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SONG TUTORING INFLUENCES FEMALE SONG PREFERENCES IN DOMESTICATED CANARIES

by

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Summary

Laboratory experiments were designed to examine the influence of previous acoustic experience on later song preferences in female domesticated canaries (*Serinus canaria*). Young females were reared in acoustic isolation (five groups). In these five groups, one was reared without tutoring and four were exposed to taped tutoring songs (playbacks of three different songs, two conspecific and one heterospecific). One of the four tutored groups was exposed to all three songs, while each of the remaining groups was exposed to one of the three songs. When adult, all females were tested using copulation solicitation displays as an index of their song preferences. We demonstrated that females reared without tutoring were especially responsive to a particular domesticated canary song. This song contained a special song phrase type (Vallet & Kreutzer, 1995) that elicits high levels of sexual response. In general, a similar preference was also observed in the groups reared with tutoring. In addition, the females' preferences in tutored groups were also positively and strongly affected by conspecific songs, when these songs had been heard during the previous tutoring. In fact, females seemed to be able to selectively respond to a song containing a special song phrase, but were also able to learn conspecific songs.

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Introduction

Auditory experience plays a vital role in birdsong development (Thorpe, 1958, 1961; Marler, 1970). Young male white-crowned sparrows (*Zonotrichia leucophrys nuttalli*) learn their songs by copying models heard during their first weeks of life (Marler, 1970). In a similar way, females also memorise song models heard during early life. Evidence for this comes from observations of female white-crowned sparrows singing in the wild (Blanchard, 1941; Baptista *et al.*, 1993) or treated with testosterone. These females vocalise native dialects (Konishi, 1965; Baptista & Morton, 1982). In most oscine birds, the females take the more active part in selecting a mate, choosing a male partly by his song (Payne, 1983). An indication of the song preferences of females can be obtained from their copulation solicitation displays — CSD (Searcy *et al.*, 1981; West *et al.*, 1981). These displays normally occur during the breeding season in response to the courtship displays of males, in the context of pair formation and copulation (Baker *et al.*, 1987). An important question is whether song models heard during the first weeks of life influence song preferences in adult females.

Laboratory studies conducted by Casey & Baker (1992) suggested that the mate-choice behaviour of female white-crowned sparrows is guided by the songs experienced early in life. These authors concluded that females mate preferentially with males that sing songs the females were exposed to during their early life. In contrast, Chilton *et al.* (1990) argue from field studies that female white-crowned sparrows do not mate preferentially with males singing songs that the female heard early in life. Rather, females in the wild choose mates on the basis of characteristics other than song type. Females probably use a variety of cues (*e.g.* territory quality or size, intersexual displays) in choosing among potential mates (Andersson, 1982; Alatalo *et al.*, 1984). Nevertheless, song preferences revealed by CSD can be studied as a potential mechanism of mate selection in wild species (Marler, 1960; King *et al.*, 1980; Salomon, 1989), as well as in domesticated species (Kreutzer & Vallet, 1991; Nagle *et al.*, 1993).

The purpose of our study was to test the hypothesis that song tutoring positively influences later song preferences in female canaries. After demonstrating that young female canaries (*Serinus canaria*) reared in an aviary environment (AVI group) exhibit the strongest sexual responses to particular songs (Experiment 1), we performed three experiments to un-

derstand the establishment of their preferences. First, we investigated the predisposition for songs in naïve young females (ISO group) reared in total acoustic isolation (Experiment 2). Second, we explored the influence of tutoring from tape recordings during the first weeks of life on later sexual preferences (Experiments 3 and 4). In Experiment 3, we reared one group of females that were exposed to three different songs (one domesticated canary song, D1; one wild canary song, W1; and one pine siskin song, P1). The results in this experiment demonstrated that this acoustic environment influences later song preferences. The sexual responses by females are stronger for the two conspecific tutoring songs than for the heterospecific tutoring song. This may be the result of competition between the heterospecific model and the conspecific ones. Thus, in Experiment 4, we study this problem by the absence of any competing influence between the tutoring songs. Three different groups were constituted. Each group was tutored with only one song (D1 or W1 or P1).

