

Audience drives male songbird response to partner's voice

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Abstract

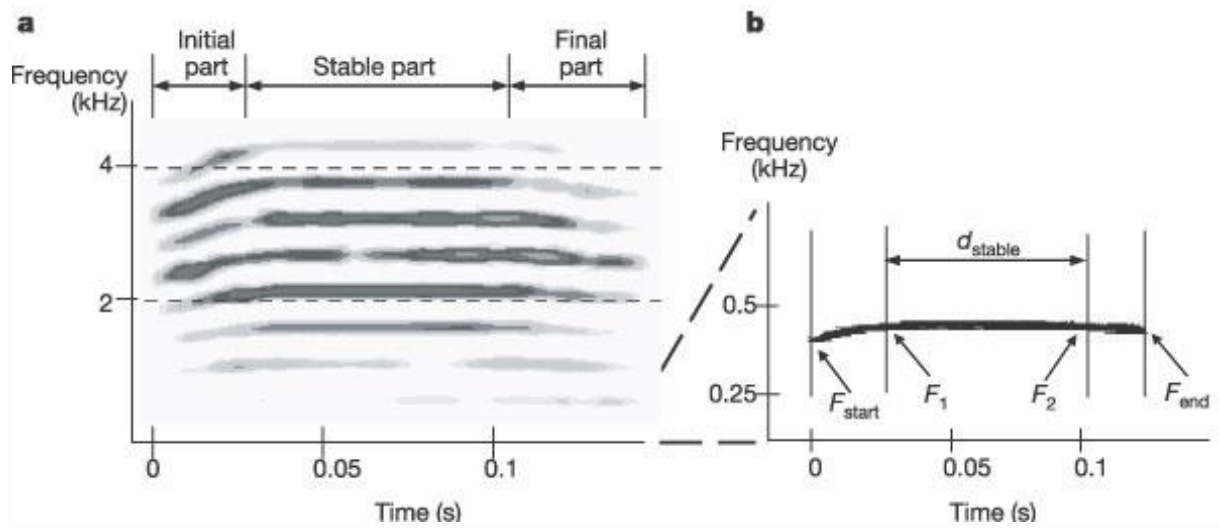
According to the social intelligence hypothesis, social context represents an important force driving the selection of animal cognitive abilities such as the capacity to estimate the nature of the social relationships between other individuals^{1,2,3,4}. Despite this importance, the influence of this force has been assessed only in primates and never in other animals showing social interactions^{5,6,7}. In this way, avian communication generally takes place in a network of signallers and receivers, which represents an audience altering individual signalling behaviours^{8,9}. Indeed, vocal amplitude¹⁰ and repertoire¹¹ are known to be socially regulated and the attitude towards the opposite sex may change depending on the audience^{8,12,13}. This 'audience effect'^{8,14,15,16} provides support for the reality of social awareness in some bird species. However no evidence has yet been found to suggest that birds are able to estimate the characteristics of the social relationships between group-mates. Here we show that the male of a gregarious songbird species—the zebra finch (*Taeniopygia guttata*)—pays attention to the mating status of conspecific pairs, and uses this information to control its behaviour towards its female partner.

Zebra finches are monogamous flock-forming birds that seem to use acoustic recognition for pair-bond maintenance^{11,17}. A number of different vocalizations are produced by this species¹¹, distance calls being the most frequently emitted by both males and females. Distance calls are used by the members of a pair to remain in contact when the flock is foraging or feeding and especially when the birds lose visual contact with each other¹¹. As in many gregarious species, vocal recognition is thus likely to be a key component of reproductive success and it should be supported in both sexes by acoustic cues of distance calls^{18,19,20}.

Previous laboratory experiments testing isolated birds demonstrated that the female zebra finch is able to recognize its mate's vocalizations from other males' vocalizations¹⁷, but never succeeded in demonstrating a mutual acoustic recognition between mates¹¹. In the natural biological context described above, it is very unlikely that wild male zebra finches do not recognize their mates' voices. Two main hypotheses can thus be envisaged: either captive zebra finches have lost some cognitive capacities because of domestication (for instance, females' calls may be less individualized, and/or males may no longer be able to recognize them), or tested males do not show preferential response to their mate's voice owing to a modification of their natural behaviour by their socially isolated position during the playback tests. Indeed social isolation could be a situation of stress in comparison to the natural context where the zebra finch lives in large groups and experiences permanent social interactions that may influence mate-directed behaviour.

