

RESEARCH PAPERS

Assessing the Importance of Social Factors in Bird Song Learning: A Test Using Computer-Simulated Tutors

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Abstract

We used a mixed live/synthetic tutoring design to investigate whether the social factors of eavesdropping on adult singing interactions and/or direct interaction with a tutor would influence song learning in song sparrows (*Melospiza melodia*). Males were brought into the laboratory at 4–5 d-old, hand-raised and then tutored by two pairs of adult song sparrows in June and July. From January through March of the next year, subjects received tutoring from computer simulations of two of the original live tutors. The first, non-interactive, model simulated one of the earlier tutors singing 'naturalistic' bouts of song with no interaction with the subject. The second, interactive, model simulated a different early tutor that behaved similarly to the non-interactive model, but synchronized its singing with the subject, and tried to match the subject's song. Subjects learned relatively more from their interactive late tutor and his early partner, and showed no tendency to learn more from their late than their early-only tutors. These results support the eavesdropping hypothesis, and also suggest that direct interaction with the tutor is a relevant social factor.

Introduction

Passerine song learning has become a major model system for the study of vocal learning, and many parallels with human language learning have been noted (Marler 1970; Brainard & Doupe 2002). One parallel that has been appreciated only recently is the key role of social factors in vocal development (Catchpole & Slater 1995; West et al. 1996; Snowdon & Hausberger 1997; Goldstein et al. 2003; Beecher & Burt 2004). The importance of social factors in bird song learning first became apparent with the discovery that birds learn more readily from singing adult birds (live tutors) than from tape-recorded song (tape tutors) (Baptista & Petrinovich 1984). The greater potency of live tutors compared with tape tutors suggests a key role for social factors in song learning, but to date much work remains to be carried out in analyzing these presumptive social factors (Nelson 1997).

The major effort to integrate social variables into song learning is a model of song learning proposed by Nelson & Marler (1994). They focus on the selective nature of song learning, on the fact that the young bird hears and memorizes many more songs during his song-learning period than he will keep for his final song repertoire. This selective process appears to operate in many species regardless of whether the species-typical repertoire size is 1, 10 or 100 song types (Marler & Peters 1982). Therefore, the bird must 'decide' which particular songs he will retain for his final repertoire. Nelson and Marler propose 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 the songs of 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 he will retain for his final repertoire. Nelson and Marler describe this later

phase as a 'selective attrition' phase because the learning consists of the bird pruning his repertoire of memorized songs, keeping some, while dropping some others. They also describe it as a phase of 'action-based' learning, in which the learning is shaped by counter-singing interactions the young bird has with his new territorial neighbors. Specifically, they suggest that the young bird attempts to match the songs of his new neighbors (matched counter-singing) and eventually pares his song repertoire down to those songs that are in fact the best matches to his neighbors' songs (Nelson 1992; Nelson & Marler 1994).

The Nelson–Marler theory is consistent with our observations on our study population of song sparrows (*Melospiza melodia*) in Washington state, USA. In this non-migratory population, the young bird typically encounters his song tutors both in the natal summer and in the following spring when he attempts to set up his breeding territory. We have found that a young song sparrow is more likely to keep songs for his final repertoire from adults who survive the winter and become the young bird's territorial neighbors in his first spring (Nordby et al. 1999). Moreover, comparison of the young birds' early (January or February) and final or 'crystallized' (April) song repertoires, reveals that they tend to keep songs that best match their spring neighbors while dropping more dissimilar ones (Nordby et al. in press). One clear prediction of this aspect of the Nelson–Marler theory, which we will call the matching hypothesis, is that a bird's crystallized song repertoire should resemble more closely those of the birds he interacts with than those of birds he does not interact with in the late phase of song learning.

One problem with the Nelson–Marler model is that it does not seem to account for those populations in which neighbors do not share songs with their close neighbors such as eastern song sparrows, chaffinches and common nightingales (Hultsch & Todt 1981; Hughes et al. 1998; Lachlan & Slater 2003; Nordby et al. in press) and thus cannot engage in matched counter-singing, i.e. cannot reply to the other bird's song with the same song type. Moreover, even in populations such as our study population in which neighbors typically share songs, birds only engage in matched counter-singing with their neighbors under certain limited circumstances; most of the time they avoid it (Beecher et al. 1996, 2000; Burt et al. 2001).

