

Nightingales respond more strongly to vocal leaders of simulated dyadic interactions

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Although vocal interactions in songbirds have been well studied, little is known about the extent to which birds attend to their conspecifics' interactions. Attending to others' interactions can provide valuable information since vocal interactions are often asymmetrical and can reflect differences in the state or quality of the signallers. Playback experiments with simulated dyadic interactions showed that male territorial nightingales (*Luscinia megarhynchos*) attend to asymmetries in interactions and respond more strongly to rivals that overlap the songs of their counterpart. In order to test if nightingales respond differently to two interacting rivals that are alternating songs asymmetrically (with leader–follower roles), we simulated an interaction using a dual-speaker design. Subjects discriminated between the simulated singing strategies and responded more intensely at the loudspeaker playing the preceding songs. This suggests that individuals whose songs precede in an interaction when there is no acoustic overlap are perceived as more serious rivals. Intense responses to the preceding songs compared with intense responses to the overlapping (non-preceding) songs in a previous study also indicate that discrimination is not the result of one specific proximate cue such as greater attention to the first- or last-heard stimulus. Thus, these results provide further evidence that by listening to asymmetries in conspecifics' vocal interactions, receivers can obtain valuable information on their relative differences.

Keywords: *Luscinia megarhynchos*; asymmetrical interactions; birdsong; eavesdropping; long-range communication; nightingales

1. INTRODUCTION

In many communication systems, interactions between two individuals are conspicuous and can be observed by others. This holds particularly in long-range acoustic interactions, and also at close range for other means of signalling, such as visual or tactile. In these cases, individuals that are not primary addressees can extract information on differences in their conspecifics by observing their interactions (Otte 1974; Freeman 1987; Endler 1992; Klump & Gerhardt 1992; McGregor & Dabelsteen 1996; Naguib & Todt 1997; Oliviera *et al.* 1998).

Such transfer of information during an interaction beyond the primary addressee can play an important role in communication and social behaviour. In interactions between two males, other observing ('eavesdropping') males could gain information on their potential competitors and use this information in subsequent behaviour. Extracting information on relative differences among males by attending to their interactions also might be an important source of information for females seeking a mate. Such a way of gathering information is particularly valuable when interactions reveal differences among the interacting individuals, as often occurs during vocal interactions in territorial song birds. So far, few studies have shown that birds indeed attend to vocal interactions of

others and use this information in their decisions to respond (Naguib & Todt 1997).

Male territorial nightingales (*Luscinia megarhynchos*) can use different singing strategies with regard to the timing of songs, either by alternating songs with a conspecific singer, by overlapping a conspecific's songs, or by not reacting specifically ('autonomous' singers). Such asymmetries in the timing of their songs are thought to reflect differences in social state and status (Hultsch & Todt 1982). Furthermore, studies in other species on timing of songs during vocal interactions have shown that difference in the timing of songs is functionally important (Todt 1981; Kramer & Lemon 1983; Popp 1989; Brindley 1991; Nielsen & Vehrencamp 1995; Dabelsteen *et al.* 1996, 1997). Song overlapping, for instance, in many cases is used and perceived as an agonistic signal (Todt & Naguib 1999).

Recent playback experiments on male territorial nightingales showed that they discriminated between two simulated rivals on the basis of asymmetries in their vocal interactions. They responded more strongly to simulated rivals that were acoustically overlapping songs of their counterpart, and thus were more threatening (Naguib & Todt 1997). The subjects' behaviour indicated that information obtained from these asymmetries is important for their decisions on how to respond. The highly dynamic vocal interactions in birds usually involve other asymmetries as well. Such asymmetries can be evident in differences in latencies of song onset during alternating singing or in vocal matching. Several studies suggested that these kinds of asymmetries also reflect differences in state or

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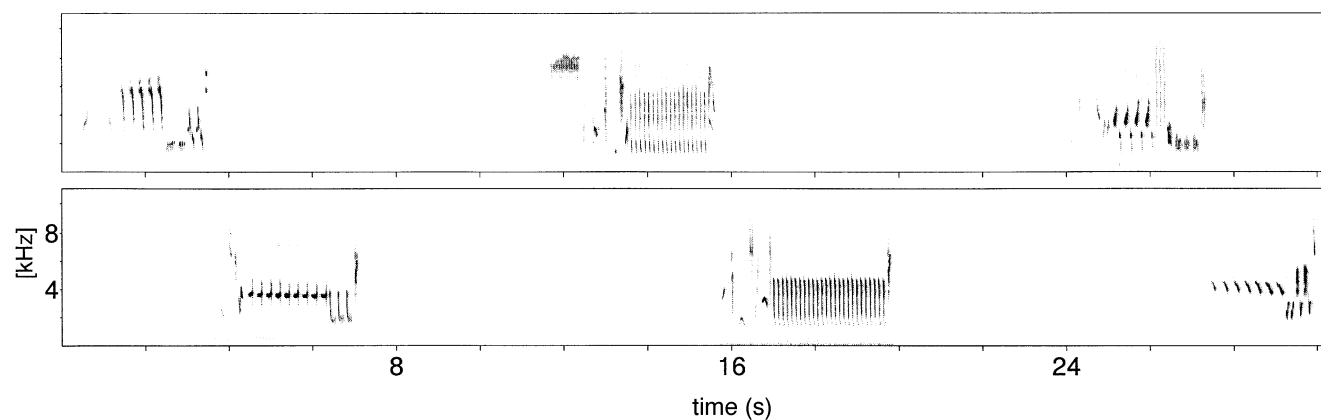