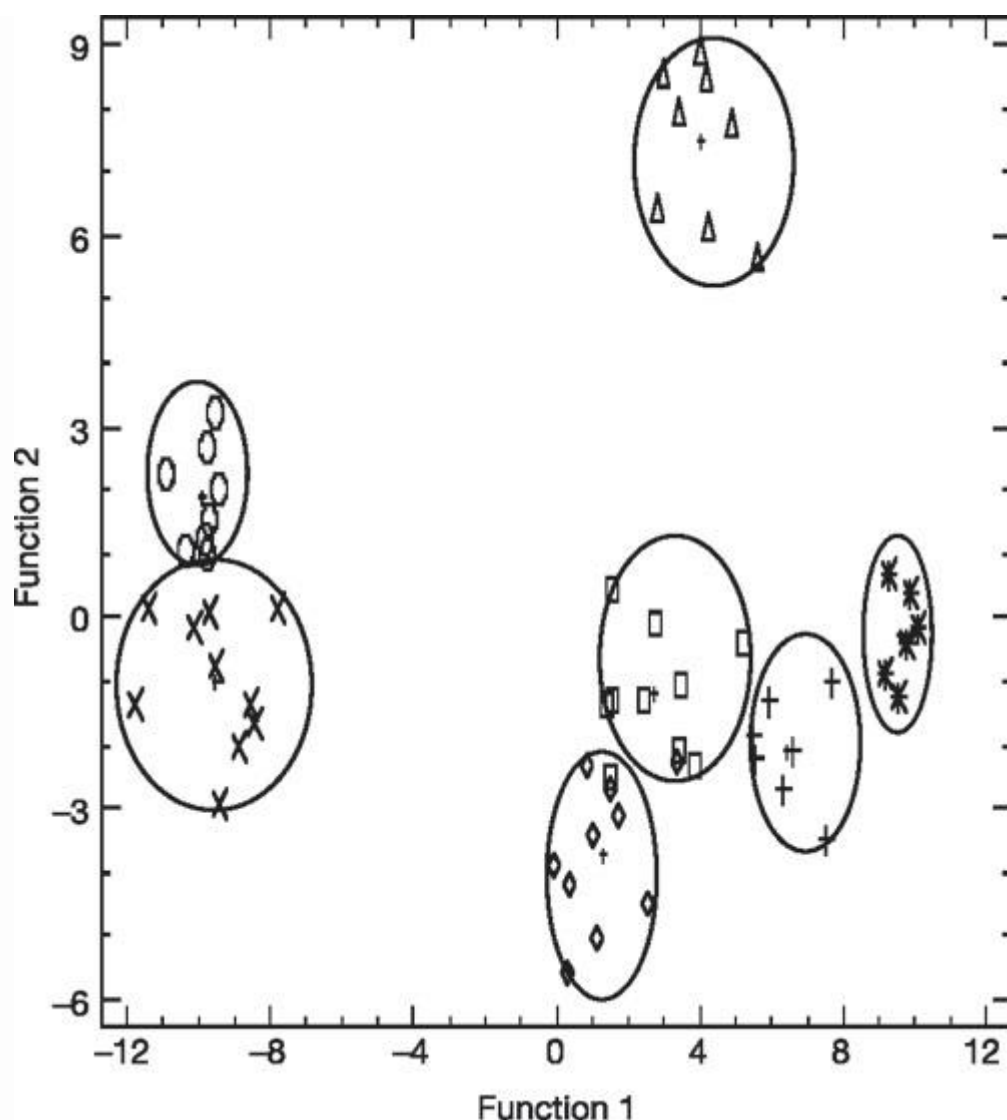
To determine whether the vocalizations of female zebra finches support mate recognition, we analysed the acoustic structure of distance calls, searching for acoustic cues which could encode the emitter's individual identity. The female distance call is a complex sound with a fundamental frequency associated with several harmonics ([Fig. 1a](#)). This sound is frequency- and amplitude-modulated. With reference to frequency-modulation characteristics, the distance call can be divided into three segments of different durations ([Fig. 1a](#)): the initial segment defined by a rapid and loud ascending frequency modulation, a long and loud second segment with no frequency modulation (the stable part), and a third segment defined by a rapid and soft descending frequency modulation. To assess which of these spectral, amplitude and temporal cues could support individual identity coding and thus vocal recognition by males, we defined a set of 17 parameters describing the acoustic structure of the call, and measured the intra-individual and inter-individual variability of each parameter with a non-parametric analysis of variance. For each measured parameter the difference between the females is significant (Kruskal–Wallis ANOVA, $P < 0.05$) and the variation within individuals is smaller than that among individuals. In particular, the four spectral parameters (F_{start} , F_1 , F_2 , F_{end} ; [Fig. 1b](#)) describing the frequency modulation of the fundamental frequency are highly individualized (potential for individual identity coding values (PIC) >2 ; see Methods). The discriminant analysis based on the whole set of analysed acoustic parameters allows us to discriminate among 100% of the seven females ([Fig. 2](#)). According to our analysis, it thus appears that female distance calls contain potential cues to support individual identity coding and thus recognition by males.

