Juvenile sparrows preferentially eavesdrop on adult song interactions

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Recent research has demonstrated that bird song learning is influenced by social factors, but so far has been unable to isolate the particular social variables central to the learning process. Here we test the hypothesis that eavesdropping on singing interactions of adults is a key social event in song learning by birds. In a field experiment, we compared the response of juvenile male song sparrows (*Melospiza melodia*) to simulated adult counter-singing versus simulated solo singing. We used radio telemetry to follow the movements of each focal bird and assess his response to each playback trial. Juveniles approached the playback speakers when exposed to simulated interactive singing of two song sparrows, but not when exposed to simulated solo singing of a single song sparrow, which in fact they treated similar to heterospecific singing. Although the young birds approached simulated counter-singing, neither did they approach closely, nor did they vocalize themselves, suggesting that the primary function of approach was to permit eavesdropping on these singing interactions. These results indicate that during the prime song-learning phase, juvenile song sparrows are attracted to singing interactions between adults but not to singing by a single bird and suggest that singing interactions may be particularly powerful song-tutoring events.

Keywords: vocal learning; radio telemetry; song learning; *Melospiza melodia*; eavesdropping; song sparrow

1. INTRODUCTION

Many species use elaborate acoustic signals, or songs, to communicate with rivals and potential mates. In some species, these important vocalizations must be learned, with most of the learning taking place early in life. Vocal learning is found in a diverse group of animals, including cetaceans, pinnipeds, bats, elephants, primates (only in humans) and birds (Jarvis 2004). Approximately half of all bird species learn to sing, with parrots, hummingbirds and Oscine songbirds each having evolved vocal learning (Catchpole & Slater 2008). Of all these animals, songbirds have been best studied and have become a major model system, in part because of the numerous features of their song learning programme that parallel human language learning (Brainard & Doupe 2002). These similarities include an early sensitive period, an innate filtering mechanism for selecting conspecific vocalizations, a babbling developmental phase, and the importance of social variables in vocal learning.

Despite the enormous attention that has been paid to song learning in songbirds, very little is known about the behaviour of young birds in nature during the song learning period. Field observations could shed light on how song learning occurs, in particular, on the mechanisms by which social factors affect learning. The importance of social factors in song learning has only recently been appreciated. The pioneering song learning studies of Thorpe (1958) and Marler (1970) used audio recordings in their tutoring regime to remove social

features and achieve rigorous experimental control. Many subsequent studies (recently reviewed by Beecher & Brenowitz 2005; Catchpole & Slater 2008) have used and extended the 'tape tutor design' and from these studies we have learned a great deal about the song learning programme, including many of the features described above. The importance of social factors was initially discovered when live birds were used for tutors in place of tape recordings (e.g. Baptista & Petrinovich 1984; Chaiken *et al.* 1993). In these studies, juveniles are typically paired with a live tutor at close quarters during the song learning phase. Juvenile birds tend to learn more readily from live tutors than tape recordings, and these studies showed that many of the previously established learning rules could be significantly altered with the addition of the social component.

Although the importance of social factors in the song learning process was revealed by substituting live tutors for tape tutors, it is still unclear exactly how social variables facilitate learning. The design of tape tutor studies implies that song learning is primarily a process of simple eavesdropping (a.k.a. interceptive eavesdropping, Peake 2005) on a solo-singing adult, as the juvenile is neither able to interact with the tape tutor, nor the tutor with the juvenile. On the other hand, the design of live tutor experiments implies that song learning takes place through *direct interaction* between a juvenile and an adult song tutor, paralleling how human language learning is commonly thought to occur. However, a recent laboratory song learning study found, surprisingly, that juvenile birds learned more from tutors that they overheard singing with another bird than from tutors they

were able to interact with directly (Beecher *et al.* 2007). This study has suggested a new model, which we have called the *social eavesdropping hypothesis*. According to this view, song learning occurs through eavesdropping on the singing interactions of adults.