In this paper, we therefore consider and test an alternative hypothesis concerning the possible role of social interaction in song learning. According to

the eavesdropping hypothesis, the young bird's choice of songs to memorize and ultimately select for his repertoire is influenced by information derived from observing countersinging interactions. The young bird attends to both sides of the interaction and extracts two unique types of information that he could not extract from solo singing of these same birds. First, he can detect asymmetries in the interactions that provide clues as to the dominance relationship between the two birds (Beecher & Burt 2004). A number of recent studies have shown that adult songbirds eavesdrop on singing interactions of neighborhood males and subsequently make decisions about whom to challenge or with whom to mate on the basis of information they have extracted concerning the dominance relationship of the singing males (Otter et al. 1999; Peake et al. 2001; Mennill et al. 2002; Naguib et al. 2004). Young males might use the same kind of information to make tutor- and song-selection decisions in the song-learning process, preferentially learning the songs of dominant birds. Second, in species with song repertoires, the young bird, by listening to interactions, can learn the rules concerning the appropriate reply songs to particular songs. For example, suppose that during this early learning phase, the young bird eavesdrops on interactions between adults 1 and 2 and learns that when adult 1 sings song X, adult 2 usually sings song Y. If the young bird stores this information and later attempts to settle next to adult 1, he potentially can retain either song X which he memorized from adult 1 or song Y of adult 2 which he memorized as an appropriate reply to song X. The bird could retain both of course, but because song learning is selective, and the bird must eliminate many memorized songs in getting down to the species typical repertoire size, the interesting decision occurs when he keeps just one or the other. The central prediction of the eavesdropping hypothesis – regardless of whether dominance relationships or song reply rules are the key factor – is that a young bird interacting with an adult may keep for his final repertoire not just that individual's songs but songs he has heard other birds singing to that individual as well.

Social interaction hypotheses for song learning have rarely been experimentally tested, primarily because neither of the two current tutoring methods used for studying song learning, live tutors and tape (or computer) tutors, are ideal for testing social variables. Live tutors provide the appropriate social stimulus, but at the expense of experimental control, while predetermined tape (or computer) playback

provides experimental control but at the expense of social context. To address this problem, we have developed the 'virtual tutor' method, a computer program that simulates a live, interactive tutor. Using the virtual tutor software, we can present an acoustic approximation of a live tutor which is more realistic than static tape or computer playback, while allowing us to control and manipulate any aspect of the tutor's behavior. Most importantly, with the virtual tutor we could present and manipulate a social stimulus not possible with simple playback: 'live' tutor–subject singing interactions.

For this experiment, we used a combination of live and virtual tutors to explicitly test the eavesdropping hypothesis. In their first spring/summer, hand-raised song sparrows were alternately exposed to two pairs of live song sparrows who shared no song types (early tutoring phase). Subjects were isolated throughout the fall, and then presented with two virtual tutors in their first winter, each simulating the singing of a different early live tutor (late tutoring phase). One of the virtual tutors did not interact with the subject, while the other virtual tutor interacted with and tried to match the subject's singing. The eavesdropping hypothesis predicts that subjects should retain songs from either one or both of the interactive late tutor and the interactive late tutor's early partner. The matching hypothesis predicts that subjects should retain the most songs from the interactive late tutor, followed by the non-interactive late tutor, and the least from tutors heard only in the early phase.

Materials and Methods

Subjects

Seven nestling male song sparrows were collected at Discovery Park, near Seattle, Washington (approx. 47°39'40" latitude, 122°24'58" longitude) at approx. 3–4 d post-hatching (hatch-dates ranged from May 2 to 27, 2004). The birds were hand-raised to independence at approx. 30 d 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.

Song Tutoring Phase 1

In the first phase of tutoring, young song sparrows were rotated between two pairs of live tutors on alternate days. We used four tutors that shared no songs so that we could unambiguously trace any

song in the young bird's final crystallized repertoire to a particular tutor. We used live birds as song tutors for this phase to increase the likelihood that the 'virtual' tutors of the late learning phase, which would be heard but not seen, would be perceived as the original live tutors.

