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ORIGINAL ARTICLE

Constraints on song type matching in a songbird

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Abstract

In an eastern population of song sparrows (*Melospiza melodia*), song type matching occurs at above chance levels but does not signal aggressiveness. One explanation for the apparent ineffectiveness of matching as a signal is that the occurrence of matching is constrained by internal rules for ordering the production of song types. This constraint hypothesis is tested here in an experiment in which the singing of territorial male song sparrows is monitored in the field in real time, and subjects are confronted with playback of one of their song types either immediately after switching away from that type (short-delay) or after having cycled through much of their repertoire since last singing that type (long-delay). Matching was not significantly more likely in the long-delay treatment than in the short-delay treatment. The probability of matching did, however, depend significantly on prior bout length: the longer was a singer's last bout of a song type, the less likely the singer was to match it. There was also a suggestive effect of frequency of usage: males were more likely to match a song type the more frequently they normally sang that type, though this result was not significant after correcting for multiple comparisons. Thus, internal rules on how songs are sequenced exert constraints on the occurrence of song type matching, and such constraints can help to explain the apparent ineffectiveness of matching as a signal in this study population.

Significance statement

Research on song type matching in songbirds has largely focused on the signal function of matching, especially on the hypothesis that matching serves as an aggressive signal directed at the matched individual. In some songbirds, however, such as our study population of eastern song sparrows, predictions of the aggressive signaling hypothesis are not supported. Here, we show that the probability that song sparrows match song playback is strongly influenced by internal rules governing the sequencing of song type production. Specifically, the probability that song sparrows will match a particular song type is inversely related to the length of their prior bout of that song type. This result demonstrates how internal syntactical rules governing song type sequencing can constrain the signal function of song type matching.

Keywords Matching · Vocal matching · Birdsong · Song sparrows · *Melospiza melodia*

Introduction

Vocal matching is a behavior in which one individual replies to a vocalization of another with an especially similar vocalization of its own (King and McGregor 2016). Vocal matching is best known in songbirds (Catchpole and Slater 2008), but has also been found in cetaceans (Janik 2000; Miller et al. 2004; Alves et al. 2014), parrots (Balsby and Bradbury 2009), primates (Sugiura 1998), and anurans (Arak 1983; Gerhardt et al. 2000). In songbirds, vocal matching most often takes the form of song type matching, where one individual replies to another with the same or a similar song type. Song type matching has been shown to occur at above chance

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frequencies in a number of species of songbirds, both in natural interactions (Schroeder and Wiley 1983; Rogers 2004; Burt and Vehrencamp 2005; Gammon et al. 2008; Price and Yuan 2011) and in response to song playback (Hinde 1958; Krebs et al. 1981; Falls 1985; Stoddard et al. 1992; Liu et al. 2018). A large body of research has examined possible signal functions of song type matching, concentrating especially on the hypothesis that matching functions as a graded signal of aggression directed at the matched individual (Krebs et al. 1981; Searcy and Beecher 2009). A second body of research has taken a more mechanistic approach, examining whether the occurrence of song type matching is affected by internal mechanisms that govern the sequencing of song types in non-interactive singing (Hinde 1958; Bertram 1970; Falls 1985; Whitney 1985). Here, we address the intersection of these two approaches, asking whether internal sequencing mechanisms operate in a way that constrains the signal function of matching in an eastern population of song sparrows (*Melospiza melodia*).

The hypothesis that song type matching has an aggressive signaling function has received support in some songbird populations (Krebs et al. 1981; Molles and Vehrencamp 2001; Vehrencamp 2001), with the strongest evidence coming from a Washington State population of song sparrows. Song sparrow song typically consists of a series of three to five phrases, starting with an introductory trill of repeated syllables (Fig. 1). Individual males possess repertoires of 5 to 13 song types (Hughes et al. 1998, 2007; Beecher et al. 2000b; Peters et al. 2000), with a median of about 8; thus, a male's random chance of matching a song type in its repertoire is often assumed to be approximately 1/8. In the Washington State population, male song sparrows match, at frequencies much higher than chance, playback of either their own songs or of shared stranger songs (Stoddard et al. 1992). These birds also match stranger songs that have only limited similarity to one of their own song types, for example in the form of the introductory trill (Burt et al. 2002). Territorial males in this population match more often in aggressive contexts, for example matching more frequently when played songs of strangers rather than neighbors (Stoddard et al. 1992) or when played neighbor songs early in the breeding season rather than later (Beecher et al. 2000a). Territory owners respond more aggressively to playback of songs that type match them than to playback of songs that they share but are not currently singing (Burt et al. 2001). Finally, early matching to playback in this population is associated with subsequent attack on a conspecific model (Akçay et al. 2013). Song type matching in these western song sparrows thus satisfies all the criteria for an aggressive signal laid out by Searcy and Beecher (2009): it increases in aggressive contexts, it elicits receiver response, and it predicts aggressive escalation.