The importance of social eavesdropping (Peake 2005) in communication networks has received much attention recently (McGregor 2005). For example, individuals in numerous species have been shown to eavesdrop on the alarm vocalizations of conspecifics and heterospecifics (e.g. Templeton & Greene 2007; Goodale & Kotagama 2008; Magrath *et al.* 2009) in order to gain information about predators. It is hypothesized that young birds may even learn to recognize dangerous predators by listening to the mobbing vocalizations of other birds (Curio 1978). There is also recent evidence that individuals eavesdrop on the conspicuous songs of birds, both to gain information about suitable breeding sites (Doligez *et al.* 2002; Dall *et al.* 2005; Betts *et al.* 2008) and to assess characteristics of specific individuals. For example, eavesdropping on singing interactions may allow females to assess the quality of a potential mate (Otter *et al.* 1999; Mennill *et al.* 2002; Kunc *et al.* 2006) or males to assess the aggression level or dominance rank of a potential competitor (Peake *et al.* 2001; Mennill & Ratcliffe 2004). It seems plausible that juveniles might eavesdrop on singing interactions for similar purposes: dominance or aggression levels might be particularly important information for a young bird preparing to establish a territory. Eavesdropping on singing interactions may also be a good way for young birds to learn the rules of singing interactions. Because many animal signalling systems (such as song overlapping or type-matching an opponent) are rule-based, they cannot be learned simply by listening to solo singing.

We examined the social eavesdropping hypothesis using song sparrows (*Melospiza melodia*). Song sparrows are known vocal learners that have been studied extensively in the laboratory and in the field (reviewed in Beecher 2008). A young male song sparrow learns 6–13 different song types from several different neighbouring adults during his first year of life (Nordby *et al.* 1999). Song sparrows in our population copy entire songs from adult tutors and preferentially learn shared songs (other populations may use slightly different rules; Hughes *et al.* 2007). Learning songs shared with future neighbours is particularly important for song sparrows because the intrasexual communication system relies heavily on the ability of a bird to reply to his neighbours with a shared song (Stoddard *et al.* 1992; Beecher *et al.* 1996; Burt *et al.* 2001). In song sparrows, singing interactions can be quite elaborate, containing a variety of ritualized vocal and visual signals. By eavesdropping on these singing interactions, juveniles may gain an ideal opportunity to learn particular songs that are shared in a given neighbourhood as well as the singing conventions for how these songs are to be used.

Here we use a field playback experiment to test one prediction of the social eavesdropping hypothesis, namely that counter-singing interactions should be more attractive to eavesdropping juvenile birds than solo singing. Using radio telemetry, we observed the movements of juvenile male song sparrows in response to the simulated songs of one bird singing alone versus two birds singing interactively. Although not mutually exclusive with the hypotheses that song learning occurs by simple eavesdropping on solo singers, or by direct interaction with an adult singer, the social eavesdropping hypotheses makes the unique prediction that singing interactions should be the most compelling stimuli for a juvenile bird during the song-learning phase. Therefore, we predicted that our radio-tagged juveniles would show the greatest interest in the interactive singing condition, by approaching the speakers so that they could better acoustically (and perhaps visually) monitor the interaction.

2. MATERIAL AND METHODS

(a) *Study site and subjects*

We conducted all fieldwork at Discovery Park, a 3 km^2 undeveloped park in Seattle, WA, USA (47°39′ N, 122°24′ W). The song sparrow population is resident year-round and includes approximately 150 breeding pairs in our study area. As part of our long-term studies, nearly all adult and many juvenile song sparrows are individually marked with unique combinations of coloured leg bands and the songs of adult males are recorded to determine complete repertoires (6–13 song types per bird; Peters *et al.* 2000). Between 26 June and 11 July 2008, we captured juvenile male song sparrows ($n = 11$) using mist nets. All birds used in this study were independent of their parents and were one to three months old (first egg laid on 14 April 2008, modal day approx. 1 May). Each subject was fitted with a small radio transmitter (Holohil Systems Ltd: BD-2) using a backpack harness (Rappole & Tipton 1991). Each radio tag weighed 0.70 g, equivalent to less than 3 per cent of the bird's body mass (Millspaugh & Marzluff 2001), and we saw no evidence that the birds were hampered by the transmitters. In addition to weighing each bird, we also measured their wing chord before attaching a transmitter. Most song sparrows in our population can be sexed by their wing chord; males and females differentiate around 65 mm, with first-year birds having slightly shorter wings. For this study, we conservatively used only birds with wing chords at least 67 mm in length to be confident that we tagged only males (females song sparrows do not normally sing). After a bird was marked with a radio transmitter, we waited at least 2 days before conducting any playback trials. Transmitters were removed at the end of the experiment.

