Song sparrows do not discriminate between their own song and stranger song

Çağlar Akçay, Michael D. Beecher

Department of Psychology, Koç University, Istanbul, Turkey
Department of Biological Sciences, Virginia Tech, Blacksburg, VA, USA
Department of Psychology, University of Washington, Seattle, WA, USA

ABSTRACT

Bird song is socially learned. During song learning, the bird’s hearing its own vocalization is important for normal development of song. Whether bird’s own song is represented and recognized as a special category in adult birds, however, is unclear. If birds respond differently to their own songs when these are played back to them, this would be evidence for auditory self-recognition. To test this possibility, we presented song sparrow males (Melospiza melodia) playbacks of their own songs or stranger songs and measured aggressive responses as well as type matching. We found no evidence of behavioral discrimination of bird’s own song relative to the (non-matching) stranger song. These findings cast doubt on an earlier proposal that song sparrows display auditory self-recognition and support the common assumption in playback experiments that bird’s own song is perceived as stranger song.

1. Introduction

Songbirds are one of the handful of taxa (including humans, bats, cetaceans, parrots and hummingbirds) that are known to learn their vocalizations socially. Laboratory studies of songbirds have revealed that a young bird’s hearing its own vocalizations plays a key role in song development: young birds deprived of auditory feedback from their own singing ultimately develop abnormal songs (Brainard and Doupe, 2000; Konishi, 1965; Price, 1979). Hearing one’s own singing also appears to be important for the maintenance of adult song: birds deafened as adults also lose the species typical consistency in their songs (Lombardino and Nottebohm, 2000; Nordeen and Nordeen, 1992). Not surprisingly, song-learning and production circuits in the songbird brain display special sensitivity to own song when these are played back from a speaker (Poirier et al., 2003; Prather and Mooney, 2004). All these results suggest that songbirds may represent their own song as a special category and may even display auditory self-recognition (Derégnaucourt and Bovet, 2016).

Field studies have raised different questions as to ways in which a bird’s own song might be special. Bird song, which typically functions in territory-defense and mate-attraction contexts (Catchpole and Slater, 2008), is often learned from other adults in the local area, usually a neighbour (Beecher, 2008). Consequently, in natural interactions, birds will often hear versions of their songs from other individuals. Bird song communication is often studied by observing a bird’s response to the playback of pre-recorded song (McGregor, 2000; Weeden and Falls, 1959). Many such playback experiments simulate realistic situations, such as an intrusion onto the subject’s territory by a neighbour, or a stranger but a particularly interesting case is when the bird’s own song is played back to him. Playback of own song of course would not simulate a realistic situation if the bird were to perceive the playback as its own song. It may however resemble a realistic situation if the bird perceives the playback song as the song of a stranger that happens to have a song very similar to his, or as a shared song of one of his neighbours. The neighbour possibility is plausible in those populations where neighbours share songs, a common occurrence for species who learn songs after they disperse from the natal area, such as indigo buntings, Passerina cyanea, or some populations of song sparrows, Melospiza melodia (Beecher et al., 1994a, 1994b; Payne, 1982). The stranger possibility is plausible in circumstances where some birds learn songs in one neighbourhood and then move to another neighbourhood leading to shared songs between distant birds. The self-recognition possibility seems least likely although McArthur (1986, 1987) claimed to have found evidence for this possibility in a study with song sparrows (see below).

One difficulty in studying auditory self-recognition in the field is...
that it is unclear how self-recognition would manifest itself in the re-
response of an individual to playback (Derégnaucourt and Bovet, 2016).
The first possibility is that the bird might type match (i.e. reply with the
same song type as the playback song) its own song at a higher rate than it
would to, say, a neighbour song, as has been found in western
meadowlarks, *Sturnella neglecta* (Falls, 1985). Note that such an effect
could simply come about because bird’s own song is by definition more
similar (indeed identical) to his than any other class of stimulus (Falls
et al., 1982). In any case, other studies found different patterns. For
instance, Stoddard et al. (1992) found that type matching levels in male
song sparrows were similar to own song and to matching stranger
songs, while type matching in response to matching neighbour songs
were lower than either. Since stranger matching songs were generally
worse matches to subject songs than either own- or neighbour-matching
songs, similarity of playback stimulus to the subject song cannot explain
the pattern of matching found in this experiment.