A strong case against an aggressive signaling function of song type matching has been made for another song sparrow population, this one in Pennsylvania (Searcy et al. 2014). Males in this eastern population also show matching behavior: territory owners type match at higher-than-expected frequencies both their own song types (Anderson et al. 2005; Searcy et al. 2006, 2013) and songs that share only the introductory trill with one of their song types (Anderson et al. 2005). As in the western population, type matching is more frequent early in the breeding season than late (Anderson et al. 2005). Territory owners, however, do not respond more strongly to playback that matches them than to non-matching playback (Anderson et al. 2008). Song type matching to a playback at the center of the territory does not predict subsequent attack on a conspecific model (Searcy et al. 2006), and matching to a boundary playback does not predict aggressive signaling and approach in response to a subsequent playback at the territory center (Searcy et al. 2013). Two separate studies found that individual males in this population are not consistent in whether they match or do not match playback of shared songs (Anderson et al. 2005; Searcy et al. 2013). By contrast, males in this population are highly consistent in aggressive approach and signaling behaviors (Nowicki et al. 2002; Hyman et al. 2004; Searcy et al. 2013). Because aggressive behavior is consistent in individuals and matching is not, matching is unlikely to be a reliable signal of aggressiveness.

Logue and Forstmeier (2008) proposed an alternative function for song type matching: matching displays the superiority of the matching male's song performance relative to that of the matched male's. This hypothesis has not been tested in song sparrows, but has been tested in a congener, the swamp sparrow (*Melospiza georgiana*). In swamp sparrows, song performance can be measured as vocal deviation, the departure of the song from an upper bound regression relating syllable bandwidth to syllable rate. This performance measure has been supported by biomechanical and developmental evidence (Podos 1996, 1997) and by results showing that both females (Ballentine et al. 2004) and males (DuBois et al. 2011; Moseley et al. 2013) respond more strongly to high performance songs. Liu et al. (2018) found, however, that male swamp sparrows are not more likely to match playback of song types that they out-perform than to match songs they under-perform, thus rejecting for this species a central prediction of the Logue and Forstmeier (2008) hypothesis.

Alongside these functional studies, a second body of work has examined whether the occurrence of song type matching can be explained by internal mechanisms governing the sequencing of song types. This research addresses a different one of Tinbergen's four questions than the functional studies, the question that Tinbergen termed "causation" rather than "survival value" (Tinbergen 1963). In an early study of matching, Hinde (1958) proposed that song sequencing in chaffinches (*Fringilla coelebs*) is governed by a mechanism that involves both facilitation and inhibition, a proposal echoed by Falls (1985) in a study of western meadowlarks