Phase 1 song tutoring began on post-hatch day 20 for each subject, and ended on day 50 (first subject started on May 22, and last subject ended on Jul. 15). Tutoring occurred for approx. 4 h per day on days 20–30 and for the full daylight hours thereafter. Subjects were taken to one of two live tutoring rooms, each of which housed two adult song sparrows in individual cages, separated by approx. 2 m of open space, and approx. 2 m equidistant from the subjects. Tutors BO and BG were housed in the North room, tutors PP and IC in the South room. Because each pair of tutors was permanently housed in one of the rooms, they became territorial about their cages and sang frequently. The subject birds were rotated between the two rooms every fourth day.

Each subject was individually housed in a small cage (dimensions 40 × 23 × 26 cm) within an acoustic isolation chamber. Isolation chambers were installed onto racks in each tutor room so that multiple subjects at a time could be housed in a tutor room. During tutoring periods, chamber doors were opened so that subjects could see and hear the tutors but could not see each other. Because the young birds had not yet begun to sing at this age, we exposed them in groups; the only songs they heard were from the two adult tutors in the room. Young males began singing subsong after approximately day 50, so from the end of phase 1 (which ranged from Jun. 20 to Jul. 15 for different subjects) until the beginning of phase 2, subjects were kept in closed chambers so that they heard no other singing.

Song Tutoring Phase 2

All subjects received phase 2 of song tutoring from January 5 through March 23, 2005. The tutors in phase 2 were 'virtual' tutors; each of these mimicked the singing of one of the early live tutors, i.e. behaved acoustically like a song sparrow and 'sang' that tutor's song types. We presented two virtual tutors to each subject. On one day a virtual tutor sang and interacted with the subject (interactive virtual tutor), and on another day a different virtual tutor sang but did not interact with the subject (non-interactive virtual tutor). The two phase 2

virtual tutor models were each programmed to simulate one of the early live tutors (BO from the North tutor room and PP from the South tutor room). For four of the subjects, virtual PP was always the interactive tutor, and virtual BO was the non-interactive tutor. For the other three subjects, virtual BO was always the interactive tutor and virtual PP was the non-interactive tutor.

Subjects received virtual tutoring in an isolation chamber every other day, and tutoring alternated between virtual BO and virtual PP, so that each subject received tutoring from a specific virtual tutor every 4 d. On their tutoring days, subjects were moved at mid-day from their home isolation chamber to the tutoring chamber. Although each tutoring session was unique because of intentionally stochastic aspects of the virtual tutor programs, the basic form of the sessions was the same: the assigned virtual tutor would sing bouts of song, punctuated by inter-bout pauses. The virtual tutors were programmed to sing a total of 300 songs/AM or PM session and then stop. Thus, regardless of the minute details of each session, every subject received 600 playback songs/tutoring day (300 in each session) in roughly the same manner. Virtual tutor songs were calibrated to play from a speaker in the chamber at approx. 70 dB SPL at 1 m distance. All subject singing was recorded, both during tutoring sessions, and while not being tutored.

The Virtual Tutor Design

The virtual tutor software was written by JMB in the MATLAB programming environment (release 14; The Mathworks, Natick, MA, USA). The non-interactive virtual tutor was given a behavioral repertoire and parameters that caused it to sing like a live song sparrow in 'free-singing' mode (i.e. when not interacting with another bird), with each song type repeated several times before it switched to a new type (e.g. AAAABBBBCCCC). We refer to the entire sequence of songs in a bout (including one or more song type switches) as a 'song bout', and the briefer sequences of songs of one type within each song bout as a 'type bout'. Each song bout duration was determined randomly at its start with a range of 1–15 min. Type bouts ranged randomly from 5 to 15 songs. Song renditions within a type bout were selected at random from the 10 different renditions of each type available to the virtual tutor. Inter-bout pauses ranged randomly from 5 to 20 min. Pauses between individual songs were also randomly determined with a range of 5–20 s.