Some studies assessed whether birds differ in aggressive responses
to own song vs. stranger or neighbour song (Derégnaucourt and Bovet,
2016). Several of these found an intermediate response to the own song,
i.e., stronger than to neighbour song, and weaker than to stranger song
(Brooks and Falls, 1975; Weeden and Falls, 1959; Yasukawa et al.,
1982). In contrast, Searcy et al. (1981) found no significant difference
in approach to own song compared to stranger song in eastern song
sparrows. Most relevant to the present study, McArthur (1986) found
that song sparrows responded with equal intensity in singing, flights or
approach measures to own song compared to stranger song while the
playback was ongoing, but birds stayed closer to the speaker after the
playback was over in the two stranger song conditions compared to the
own song condition. McArthur interpreted this one difference in his six
response measures as evidence of ‘auditory concept of self’ (McArthur,
1986). This interpretation has been criticized (Suarez and Gallup,
1987).

In the present study we studied the same western population studied
by Stoddard et al. (1992). Male song sparrows have a repertoire of
about 9 distinct song types (median: 9, range: 6–13 songs) and in this
population they show high levels of song sharing among neighbours
(Beecher et al., 1994a, 1994b; Hill et al., 1999). This song sharing
comes about by birds copying whole songs of older birds (‘tutors’), who
are often also neighbours (Beecher et al., 1994a, 1994b; Nordby et al.,
1999). This fact means that any particular song in a song sparrow’s
repertoire is invariably more similar in acoustic structure to a song in
another bird’s repertoire (e.g. the tutors or neighbours) than it is to one
of the other songs in his own repertoire. Additionally, song sparrow
songs do not have distinctive ‘signature’ or voice characteristics identi-
fying them as the songs of that individual (Beecher et al., 1994a,
1994b).

Thus, when we play own song to a bird in the field, it is plausible
that he would perceive it as the similar song of one of his neighbours.
Song sparrows, like many other territorial animals display reduced
aggression towards neighbours compared to strangers, i.e. the Dear
Enemy effect (Fisher, 1954; Stoddard et al., 1991; Temeles, 1994).
Thus, if own song is perceived as a neighbour song we expect subjects to
respond more weakly to own song than to stranger song (Stoddard
et al., 1991). Alternatively, he might perceive own song as a stranger
who happens to share a song with him, given that song types
do spread beyond the immediate neighbourhood (Nordby et al., 1999).
In this case we would expect him to respond equally strongly to own
and stranger song. Finally, it is also possible that playback of own song
is especially salient, either because his own songs will have been the
songs he has heard more than any others or because it is represented as
a distinct category for recognition. In this case, we would expect a
difference in response between stranger and own song, although which
direction this difference should go is unclear, as discussed above.

We were also motivated to carry out this experiment for methodo-
logical reasons: Bird’s own song is a powerful stimulus for studying
behaviours like song type matching. Using bird’s own song is also a
convenient way to match stimulus song for relative quality, familiarity
and similarity to each subject while avoiding pseudoreplication.
Consequently, a number of studies have used bird’s own song as a sti-
minus in playback experiments (e.g. Akçay, Tom et al., 2013; Anderson
et al., 2005; Searcy et al., 2019), with the assumption that this song is
perceived as a stranger song. The present study provides a test of this
assumption.

2. Methods

2.1. Study site and subjects

We studied adult male song sparrows in a population in Discovery
Park, Seattle, WA that has been studied since 1986 (Beecher et al.,
1994a, 1994b). We carried out this experiment between 17 and 22 June
2019. The subjects used in this study were not banded but we had no
more than 4 days between the initial recordings of the songs of subjects
and the trials to ensure that the individual recorded for own song
playbacks was still there at the time of the trials. Given that territories
are extremely stable in song sparrows even across multiple years (e.g.
Akçay et al., 2015) this assumption is reasonable. We also corroborated
the identities of the birds by matching the song types recorded in the
recording sessions before the trials and songs recorded during the trials.