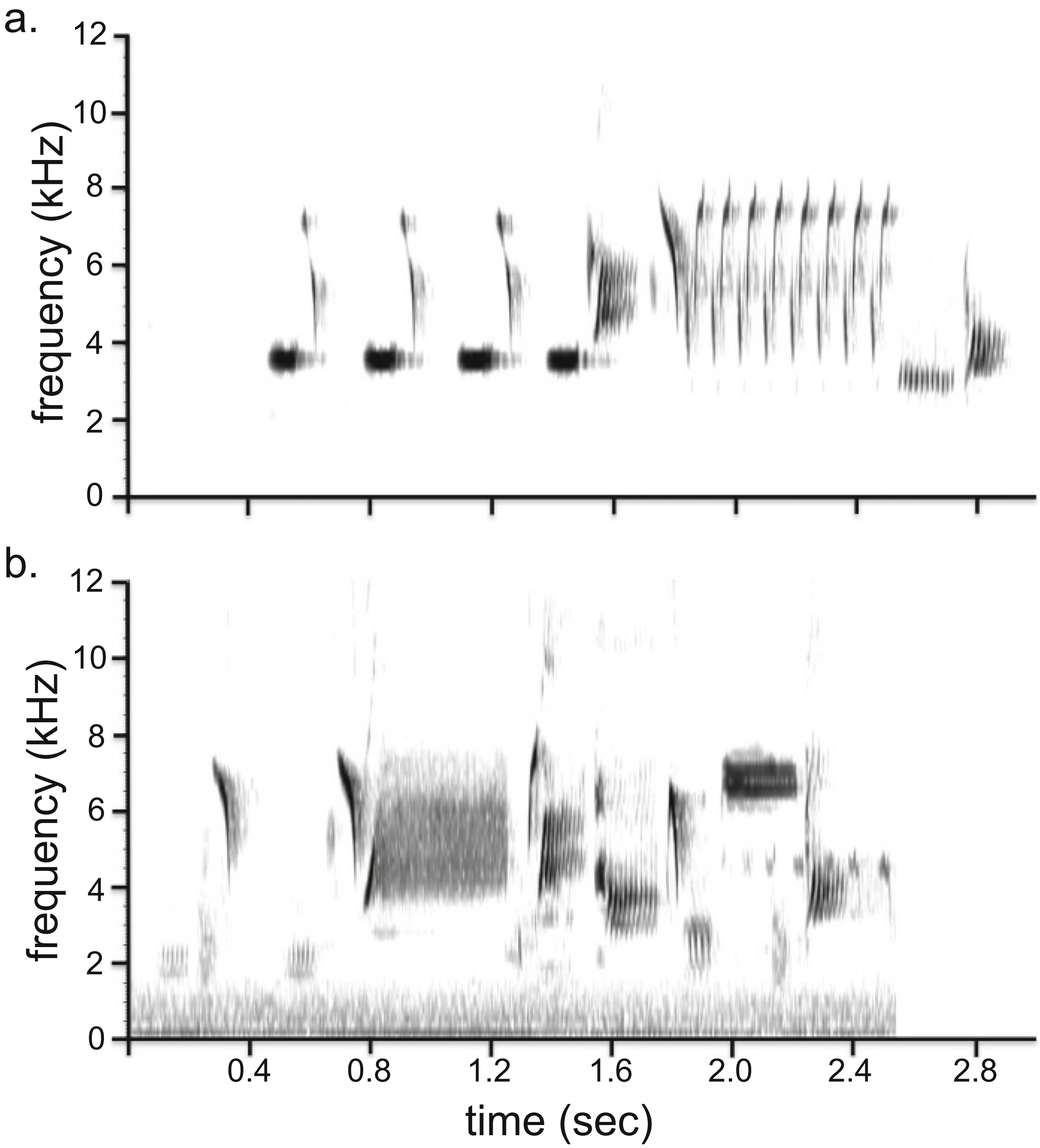

Fig. 1 (a) A spectrogram of a song sparrow song used as the playback signal in one trial. Note that the song starts with an introductory trill consisting of a repeated syllable and that throughout the song trills alternate with groups of unrepeated elements ("note complexes"). (b) The song used by the subject to reply to playback of the song in (a.) This field recording is not as clear as the one used for playback, but nonetheless is obviously not a match

(*Sturnella neglecta*). Both these species, like song sparrows, have repertoires of multiple song types that they sing with eventual variety, meaning that they sing multiple renditions of one song type before moving on to the next. In song sparrows, bout lengths average around 10 repetitions but with a great deal of variance (Kramer and Lemon 1983; Searcy et al. 2000). Facilitation is invoked to explain why renditions of one song type are produced together to form a bout, and inhibition is invoked to explain why a bout eventually ends with a switch to another song type. The facilitation mechanism can explain the occurrence of matching, if it is assumed that hearing a shared song from an external source activates the same mechanism as when a singer hears a song produced by itself (Falls 1985). As Bertram (1970, pp. 179-180) put it in a study of call type matching in hill mynahs (*Gracula religiosa*): "hearing a call type, whether made by a neighbour or made by the bird itself, increases the probability that this call type will be made," so that "matching ... is thus essentially a side effect of the mechanism of ordering a bird's own call types."

These internal mechanisms can produce additional sequencing patterns that affect matching. Some songbirds, including great tits (*Parus major*) (Krebs 1976) and song sparrows

(Cassidy 1993), tend to cycle through their repertoires before repeating a song type, a pattern that might be explained by the gradual waning of inhibition of a song type following production of a bout of that type. Such a cycling mechanism predicts that a bird should be more likely to match a song type the more type switches it has made since last singing that type, a prediction that Krebs et al. (1981) confirmed for great tits. Another pattern that might be produced by the inhibition mechanism is one in which a long bout of a particular song type is followed by a longer gap before that song type is produced again. Such a "bout length rule" would be predicted to make matching a particular song type less likely following a long bout of that type than following a short bout.

Two additional song sequencing patterns have been suggested that do not seem related to facilitation and inhibition, but which nonetheless might affect matching. First, in some songbird species, including song sparrows (Lapierre et al. 2011), individuals seem to prefer singing certain of their song types more than others. When such "usage preferences" exist, a singer might be more likely to match if challenged with one of its favored song types than if challenged with a less favored type. Second, in some species, especially those that sing with immediate variety, song types are typically sung in a fairly set order, so that certain transitions between song types are much more common than others (Verner 1975; Hedley 2016). Such "transition preferences," where they exist, might well affect matching; for example, if a particular singer preferred to transition from type I to type J, it might be more likely to match J when singing I than when singing some other type.

Here, we are interested in the hypothesis that internal sequencing rules such as those just discussed constrain the functional usefulness of matching as a signal. To this end, we test the effects of four putative sequencing rules on the occurrence of song type matching in our study population of eastern song sparrows. First, the "cycling rule," which proposes that singers tend to cycle through most or all of their repertoire before returning to a song type, predicts that a subject will be more likely to match a song type the more type switches it has made since last singing that type. Second, a "bout length rule," which assumes that longer bouts of a song type produce stronger inhibition of the type, predicts that a singer will be more likely to match a song type the shorter was its last bout of that type. A "usage preference rule," whereby a singer favors producing certain song types over others, predicts that matching should be more likely for favored song types than for less favored ones. Finally, a "transition preference" rule, which specifies that some transitions between song types are favored, suggests a fourth prediction: matching will be more likely the more favored is the specific transition that will produce matching. We designed an experiment to test the first prediction directly; data from the experiment also allow post hoc correlational tests of the other three predictions.

Methods

The study was carried out during May and June of 2017 in Crawford County, Pennsylvania, USA, on Pennsylvania State Gamelands 214 and along the shores of Pymatuning Reservoir. The subjects were 22 adult male song sparrows holding territories in old fields and forest clearings and along the margins of lakes and ponds. Twelve of the 22 subjects were banded with metal and colored plastic leg bands for individual recognition. The remaining 10 subjects were individually recognizable by spectrographic analysis of their songs, as song sharing is low in this population of song sparrows (Hughes et al. 1998; DuBois et al. 2016), allowing most individuals to be recognized by viewing one or two song types.

We recorded the song type repertoires of all subjects prior to their playback trials using digital recorders (Marantz PMD 660 or 670) and omnidirectional microphones (Shure SM58) in parabolic reflectors (Sony PBR-330). Recordings were made with a sampling rate of 44.1 or 48 KHz and stored as wav files. Previous work with eastern populations of song sparrows has shown that recording 200 songs captures the complete repertoires of most males, with a new song type occasionally being found between 200 and 300 songs (Searcy et al. 1985). We recorded more than 300 songs for 21 of the 22 subjects (range 305–386). For the one remaining male, we recorded only 230 songs during pre-trial recording, but we recorded an additional 113 songs during the two playback trials with this male without encountering any new song types. For the other 21 subjects, we recorded a mean of 156 additional songs (range 84–262) during playback trials and again found no new song type for any male.