(b) *Playback stimuli*

Playback stimuli were selected from high-quality recordings of adult birds that had died before the current breeding season. This ensured both that subjects heard songs from the correct population-specific dialect and that none of the subjects had had any prior experience with the specific adult's songs. From these recordings, we used Syrinx (John Burt; www.syrinxpc.com) to construct playback stimuli that mimicked the natural singing behaviour of adult song sparrows. A single song (2–3 s in length) was presented every 10 s for 150 s, at which point the playback switched to a second song from the same adult for an additional 150 s. Thus, the playback stimuli lasted for 5 min and contained approximately 15 iterations each of two different song types. The playback stimuli were arranged in a two-channel, uncompressed wave file that could be controlled from a field computer using Syrinx.

We used two speakers to simulate two different birds singing for each playback trial. The playback experiment tested the response of juvenile birds to three different conditions: two song sparrows singing interactively, one song sparrow singing solo and control songs from black-capped chickadees (*Poecile atricapilus*). In the first condition ('interactive'), we used the songs of two different adult song sparrows (one per speaker) to simulate a typical counter-singing interaction. We simulated counter-singing by delaying the songs in one channel 5 s relative to the other channel so that the two speakers alternated songs during the playback but did not overlap in time. We used matching songs for each of the playback stimuli, as these are frequently used during interactive singing in western song sparrows (Stoddard *et al.* 1992; Burt *et al.* 2001). Both channels of the playback recording switched song types (to another matching type) after 150 s, as described above. To avoid pseudoreplication (Hurlbert 1984; Kroodsma *et al.* 2001), we used different exemplars for each subject ($n = 11$, two channel playback exemplars of 22 adult birds). In the second condition ('solo'), we used one channel of song sparrow song and one channel of chickadee song (one in each speaker). The 'solo' song sparrow stimuli were selected from the same stimuli used in the interactive playbacks, so that one of the playback channels (a given adult) from each interactive playback was also used for a solo playback trial (always for a different subject). In the second channel, we played 'fee-bee' songs from a black-capped chickadee, which were arranged in a similar fashion to sing opposite the song sparrow (i.e. 2–3 s of song every 10 s, delayed 5 s relative to the song sparrow playback, so that the chickadee appeared to counter sing with the song sparrow but never overlapped the song sparrow songs). Chickadees are common in our study area and their songs are frequently heard by song sparrows. Using chickadee songs from one speaker during the solo treatment allowed us to control for the overall timing and amount of acoustic stimuli (total number of songs played) between the solo and interactive treatments. For the last condition ('control'), we played the songs of two chickadees singing interactively from two speakers in the same manner.

(c) *Procedure*
Prior to the start of a trial, two observers (M.D.B. and Ç.A.) located the subject by radio telemetry (Communication Specialists R-1000 receivers with three element Yagi antennae). We conducted a 5 min pre-trial observation period to ensure that the birds were not moving erratically before the playback began. During the pre-trial period, a third observer (C.N.T.) set up and ran the playback apparatus. We positioned two playback speakers (Pignose Model No. 7-100R) 10 m apart and approximately 50 m from the subject. These speakers were attached to a Dell laptop computer running SYRINX software, via two 20 m cables. If the subject moved during the pre-trial period, we relocated the speakers so that they were once again approximately 50 m from the subject prior to initiating playback. Prior to the start of the trial, the two observers located themselves in a position to best assess the movements of the bird through triangulation (typically at right angles relative to the focal bird and speakers), without having to move during the trial. Each of these observers had a walkie-talkie which was used to relay information back to the third observer. During the trial, each observer continuously tracked the subject bird, noting the distance and direction relative to the speakers of all