We tested 24 males. The sample size was determined a priori with a
power analysis, aiming for a power of 0.80, and an effect size of
d = 0.6. This effect size is smaller than the significant effects we de-
tected in our studies of individual discrimination of different classes of
individuals (Akçay et al., 2017; Akçay, Reed et al., 2010; Akçay et al.,
2009; Stoddard et al., 1991).

2.2. Stimuli and design

We recorded each subject for at least 15 min which was enough to
obtain at least two or three good songs types. We did not attempt to
record the entire repertoire of the males. During these recordings we
occasionally used playbacks both to elicit song, and to determine the
extent of the territory for the trials. The recordings were made with a
directional microphone (Sennheiser ME67/K6) and a digital recorder
(Marantz PDM660). We viewed the recordings in Syrinx (John Burt,
Portland, OR) and chose one good rendition of a song type for each
subject for own song stimulus. We manually filtered low-frequency
noise and added a silent period to the end of the song to create a 10 s
wave file. This wave file was played during the trial in a loop so that
playback stimulus rate was one song every 10 s (song sparrow songs last
about 3 s).

Each stimulus song was used once as an own song and once as a
stranger song for a different subject at least 4 territories away (average
distance: 667 m, range: 490 – 961 m). This definition of stranger is
consistent with previous studies on this species (Kroodsma, 1976; Se-
arcy et al., 1981; Stoddard et al., 1991). Each subject was tested
twice, once with his own song and once with the stranger song in a
counterbalanced order such that half of the subjects received the own
song first, while the other half received the stranger song first. The trials
were carried out on consecutive days with about 24 h in between.

The own song stimulus by definition was one which the subject
could match. Because we did not attempt to record the entire repertoire
of the subjects, we did not ensure that the stranger stimulus song could
be matched but we observed no type matching during the stranger
trials. Because song sharing with non-neighbours is low in our popu-
lation (Hill et al., 1999), we assumed that most, if not all of the stranger
songs were non-shared with the subject.

2.3. Procedure

For each trial, we placed a Bluetooth speaker (Anker SoundCore,
Anker Inc.) on a natural perch at a height of about 1.5m above ground
at a central location of the territory. There were three reasons for carrying out the playbacks near the territory centre as opposed to near a boundary. First, playback from the centre was a key part of the design of the McArthur (1986) study, and our study is in part a replication of his. Second, differences between familiar and stranger songs are not always reduced in the center of the territory, e.g., Akçay et al., 2017, where we found greater response to primary tutor song than to stranger playback in the center of the territory. Third, and most important, the self-recognition hypothesis is logically better tested in the center for the following reason. In this song-sharing species, self-song is less likely to be confused with neighbour song in the center than at a neighbour boundary where that neighbour might share that song. At the center, however, this confusion is much less likely, and if per hypothesis the song is perceived as own song, his response should be weaker to it than to stranger song, whereas if it is perceived as from a stranger or an intruding neighbour, the response should be similar to response to (the official) stranger song.

The speaker volume was adjusted to play the stimulus songs at about 85 dB SPL measured at 1 m, corresponding to natural levels of broadcast song in this species. We then moved to about 10–15 m from the speaker and started the playback, which lasted for 3 min after the subject’s first response (approach or song). This trial duration was the same as in previous studies on recognition of song in song sparrows (Searcy et al., 1981; Stoddard et al., 1991) and initial responses to three minutes of playback predict an eventual attack on a taxidermic mount (Akçay et al., 2013). In all cases, the birds responded within about 10–20 seconds of the start of the playback (to the first or second playback song). During the playback, the observers narrated the trial and recorded the vocal response of the subject using the same equipment as above. We recorded each flight (any airborne movements), distance with each flight, songs (loud and soft, see below), and wing waves. After the playback ended, we recorded the same behaviors for another 2 min. We avoided testing neighbours on the same day and carried out consecutive trials at least 200 m apart, where we could not hear the previous subject.