Recorded songs were categorized into song types by visual inspection of spectrograms produced using Syrinx software. All song sparrow song types are variable to some extent (Podos et al. 1992), but playback experiments have shown that within-song type variation is less salient to song sparrows than are differences between song types (Searcy et al. 1995, 1999). Two songs were classified as the same song type if they shared the same introductory phrase and half or more of their total phrases. Classification of songs into song types was done for each male prior to that male's playback trials. A catalog containing spectrograms of two or three variants of each of a male's song types was printed out to aid in identification of song types produced by the subject during playback trials.

Playback stimuli

We assembled three digital playback stimuli for each subject from three of its own song types ("self songs"), choosing which song types to use based on recording quality (i.e., those songs with the lowest background noise and clearest signals). Self songs have been used extensively in matching experiments (Hinde 1958; Krebs et al. 1981; Todt 1981;

Templeton et al. 2012), including in several tests of the signal function of type matching in song sparrows (Anderson et al. 2005; Akçay et al. 2011; Akçay et al. 2013; Searcy et al. 2013). Song sparrows do not seem to recognize voice quality similarities across the song types of an individual and instead classify songs by song type similarities (Beecher et al. 1994); thus, self songs may be perceived as especially similar stranger song types. In practice, song sparrows treat self song similarly to stranger song in terms of both aggressive response (Searcy et al. 1981) and matching (Stoddard et al. 1992).

We copied each of the chosen songs from the field recordings in RavenPro 1.4 (Cornell Lab of Ornithology). Using the bandpass filter command in RavenPro, we filtered out sound below 1500 kHz and above 18,000 kHz and saved the filtered song as a 16-bit wav file. Using Audacity (https://audacityteam.org/), we normalized the peak amplitude to a constant level across all stimulus songs, added silence to produce a segment 10 s long, and repeated the segment 18 times. This procedure resulted in three playback stimuli per male, each consisting of one of that male's song types repeated 18 times in a 3-min period. The resulting bout lengths and song rates are within the natural range of variation. We refer to the three playback song types as the "target songs."

Experimental procedures

Each of the 22 subjects was tested in two trials 3–5 days apart, once with a "short-delay" treatment and once with a "long-delay" treatment, with treatment order randomized and counterbalanced. In both treatments, the subject's use of song types was monitored in the field by recording with a Shure SM58 microphone in a Sony PBR330 parabola to a PC laptop. The laptop ran Syrinx software that allowed us to view spectrograms of the songs produced by the subject in real time. Spectrograms on the screen were compared with the printed catalog of the subject's repertoire to identify song types. In the first trial with a subject, countdown to playback was triggered by the subject's singing any one of the three target song types for which we had made playback stimuli. In the second trial, countdown to playback was triggered by the subject's singing one of the two remaining target songs. Thus, two of the three target songs were used in playback, on separate trials.

In the short-delay treatment, playback was triggered by the subject's first switch from the target song to a new song type. Subjects sang a mean of 5.4 repetitions (range 2–10) of the new type before the first playback song was produced; no subject switched song types again before we were able to initiate playback. In the long-delay treatment, playback was started after the third song type switch following the target song for subjects with a repertoire of 6 song types and after the fourth switch for subjects with a repertoire of 7 or more song types. During this interval, subjects sang a mean of 45.6 songs (range 19–78).

Playback stimuli were broadcast from an iPod touch connected to an iMainGo X speaker (Portable Sound Laboratories, Van Nuys, CA, USA). The speaker was placed in a small box lined on five sides with polyurethane composite foam (Acoustical Surfaces, Inc., Chaska MN, USA) and open on the sixth. The box and speaker were placed on a tripod at a height of approximately 1.2 m and positioned on the subject's territory near a boundary, with the speaker pointed towards the territory center. Songs were broadcast forward at 84–88 dB SPL measured at 1 m with a B&K Precision 32A sound level meter, A weighting. The acoustic foam reduced sound amplitude to the rear of the box by approximately 20 dB, lowering the chance of response by neighbors.

Analysis of responses

We continued recording subjects after playback began until they switched to a new song type as determined by visual inspection of the real-time spectrograms in the field. Subsequently, the identity of the first exemplar of the new song type was determined by consensus of two observers through comparison of its spectrogram to the catalog of song types previously prepared for the subject. A third experienced observer independently identified each of these response songs to song type while blind to the treatment, the identity of the playback song, and the previous consensus assignment. The blind scoring agreed with the previous consensus scoring as to the song type of the response song in 43 of 44 cases (97.7%) and as to whether matching of the playback song had occurred in 44 of 44 cases (100%). Figure 1 gives an example of a comparison of a response song to a playback song.

We tested for an effect of treatment on song type matching in two ways: (1) with a Chi Square test comparing the numbers of subjects that type matched and failed to type match during the long-delay and the short-delay treatments and (2) with a generalized linear mixed model (GLMM). The GLMM was from the binomial family with a logit link and was fit by maximum likelihood in the glmer function in the lme4 package of R. Individual was entered as a random effect and five variables were entered as fixed effects: treatment (short-delay versus long-delay), date, type frequency, transition frequency, and prior bout length. All fixed effects variables showed low association with each other ($P > 0.15$ in all cases). Type frequency is the frequency with which the subject sang the playback song type during the repertoire recordings. Transition frequency is the frequency in the repertoire recordings of the song type transition needed to produce a match (e.g., type B to type D if the subject was singing B when playback of D was initiated). Prior bout length is the number of repetitions of the target song used for playback that the subject produced in the bout of the target song that triggered playback.