movements. The direction of movement was categorized simply as towards, away from or parallel to the speakers. The latter type of movement was defined as a movement detected by the observer located in line with the bird and speakers which could not be detected by the observer who was positioned at a 90° angle to this line (the second observer could more readily determine movements towards and away from the speaker). Data were recorded onto compact flash media, using a Sennheiser ME67 microphone and Marantz PMD 660 recorder, by the third observer and saved for later analysis.

We used a repeated measures design, so that all subjects received each of the three playback treatments. The treatment order for each bird was chosen randomly and each subject received only one trial per day. Six subjects were tested on 2–5 July and five additional subjects were tested on 14–16 July 2008, for a total of 33 playback trials. After each trial, we scanned the radio frequencies of the other subjects to be sure that none were nearby and had heard unintended song playback trials (none did). If a bird did not move during a given trial, we confirmed that he was still alive by gently flushing him after the end of the trial.

(d) *Data analysis*
We measured the subject's response to each playback trial using the latency to approach the speakers, the closest approach to the speakers, and the overall distance and direction moved during the playback period, in relation to the speaker locations. If the subject did not approach the speakers during the playback trial, we assigned a latency of 300 s, corresponding to the length of the playback. Similarly, we assigned 50 m (the starting location) as the closest approach distance for subjects that moved away or parallel instead of towards the speakers. All three measures were highly correlated and thus we performed a principal components analysis (PCA) to generate a single approach score based on the three measures. The first principal component (PC) had an eigenvalue of 2.6 and explained 86.5 per cent of the variance in the data (loading coefficients are listed in figure 2), so we used only PC1 in further analyses.

To assess differences among playback treatments, we used these PCA movement scores in a repeated-measures analysis of variance (ANOVA; $n = 11$ subjects). We conducted post hoc paired *t*-tests to determine specific differences among the three treatments. In addition, we analysed the overall direction the subject moved relative to the speakers (towards, away, parallel, no movement) with a multinomial logistic regression, using both playback treatment and subject (to control for individual variation) as factors. All statistical tests were two-tailed and were calculated in JMP 7 (SAS Institute Inc, Cary, NC, USA).

3. RESULTS
We found a strong difference in the movement of juvenile male song sparrows in response to different types of song playback (repeated measures ANOVA using PCA scores: $F = 15.19$, $p < 0.0001$; figure 1). Birds moved closer to the speakers during the playback simulating two song sparrows engaged in a song interaction than to either the solo song (paired *t*-test: $t = 3.85$, $p = 0.0032$) or control chickadee song (paired *t*-test: $t = 5.79$; $p = 0.0002$) playbacks. There was no difference in the movement score between solo song and the control playback
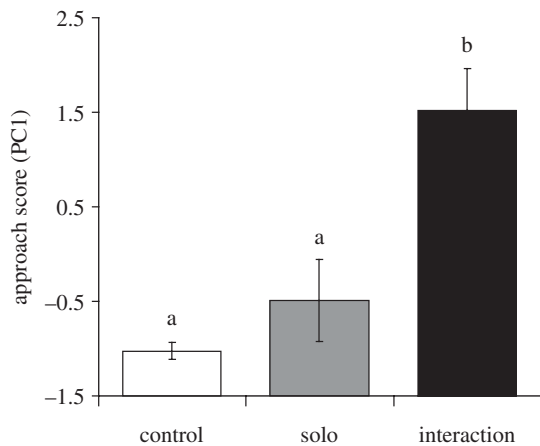
Figure 1. Juvenile male song sparrows approach playback speakers broadcasting two birds singing interactively more than they do for solo song or control playback trials ($p < 0.0001$). Approach scores are derived from PC1 from the PCA and are represented as mean $\pm$ s.e. Higher approach scores indicate a stronger response. Different letters represent statistically significant groups. Data from each individual variable that factored into the PCA are shown in figure 2.