Song types for type bouts were chosen by the virtual tutor using a weighted random function that favored types not recently sung, and prohibited reselection of the current and immediately prior types. The song type selection function was designed to mimic a '7±2 rule' for short-term memory of recent songs sung (sensu Miller 1994), and to avoid repeating recent song types, a pattern observed in free-singing song sparrows (Nice 1943). A simplified flowchart of the non-interactive virtual tutor's behavior is shown in the white boxes of Fig. 1.

The interactive virtual tutor had the same parameters and behaved similarly to the non-interactive virtual tutor, except that it additionally received input from an acoustic feedback system that monitored the subject's vocalizations, allowing it to respond interactively to the subject's vocalizations. The first stage of the feedback system consisted of a sound detector program that monitored sound from a microphone in the subject's isolation chamber. The sound detector was designed to be sensitive enough to detect quiet singing, but reject cage noises and non-song vocalizations with greater than 90% accuracy. The detector also deactivated during tutor song playback so that tutor songs were not detected as subject songs. When a subject song was detected, it was then passed to a classifier that attempted to determine whether the song was similar to one of the tutor's songs.

The song classifier program used a spectrograph-cross-correlation algorithm to compare the detected subject's song against examples from the tutor's repertoire. The classifier returned a score indicating the similarity of the detected subject song to each of the tutor examples. If the score of the most similar tutor example type was above a fixed threshold, then the virtual tutor was informed that the subject had sung that type, otherwise it was informed that the subject had sung an unknown type. The virtual tutor then acted upon this information, based on its behavior rules and the current context (see below). The classifier parameters and similarity threshold were calibrated a priori using a test set of different song sparrow songs to maximally agree with our own judgments of similarity, and the classifier output was periodically assessed during tutoring to verify that it was working reasonably.

The grayed-in boxes in the Fig. 1 flowchart show the parts of the interactive virtual tutor's acoustic feedback system, which were lacking in the non-interactive virtual tutor; both virtual tutor models shared the same program flow shown in the white boxes. The interactive virtual tutor responded to