Each subject was tested for matching with both the long-delay treatment and the short-delay treatment, allowing a test for individual consistency as in Anderson et al. (2005). Individuals were consistent if they either matched on both trials or failed to match on both trials and were inconsistent if they matched on one trial but not the other. Expected numbers in each category were estimated using the frequency of matching in the long-delay treatment, the frequency of matching in the short-delay treatment, and the number of subjects, and expected numbers were compared with the observed using a chi-square test. All probabilities are two-tailed.

Data availability Data from this study will be available from the Dryad Digital Depository (https://doi.org/10.5061/dryad.dn61nt7) after a 1-year embargo.

Results

The male song sparrows used as subjects had a mean repertoire size of 7.6 song types, and thus had a mean of 6.6 song types to choose from when they performed their first song type-switch after playback began. The chance of type matching the playback at random was therefore 1/6.6 or 15%. The subjects type-matched in response to the long-delay treatment on 8 of 22 trials (36%), which was significantly more often than expected by chance ($X^2 = 7.88$, df = 1, $P = 0.005$). Subjects type-matched in response to the short-delay treatment on 6 of 22 trials (27%), which was not significantly more often than expected ($X^2 = 2.60$, df = 1, $P = 0.107$). The difference in response was marginal in the predicted direction of more matching in the long-delay treatment than in the short-delay treatment, but this difference was not significant ($X^2 = 0.419$, df = 1, $P = 0.517$).

In the generalized linear mixed model (Table 1), the effect of treatment (long-delay versus short-delay) was not statistically significant. The effect of prior bout length, however, was significant, with a low enough *P* value ($P = 0.008$) to survive a Bonferroni correction for multiple comparisons (Rice 1989). What this result means is that the more repetitions of a target song a male had produced in its most recent bout of that song type, the less likely the male was to match the song type when it was presented via playback. Figure 2 shows a visual representation of this result. The GLMM also shows a marginal effect of song type frequency (Table 1), with a P value ($P = 0.042$) below the alpha = 0.05 threshold but not low enough to survive a sequential Bonferroni correction (Rice 1989). Taken at face value, what this effect means is that the more frequent a song type is in a male's general usage, the more likely the male is to match it. Date and transition frequency had no statistical effect on matching.

Table 1 Results of the GLMM examining effects of singing behaviors on the occurrence of song type matching

Intercept	Effect 0.214	SE 1.51	*z* 0.142	*P* 0.89
Treatment (short-delay)	− 0.816	0.815	− 1.001	0.32
Date	− 0.117	0.076	− 1.550	0.12
Transition frequency	0.044	1.89	0.023	0.98
Type frequency	21.2	10.4	2.032	0.042
Prior bout length	− 0.158	.060	− 2.649	0.008

Individual consistency in matching is expected if matching is associated with any consistent individual trait, including not only aggressiveness but also body size, age, and boldness. Slightly more of the subjects were consistent in type-matching (matching twice or never matching) and slightly fewer were inconsistent (matching once in two opportunities) than expected by chance (Table 2). The difference from random expectation was not, however, statistically significant ($X^2 = 0.70$, df = 2, $P = 0.705$).

Discussion

Male song sparrows were slightly more likely to match the playback song type when they had just switched away from singing that type than when they had cycled through much of their repertoire since last singing it, but this difference was not significant. Thus even though male song sparrows appear to follow the cycling rule in song production overall, this rule did not have a significant effect on whether they song type matched in the context of our experiment. Nevertheless, we found strong correlational evidence that at least one internal sequencing rule does affect matching, namely the prior bout length rule: males were less likely to switch to the matching song type the more repetitions of the type they had sung in their most recent bout of that type. We also found equivocal support for an effect of a usage preference rule, whereby males prefer singing certain of their song types more than others. Males were more likely to match the playback song type the more frequent their general usage of that song type, but that effect was not significant after a correction for multiple comparisons.

The effect of prior bout length on matching is consistent with male song sparrows possessing internal sequencing mechanisms whereby hearing a certain song type facilitates production of that song type, and repeated production of a song type inhibits its subsequent production. The pattern that Krebs et al. (1981) found in great tits, in which males are more likely to match a song type the more type switches they have made since last singing it, also supports the inhibitory mechanism. Also compatible with the facilitation mechanism are certain singing behaviors observed in immediate variety singers (those that usually sing each song type just once

