ANIMAL BEHAVIOUR, 2007, 73, 929–935
doi:10.1016/j.anbehav.2006.10.013

ARTICLES

Bird song learning in an eavesdropping context

MICHAEL D. BEECHER*†, JOHN M. BURT*, ADRIAN L. O'LOGHLEN*, CHRISTOPHER N. TEMPLETON† & S. ELIZABETH CAMPBELL*

*Department of Psychology, University of Washington
†Department of Biology, University of Washington

(Received 28 July 2006; initial acceptance 4 September 2006; final acceptance 17 October 2006; published online 4 May 2007; MS. number: A10523R)

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

Correspondence: M. D. Beecher, Department of Psychology, University of Washington, Seattle, WA 98195, U.S.A. (email: beecher@u.washington.edu).

0003–3472/07/$30.00/0

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.

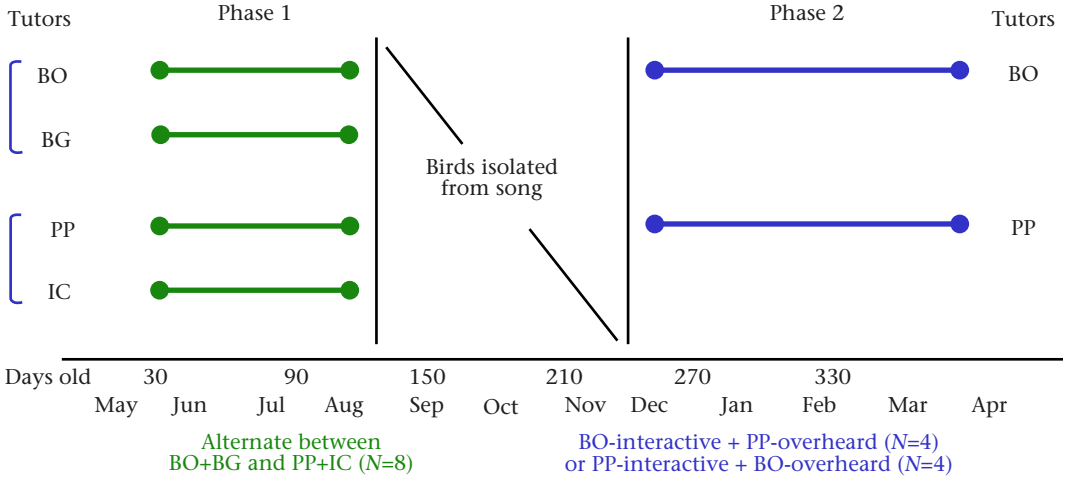

Figure 1. In Phase 1, young song sparrows as a group were exposed to two pairs of tutors; the group was moved from the room housing tutors BO and BG to the room housing tutors PP and IC every fourth day. In Phase 2, individual subjects interacted with one of the four tutors from Phase 1 and overheard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