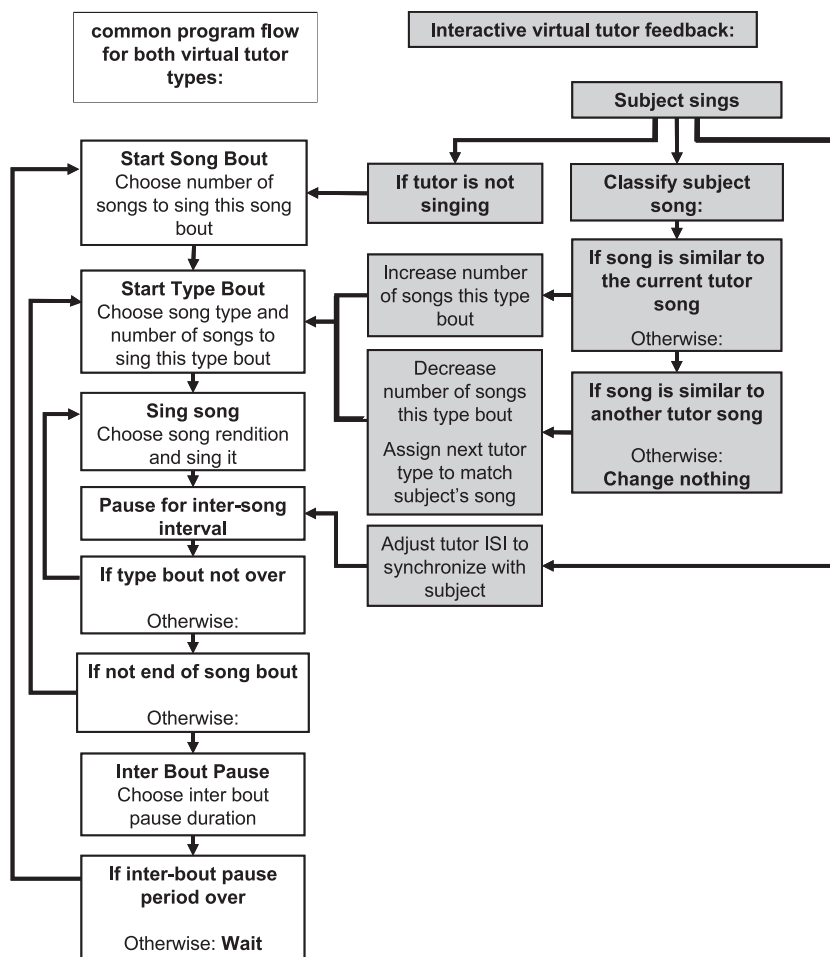


Fig. 1: Virtual tutor program behavior flow-chart. White background boxes indicate program flow common to both the interactive and non-interactive virtual tutors. Shaded boxes depict the interactive feedback loop found only in the interactive virtual tutor.

input from the feedback system in three ways. First, a song from the subject induced the virtual tutor to begin a song bout, if it was not already singing. Second, the virtual tutor would reset its internal song timer after a subject song so that its next song would occur 2 to 4 s later, which synchronized the virtual tutor’s playback to the subject’s singing. Third, if the subject’s song was deemed similar to the tutor’s most recently sung type, then the virtual tutor would prolong its bout of that type. This behavior simulated a stay-on-type response to being type matched, which we have observed in the field (Burt et al. 2001). If the subject’s song was similar to another of the virtual tutor’s songs, then the virtual tutor would greatly reduce the current type bout duration and assign the next type switch to be the virtual tutor’s similar type (i.e. the virtual tutor would switch to ‘match’ the subject). If the classifier could not identify the subject’s song, then there were no changes to the virtual tutor’s type bout parameters.

Song Analysis

On Mar. 23, we stopped all tutoring, but continued to record and monitor subject singing. By Mar. 28, all of the subjects had crystallized to adult song sufficiently well that we could identify their final repertoires (this date roughly coincides with dates of crystallization in the field). Using the SYRINXPC sound analysis software (John Burt, <http://www.syrinxpc.com>), we built a comprehensive repertoire of each subject’s song types and their variations by scanning the most recent 3 d of his singing (or 1000 songs minimum). Then, we visually compared the spectrographs of each subject’s repertoire against the comprehensive repertoires of the four live tutors, and identified which tutor song type(s) were the likely model(s) for each subject song type. Comparisons were made by three trained observers (MDB, JMB, SEC) using methods described previously (Nordby et al. 2000).

The majority of song types the subjects learned shared more than three-fourth of their elements (notes, trills, buzzes, etc.) with one tutor type (39/58 types or 67.2%), which we classified as a whole copy. The remaining subject types were hybrids of two different tutor types (11/58 or 19.0%), or three or more tutor types (8/58 or 13.8%). For subject types that were hybrids of two or more tutor types, we applied a winner-take-all scoring rule, where the tutor whose song elements comprised the majority of a subject's type was given full credit. Although a few subject types contained some elements that could not be attributed to a particular tutor, there were no completely unique song types, and thus by the winner-take-all scoring rule all subject types could be assigned to a particular tutor type.

Prediction and Statistical Analysis

The *matching hypothesis* predicts that subjects should retain more songs from the two late tutors, and in particular the interactive (matching) tutor, than from the two early-only tutors. The *eavesdropping hypothesis* predicts that subjects should retain songs from one or both of the interactive tutor and the interactive tutor's early partner. Given the design of the experiment, however, the hypothesis does not yield a prediction of from which of the two (interactive tutor or the early partner) the subject should learn more. First, if dominance is important, then because we neither evaluated nor manipulated the dominance relationship of the tutor pairs, we cannot predict from which of the two tutors the birds might learn more songs. Second, if dominance is not important and only song reply rules are, then we can only predict that the bird should learn some songs from the early partner of the interactive tutor. But in either case we can predict that the bird should learn more from the interactive tutor and his partner combined than from the non-interactive tutor and his early partner combined. Thus when the interactive tutor is virtual BO, we predict that the bird will learn/retain more songs from tutors BO and BG, and when the interactive tutor is virtual PP, the subject should learn/retain more songs from tutors PP and IC. To evaluate this prediction, we used a repeated-measures analysis of variance, with the interactive tutor (BO vs. PP) as the between-subjects variable, and the number of songs learned from the tutor pairs (BO + BG vs. PP + IC) as the within-subjects variable (SPSS v. 14; SPSS Inc., Chicago, IL, USA).