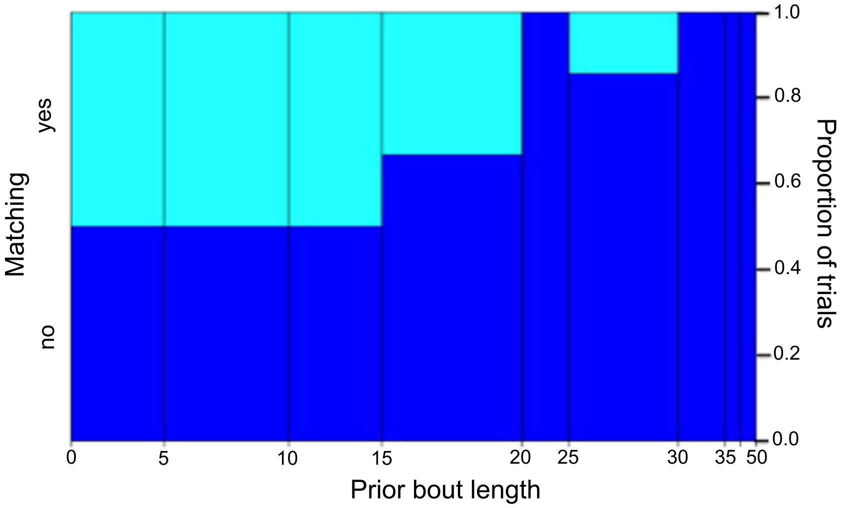

Fig. 2 Proportion matching versus prior bout length in the playback trials. The widths of the intervals on the *X*-axis are proportional to the number of trials falling in the interval. Male song sparrows were less likely to match a song type the longer was their previous bout of that type ($z = -2.649$, $N = 44$ trials, $P = 0.008$)

before switching to another). Whitney (1985) found that male wood thrushes (*Hylocichla mustelina*) sing their songs in a preferred order with respect to their B-phrases, for example B1–B2–B3–B4–B1. He then showed that when male wood thrushes were played songs that were similar to one of their own song types, they would preferentially reply with the next song in their usual sequence; for example, if played B2, the male above would reply preferentially with B3. Such "song advancing" (Hedley et al. 2017) has also been observed in other immediate variety singers (Todt 1971; Verner 1975; Kroodsma 1979; Hedley et al. 2017). Whitney (1985, p. 1250) suggested that song advancing occurs because hearing a song type triggers a "mechanism by which one song facilitates, via a loop involving audition, the production of the next song in the sequence." Thus, a variety of evidence from both immediate and eventual variety singers is in accord with the idea that the auditory stimulus of hearing an external song can be incorporated into the internal mechanisms controlling the sequencing of song production. The confirmatory evidence is rather indirect, however, so more direct neurobiological tests for the proposed audition-dependent sequencing mechanisms would be valuable.

Whatever its mechanistic basis, the prior bout length rule puts a constraint on the value of song type matching as a signal. The more that variation in matching behavior is explained by internal sequencing rules such as this one, the less information matching can carry about aggressiveness or any other parameter of interest to receivers. For example, to the extent that matching conveys the singer's prior bout length rather than its aggressiveness, matching will be less useful in intimidating an intruder. The existence of such constraints therefore helps explain the evidence against an aggressive signaling function of matching in our study population, such as the evidence that matching does not predict aggressive escalation (Searcy et al. 2006, 2013). Such constraints can also explain why matching is not consistent within individuals (Anderson et al. 2005; Searcy et al. 2013): if whether matching occurs depends importantly on the length of the subject's prior bout of the target song, and if prior bout length varies randomly between trials, then individuals would not be expected to be consistent in matching behavior.

Table 2 The number of subjects that were consistent in matching (never matching or matching twice) versus the number that were inconsistent (matching on one trial but not the other)

	Never matched	Matched once	Matched twice
Observed	11	8	3
Expected	10.3	9.6	2.1

It is possible that even if much of the variation in matching reflects sequencing rules of no interest to receivers, there remains some variation associated with information that is important to receivers. Moreover, it can be argued that receivers could compensate for such sequencing rules in order to extract additional information from matching. Thus, if a singer matched a particular song type despite having recently produced a long bout of that type, a receiver could judge that singer to be especially aggressive. This kind of compensatory evaluation requires significant cognitive processing on the part of the receiver, which would have to keep track of what song types an opponent sings and how many repetitions of each it produces. No evidence exists that songbirds acquire and retain such detailed information on the recent singing activity of others. For these reasons, we think compensatory evaluation is unlikely.

A bout length rule and a cycling rule can be considered to be aspects of song sparrow syntax, where syntax refers to a set of rules governing how communicative items are assembled into combinations (Berwick et al. 2011; Hurford 2012). Songbirds in general assemble songs into bouts, with rules that differ between species in how such sequences are formed. Evidence of complex "compositional" syntax, in which the ordering of elements affects the meaning of the whole, has recently been found for call combinations in Japanese great tits (Suzuki et al. 2016, 2019). The syntax of song bouts, by contrast, is generally thought to be quite simple, with the ordering of song types having little or no effect on meaning (in the sense of the information conveyed to receivers). Our results illustrate one way in which syntactical rules in birdsong can affect song function without affecting meaning per se.

In conclusion, variation in song type matching in our study population is affected by internal syntactical rules for ordering song types: very probably by a prior bout length rule, by which the probability of matching goes down as the length of the prior bout of the matching type goes up, and perhaps by a usage preference rule, whereby certain song types are preferred and are therefore more likely to be matched. Our results do not demonstrate an effect of a cycling rule, under which singers should be less likely to match recently sung song types, but that rule deserves further testing. Effects of internal syntactical rules on matching might occur in any animal that produces vocalizations in sequences governed by syntactical rules, including not only other songbirds but also perhaps some cetaceans as well. Whenever such syntactical rules exist, they may constrain signal function, as seems to be the case in eastern song sparrows.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures used in this study were approved by the Institutional Animal Care and Use Committees of the University of Miami (protocol no. 17–046), Duke University (protocol no. A004-17-01) and the University of Pittsburgh (protocol no. 15045539). All applicable national and institutional guidelines for the use of animals were followed. Playback trials were kept brief (≤3 min) to minimize disturbance to our subjects.

