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Differential response of female starlings to shared and nonshared song types

M. Hausberger, M. Forasté, M.A. Richard-Yris, C. Nygren

Ethologie,Evolution, Ecologie, UMR CNRS 6552, Université de Rennes I, Avenue du Général Leclerc, F - 35042 - Rennes Cedex.

ABSTRACT: *Differential response of female starlings to shared and nonshared song types.* The behavioural reactions of isolated male and female starlings to different categories of songs were tested using playback experiments. The categories tested included song types that the experimental bird shared with a particular conspecific in an earlier social situation, song types of familiar but not socially associated females, self songs and individual-specific songs. No vocal response was given to the playbacks in the test situation but video-recordings showed differential responses (measured in head movements) to the different stimuli. The strongest reactions were observed for the shared song types, especially in the own songs. These results reveal a long term memory of the particular social value of shared signals.

KEY WORDS: Starling; Song; Song sharing; Social recognition

Introduction

Individual recognition of song has been mostly investigated using responses of territorial male songbirds to playbacks of songs of neighbours vs non neighbours (Falls et al, 1982). Using their aggressive responses, it has been shown that birds do discriminate on the basis of shared songs but also non shared songs, sometimes even atypical (Richards, 1979; Kreutzer, 1987). Birds can memorize the song types of their neighbours even if they do not sing them (Mc Gregor et al., 1986) and even if the repertoires are large (Stoddard et al, 1992). Beletsky (1983) used the same type of procedure to test individual recognition in female red-winged blackbirds (*Agelaïus phoeniceus*). The experiment failed to show any such recognition but the procedure (test in the center of the territory) may not have been adequate to show it. Although the reactions of females to male song characteristics have been extensively studied in laboratory, little is known on their ability to discriminate the song types of their mates (see Halkin, 1995) or of other females. This question is especially interesting in European starlings (Sturnus vulgaris), since it has been shown that song sharing in this species clearly reflects the social organization outside the breeding season (Hausberger et al 1995 b). In particular, females tend to form social pairs where both partners spend most of their time in close proximity and share most of their repertoire.

Such an association between social affinities and vocal sharing has been found in different species recently (e.g. Brown E.D. and Farabaugh S., 1997) and the significance of these shared songs for the birds themselves is intriguing, especially for females.

In the present preliminary study, we test the following questions in extensively studied birds whose social associations were well known.

- do the shared song types have a special meaning for the bird: are they clearly discriminated from the other types in the other's song as well as in the own song?

- does a separation from the social mate prevent discriminating shared songs?

- does a bird discriminate the past social partner's individual types from those of other non socially associated but well known birds ?

- do males show any reaction to songs of females, with whom they have been housed but were not paired?

Starlings do not readily show vocal responses when placed in isolation, and therefore we had to use behavioral criteria to test for a response. Even very slight behavioral responses can have a significance and reveal discriminations (West & King, 1988).

We especially tested the reactions of females to:

1) their own song types: shared or *2)* non shared, *3)* the songs of their past social mate: shared or *4)* non shared, *5)* the songs of familiar females, *6)* the songs of a familiar female that died one year ealier. Social partners had been separated for 8 months.The reactions of males to the songs of familiar females (but not paired with them) were also tested.

MATERIAL AND METHODS

Subjects and housing conditions

The reactions of 4 male and 4 female European starlings to playback of female song were tested. All of them had been wild caught as adults and were between 1 and 5 years old at the beginning of the experiment. After their songs were recorded in individual rooms at their arrival (November 1991), the birds were placed in two adjacent indoor aviaries (M1,M3,F5,F6 in aviary 1, M5,F2,F3 in aviary 2 plus other birds) between December 1991 and March 1992. Behavioural observations showed that F5 and F6 were socially associated as were F2 and F3. None of these males and females were paired together (Hausberger et al, 1995 b). No song could be recorded from the females at that time although some could be heard.

In May 1992, the songs of the females were recorded in separate individual rooms (for more details see Hausberger et al. (1995 a)). They were then kept together until July when F5 and F3 were released in an outdoor aviary with the males and F(6) and F(2) were with two other females in another indoor aviary. Some spontaneous song could be recorded from these females whereas those in the outdoor aviary did not sing.

In October 1992, the four females were placed in individual cages in separate anechoic rooms and injected with testosterone in order to record their songs. In November and December, they were kept in two separate rooms: F5 and F3 in one cage, F2 and F6 in one cage in the other room.