Materials and methods

We studied captive domesticated common canaries, an outbred form with a heterogeneous genetic background. Between 1992 and 1994, males and females were mated at random. Six different groups were formed with the daughters of these pairs. One group (AVI) was made up of nine females raised in an aviary (Experiment 1), one group (ISO) of 10 females was reared in total acoustic isolation (Experiment 2), one group (D1W1P1) of seven females was reared in acoustic isolation from other birds and exposed to three different tutoring songs (Experiment 3) and three different groups of 6 females each was reared in acoustic isolation from other birds and exposed to a taped tutoring song (groups D1T, W1T and P1T, respectively; see below for details of the treatment, experiment 4). For all groups the females, when 20 weeks old, were for 9 weeks subjected to a short day photoperiod (LD 8 : 16). After that, the photoperiod was changed to long days (LD 16 : 8). The females were placed in individual cages (38 × 33 × 26 cm) and provided with nest bowls (10 cm in diameter) and nesting materials (coconut fibres, shredded linen). These conditions led the females to reach a state of reproductive readiness appearing from their copulation solicitation displays (CSD) given in response to taped recordings of male songs. At that time, females were tested to measure their preferences for acoustic stimuli during test sessions. All birds were provided daily with seeds, fresh food, water and vitamins.

Two test sessions were carried out each day for each female between 10:00 and 18:00 (one in the morning and the other in the afternoon) from the end of November until the middle of December (3 weeks allowing for a total of 42 test sessions). During a test session, six different 'song bouts' were successively presented. The order varied at random from one session to another. Each song bout consisted of six repetitions of the same song (duration 8 s) followed by a silent period of 10 s allowing full female displaying. So the total duration

of each song bout is 98 s. A delay of 90 seconds of silent period separated the playbacks of two successive song bouts. Six songs were used: two domesticated common canary songs — D1 and D2, two wild canary songs — W1 and W2 — and two pine siskin songs — P1 and P2 (Fig. 1). The pine siskin *Carduelis spinus*, like the canary, is a member of the family Fringillidae. All songs were copies of natural songs selected to avoid the occurrence of identical syllables. They were edited using an analysis and synthesis software developed by Richard (1991).

Tests were conducted in sound-proof chambers (52 × 50 × 40 cm inside, 80 × 72 × 70 cm outside). Each bird was housed singly in a cage placed in front of a loudspeaker. Playback stimuli were given by a Panasonic tape recorder (RQ-P 155, 50–14 000 Hz) over an Aiwa full range speaker, power booster (SC-A8, 100–18 000 Hz). An observer scored the female's response by watching through a one-way glass and counted the number of copulation solicitation displays during each test. In a complete CSD, the responding female crouches, arches her back, and simultaneously brings her tail forward and her head back. The wings are moved away from the body and are brought in vibration. The feathers surrounding the cloacal region are spread. Incomplete CSDs also occur. In this case, the display is shorter and lacks wing vibration and/or the complete tail movement (Baker *et al.*, 1981). We scored the responses as follows: 0 for no display, 0.5 for an incomplete display and 1 for a complete display. Scores for the different songs for each group of females were compared and tested for significance using the Friedman two-way analysis of variance (F), followed by Student-Newman-Keuls (SNK) for multiple comparisons (Winer, 1971). Scores for the same songs between groups were compared according to the hypothesis that tutoring with a particular song positively influences the later responses to this song. Significances were tested using either the Wilcoxon-Mann-Whitney two sided (WMW) or the Kruskal-Wallis one way analysis of variance by ranks (KW) depending on the hypothesis.

Experiment 1 (aviary females — AVI group)

Nine young females were raised in an aviary environment by their parents until they were 35 days old (or could feed independently). These young females were then placed in an aviary (300 × 200 × 200 cm) where they experienced the songs of several adult males. They had never heard the test songs used in this study before the test sessions.

Experiment 2 (isolated females — ISO group), Experiment 3 (tape-tutored females with 3 different songs) and Experiment 4 (tape-tutored females — DIT, WIT and PIT groups)

Thirty-five females were raised in sound-proof chambers by their mothers alone (the fathers were taken away after copulation). Thirty-five days after hatching, young females were separated from their mothers and brothers (just before the subsong onset of the latter). They were housed 2 or 3 per cage in sound-proof chambers. When 30 weeks old, they were housed separately and were tested. One week after hatching, the 35 females were divided into five groups, distributed as follows.

(1) Isolated females (ISO group)

Ten young females remained isolated from live males or taped tutoring songs in sound-proof chambers. These birds are referred to as the 'isolated females'.

