

# Sexual equality in zebra finch song preference: evidence for a dissociation between song recognition and production learning

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Song in oscine birds is a culturally inherited mating signal and sexually dimorphic. From differences in song production learning, sex differences in song recognition learning have been inferred but rarely put to a stringent test. In zebra finches, *Taeniopygia guttata*, females never sing and the species has one of the greatest neuroanatomical differences in song-related brain nuclei reported for songbirds. Preference tests with sibling groups for which exposure to song had been identical during the sensitive phase for song learning in males, revealed equally strong influence of the tutor's song (here the father) on males' and females' adult song preferences. Both sexes significantly preferred the father's over unfamiliar song when having free control over exposure to playbacks via an operant task. The sibling comparisons suggest that this preference developed independently of the song's absolute quality: variation between siblings was as great as between nests. The results show that early exposure has an equally strong influence on males' and females' song preferences despite the sexual asymmetry in song production learning. This suggests that the trajectory for song recognition learning is independent of the one for song production learning.

**Keywords:** song recognition learning; sex differences; song preferences; *Taeniopygia guttata*; operant conditioning; receiver learning

## 1. INTRODUCTION

Song in oscine birds is acquired through social learning during development (Catchpole & Slater 1995). Across species, song usage and function can vary greatly between the sexes but males are typically the vocally displaying sex and females the choosing one, singing less or not at all (Catchpole & Slater 1995; but see Langmore 1998). With culturally transmitted mating signals, the question arises to what extent song production learning is mirrored by learning on the receiver side and whether sex differences in song production (learning) predict differences in song recognition (learning). Forebrain nuclei that were identified as part of the song-controlling neural circuitry are usually larger in oscine males than females (Brenowitz & Kroodsma 1996; MacDougall-Shackleton & Ball 1999; but see Gahr *et al.* 1998). Sex difference in song recognition could arise because the sex with the smaller song nuclei (females) is less proficient in discriminating conspecific song (Nottebohm *et al.* 1990) or because learning to sing particular songs will influence the way other songs are perceived (Nottebohm *et al.* 1990; Cynx & Nottebohm 1992; Pytte & Suthers 1999). In contrast, ultimate arguments predict that females should be the more discriminating sex, as mistakes in song recognition leading to suboptimal mate choice have higher fitness costs for females than for males (Searcy & Brenowitz 1988).

However, current evidence regarding sex differences in song recognition is not conclusive. Sex differences in song usage and function resulted in different methodological approaches to investigating song recognition, thus when comparing males and females across studies, possible sex differences cannot be separated from effects resulting from different test songs or motivational contexts (Johnsrude *et al.* 1994; Ratcliffe & Otter 1996). The lack of control of early learning processes should be added as another caveat. The consequences are best illustrated in the zebra finch. There is ample evidence that song perception is influenced by early exposure leading to preferences for particular songs in both sexes (Miller 1979; Clayton 1988; Adret 1993; Houx & ten Cate 1999a,b; Riebel 2000). However, a comparison of the strength of preferences across sexes remains wanting as all studies tested only one sex, with one exception (Clayton 1988). In the latter study, the developmental time window of exposure to a particular song, but not the sex of the subjects, influenced whether this song was preferentially approached in a phonotaxis test. This is in contrast to studies that report females to differ significantly from males in learning to recognize and categorize songs in discrimination tasks (Cynx *et al.* 1990; Cynx & Nottebohm 1992; but see Sturdy *et al.* 1999). Given the importance of the zebra finch as a model system for the study of vocal learning, and the possible evolutionary consequences of an asymmetry in sender and receiver learning, our study re-addresses the question of possible sex differences in preference learning. Contrary to other tests, we explicitly considered sibship, as well as sex, as factors in the