Figure 1: Acoustic structure of the distance call of the female zebra finch.



a, Spectrogram of the call of a female zebra finch. The call can be divided into an initial part (rapid and loud ascending frequency modulation), a long and loud second part with no frequency modulation (the stable part) and a final part (rapid and soft descending frequency modulation). The amplitude modulations are represented by a greyscale. **b**, Acoustic cues characterizing the fundamental frequency: the beginning frequency (F_{start}), the frequencies at the start and at the end of the second part (F_1 , F_2), the frequency at the end of the third part (F_{end}), and the duration of the second part (d_{stable}).

Figure 2: Discriminant analysis on the 17 acoustic parameters of the female call.



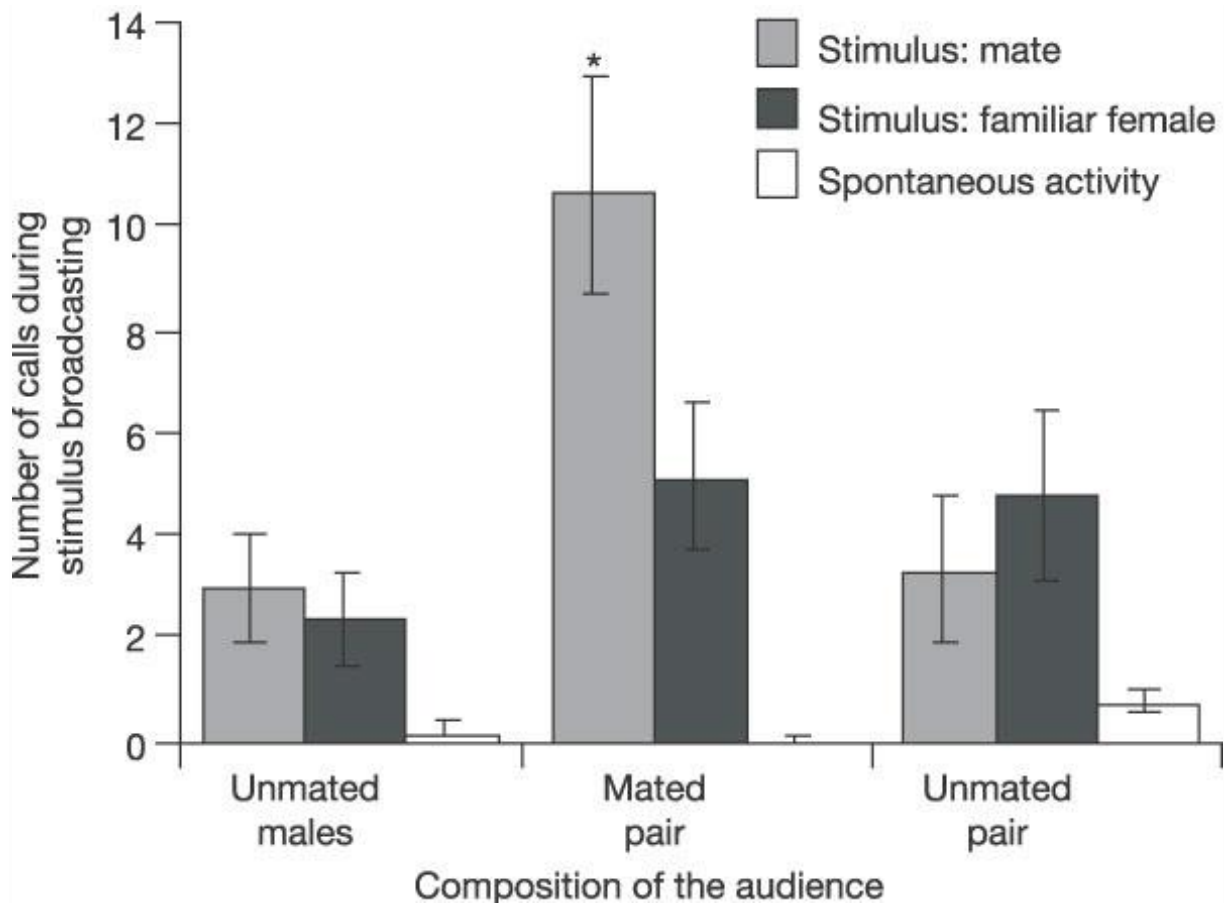
The calls of seven individuals are represented according to the two main functions of the analysis. Each female is represented by one symbol and each point corresponds to one analysed call. The seven females are discriminated, so the distance calls could support individual identity coding.