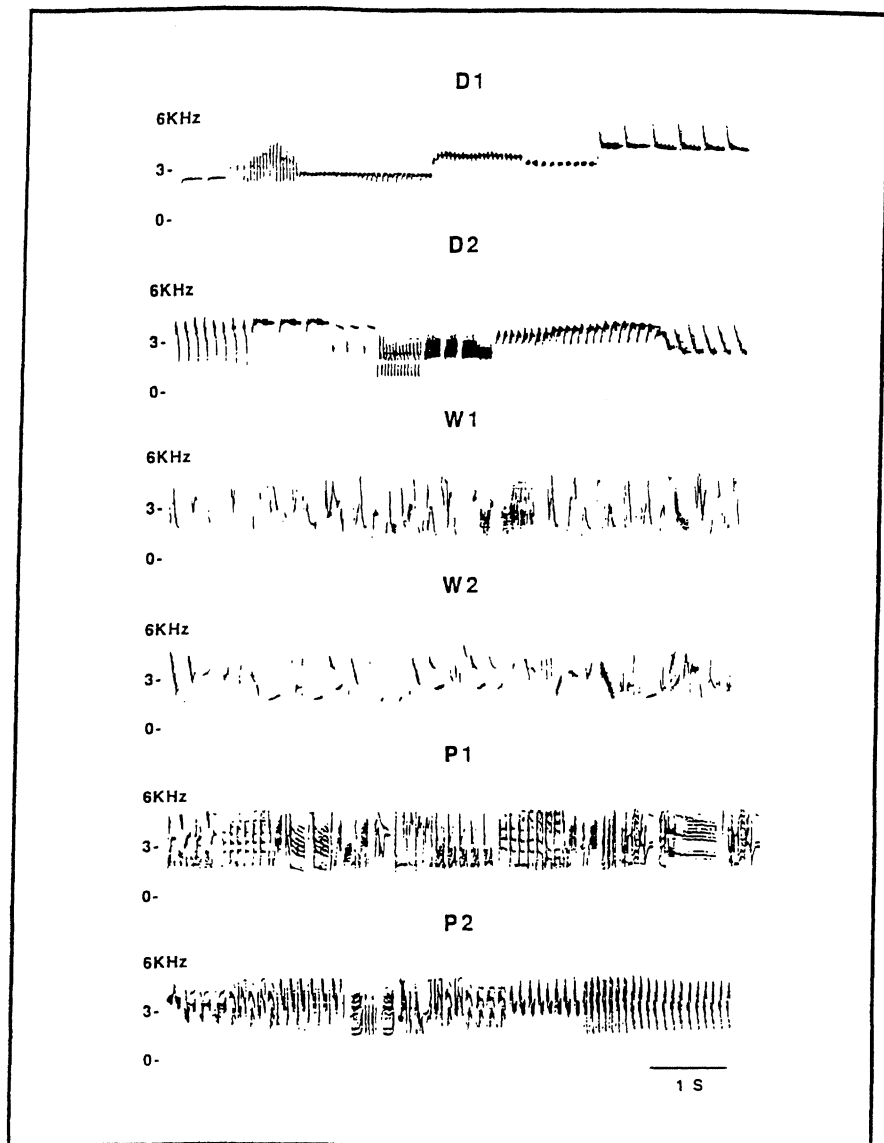


Fig. 1. Sonograms of playback songs used in experiments. From top to bottom: four conspecific songs (two common canary songs — D1 and D2 — and two wild canary songs — W1 and W2) and two heterospecific songs (pine siskin — P1 and P2). Group D1W1P1 was tutored with D1, W1 and P1; group D1T with D1; group W1T with W1 and group P1T with P1.

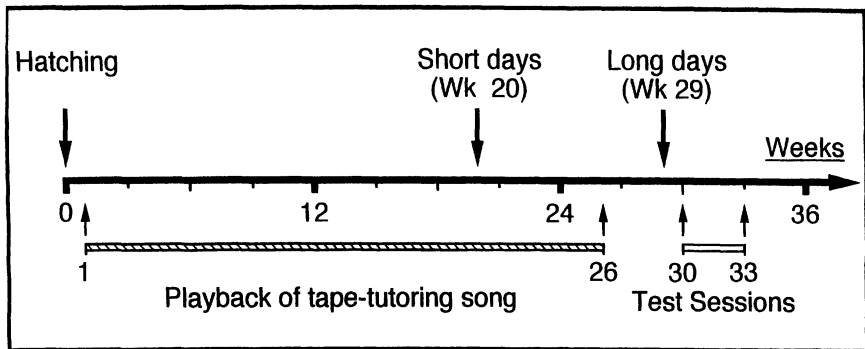


Fig. 2. Outline of the experimental design for groups D1W1P1, D1T, W1T and P1T.