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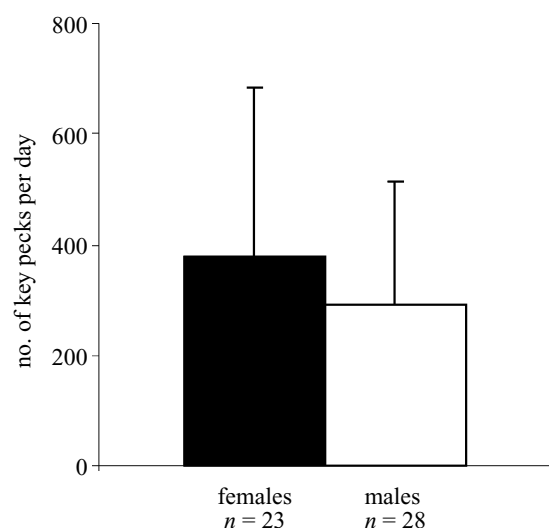


Figure 1. Mean ( $\pm 1$  s.d.) number of pecks per day.

design and analysis. Siblings were raised and tested the same way, thereby keeping possible genetic, environmental and cultural effects on song preference the same within a clutch and allowing for a more stringent test of sex differences. Using an operant task with song as a reward (Houx & ten Cate 1999b; Riebel 2000) allows the repeated testing of males' and females' active choices over several days, thereby addressing the critique on the validity of single phonotaxis tests regarding quantification and comparison of preference strength on an individual scale (Wagner 1998).

## 2. MATERIAL AND METHODS

### (a) Subjects

Subjects for this study were 62 zebra finches (26 females, 36 males) from 19 nests and 13 different pairs in an outbred laboratory population. Breeding was initiated by housing a pair in an individual cage (80 cm (length)  $\times$  40 cm (width)  $\times$  43 cm (height)) fitted with a nest box in a large bird room set on a 13.5 L : 10.5 D photoperiod. Fledglings remained within their family group in the natal cage until  $74 \pm 16$  days post-hatching (mean s.d. of median hatching day of each clutch). From then onwards, they were housed in unisex groups with the exception of the preference test at  $113 \pm 28$  days post-hatching. Group size was random and ranged from a minimum of 3 to a maximum of 11, and differed within and between subjects during the experiment in a non-systematic fashion, but was always the same for siblings of the same sex and the same clutch.

### (b) Preference tests

The experimental set-up has been reported elsewhere (Riebel 2000). Briefly, experimental cages (70 cm  $\times$  30 cm  $\times$  45 cm) had five perches (at 8, 23, 35, 47 and 62 cm length), with perches 1, 3 and 5 at heights of 21 cm and perches 2 and 4 at heights of 26 cm. Perched on the first or fifth perch, birds could peck red response keys (diameter: 1 cm) with a red light-emitting diode (LED) light in the centre (diameter: 2 mm) fitted into the rear wall. Pecking one key triggered one playback of the song assigned to it. A custom-built control-registration unit kept a datalog and controlled the playbacks (soundchip Oki MSM6388, Tokyo, Japan). Songs were broadcasted at 70 dB (re 20  $\mu$ Pa; CEL-231 sound-level meter, fast response setting) peak amplitude at 30 cm from the loudspeaker (Quart 250 or JBL Control 1), which was fitted behind an opening (diameter: 9 cm) in the rear, halfway between the keys.

To start a test, a subject was moved into one of the experimental cages with the pecking keys' LED lights switched on (when the light in the chamber was on) until the end of the day when it had started pecking both keys. This day was designated day 0, which was on average  $3.5 \pm 3.9$  days from the starting day (range 1–16), and this did not differ between males and females (Mann-Whitney *U*-test,  $U = 295$ ,  $N_1 = 23$ ,  $N_2 = 28$ ,  $p = 0.6$ ). The subsequent day was designated day 1 of the preference test, which lasted 4 days or two blocks (one block = 2 days, each song having been presented for 1 day on either side). Most birds learned the task without shaping, those who had not after 5 days were shaped in training sessions (details in Houx & ten Cate (1999b)). Throughout the testing period, food and water were available *ad libitum* and all procedures reported in this paper were approved beforehand by Leiden University's animal experimentation committee (UDEEC) according to Dutch law on animal experimentation.