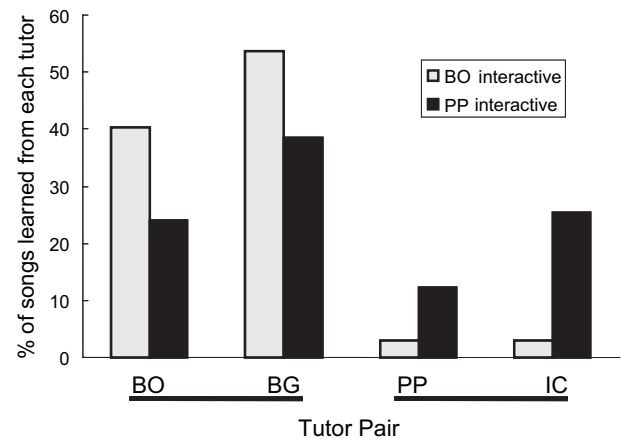


Fig. 2: Overall percentage of songs learned from each of the four tutors. Although birds learned more songs from BO or BG than they did from PP and IC, they learned (or retained) more from a bird when it was the interactive virtual tutor (BO light, PP dark) than when it was the non-interactive virtual tutor, and they retained more from the partner of the interactive virtual tutor than from the partner of the non-interactive virtual tutor.

Results

There were three major findings (Fig. 2). First, subjects showed a strong bias in favor of learning from the BO–BG tutor pair (44/58 or 76% of all songs, $F = 15.2$, $df = 1$, $p = 0.011$), regardless of who their late interactive tutor was (BO or PP). Second, the direction of the results was opposite that predicted by the matching hypothesis. Subjects learned fewer songs from the late member of a tutor pair (BO or PP) than from the early member (BG or IC), regardless of whether the late member was interactive or non-interactive: 46% (12/26) from BO vs. BG when BO was interactive and 39% (7/18) when BO was non-interactive, 33% (4/12) from PP vs. IC when PP was interactive and 50% (1/2) when PP was non-interactive. This surprising result is in the opposite direction from that predicted by the matching hypothesis, according to which more than 50% of learned songs should have been from the late tutors, especially the late interactive tutor. Third, as predicted by the eavesdropping hypothesis, subjects learned more songs from an early tutor pair when the late tutor of the pair was the interactive tutor than when he was the non-interactive tutor. This effect is seen as an interaction between the number of songs learned from each of the two tutor pairs and the role (interactive or not) of the late member of the tutor pair ($F = 7.01$, $df = 1$, $p = 0.045$); although birds learned more from BO and BG than

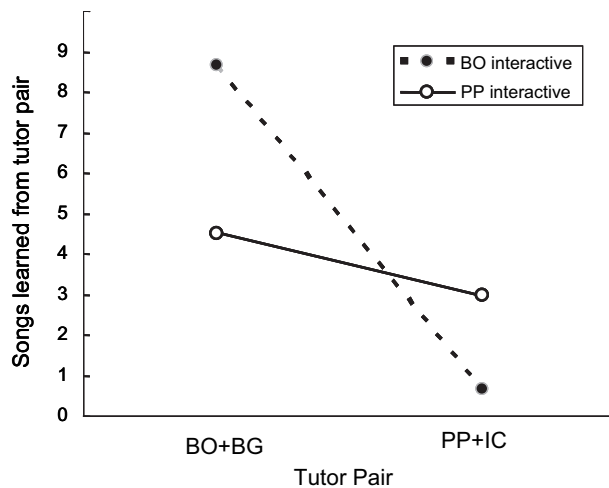


Fig. 3: Number of songs learned from the two tutor pairs (BO and BG combined, PP and IC combined). Although birds learned more in general from BO and BG than from PP and IC, this factor interacted with whether or not the late member of a pair was the interactive tutor (BO dotted line, PP solid line) or non-interactive tutor.

PP and IC in general (result 1), they learned relatively more from BO and BG when BO was the late interactive tutor than when PP was, and they learned relatively less from them when PP was the late interactive tutor than when BO was (Fig. 3).