(2) Tape-tutored females (D1W1P1, D1T, W1T and P1T groups)

The interest of these experiments was to determine whether female reproductive response behaviour (CSD) was stimulated by a song heard during their first weeks of life. We hypothesised that tutoring influences female sexual response (Casey & Baker, 1992). Seven females were exposed to D1, W1 and P1 songs during rearing. One week after hatching, young females got playback sessions for 2 h in the morning and for 2 h in the afternoon each day. A 2 h playback session consisted of successive blocks of 10 min, in each block the same song was repeated and each song (duration 8 s) was separated from the others by a pause (duration 10 s). The different blocks corresponding to each song were alternated at random and from one playback session to another the beginning block was also alternated at random.

For the groups tape-tutored with one song, six females (D1T group) were tutored with the taped song D1 (domesticated common canary), six females (W1T group) with the taped song W1 (wild canary) and six females (P1T group) with the taped song P1 (pine siskin). The tape tutoring songs were broadcast 2 h in the morning and 2 h in the afternoon. Each of these playback sessions was composed of the repetition of the same songs (duration 8 s) separated by pauses (10 s).

The taped tutoring songs in all experiments (D1W1P1, D1T, W1T and P1T groups) were broadcast during 25 weeks and was stopped one month before the test sessions. The experimental design for tape-tutored females is shown in Fig. 2.

Results

Intra-group comparisons

There was a significant heterogeneity in the response to the six different songs for the number of copulation solicitation displays in each group (Friedman — F — two-way analysis of variance, aviary group $p < 0.0001$;

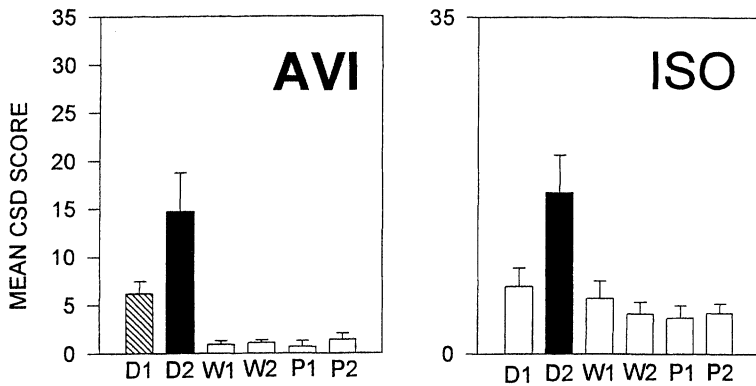


Fig. 3. The mean display score (\pm SE) measures the number of copulation solicitation displays (CSD) of the female canaries for each kind of song: domesticated common canary (D1 and D2), wild canary (W1 and W2), pine siskin (P1 and P2). Significant heterogeneity was tested by using Friedman two-way analysis of variance by ranks. AVI = aviary group (nine females reared in aviary environment exposed to adult domesticated common canary songs in aviary environment), ISO = isolated group (10 females reared acoustically isolated from adult songs). Dark columns indicate significant differences with open columns, hatched column indicates significant differences with both dark and open columns ($p < 0.05$, Student-Newman-Keuls tests). All statistics were non-parametric, so mean values are for illustration only.

isolated group $p < 0.0001$; D1W1P1 group $p < 0.0001$, D1T group $p < 0.0002$; W1T group $p < 0.001$; P1T group $p < 0.006$).

Experiment 1 (aviary females, AVI group)

In this experiment, females were reared in an aviary. All nine females of this aviary group (AVI) gave significantly stronger responses to the playback of D1 and D2 songs than to the playback of the other songs (Student-Newman-Keuls test — SNK — two-tailed, $N = 9$, $p < 0.05$). Females discriminated significantly between D1 and D2 ($p < 0.05$). The song D1 elicited a level of response intermediate between D2 and the other songs (Fig. 3 AVI).

Experiment 2 (isolated females, ISO group)

The females of the isolated group (ISO) responded significantly more often to D2 than to the other songs (SNK two-tailed, $N = 10$, $p < 0.05$).