### (c) Stimulus songs

There was one stimulus set per clutch: the father's song and the song of an unfamiliar male. In six cases, breeding pairs contributed two clutches to the sample: for half of these ( $N = 3$ ), the original stimulus set was re-used, for the other ( $N = 3$ ), a different recording of the father's song and of a different unfamiliar male. Recordings of undirected song (Zann 1996) were made with a Sennheiser MKH40 microphone and Sony TC-D5 Pro II cassette recorder in the sound attenuation chambers later used for preference testing. From each male, a song bout of 5–6 s duration was digitized (sample rate 25 000 Hz) with the SIGNAL-RTS software (Engineering Design, Belmont, MA, USA) and a low-pass filter (cut-off frequency 10 000 Hz, Frequency Devices 900C/9L8B, USA). Unfamiliar songs had not been heard by the subjects before the tests: they stemmed from males in different bird rooms or from other breeding colonies in the

Table 1. Generalized linear model for key pecks per day.

(Sex and parents are fixed factors. Expected mean squares are based on type III sum of squares.)

| source of variation  | all birds |                     |          |          | one clutch per parents only |                     |          |          |
|----------------------|-----------|---------------------|----------|----------|-----------------------------|---------------------|----------|----------|
|                      | d.f.      | mean sum of squares | <i>F</i> | <i>p</i> | d.f.                        | mean sum of squares | <i>F</i> | <i>p</i> |
| sex                  | 1         | 97 602              | 1.39     | 0.25     | 1                           | 74 765              | 0.73     | 0.41     |
| parents              | 12        | 91 298              | 1.30     | 0.28     | 12                          | 79 131              | 0.77     | 0.67     |
| sex $\times$ parents | 12        | 43 441              | 0.62     | 0.81     | 11                          | 40 777              | 0.40     | 0.93     |
| error                | 25        | 70 128              | —        | —        | 13                          | 101 714             | —        | —        |

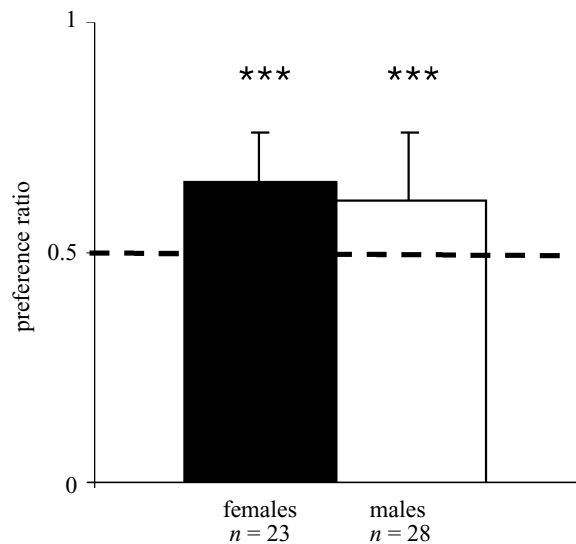


Figure 2. Mean ( $\pm 1$  s.d.) preference ratio (total number of pecks for father's song divided by grand total). Asterisks denote a mean preference ratio that was significantly different from a 0.5 (dashed line) preference ratio (one-sample  $t$ -tests,  $p < 0.001$ ).

Netherlands, or from newly acquired birds. Stimuli sets were adjusted to have the same peak amplitude and were approximately of the same duration (fathers' songs =  $5.9 \pm 0.8$  s, unknown songs  $5.8 \pm 0.9$  s).

#### (d) Analysis

No data were obtained for 11 out of the 62 subjects, because birds did not learn to press both ( $N = 6$ ) or one key ( $N = 2$ ), or because of technical problems ( $N = 3$ ), thus leaving a total of 51 birds (23 females and 28 males). Preference tests lasted 4 days or two blocks (one block = 2 days, each song 1 day on each side). For eight birds, data could be obtained for the first block only, due to technical problems. However, a comparison showed that activity levels and preference ratios were the same between block 1 and 2 for those birds tested on 4 days (see § 3), thus data for those birds tested for only 2 days were included in the analysis. Effects of sex and siblingship on preference strength and activity levels (key pecks per day) were tested with two-way general linear models. All statistical tests were calculated with the SPSS statistical package (v. 8.0.1) and were two tailed. Means are given  $\pm 1$  s.d.