The playback experiments were made in January 1993. Four anechoic rooms were used for the experiments, where the animals were individually housed for a week before the experiment started. (see Fig. 1).

In all conditions, water and food (commercial pellets and apples) were provided ad libitum.

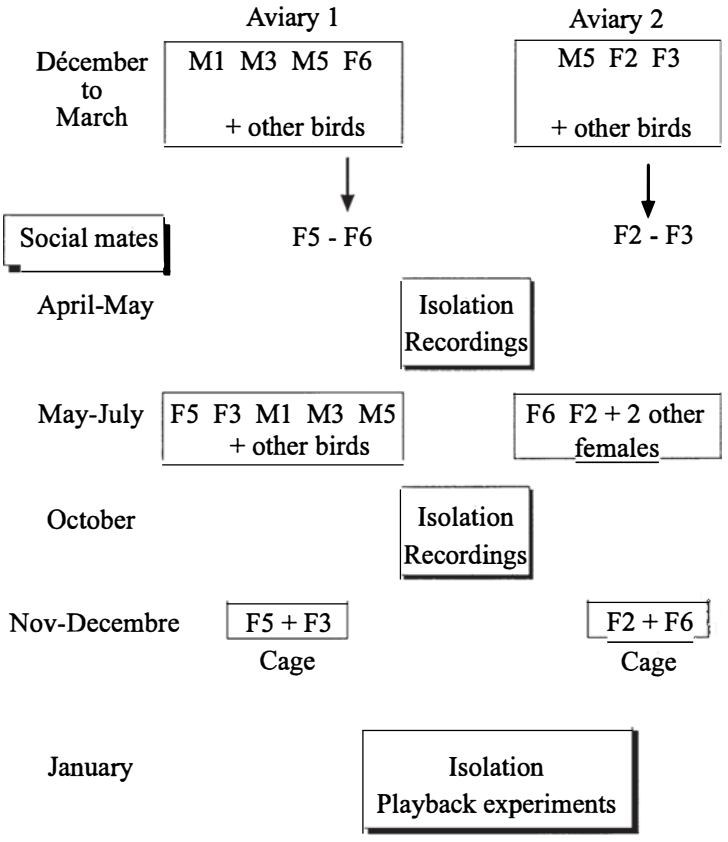

Figure 1: Social conditions of the birds before testing them in January 93. All the observations made in the year before are reported in Hausberger et al, 1995 a, 1995 b.

Only the social mates shared song types, that is F5-F6 and F2-F3. Note that they have been separated for about 10 months when the playback experiments were started.

Experimental tapes

Four groups of female whistles were tested:

* self songs- shared SSS
- unique SSU
* social mate's song types
- shared SMS
- unique SMU
* familiar female's song types:
- shared with her own social mate FFS
- unique FFU

* song types produced by a female with whom none of the females was associated and who disappeared one year earlier, a "control": FC

Given the limited individual repertoire size of whistles (between 7 and 10), only a few whistle types were available for each category. Four types were used from the repertoire of each female: 2 SSS and 2 SSU. Therefore each female could be tested for their reactions to 2 SSS and 2 SSU, the two shared songs produced by their social mate (SMS), 2 unique songs of their social