The females did not discriminate significantly between the other songs (Fig. 3 ISO).

Experiment 3 (tape-tutored females with 3 different songs, D1W1P1 group)

The seven females of group D1W1P1 responded significantly more often to D1, D2 and W1 than to the other songs (SNK two-tailed, $N = 7$, $p < 0.05$). The females did not exhibit a significantly different response to W2, P1 and P2 (Fig. 4 D1W1P1).

Experiment 4 (tape-tutored females D1T, W1T and P1T)

For the six females tutored with song D1 (D1T group), the songs D1 and D2 significantly elicited most of the CSD (SNK two-tailed, $N = 6$, $p < 0.05$). The response scores on the two preferred songs did not differ significantly (Fig. 4 D1T).

In the W1 tape group (W1T), the number of displays given to song W1 was significantly higher than the number of displays given to the other songs (SNK two-tailed, $N = 6$, $p < 0.05$). The group W1T tended to respond more to D2 than to the other songs but the difference was not significant (Fig. 4 W1T).

For the six females tutored with pine siskin song P1 (P1T group), there was significant discrimination between D2 and the other songs (SNK two-tailed, $N = 6$, $p < 0.05$). Responses to the other songs were not significantly different (Fig. 4 P1T). Thus, they preferred the conspecific song D2 and not the tutoring song P1.

Inter-group comparisons

All of the 44 females in the six groups responded with copulation solicitation displays (CSD) to at least one of the six stimuli. With regard to the total number of CSD given by each female to six songs we could calculate and compare the mean \pm SE score displays between the six groups. These scores were 25.1 ± 6.08 for the aviary group ($N = 9$), 40 ± 9 for the isolated group ($N = 10$), 42.8 ± 14.13 for the D1W1P1 group ($N = 7$), 53.2 ± 24.61 for the D1T group ($N = 6$), 41.8 ± 26.43 for the W1T group ($N = 6$) and 45.2 ± 10.33 for the P1T group ($N = 6$). Differences among groups were not significant (KW, $p = 0.517$). But the variability between

the females for their responsiveness in any group was important. Some females gave many CSD while others only a few. So in order to compare the different experimental groups for similar songs we used a ratio. The responses (number of CSD) of each female in each group for each of the following songs — D1, W1, W2, P1, P2 — were divided by their responses to D2 (used as a ‘reference song’). As all the females in any group responded strongly to this song, we first compared the different groups for this song. After that, inter-group comparisons were conducted according

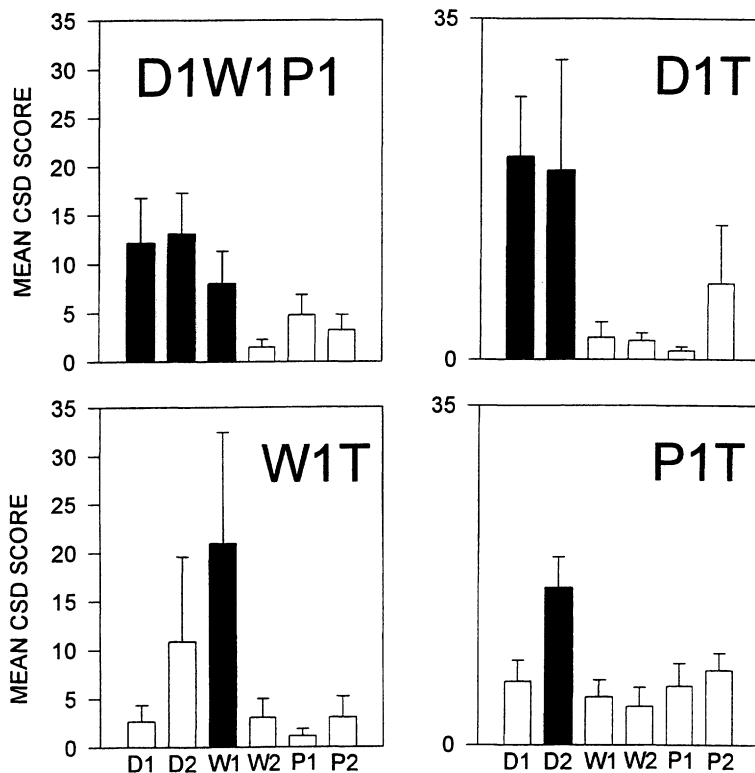


Fig. 4. Mean display score (\pm SE), significant heterogeneity, multiple comparisons and labelling for songs as in Fig. 3. D1W1P1 = seven females tutored with D1, W1 and P1 songs; D1T = six females tutored with D1; W1T = six females tutored with W1 and P1T = six females tutored with P1. Dark columns indicate significant differences with open columns, ($p < 0.05$ in all cases, Student-Newman-Keuls tests). For inter-group comparison between experimental conditions to similar songs see the text. All statistics were non-parametric, so mean values are for illustration only.

to the hypothesis that tutoring with a particular song should increase the preferences for that song.