### 3. RESULTS

The two main measures—preference ratio (total number of key pecks for the father's song divided by grand

total) and key pecking (mean per day)—did not change during the duration of the test period. For all subjects tested on 4 days ( $N = 43$ ), a comparison between the first 2 days (block 1) and days 3–4 (block 2) of the preferences test showed no differences across the two blocks (preference ratio: females  $t_{16} = 1.7$ ,  $p = 0.2$ ; males  $t_{25} = 1.7$ ,  $p = 0.1$ ; key pecking: females  $t_{16} = 0.1$ ,  $p = 0.9$ ; males  $t_{25} = 1.1$ ,  $p = 0.27$ , paired  $t$ -tests). Due to the fact that the first block did not differ from the second, and because both measures (pecks per day and preference ratio) were relative, we pooled the data of subjects tested on 4 days ( $N = 43$ ) with those tested on only 2 days ( $N = 8$ ).

Males and females showed no differences in activity levels, i.e. the mean number of key pecks per day did not differ significantly between them (figure 1 and table 1), and this was also true for the preference ratios for the father's song (figure 2 and table 2). Furthermore, there was no 'parents' effect and no interactions between factors. Some parents contributed more than one clutch. However, re-running the analysis including only one clutch per parental pair did not change the outcome (see second columns in tables 1 and 2). The preference for the father's song was significant in both males and females (tested as a deviation from a 0.5 preference ratio with one-sample  $t$ -tests; mean preference ratios: males =  $0.61 \pm 0.14$ ,  $t_{27} = 4.0$ ,  $p < 0.001$ ; females =  $0.65 \pm 0.11$ ,  $t_{22} = 6.3$ ,  $p < 0.001$ ).

### 4. DISCUSSION

Exposure to song during the sensitive phase for song (production) learning equally influenced song preferences in male and female zebra finches. Both adult males and females preferentially chose their father's song over an unfamiliar one during a test period of 4 days with free access and control over playbacks of either song via key pecking. Conspecific song has previously been shown to be reinforcing for adult untutored zebra finches (Braaten & Reynolds 1999). The present study demonstrates that the relative reinforcing quality of different variants of the species-specific song was equally influenced by early learning in both sexes. Males worked as hard for song exposure as females. This strongly suggests a role for song also in male–male communication, which has so far not been contemplated in this non-territorial but colonial species (Zann 1996). The strongest implication of this is, however, that sex differences in song production learning are not predictive of song recognition learning in a species listed as one of the most behaviourally and neuroanatomically dimorphic of the songbirds (Brenowitz & Kroodsm

Table 2. Generalized linear model for preference ratio for the father's song over an unfamiliar song. (Sex and parents are fixed factors. Expected mean squares are based on type III sum of squares.)

| source of variation  | all birds |                     |      |      | one clutch per parents only |                     |      |      |
|----------------------|-----------|---------------------|------|------|-----------------------------|---------------------|------|------|
|                      | d.f.      | mean sum of squares | $F$  | $p$  | d.f.                        | mean sum of squares | $F$  | $p$  |
| sex                  | 1         | 0.058               | 2.6  | 0.12 | 1                           | 0.051               | 2.2  | 0.16 |
| parents              | 12        | 0.018               | 0.53 | 0.87 | 12                          | 0.011               | 0.48 | 0.89 |
| sex $\times$ parents | 12        | 0.017               | 0.77 | 0.67 | 11                          | 0.018               | 0.75 | 0.68 |
| error                | 25        | 0.022               | —    | —    | 13                          | 0.025               | —    | —    |

1996; MacDougall-Shackleton & Ball 1999). This is in line with recent neurobiological findings, which identified brain regions outside the sexually dimorphic parts of the song circuitry as possible neural substrates for song memorization. Both the caudo-medial part of the neostriatum and of the hyperstriatum ventrale were recently suggested to be involved in song recognition memory both in males (Bolhuis *et al.* 2000, 2001a) and females (MacDougall-Shackleton *et al.* 1998; Bolhuis *et al.* 2001b). So far, no sex differences have been reported for these regions.