(paired *t*-test: $t = 1.29$, $p = 0.226$). The raw movement data for each of the behavioural variables that factored into the PCA are depicted in figure 2. In addition to differences in the overall movement scores, the predominant direction juvenile birds moved during playback varied among treatments (multinomial logistic regression, treatment effect: d.f. = 6, $\chi^2 = 18.94$, $p = 0.0043$) indicating that birds responded differently to different types of simulated singing interactions. Birds tended to approach the speakers during the interactive playbacks (8 of 11 subjects) but moved away or did not move during the control and solo playbacks (with 0 of 11 approaching during the control treatments and only 3 of 11 subjects approaching the speakers during the solo trials; figure 3). Although juveniles sometimes sing in the late summer, no subjects sang sub-song or plastic song in response to any of the playback treatments.

4. DISCUSSION

There are currently three main hypotheses concerning the role of vocal interactions in songbird song learning: the 'social eavesdropping' hypothesis that juvenile birds learn to sing by eavesdropping on singing interactions between adult birds; the 'simple eavesdropping' hypothesis that they learn by just listening to a solo singing adult, and the 'direct interaction' hypothesis that they learn to sing by directly interacting (including singing) with an adult bird. The social eavesdropping hypothesis predicts that during the prime song learning period in the natal summer, juveniles should be especially attracted to singing interactions between adult birds. Although the three hypotheses are clearly not mutually exclusive, the simple eavesdropping and direct interaction hypotheses imply that juveniles will be just as attracted to the solo singing of an adult bird as they are to the interactive singing of two birds. In this experiment, we found that juveniles were more likely to move towards the speakers,

approaching closer and more quickly, during the simulated singing interactions than during either solo singing or control playback trials. Their response to solo song sparrow song was minimal and virtually identical in their response to the control playback (two chickadees singing). Although the young birds approached the simulated counter-singing song sparrows, neither did they approach too closely, nor did they vocalize themselves, consistent with the hypothesis that the primary function of approach is to permit eavesdropping on these singing interactions. Our finding, that juvenile song sparrows are attracted to the singing interactions of adult birds during the song-learning phase, is consistent with the social eavesdropping hypothesis (Beecher *et al.* 2007) and indicates that eavesdropping on singing interactions may be a central event in juvenile song learning.

There may be a number of advantages to learning song by eavesdropping on singing interactions. Beecher *et al.* (2007) suggested that one reason laboratory birds might learn better via eavesdropping is that direct interactions may be intimidating, thereby suppressing learning. For example, one obvious method of learning new vocalizations might involve a juvenile repeating what he hears an adult sing. However, in most songbirds, repeating the same song type, or 'song-matching', is considered an aggressive signal (Krebs *et al.* 1981; Burt *et al.* 2001; Vehrencamp 2001), and potentially could provoke a chase or attack by the adult 'tutor'. Although the inhibitory effect of direct interactions may still be important, the results of the present study suggest that eavesdropping on interactions may have unique benefits. The fact that juvenile song sparrows approached simulated song interactions in our study suggests that they may seek out these types of interactions as an opportunity for learning songs and how to use them.

To make the playback stimuli as natural as possible, we used natural song rates for interactive and solo singing, and therefore subjects heard twice as many song sparrow songs during the interactive treatment. This experimental design thus had realistic singing rates in both song sparrow treatments, which we judged as preferable to other potential designs that would instead have controlled for total song rate (i.e. half-normal singing rate for each of the two simulated song sparrows, or a twice-normal singing rate for the single simulated song sparrow). Although it is possible that juveniles were more attracted to our interaction treatment simply because of its higher song rate, if that were so we should have observed an intermediate response in the 'solo' condition, which contained half as many song sparrow songs as the 'interaction' condition, and many more than the 'control' condition. The birds did not show a graded response, however, but instead their response to the solo condition was essentially indistinguishable from the control condition. These results thus suggest that the key feature of the interactive treatment was interactivity rather than song rate.