2.4. Response measures

From the trial recordings we extracted the following information: flights of the subject (any airborne movements), distance to the speaker with each flight, loud songs, soft songs and wing waves. Soft songs are low amplitude songs that reliably predict a physical attack (Akçay et al., 2013; Nice, 1943; Searcy et al., 2006). Loud songs and soft songs can be distinguished in the field by an experienced observer (in this case, CA) despite the fact that amplitude variation in singing is continuous (Anderson et al., 2008). We further distinguished between two types of soft songs: crystallized and warbled soft songs which differ in their acoustic structure (Anderson et al., 2008). Wing waves are rapid flutering of one or both wings without taking off, which also predict a subsequent attack in our population (Akçay et al., 2013). Loud songs, in contrast do not predict attack in this species (Akçay et al., 2013; Searcy et al., 2006). We converted counts of behaviours into rates to account for slight variation in playback duration (mean duration ± SD: 180.66 ± 2.95 s). We extracted the same response variables for the 2-minute post-playback duration as well.

2.5. Data analyses

Most of the rates were non-normally distributed. We therefore used permutation tests (1000 iterations) to compare responses to the own song with responses to stranger song. We report the effect sizes and 95 % confidence intervals along with the comparisons. Finally, we also report repeatability of the behaviours for completeness sake. The analyses were carried out in R (R Core Team, 2012) using packages ez (Lawrence, 2016) and rptR (Nakagawa and Schielzeth, 2010). To assess whether type matching was greater than random we ran a binomial test. Because we did not record the entire repertoire of the subjects, we did not know their repertoire size to exactly determine the chance level of matching. Previous samples of males in our population have consistently yielded average repertoire sizes larger than eight (e.g. Hill et al., 1999; Nordby et al., 1999). Therefore, we conservatively assumed a chance level of matching of 1/8.

2.6. Ethical note

The experiments lasted less than 10 min between arrival on territory and leaving (with only about three minutes of playback) to minimize disturbance to the subjects. The subjects were not captured at any time for this study. The procedures conform to the guidelines of ASAB/ABS for the treatment of animals in behavioral research and teaching.

3. Results

There were no differences between responses to own song and stranger song during either the 3- minutes of playback (Table 1) or the 2-minute period after the playback (Table 2). The response variables during the playback period were highly repeatable (Table 1). Subjects type matched own song playback in 6 of the 24 trials. In an additional 3 trials, the subjects were singing the same song type as playback song when we started (thus we type matched the subject). In those cases, the subjects stayed on type. We counted them as type matching as well. This level of type matching (9/24 = 0.375) was higher than the expected level of type matching (1/8, p = 0.0013). When we excluded the three trials on which the subjects stayed on type the observed type matching levels (6/21 = 0.286) was still higher than the expected level

### Table 1

Results of the permutation tests (p-values) for each response variable measured during the trial, along with effect sizes (Cohen's d and 95 % confidence intervals) and repeatability (intra-class correlation coefficients; standard errors are given in parentheses and p-values associated with the coefficients).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Permutation p-value</th>
<th>Cohen's d</th>
<th>95 % CI</th>
<th>ICC (SE)</th>
<th>ICC p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flight rate</td>
<td>0.233</td>
<td>0.136</td>
<td>−0.43, 0.71</td>
<td>0.86 (0.076)</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Proportion of time spent &lt; 1m</td>
<td>0.174</td>
<td>0.265</td>
<td>−0.28, 0.90</td>
<td>0.58 (0.14)</td>
<td>0.001</td>
</tr>
<tr>
<td>Warbled soft songs</td>
<td>0.17</td>
<td>0.277</td>
<td>−0.25, 0.86</td>
<td>0.49 (0.17)</td>
<td>0.0067</td>
</tr>
<tr>
<td>Crystallized soft songs</td>
<td>0.84</td>
<td>0.0481</td>
<td>−0.54, 0.62</td>
<td>0.43 (0.18)</td>
<td>0.01</td>
</tr>
<tr>
<td>Wing waves</td>
<td>0.69</td>
<td>0.0671</td>
<td>−0.52, 0.60</td>
<td>0.69 (0.12)</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Loud songs</td>
<td>0.35</td>
<td>−0.154</td>
<td>−0.77, 0.39</td>
<td>0.72 (0.095)</td>
<td>&lt; 0.0001</td>
</tr>
</tbody>
</table>