How do the present findings relate to the reported sex differences in song discrimination in the zebra finch? Females were reported to need more trials than males in learning acoustic discrimination tasks (e.g. Cynx *et al.* 1990; Cynx & Nottebohm 1992), but once they had acquired it they performed any of the subsequent discriminations as well as males did in one study (Cynx *et al.* 1990). In another study, females only differed from males in learning to discriminate between two songs from familiar aviary companions, but not to discriminate between two songs of unknown males (Cynx & Nottebohm 1992). Thus, having known the songs (or singers), rather than the ability to discriminate between two conspecific songs, might have influenced the way females, but not males, categorized the song. This would explain an absence of sex differences in learning, as well as categorizing, conspecific syllables (Sturdy *et al.* 1999). Thus, it is perhaps not the discrimination and memorization abilities *per se* that differ between the sexes, but the way sex-specific cognitive processes influence perception. Early learning processes seem to have an important role not only in developing preferences for particular songs (Miller 1979; Clayton 1988; Adret 1993; Houx & ten Cate 1999a,b; Riebel 2000), but also in shaping more general perceptual filters (Neubauer 1999; Riebel 2000). Future work will have to disentangle further the degree to which the consequences of early learning processes on perception correspond or diverge between the sexes.

Preference strength did not differ significantly between sibling groups. This suggests that the overall quality of the father (or his song or song output) does not influence how much a song is preferred, memorized or copied (for concurrent evidence, see Pearson *et al.* 1999; Houx *et al.* 2000). Variation between siblings could be developmental consequences of genetic differences between them, but genetic variance between siblings should be smaller than between non-siblings. As for parental effects on phenotype, the quality and quantity of interactions with the father differ between siblings. Despite considerable research effort confirming such differences, their effect on song learning remains unclear (discussion in Pearson *et al.* 1999; Houx *et al.* 2000). Laying-hatching order covaries with hormone and nutrient contents in the egg (Gil *et al.* 1999), fledgling weight (Kilner 1998) and with song learning (Tchernichovski & Nottebohm 1998). Endocrinological and physiological differences could influence the duration of the sensory and motor learning phase. How these factors interact and which of them covary with the observed differences in adult song preference strength will have to be addressed in future studies.

This study clearly demonstrates how perception of the species-specific mating signal is influenced by cultural

inheritance. The effects of a learned preference for a particular type of song on actual mate choice remain to be tested, but it seems likely as song has an important role in female mate choice in zebra finches (reviewed in Zann 1996). Furthermore, a learned preference for a particular song seems to lead to some generalization. Females that were crossfostered between the two zebra finch subspecies, showed more sexual displays during playback of unfamiliar foster species songs than of unfamiliar own species songs (Clayton 1990). A preference for the father's song in females seems puzzling at first—but should perhaps be replaced with the notion of a preference for songs heard during this sensitive period. In the wild, young zebra finches might start to join flocks as early as 35 days, but although they come in contact with a number of other songs, a majority of young males predominantly learn the father's song (Zann 1996). However, songs of flock-mates might also be memorized during this period. Although they were exposed to a multitude of songs in the bird room, our birds stayed within the family group for at least 70 days, thereby being exposed to their father's song in close contact longer than they might have in the wild. This might have led to an unusually strong preference for it. However, exposure to tape-tutored song (Houx & ten Cate 1999b; Riebel 2000), or the song of a tutor other than the father (Clayton 1988), during this period will also lead to a preference for it. Whether learning during this period normally encompasses more than one song remains to be tested, as well as whether behavioural consequences of learned song preferences are the same for both sexes. Song preferences could affect affiliative behaviour (influencing grouping and socializing decisions) as well as sexual behaviour (influencing mate choice) but also settling in a particular colony. At this stage, we do not know what the possible adaptive significance of a learned song preference is, but bird song learning takes place both on the sender and receiver side and both are influenced by early exposure. The evolutionary consequences of receiver learning have probably been seriously underestimated, as recent work on brood parasites suggests (Payne *et al.* 2000; Smith *et al.* 2000), and still have to be explored in other songbird species (for further references on female song preference learning, see Riebel & Slater 1998; Riebel 2000). Given a communication system with a learned mating signal, we should not be surprised to find receivers as apt at learning as senders.

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