Comparisons to song D2

There are no significant differences between the six groups to song D2 (KW, $p = 0.15$). Even a comparison between all the groups tutored or experienced with domestic canary songs (AVI, D1W1P1 and D1) and the others (ISO, W1 and P1) shows that there are no significant differences (WMW, $p = 0.897$).

Comparisons to song D1

The groups that got experience with domestic canary songs (AVI) or were tutored with song D1 (D1W1P1 and D1) differ significantly (WMW, $p = 0.015$) from the others (ISO, P1 and W1). There are no significant differences as a whole between these three groups (KW, $p = 0.16$) and respectively between AVI and D1W1P1 (WMW, $p = 0.54$), AVI and D1 (WMW, $p = 0.67$), D1W1P1 and D1 (WMW, $p = 0.25$).

Comparisons to song W1

The groups tutored with W1 (D1W1P1 and W1) differ significantly (WMW, $p < 0.0001$) from the others (AVI, ISO, D1 and P1). There is also a significant difference between the groups W1 and D1W1P1, with females responding more often in group W1 (WMW, $p = 0.005$).

Comparisons to song P1

The groups tutored with P1 (D1W1P1 and P1) differ significantly (WMW, $p = 0.016$) from the others (AVI, ISO, D1 and W1). But there are no significant difference between the groups D1W1P1 and P1 (WMW, $p = 0.93$).

Comparisons to song W2

There are no significant differences for W2 between the groups tutored with the wild canary song W1 (D1W1P1 and W1 *versus* all the others groups; WMW, $p = 0.55$). So tutoring with W1 did not induce a generalisation to W2 of the preferences observed for W1.

Comparisons to song P2

There are no significant differences for P2 between the groups tutored with the pine siskin song P1 (D1W1P1 and P1 *versus* the others groups; WMW, $p = 0.30$). So tutoring with P1 did not induce a generalisation to P2 of the preferences observed for P1.

Discussion

As a whole the results are in agreement with the hypothesis that female song preferences are influenced by previous auditory tutoring and experience. However these acoustic experiences did not override the tendency to display high levels of response to another song (D2) because females, whatever their tutoring, always responded strongly to D2. The females tutored with either W1 or P1 did not show high levels of responses to songs W2 or P2, respectively.

The females of the aviary group AVI (reared hearing adult domesticated common canary songs in an aviary environment) responded preferentially to the two songs of domesticated canaries (D1 and D2). The other songs elicited only a small number of CSDs. Thus, the young females of the aviary group exhibited high levels of sexual behaviour (CSD) when hearing songs with the phonology and syntax of their own subspecies. These results agree with those of Clayton & Pröve (1989), who showed that female zebra finches (*Taeniopygia guttata*) exhibited significantly more responses to playback songs from conspecific males of their own subspecies than to the playback songs from other subspecies or to heterospecific songs.

For females of the isolated group (ISO), we observed that song D2 elicited significantly more responses than other songs. These young naïve females are able to recognise a song of their subspecies without having had prior experience with it. Our results agree with those of other researchers who demonstrated that young female white-crowned sparrows (Nelson & Marler, 1993) and swamp sparrows *Melospiza georgiana* (Dooling & Searcy, 1980), hand-reared and isolated from exposure to conspecific song, can recognise conspecific songs. But in our experiment the high female response was only to song D2 and not to song D1. Moreover we also observed that the females displayed most of their sexual responses when hearing the playback of a special song phrase in D2. These observations are