We cannot say which particular aspects of the interactive singing condition were critical. In particular, the fact that the two simulated birds were song-matching one another may or may not have been critical. Future experiments comparing different sorts of song interactions (e.g. two birds singing different song types instead of type matching, one bird overlapping the other, etc.) will be
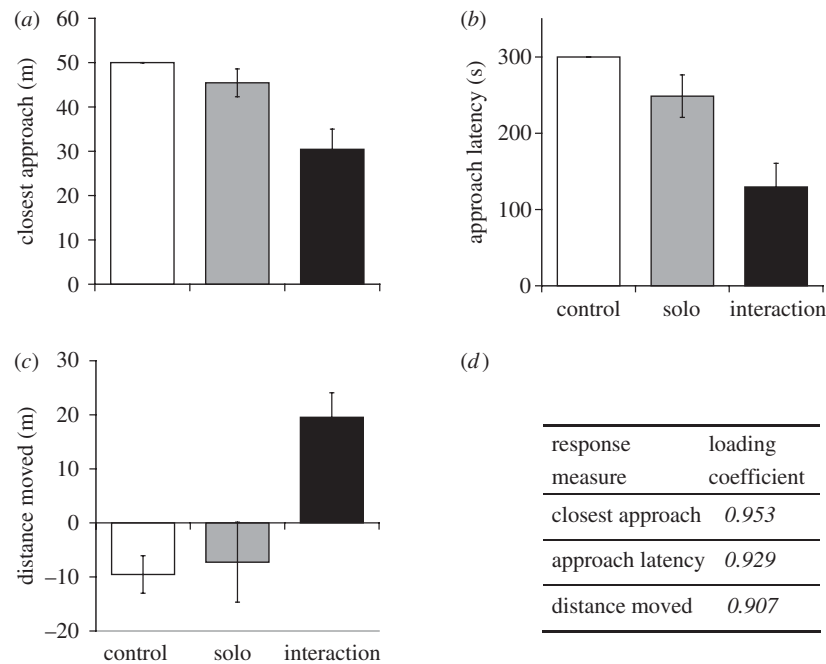
Figure 2. Behavioural measures that were factored in the PCA: (*a*) the closest approach to the speakers; (*b*) latency to approach the speakers; and (*c*) overall distance moved in relation to the speakers (positive values denote movements towards the speakers, negative values denote movements away). Data are shown as means ± s.e. These data were analysed together in a PCA (figure 1); (*d*) shows PCA loading coefficients for each variable on PC1, which explained 86.5% of the variation in the data.

needed to pinpoint whether particular aspects of counter-singing are especially attractive. It is possible that the key attractant is simply that the two birds are counter-singing, i.e. singing back and forth in a synchronized fashion.

Song matching may be one form of counter-singing that is particularly attractive for a young song-learning bird. In our population of western song sparrows, neighbours typically share a number of song types, and two neighbours will preferentially use songs they share when counter-singing (Beecher 2008). Previous research (Beecher *et al.* 1994) shows that young song sparrows also preferentially learn shared songs, and hearing shared song types used in the counter-singing context might be the key to this preference. Sharing songs with neighbours is strongly related to the success of an adult male (Beecher *et al.* 2000), so learning shared songs is critical for juveniles. A juvenile eavesdropping on inter-actions will have the opportunity to quickly learn which songs are shared by adults in that particular neighbour-hood. Because many juveniles move through a number of different neighbourhoods during their first year (C. N. Templeton, H. F. Boyce, S. E. Campbell, A. E. Illes, & M. D. Beecher 2009, unpublished manuscript), they may focus on these shared songs when making decisions about which song types to learn and keep for their final repertoire. Because males may vary in their ability to perform different song types (Podos 1997), eaves-dropping on song contests with matching types might also allow a juvenile to evaluate two adults' renditions of a song and compare different variations of a given song type (a similar idea has been proposed for adults by Logue & Forstmeier (2008), information which could be useful in both selecting song tutors and obtaining information about the quality of territorial adults.