References

Akçay C, Tom ME, Holmes D, Campbell SE, Beecher MD (2011) Sing softly and carry a big stick: signals of aggressive intent in the song sparrow. Anim Behav 82:377–382

Akçay C, Tom ME, Campbell SE, Beecher MD (2013) Song type matching is an honest early threat signal in a hierarchical animal communication system. Proc R Soc B 280:20122517

Alves A, Antunes R, Bird A, Tyack PL, Miller PJO, Lam FPA, Kvadsheim PH (2014) Vocal matching of naval sonar signals by long-finned pilot whales (*Globicephala melas*). Mar Mammal Sci 30:1248–1257

Anderson RC, Searcy WA, Nowicki S (2005) Partial song matching in an eastern population of song sparrows, *Melospiza melodia*. Anim Behav 69:189–196

Anderson RC, Searcy WA, Nowicki S (2008) Testing the function of song-matching in birds: responses of eastern male song sparrows *Melospiza melodia* to partial song-matching. Behaviour 145:347–363

Arak A (1983) Vocal interactions, call matching and territoriality in a Sri Lankan treefrog, *Philautus leucorhinus* (Rhacophoridae). Anim Behav 31:292–302

Ballentine B, Hyman J, Nowicki S (2004) Vocal performance influences female response to male bird song: an experimental test. Behav Ecol 15:163–168

Balsby TJS, Bradbury JW (2009) Vocal matching by orange-fronted conures (*Aratinga canicularis*). Behav Process 82:133–139

Beecher MD, Campbell SE, Burt JM (1994) Song perception in the song sparrow: birds classify by song type but not by singer. Anim Behav 47:1343–1351

Beecher MD, Campbell SE, Burt JM, Hill CE, Nordby JC (2000a) Song-type matching between neighbouring song sparrows. Anim Behav 59:21–27

Beecher MD, Campbell SE, Nordby JC (2000b) Territory tenure in song sparrows is related to song sharing with neighbours, but not to repertoire size. Anim Behav 59:29–37

Bertram B (1970) The vocal behaviour of the Indian hill mynah, *Gracula religiosa*. Anim Behav Monogr 3:79–192

Berwick RC, Okanoya K, Beckers GJL, Bolhuis JJ (2011) Songs to syntax: the linguistics of birdsong. Trends Cogn Sci 15:113–121

Burt JM, Vehrencamp SL (2005) Dawn chorus as an interactive communication network. In: McGregor PK (ed) Animal communication networks. Cambridge University Press, Cambridge, pp 320–343

Burt JM, Campbell SE, Beecher MD (2001) Song type matching as threat: a test using interactive playback. Anim Behav 62:1163–1170

Burt JM, Bard SC, Campbell SE, Beecher MD (2002) Alternative forms of song matching in song sparrows. Anim Behav 63:1143–1151

Cassidy ALEV (1993) Song variation and learning in island populations of song sparrows. Dissertation, University of British Columbia

Catchpole CK, Slater PJB (2008) Bird song: biological themes and variations. Cambridge University Press, Cambridge

DuBois AL, Nowicki S, Searcy WA (2011) Discrimination of vocal performance by male swamp sparrows. Behav Ecol Sociobiol 65:717–726

DuBois AL, Nowicki S, Searcy WA (2016) A test for repertoire matching in eastern song sparrows. J Avian Biol 47:146–152

Falls JB (1985) Song matching in western meadowlarks. Can J Zool 63: 2520–2524

Gammon DE, Hendrick MC, Baker MC (2008) Vocal communication in a songbird with a novel song repertoire. Behaviour 145:1003–1026

Gerhardt HC, Roberts JD, Bee MA, Schwartz JJ (2000) Call matching in the quacking frog (*Crinia georgiana*). Behav Ecol Sociobiol 48: 243–251

Hedley RW (2016) Composition and sequential organization of song repertoires in Cassin's Vireo (*Vireo cassinii*). J Ornithol 157: 13–22

Hedley RW, Denton KK, Weiss RE (2017) Accounting for syntax in analyses of countersinging reveals hidden vocal dynamics in a songbird with a large repertoire. Anim Behav 131:23–32

Hinde RA (1958) Alternative motor patterns in chaffinch song. Anim Behav 6:211–218

Hughes M, Nowicki S, Searcy WA, Peters S (1998) Song-type sharing in song sparrows: implications for repertoire function and song learning. Behav Ecol Sociobiol 42:437–446

Hughes M, Anderson RC, Searcy WA, Bottensek LM, Nowicki S (2007) Song type sharing and territory tenure in eastern song sparrows: implications for the evolution of song repertoires. Anim Behav 73: 701–710

Hurford JR (2012) The origins of grammar. Oxford University Press, Oxford

Hyman J, Hughes M, Searcy WA, Nowicki S (2004) Individual variation in the strength of territory defense in male song sparrows: correlates of age, territory tenure, and neighbor aggressiveness. Behaviour 141:15–27

Janik VM (2000) Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). Science 289:1355–1357

King SL, McGregor PK (2016) Vocal matching: the what, the why and the how. Biol Lett 12:20160666

Kramer HG, Lemon RE (1983) Dynamics of territorial singing between neighboring song sparrows (*Melospiza melodia*). Behaviour 85: 198–223

Krebs JR (1976) Habituation and song repertoires in the great tit. Behav Ecol Sociobiol 1:215–227

Krebs JR, Ashcroft R, Van Orsdol K (1981) Song matching in the great tit *Parus major* L. Anim Behav 29:918–923