in agreement with Kreutzer *et al.* (1994) and Vallet & Kreutzer (1995) who demonstrated that adult female canaries are especially responsive to this particular song phrase type. This observation also explains the significant difference between D1 and D2 in an aviary group. In D2, the preferred song phrase contains bipartite syllables composed of abrupt frequency falls and short silences, this kind of syllable was found only in male songs and was never recorded in any female songs, even when the females were implanted with testosterone and sang male-like songs (Pesch & Güttinger, 1985; Vallet *et al.*, 1996). This syllable type also has no similarity with any calls emitted by adult or young canaries. So an influence of the prior acoustic environment, when these young females were with their mother, brothers and sisters, on their later responses is not relevant. One may hypothesise that young female canaries possess a 'perceptual predisposition' (Dooling & Searcy, 1980) or a 'sensory bias' (Ryan *et al.*, 1990) that facilitate the establishment of sexual preferences. But other hypotheses may attempt to account for the female preferences. This syllable is highly comparable to some of the syllable types studied by Nottebohm & Nottebohm (1976) and Hartley & Suthers (1990). These authors stated that the left and right syrinx were both needed to control and produce such a type of syllable. Thus, a special complex syllable is better than other syllables in eliciting female preferences, because a complex signal may be either (1) 'honest', because costly to the emitter, or (2) related to particular male abilities that are important for female mate choice (Zahavi, 1975; Kirkpatrick & Ryan, 1991).

Females raised hearing three different songs (D1, W1, P1) preferred the songs D1, D2 & W1. This result shows that female domesticated canaries have developed strong preferences for two conspecific songs (W1 and D1). Thus, acoustic tutoring influences the development of female song preferences. We also observed that the song D2 elicited significantly more responses than songs W2, P1 and P2, although this song has never been heard by these females (D1W1P1 group). This again indicates that song D2 may contain a song phrase which appertains to the supposed 'perceptual predisposition' of females or the honest signalling of the males. The females of this D1W1P1 group responded less to the pine siskin song P1. The broadcast of three songs simultaneously, in particular one song of the domesticated common canary and one song of the wild canary, may have

prevented the influence of the pine siskin song. If song P1 was played back alone during tutoring, a stronger influence may be observed. In order to address this question we tested tape-tutored females with song P1.

In the group P1 (females reared hearing song P1) there was a significant difference between D2 and the other songs. The number of displays given to song P1 was not significantly different from that of the other songs D1, W1, W2 and P2. But inter-group comparisons demonstrated that the two groups tutored with P1 differs significantly from the others. So compared to tutoring songs D1 and W1, the influence of tutoring song P1 is weaker, as revealed by intra-group comparison, but an influence can be detected by inter-group comparison. Such a weak influence of heterospecific songs was already demonstrated in male song learning (Marler & Peters, 1988). One other possibility for explaining the weaker responses to P1 is that the females do memorise and learn song P1, but that this song does not trigger CSD as conspecific songs do.

All the females tutored with the taped song of the domesticated common canary D1 (D1T group) gave significantly stronger responses to songs D1 and D2 than to the others. Females did not discriminate significantly between D1 and D2. These results are not comparable to those found in the aviary group AVI where D2 was the most salient song.

For the W1 tape group (W1T), our results indicate that young females that had been exposed to wild canary song, exhibited higher levels of CSD when hearing this taped tutoring song (W1) than when hearing the other songs. But inter-group comparisons also demonstrated that when W1 is not in competition with any other tutoring songs there is a stronger influence on later preferences. This effect was not observed with P1 (group D1, W1, P1 *versus* group P1). These results demonstrate first that female domesticated common canaries are able to develop preferences for one conspecific song with different characteristics (syntax and phonology) from their own subspecies and second that 'tutor competition' may influence learning processes for some songs.

In previous studies, attempts to test for song learning in female birds measured either female song production (mostly induced with testosterone) or female song preference (counting CSD when hearing songs). With regard to female song production, learning was demonstrated with females captured in the wild and induced to sing local dialects with testosterone

(Konishi, 1965; Baptista & Morton, 1982). But under laboratory conditions, experiments failed to demonstrate the similarity between female song in adulthood and the songs learned from live tutors when the females were young (e.g. female white-crowned sparrows: Cunningham & Baker, 1983; Baptista & Petrinovich, 1986; Petrinovich & Baptista, 1987). With regard to female song preferences, learning was demonstrated using live tutors (Clayton, 1990) or live tutors reinforced by song playbacks (Casey & Baker, 1992). Our results firstly support the hypothesis that females are more responsive to a song containing a special song phrase whatever their acoustic experiences are and secondly demonstrate that tutoring induces female songbirds to develop an 'acoustic model' which drives their adult song recognition and sexual preferences.

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