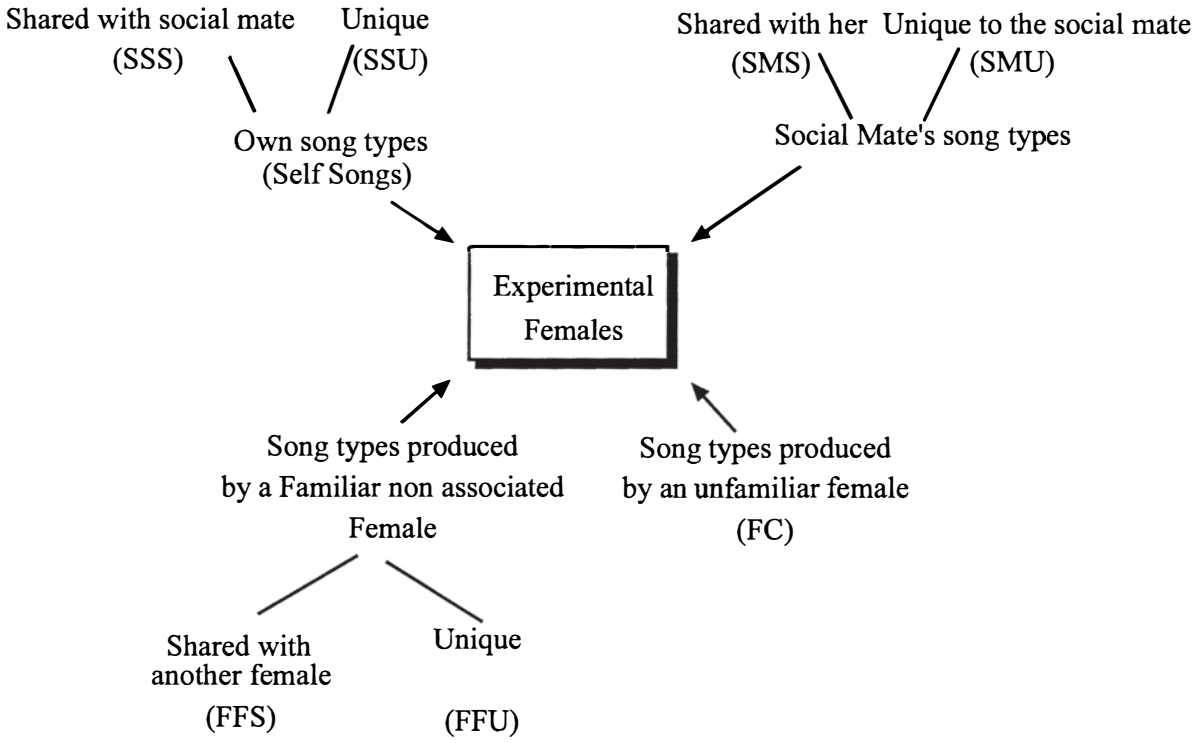

Figure 2: The experimental stimuli. The experimental female is tested with four main categories of songs (see also text).

As an example, if the females F5 is tested, she will have as SMS F6's songs that are shared with her, SMU F6's songs that are unique to F6. FFS will be for example F2's songs that are shared with F3, FFU will be F2's own songs.

mate (SMU), 4 unique song types of each of their familiar females (FFU), 4 song types shared by the 2 familiar females (=4 FFS) plus 4 whistle types unique to FC. (see Fig. 2)

The reactions of the males were tested using the same song types. A tape was constructed using those 20 whistle types that were distributed randomly in regard to category. Successive whistles were separated by 2 mn. Each whistle type was broadcast only once. The total playback lasted for about one hour. The same tape was used for all females so that the same categories of whistles did not appear in the same order for the different females.

Measurement of responses

No vocal response was observed for either males or females under those conditions. The behaviour of the birds was continuously video recorded during the whole playback session. Different parameters were measured afterwards on the tapes (flights, approaches, body movements etc..). The only aspect that seemed to be affected by playback was the movement of the head. Any change in the position of the head (compared to the body axis) was noted. The number of head movements was counted 10 seconds before and 10 seconds after each whistle broadcast.

Material

The songs had been recorded using a Sony TCD5M cassette recorder and Sennheiser MD421 microphones. Sound analysis was made using an Amiga microcomputer, which was also used to build the experimental tape (Richard, 1991). The playbacks were made using a Sony TCD5M cassette recorder and a Sony loudspeaker. The amplitude was adjusted on the Amiga computer so that all whistles were similarly loud and close to natural production.

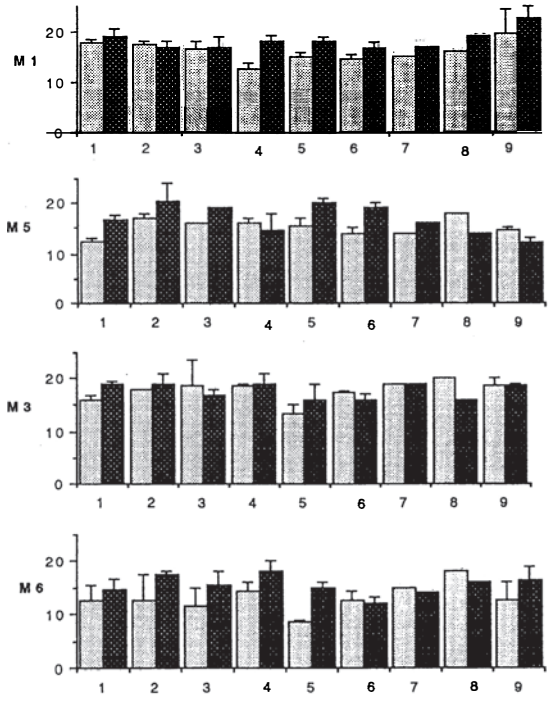

Figure 3: Mean number of head movements (and SD)) of males before and after the playback of females whistles. M1, M3, M5, M6: the individuals males. Before: light grey, after: dark grey.