Eavesdropping on singing interactions may have other benefits for song learning. For example, juveniles may need to learn the *rules* for singing in addition to the particular songs, and listening to the *way* in which adults interact may be extremely important in this regard. The young bird may need to learn not only which songs are effective in his neighbourhood, but the way in which those songs are used in singing interactions (e.g. type-matching, repertoire-matching, etc.). The rules for using songs to communicate cannot be learned via simple eaves-dropping on a single adult's songs; these rules can only be learned via eavesdropping on song contests or by directly interacting with an adult. Although we observed a number of birds approach the playback speakers during the interaction treatment, none of our subjects sang during these or the solo trials, suggesting that they were attracted to the playback for the opportunity to eavesdrop rather than to directly interact with the adult they heard sing. It is possible that juveniles might initially learn specific songs by other processes, e.g. simple eavesdropping, but are attracted to song interactions primarily to learn the semantics of using these songs to communicate.

Finally, juveniles may be able to glean information about the relationship between two adults by eavesdropping on their singing contests, as has been shown for male and female adults of other species (McGregor 2005). For example, juveniles may assess territory boundaries, territory stability, dominance relationships or relative aggression levels of each adult by listening to these interactions. This information may then be used to make future decisions about which songs to learn in relation to where each juvenile will attempt to establish a territory the next spring.
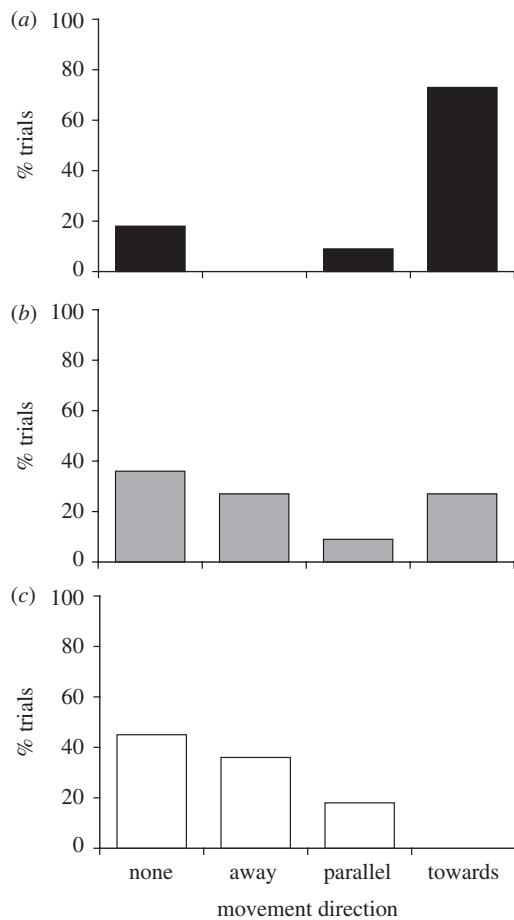
Figure 3. The direction birds moved during the playback varied with the type of singing interaction broadcast over the speakers ($p = 0.0043$). The per cent of trials for each direction moved is shown for (*a*) interactive playbacks; (*b*) solo playbacks; and (*c*) chickadee song control trials.

Our results may have interesting implications for language learning in humans. The ontogeny of bird song has served as an important model for the development of speech because of the number of similarities between vocal learning in songbirds and humans. Although it is often assumed that infants learn language primarily through direct interactions with their parents, recent research suggests that eavesdropping on the conversations of older individuals may also be important for learning language (Saffran *et al.* 1997; Akhtar *et al.* 2001; Floor & Akhtar 2006). In fact, some aspects of language seem to be better learned by eavesdropping on two interacting individuals than through active teaching (Oshimatakane 1988), a finding consistent with the fact that language comprehension by infants typically advances well ahead of their vocal production. Our results are consistent with these findings and suggest that vocal learning via eavesdropping on vocal interactions is yet another interesting parallel between human and songbird vocal development.

This research was conducted in accordance with the ABS/ASAB Guidelines for the Treatment of Animals in Behavioral Research and Teaching, with approval from the University of Washington IACUC (no. 2207-03) and USFWS bird banding permit (no. 20220).

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