor was somewhat inhibitory. Then, the greater effectiveness of the overheard tutor could be attributed purely to a late but noninhibitory influence. We would question this interpretation for three reasons. First, as noted above, subjects learned or retained more songs from the interactive tutor than from the early-only tutors. Second, all previous experiments that have compared a solo tape or computer tutor with a live interactive tutor have found the latter to be more effective. Third, several previous live tutor experiments have suggested that aggressive interactions between older males and younger males can be associated with increased song learning in indigo buntings, *Passerina cyanea*, (Payne 1981) and in zebra finches, *Taeniopygia guttata* (Clayton 1987; Jones & Slater 1996).

What is it about the overheard interaction that makes it more effective than direct interaction as a stimulus for song learning? The recent studies of eavesdropping on song in other contexts have suggested the eavesdropper detects and subsequently exploits social asymmetries. In our experiment, however, the young bird had the same lower-status relationship to his interactive tutor as the yoked subject had to his tutor, so why should the overheard tutor have been more worthy of copying than the bird's own interactive tutor? We suggest instead that overheard interactions may be more effective than direct interactions because they are less threatening. That the direct tutoring environment may have been too intense for the young birds in our experiment is suggested by the slightly better interactive tutoring observed when there was a blind between the tutor and the young bird. The general problem with direct song tutoring is that, for most songbirds, replying with the same or similar song type, 'song matching', is a threat (Burt et al. 2001; Beecher & Brenowitz 2005; Beecher & Campbell 2005). Thus, if the young bird in the early or 'plastic' song stage sings a version of one of his interactive tutor's song types and his tutor then replies with his version of the song type, this interaction may suppress rather than promote song learning. Moreover, in contrast to the human vocal learning situation, the songbird tutor may not be motivated to teach the young bird, and in this sense 'tutor' is a misnomer, because the two have conflicting interests (i.e. the student may be perceived as a potential usurper of the tutor's territory and mate).

We plan to test possible hypotheses for the effectiveness of eavesdropping in song learning in future experiments. In our most recent experiments we are using a 'virtual tutor' to better manipulate the key variables. The virtual tutor is a computer program that can present digitized songs to the subject in ways that simulate realistic singing interactions. The program can simulate singing interaction between two birds on which the subject eavesdrops, or it can directly interact with the young bird, replying to the subject's songs according to appropriate rules (e.g. it can attempt to match the young bird's songs; Beecher & Burt 2004). In addition, we have recently begun radiotracking studies of young song sparrows in the field and hope to compare the relative importance of direct and indirect social interactions in song learning under natural circumstances.

In conclusion, our finding that young sparrows learned more songs from tutors that they overheard singing to others than they did from tutors with whom they directly interacted suggests the hypothesis that young birds may normally form their song repertoire more by eavesdropping on older birds than by direct 'tutoring' interactions with them. Despite the basic differences between songbird and human vocal learning that we have noted, our results also suggest an interesting direction for research on human language learning. Most studies of language learning by infants have focused on infant–parent interactions (Goldstein et al. 2003), and as one language researcher recently noted, 'there appears to be an implicit assumption that children learn language mainly (if not solely) from speech directed at them' (Akhtar 2005, page 207). But perhaps infants may learn language in part by eavesdropping on verbal interactions between other (usually older) individuals. Such a process would be consistent with the finding that language comprehension in infants typically advances well ahead of language production.

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