### Table 2

Results of the permutation tests (p-values) for each response variable measured during the 2 min after the playback, along with effect sizes (Cohen’s d) and their 95 % confidence intervals.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Permutation p-value</th>
<th>Cohen's d</th>
<th>95 % CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flight rate</td>
<td>0.57</td>
<td>−0.107</td>
<td>−0.56, 0.24</td>
</tr>
<tr>
<td>Proportion of time spent &lt; 1m</td>
<td>0.97</td>
<td>−0.0065</td>
<td>−0.45, 0.45</td>
</tr>
<tr>
<td>Warbled soft songs</td>
<td>0.54</td>
<td>−0.18</td>
<td>−0.57, 0.22</td>
</tr>
<tr>
<td>Crystallized soft songs</td>
<td>0.43</td>
<td>0.17</td>
<td>−0.30, 0.50</td>
</tr>
<tr>
<td>Wing waves</td>
<td>0.64</td>
<td>0.22</td>
<td>−0.12, 0.65</td>
</tr>
<tr>
<td>Loud songs</td>
<td>0.19</td>
<td>0.266</td>
<td>−0.13, 0.75</td>
</tr>
</tbody>
</table>
by a binomial test $p = 0.028$.

4. Discussion

We found no evidence that male song sparrows discriminated between their own song and a stranger song: on no response variable were responses to self and stranger songs significantly different. The non-significant differences includes proximity to the loudspeaker after the playback period (as measured by proportion of time spent within 1 m during the 2 min after playback), the only measure of six for which McArthur (1986) found a significant difference between self and stranger conditions, and which served as the basis of his claim for an auditory self-concept. The present results therefore offer no support for the existence of an auditory self-concept in song sparrows and also corroborate an earlier finding of no discrimination between self and stranger songs in song sparrows (Searcy et al., 1981).

The observed levels of type matching in response to own song (9 out of 24 trials) was slightly lower than the matching to own song (6 out of 10 subjects) or to stranger song (5 out of 10 subjects) that was observed in a previous study in our population (Stoddard et al., 1992) but not significantly so (Fisher’s exact test: $p = 0.41$ and 0.72 respectively). Note also that the song playbacks in that earlier study were carried out in early Spring (March) when type matching interactions are generally higher between neighbouring birds (Beecher et al., 2000). Thus, the observed levels of type matching in our present experiment are consistent with previous estimates of song type matching against own or stranger song and corroborates the lack of discrimination between these two categories.

One potential caveat is that lack of discrimination does not always indicate lack of recognition. For instance, song sparrows in our population display the Dear Enemy effect (i.e. reduced aggression towards neighbours compared to strangers) when the songs of these neighbours are played from the correct boundary (Stoddard et al., 1991). When the neighbour and stranger songs are played at the centre or an incorrect boundary however, males respond equally strongly to the neighbour and stranger songs (Stoddard et al., 1991). This is not because of a lack of discrimination, as evidenced by the fact that intrusions by a neighbour are retaliated upon even after the neighbour “retreats” to his own territory (Akcay et al., 2010, 2009). Rather, the lack of discrimination between strangers and neighbours at the territory centre likely comes about because a bird singing in your own territory is a high threat to territorial integrity or paternity whether he is a stranger or neighbour.

In summary, we think it is unlikely that song sparrows recognize their own song as such, given the only previous evidence for such recognition in song sparrows was based on a very similar conceptualization, methodology, investigation, writing - original draft, funding acquisition. Michael D. Beecher: Conceptualization, methodology, investigation, writing - review & editing.
Acknowledgement

This study was supported by a Young Investigator Award (BAGEP) to Ça from the Science Academy of Turkey.

References