To investigate whether mate recognition by males is affected by the current social context, we tested to see whether the vocal response of males to their partner's calls and to the calls of a familiar female changes depending on the composition of the audience. We performed playback experiments with 15 male zebra finches. Each of these birds was paired for several months with a different female and raised at least one brood. The tested male was separated from its mate, put in an experimental cage one night before the test, and assigned to one of the following social contexts: (1) the 'unmated males' context: two single males were placed in a companion cage near the experimental cage, (2) the 'mated pair' context: a normal male-female pair was placed in the companion cage, and (3) the 'unmated pair' context: a male and a female that were not paired were placed in two different companion cages. During playback, the male, accompanied by its audience, was presented with two sets of stimuli: a series of calls of its mate and a series of calls of a familiar female. The male's response was

assessed by counting the number of calls emitted during the stimulus broadcasting. The audience behaviour in response to stimuli was also monitored. Before the playback, the 'spontaneous' activity of the male was always very low (Fig. 3) and not dependent on the audience (Kruskall–Wallis ANOVA, $P = 0.069$). Whereas the audience behaviour seems to be fully independent of which female's calls were being presented (Wilcoxon matched-pairs test: 'unmated males', $P = 0.892$; 'mated pair', $P = 0.419$; 'unmated pair', $P = 0.715$), the sex and the mating status of the accompanying birds modified the response of tested males to the playback of the calls of their mate (Kruskall–Wallis ANOVA, $P < 0.04$) (Fig. 3). When the male was in the presence of an established male–female pair, its vocal response was significantly stronger to its partner's calls than to the familiar female's calls (Wilcoxon matched-pairs test, $P < 0.05$). Alternatively, when the male was in the presence of unmated conspecifics, that is, two single males or one single female and one single male, its response did not differ significantly between the two stimuli sets (Wilcoxon matched-pairs test, $P = 0.593$ and 0.138 , respectively), showing no preference to the calls of its own mate.

Finally, the audience did not seem to influence the male's response to the calls of a familiar female (Kruskall–Wallis ANOVA, $P = 0.348$). These experiments clearly show that male zebra finches have the ability to recognize their mate's voice, but that partner acoustic recognition is expressed differently according to the social relationships between accompanying birds. This effect of social context on acoustic communication in songbirds is in accordance with neurophysiological data: birds recorded in isolation or in visual and auditory contact with a female show different levels of electrophysiological activity²¹ and ZENK gene expression²² within auditory brain nuclei.

Figure 3: Response of male to female voices as a function of the mating status of the audience.



The tested males were placed in different social contexts: (1) 'unmated males' (two single males placed in a companion cage), (2) 'mated pair' (a normal male–female pair in a companion cage), and (3) 'unmated pair' (a male and a female, not paired, in two different companion cages). Asterisk, significant difference between the male responses to mate and familiar female in the 'mated pair' context. The 'spontaneous' activity of the male (in the absence of any playback stimulus) is reported. Error bars indicate standard errors.

The present results support the idea that songbirds are capable of behaviours that are not just "incidentally communicative"^{12, 13}. In spite of the fact that recognizing one's partner is often crucial to reproductive success, the vocal response to one's mate does not seem to be reflexive but can be modulated by the presence of companions. Moreover, this precise regulation of signalling behaviour with regard to the mating status of conspecifics provides evidence that songbirds experiencing gregarious life can show awareness of social relationships comparable to those demonstrated by social mammals such as primates⁷. This ability might be linked to the cognitive demands of social living^{3, 4}, which are potentially an important force driving the evolution of intelligence. Indeed, one possible ultimate explanation of why male songbirds may respond to their partner's voice in the presence of a paired audience might be that the presence of a mated male expressing female-guarding behaviour could stimulate similar mate-guarding signalling by the tested male. Finally, our work emphasizes that playback results can be influenced by the presence of a particular audience, stressing the importance of considering the social environment during experiments.