Kroodsma DE (1979) Vocal dueling among male marsh wrens: evidence for ritualized expressions of dominance/subordinance. Auk 96:506–515

Lapierre JM, Mennill DJ, MacDougall-Shackleton EA (2011) Spatial and age-related variation in use of locally common song elements in dawn singing of song sparrows *Melospiza melodia*: old males sing the hits. Behav Ecol Sociobiol 65: 2149–2160

Liu IA, Soha JA, Nowicki S (2018) Song type matching and vocal performance in territorial signalling by male swamp sparrows. Anim Behav 139:117–125

Logue DM, Forstmeier W (2008) Constrained performance in a communication network: implications for the function of song-type matching and for the evolution of multiple ornaments. Am Nat 172:34–41

Miller PJO, Shapiro AD, Tyack PL, Solow AR (2004) Call-type matching in vocal exchanges of free-ranging resident killer whales, *Orcinus orca*. Anim Behav 67:1099–1107

Molles LE, Vehrencamp SL (2001) Songbird cheaters pay a retaliation cost: evidence for auditory conventional signals. Proc R Soc Lond B 268:2013–2019

Moseley DL, Lahti DC, Podos J (2013) Responses to song playback vary with the vocal performance of both signal senders and receivers. Proc R Soc B 280:20131401

Nowicki S, Searcy WA, Krueger T, Hughes M (2002) Individual variation in response to simulated territorial challenge among territory-holding song sparrows. J Avian Biol 33:253–259

Peters S, Searcy WA, Beecher MD, Nowicki S (2000) Geographic variation in the organization of song sparrow repertoires. Auk 117:936–942

Podos J (1996) Motor constraints on vocal development in a songbird. Anim Behav 51:1061–1070

Podos J (1997) A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). Evolution 51:537–551

Podos J, Peters S, Rudnicky T, Marler P, Nowicki S (1992) The organization of song repertoires in song sparrows: themes and variations. Ethology 90:89–106

Price JJ, Yuan DH (2011) Song-type sharing and matching in a bird with very large song repertoires, the tropical mockingbird. Behaviour 148:673–689

Rice WR (1989) Analyzing tables of statistical tests. Evolution 43:223–225

Rogers D (2004) Repertoire size, song sharing and type matching in the rufous bristlebird (*Dasyornis broadbenti*). Emu 104:7–13

Schroeder DJ, Wiley RH (1983) Communication with shared song themes in tufted titmice. Auk 100:414–424

Searcy WA, Beecher MD (2009) Song as an aggressive signal in songbirds. Anim Behav 78:1281–1292

Searcy WA, McArthur PD, Peters SS, Marler P (1981) Response of male song and swamp sparrows to neighbour, stranger, and self songs. Behaviour 77:152–163

Searcy WA, McArthur PD, Yasukawa K (1985) Song repertoire size and male quality in song sparrows. Condor 87:222–228

Searcy WA, Podos J, Peters S, Nowicki S (1995) Discrimination of song types and variants in song sparrows. Anim Behav 49: 1219–1226

Searcy WA, Nowicki S, Peters S (1999) Song types as fundamental units in vocal repertoires. Anim Behav 58:37–44

Searcy WA, Nowicki S, Hogan C (2000) Song type variants and aggressive context. Behav Ecol Sociobiol 48:358–363

Searcy WA, Anderson RC, Nowicki S (2006) Bird song as a signal of aggressive intent. Behav Ecol Sociobiol 60:234–241

Searcy WA, DuBois AL, Rivera-Cáceres K, Nowicki S (2013) A test of a hierarchical signalling model in song sparrows. Anim Behav 86: 309–315

Searcy WA, Akçay C, Nowicki S, Beecher MD (2014) Aggressive signaling in song sparrows and other songbirds. Adv Study Behav 46: 89–125

Stoddard PK, Beecher MD, Campbell SE, Horning CL (1992) Song-type matching in the song sparrow. Can J Zool 70:1440–1444

Sugiura H (1998) Matching of acoustic features during the vocal exchange of coo calls by Japanese macaques. Anim Behav 55:673–687

Suzuki TN, Wheatcroft D, Griesser M (2016) Experimental evidence for compositional syntax in bird calls. Nat Commun 7: 10986

Suzuki TN, Griesser M, Wheatcroft D (2019) Syntactic rules in avian vocal sequences as a window into the evolution of compositionality. Anim Behav 151:267–274

Templeton CN, Ríos-Chelén AA, Quirós-Guerrero E, Mann NI, Slater PJB (2012) Female happy wrens select songs to cooperate with their mates rather than confront intruders. Biol Lett 9: 20120863

Tinbergen N (1963) On aims and methods of ethology. Z Tierpsychol 20: 410–433

Todt D (1971) Äquivalente und konvalente gesangliche Reaktionen einer extrem regelmässig singenden Nachtigall (*Luscinia megarhynchos* L.). Z Vergl Physiol 71:262–285
Todt D (1981) On functions of vocal matching: effects of counter-replies on song post choice and singing. Z Tierpsychol 57:73–93
Vehrencamp SL (2001) Is song-type matching a conventional signal of aggressive intentions? Proc R Soc Lond B 268:1637–1642
Verner J (1975) Complex song repertoire of male long-billed marsh wrens in eastern Washington. Living Bird 14:263–300
Whitney CL (1985) Serial order in wood thrush song. Anim Behav 33: 1250–1265