1,2... the whistles broadcast:: FC, 2: F6 (unique), 3: F6 (shared with F5), 4: F5 (unique), 5: F5 (shared with F6), 6: F3 (unique), 7: F3 (shared with F2), 8: F2 (unique), 9: F2 (shared with F3). (see text).

Statistical treatment

Three types of analyses were performed:
- Individual responses: given the low number of whistle types that could be tested, data concerning a same category were summed for each bird in order to compare the number of head movements before and after playback using a X2 test. General responses to song categories: comparisons of behaviour before and after playback according to song category were made using a Wilcoxon test on clumped data for all females together. In this case, each playback was considered as an independent event (e.g. N=8 for SSS). -Finally, an Anova was performed on the whole data, testing the difference before and after playback in the head movements (number) according to the whistle category broadcast. The data were pooled for the different birds for each category.

The same analysis were made for the males, but of course the categories differed and we compared the reactions to e.g. F2 unique, F2 shared etc.

Results

1 - Males:

No important change was observed in the number of head movements before and after playback for each individual bird (Fig 3). Only slight tendencies could be observed. The Wilcoxon test made on clumped data for all males revealed one significant change after playback: all males tended to increase slightly their number of head movements after hearing the whistles of the female FC (N = 15 T = 13, p = 0.01). However, no difference was observed in the reactions to the different whistle types using the ANOVA (p =0.2).

Therefore, the males did not show any important reaction to the female whistles, as measured by head movements.

They only showed a slight increase of their movements to an unfamiliar female. All songs of the familiar females seemed to be just a "normal background".

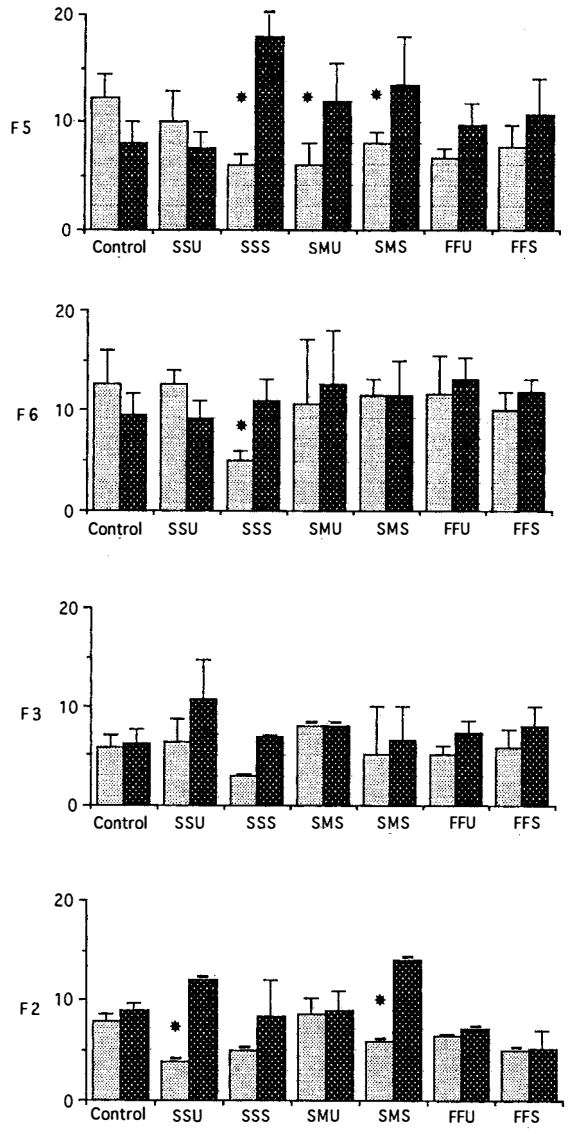

Figure 4a: Mean number of head movements (and SD) of females (light grey) or after (dark grey) the playback of female whistles. F5, F6....: females tested; the whistle categories broadcast; Control: FC songs; SSU: self songs (unique); SSS: self songs (shared with other female); SMU: social mate's unique songs; SMS: social mate's shared songs; FFU: familiar female (unique); FFS: familiar female (shared whith other female. (see text). Significant differences: *: $p<0.05$.