Methods

Adult zebra finches (*Taeniopygia guttata*) served as the subjects for this study and were naive to all testing procedures. Birds were bred in an aviary (12 h light/12 h dark photoperiod with adapted wavelengths); food and water were provided *ad libitum* and temperature was maintained between 23 and 25 °C. All birds were paired for several months and raised at least one brood. All experiments occurred between 9 a.m. and noon. During testing periods, temperature, food and water conditions were the same as in the aviary. The experimental protocols were approved by the Jean Monnet University's animal care committee.

Seven female zebra finches were recorded for analysis of female distance calls. Each female was isolated from its mate and seven to ten distance calls were recorded with a Sennheiser MD42 microphone, placed 0.3 m above the cage, connected to a Marantz PMD690/W1B recorder with 22,050-Hz sampling rate. We analysed a total of 65 female distance calls using Syntana software²³ and Praat version 4.0.19. We defined seventeen spectral, temporal and amplitude acoustic cues to describe the calls' acoustic structure. These measured parameters allowed statistical analysis of the cues potentially supporting individual identity coding and thus recognition by males. We performed a non-parametric analysis of variance (Kruskall–Wallis ANOVA, $P = 0.05$) and a principal components analysis, followed by a discriminant analysis. To describe the intra-individual and inter-individual variations of each parameter we used the coefficient of variation (CV)²⁴. For each parameter we calculated CV_i (within individual CV) and CV_b (between individual CV) according to the formula for weak samples: $CV = \{100(SD/X_{\text{mean}})[1 + 1/(4n)]\}$ where SD is standard deviation, X_{mean} is the mean of the sample and n is the population sample²⁵. To assess the potential of individual coding (PIC) for each parameter, we calculated the ratio $CV_b/CV_{i, \text{mean}}$ ($CV_{i, \text{mean}}$ being the mean value of the CV_i of all individuals). For a given parameter, a PIC value greater than one suggests that this parameter may be used for individual recognition because its intra-individual variability is smaller than its inter-individual variability.

A synthetic copy of three distance calls of each female was created with Avisoft-SAS Lab Pro software (version 4.16, 2002) in order to have experimental signals with neither any background noise nor sound degradation. These synthetic calls were used for playback tests. For playback tests, each tested male bird ($n = 15$) was separated from its mate and placed in an experimental cage (240 × 50 × 50 cm, equipped with roosts) one night before the start of stimulus presentation. The experimental cage was in a soundproof chamber with a 12 h light/12 h dark photoperiod. Another cage was placed near the experimental cage in the chamber: this companion cage contained the two birds defining the social context. This audience was composed of different individuals during each trial. The playback equipment was constituted by two high-fidelity speakers (JBL TLX 12) connected to a DAT recorder (Sony DTC-ZE 700) placed at either end of the cage. During each test only one randomly chosen speaker emitted the playback stimuli (sound level, 70 dB at 1 m). The tested male was presented with two sets of stimuli: a series of distance calls of its mate and a series of distance calls of a familiar female (series were broadcast at random; series duration, 5.0 s, one call per second; interval between series, 30 s). As all the birds (audience birds, tested males and their mates, familiar females) had been bred in the same aviary, all acoustic stimuli can be considered as perceptually equivalent for the audience birds. The vocal and locomotor activity of the bird was recorded with a video recorder (Sony DCR-TRV24E) and the number of distance calls emitted during the broadcasting of the stimuli was counted. The audience behaviour was similarly assessed. Before the playback broadcasting, the male 'spontaneous' activity (call rate per 5.0 s) was also measured. The effects of the mating status of the accompanying birds on the 'spontaneous' activity of males and on the response of males to the playback of the calls of their mate or of a familiar female were analysed with Kruskal–Wallis ANOVAs ($P = 0.05$). Complementary tests (Wilcoxon matched-pairs test²⁴, $P = 0.05$) were performed to compare the responses to both stimuli in each social context. We also tested whether the audience behaviour was independent of which female's calls were being presented (Wilcoxon matched-pairs test, $P = 0.05$).

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Competing interests statement

The authors declare no competing financial interests.