Discussion

In this experiment, we exposed young song sparrows to the songs of two pairs of adult tutors in the early phase of song learning and then in the late phase of song learning, re-exposed them to the songs of two of those tutors, one from each pair. The early exposure was to songs of the actual birds, the late exposure to songs generated by computer simulations (virtual tutors) of these birds. One of the late tutors interacted with the subject, while the other sang without regard to the subject's singing. Contrary to the matching hypothesis, birds actually retained more songs from early tutors than from late tutors (34 vs. 24, respectively). As predicted by the eavesdropping hypothesis, however, the late interactive tutoring did have an effect: subjects were more likely to learn (retain) the songs of the late tutor *and* his early partner if the late tutor was the interactive tutor rather than the non-interactive tutor. This result points to the importance in song learning of both (1) late interaction with a particular adult, and also (2) eavesdropping on interactions between that adult and another bird. The eavesdropping occurred early in this experiment, in the first phase of

learning, but it is reasonable to suppose that the same effect might be obtained with late eavesdropping as well.

Although the results of this experiment are not consistent with the matching hypothesis, we derived from Nelson–Marler theory of 'action-based' learning, they are still consistent with the theory's general idea that late social interactions are crucial in shaping the bird's final song repertoire. The results simply suggest an interesting twist on this theory: when the young bird finds himself interacting with a particular adult male, call him A, the young bird may choose to select for his final repertoire not only songs of bird A, but also songs of other adults he has overheard interacting with A. The next question is what makes this latter class of songs attractive? Is it that the young bird has heard the songs of bird B as appropriate or effective reply songs to bird A, or is it that he has detected that bird B is dominant to bird A? Clearly these are not mutually exclusive possibilities.

The finding in the present study that birds actually retained more songs from the early 'partner' of the late tutor than from the late tutor himself is initially surprising given the finding of our previous field and laboratory studies that song sparrows learn more from tutors present early and late than from those present only early (Nordby et al. 1999, 2001; Beecher; unpubl. data). On the other hand, it may help explain why birds in the field often retain for their final repertoire some songs of adults who did not survive the winter (i.e. early-only tutors). From the perspective of the eavesdropping hypothesis, this paradoxical effect is actually a late learning effect, with the young bird retaining from his earlier-memorized songs those that he has heard as appropriate or effective replies to the bird with whom he now finds himself interacting.

It is possible that birds learned more from BG than BO and more from IC than PP because BG was perceived as dominant to BO and IC as dominant to PP. In future experiments, we plan to manipulate the 'social dominance' of the tutors using virtual rather than live tutors. Although we do not yet completely understand if and how dominance is communicated by song in this species, we do know that more aggressive birds show a suite of distinctive traits in singing interactions (Kroodsma 1979; Naguib 1999; Burt et al. 2001; Bower 2005; Hyman & Hughes 2006). These include replying to the opponent, type-matching if possible, staying on the same song type if type-matched, overlapping the opponent's song, and being the last to sing in

the interaction. We are presently carrying out field experiments with the goal of correlating singing style with social dominance (see also Hyman & Hughes 2006). Although in nature birds surely use multiple sources of information to evaluate the dominance status of territorial adults, we suspect that the pattern of counter-singing between these birds is one important component of this information. If this is the case, we can incorporate these singing rules into our virtual tutor. We can then let the young bird eavesdrop on two virtual tutors that have a defined dominance relationship and see if the young bird shows a learning preference for the songs of the more dominant tutor.

For methodological reasons, the tutoring stimuli used in this experiment deviated in two important ways from what young song sparrows in our wild population would normally experience. First, the tutors (live and virtual) shared no song types. In our Seattle population, the majority of neighbors (although not all) share some song types and thus young birds might be able to assess tutors based on the song signals that sharing neighbors can use, whereas the experimental subjects could not (subjects could have assessed early live tutors by their other song signals). A second major deviation from the normal song experience in the wild is that subjects did not hear adult–adult interactions in the later stage of song learning. In future experiments, the importance of tutor song sharing and late eavesdropping will be explicitly tested using virtual tutors.

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