2 - Females:

The reactions of the individual females tended to be similar, with no obvious response to the familiar non associated females for any of them (Fig 4). The only significant responses were observed for self songs or the social mate's songs. There was a general tendency for an increase of the head movements for the SMS. But the most obvious trend is a clear increase in response to the playback of the self shared songs. Interestingly, there was little evidence of a response to the self songs that are unique to the bird, apart from the female F2. These findings were confirmed when the general responses to the categories of whistles were considered. The only significant response corresponded to a clear increase in the number of head movements after the playback of the shared self songs (N8, T = 0, p =0.03).

Looking now at the differences in the number of head movements, it appears clearly that the different categories of whistles elicit differential responses (anova p=0.009). The increase of head movements is higher for SSS compared to the songs of familiar non associated females and the "control" ($p<0.02$, $p< 0.003$, Fig. 3). No significant difference was found between the SSS and the social mate's songs (SMS or SMU).

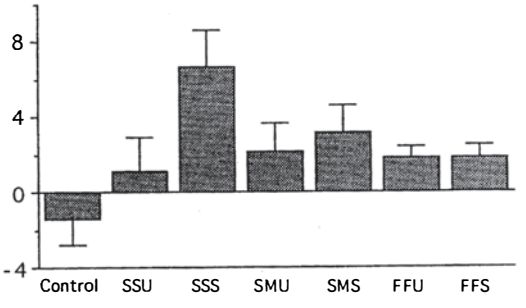

Figure 4b: Changes in the number of head movements after playback of female whistles to females (number of movements after minus the number before): mean and SD. The data are clumped for the 4 females tested.

Discussion

This preliminary study shows that it is possible to test the discrimination of song types by female starlings by measuring slight behavioral changes in response to playbacks. The females reacted mostly for their own song types but only if they were shared with a social partner. They did not show any special reaction to their own unique songs or to the songs of familiar non socially associated females, nor did the male react to these songs. The shared songs therefore appeared as a particular category for the birds, even though they corresponded to social associations that were stopped for more than eight months.

Non vocal responses could be observed which confirms the importance of context in the types of response to playback (Smith, 1991). Visual input or a more interactive condition might be necessary to elicit the usual song matching interactions observed. Most studies of song type discrimination in captivity have used a conditioning procedure (Stoddard et al, 1993; Dooling et al 1986). Perceptual abilities of starlings have been tested using such methods (Hulse & Cynx, 1985; Klump & Maier, 1989). By conditioning, the animals may however learn to do more discriminations than they would in a naturalistic situation (Snowdon, 1987) and many recent studies on categorization use sensory reinforcement (Thompson, 1995). Using visual items, it is possible to observe the direction of gaze; such active "search for perception" is more difficult to assess when auditory stimuli are involved. Few types of studies use precise behavioral measurements on isolated animals when testing responses to playback. In general, their aim is to test the signal value with regard to reproduction with an emphasis on the sollicitation displays of females under hormonal treatment (Searcy & Marler, 1981) or not (Nagle et al, 1993). However very fine changes of behaviour can reflect a discrimination of song types (King & West, 1983).

In our study, amongst all behavioral measurements, only the head movements seemed to reflect reactions to different song types. This may show an active search for the animal for the origin of the stimulus heard: moving the head may help detect the direction. Such measurements are therefore reminding of measurements of the direction of gaze in experiments using visual items. Such experiments aim at understanding how individuals react and therefore few animals can be considered, especially if, as it was the case here, an extensive knowledge of the social life and song repertoires of each animal had to be acquired first. The experimental design was adapted to questions on individual reactions (one bird, several stimuli) rather than the more usual approach using many subjects with few stimuli (Kroodsma, 1989). Despite of this limited sample, general trends appeared. None of the males or females showed any clear reaction to the playback of the songs of familiar birds, with whom they did not have a particular social bond. In this context at least, female whistles did not seem to elicit any response in the males. For females, shared songs obviously had a particular significance, especially in self-songs. In general, they did not react particularly to their own unique songs, which implies that shared songs really are special. These song types had not been produced more than non shared types and moreover some of them had not been emitted by the experimental birds since they had been separated from their social mate (Hausberger et al, 1995 b). This suggests that this special attention to shared songs reflects a long term memory of a particular social value of these themes. Long term memory has also been shown to be involved in the song learning process in starlings (Chaiken et al, 1994) This may be a memory of a given emotional level for example rather than of an "image" of the social mate, since this higher level of reaction is observed more in own songs than in recordings of the mate itself. Song matching between social mates is frequent and an associative learning may have occurred between shared songs and a positive social interaction. Further investigations are needed but this phenomenon might be another example of "social categories" in animals (Cheney et al, 1986).

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