Figure 1. Sonagrams of part of a song sequence used for playback. Songs on channel 2 (below) follow songs on channel 1 (above) with short latencies (see text).

motivation of the two singers (Kroodsma 1979; Todt 1981; Wolffgramm & Todt 1982; Popp 1989).

In this study we investigated whether or not male territorial nightingales discriminate between two interacting rivals that are alternating songs asymmetrically. We used the same dual-speaker playback design as in a previous experiment (Naguib & Todt 1997) to simulate an asymmetrical interaction of two rivals near a subject's territorial boundary.

Songs from one loudspeaker followed songs from the other loudspeaker with shorter latencies than vice versa (figures 1, 2*a*). This design allowed us to assess further functional consequences of asymmetrical vocal interactions, and to make comparisons with the previous experiment. The three possible outcomes and their explanations were:

- (i) if asymmetries in vocal interactions play a role only when there is acoustic overlap, then subjects should not discriminate between the loudspeakers; or
- (ii) if they were to regard the rival that sings the following songs as being more salient, then they should respond more intensely to the loudspeaker that broadcast the following songs; or
- (ii) if they regard the rival singing the preceding songs as more salient, they should use a different proximate cue than they did in the previous experiment on song-overlapping, and respond more to the loudspeaker that broadcast the preceding songs.

2. METHODS

(a) General

We conducted playback experiments from 1 to 5 May 1997 on 19 male territorial nightingales in Berlin, Germany. The birds started to establish territories by singing during the last week in April. We mapped subjects' territories by observing birds and by plotting song posts on a map of the study area, starting a few days after arrival of most singers and continuing throughout the time in which playbacks were conducted.

(b) Experimental procedure

(i) Selection of songs and construction of playback tapes

The songs that we used for playback were recorded in preceding years from nocturnally singing nightingales at locations out of earshot from the territories used for the

experiment. We then selected 15 different song types from each of four individuals. All songs were digitized with 16-bit accuracy and a sampling rate of 22 500 Hz on a PC using Avisoft-pro software (R. Specht, Berlin). Songs were then high-pass filtered with a cut-off frequency at 500 Hz (using a Butterworth filter function).

Because we intended to simulate a vocal interaction between two rivals we constructed stereo files using Creative Wave Studio (Creative Technology Ltd) on a PC with 15 songs of one individual on one channel and 15 songs of another individual on the other channel. To avoid confounding influences by particular songs or individuals we constructed four such tapes. Songs from the same two individuals were used for two different tapes, with songs from each individual being the preceding songs on one tape and the following songs on the other tape.

We arranged songs asymmetrically with each song on channel 1 being followed by short latencies (after 80–140 ms) by a song on channel 2 (figures 1, 2*a*). In order to allow subjects to sing without being overlapped by songs from either channel, each subsequent song on channel 1 then started after longer latencies (3.4–4.2 s) after the end of the song on channel 2. Song lengths and lengths of silence between songs were the same as in the previous experiment with song overlapping (figure 2*b*; Naguib & Todt 1997) to avoid such variables affecting responses differently in the two experiments.

(ii) Playback experiments

We conducted all playbacks between 04.55 and 10.00 except one playback which started at 19.30. Each subject received one playback treatment. We used the stereo tapes described above to simulate an interaction between two rivals by two loudspeakers (Olympus SP5 active loudspeakers) connected to the two channels of a Sony TCD-D10 DAT recorder.

We set up loudspeakers only when a subject was singing, so that we knew its location. We then positioned the loudspeakers *ca.* 25 m apart and at *ca.* 15 m from a subject's song post, but at least 5 m inside the estimated territory. We positioned the loudspeakers in a tree 1.5–2 m above the ground. In order to minimize effects of absolute and relative locations of the loudspeaker, we set up speakers only when subjects were singing on a post that allowed us to position the speakers at locations that we assessed as equally salient for the territory. Both loudspeakers were connected via a stereo-adaptor to the headphone output of the DAT recorder. We then recorded subjects' vocal responses during the playback and during the following 10 min with a Sennheiser ME66/K6 ultra-directional microphone on one

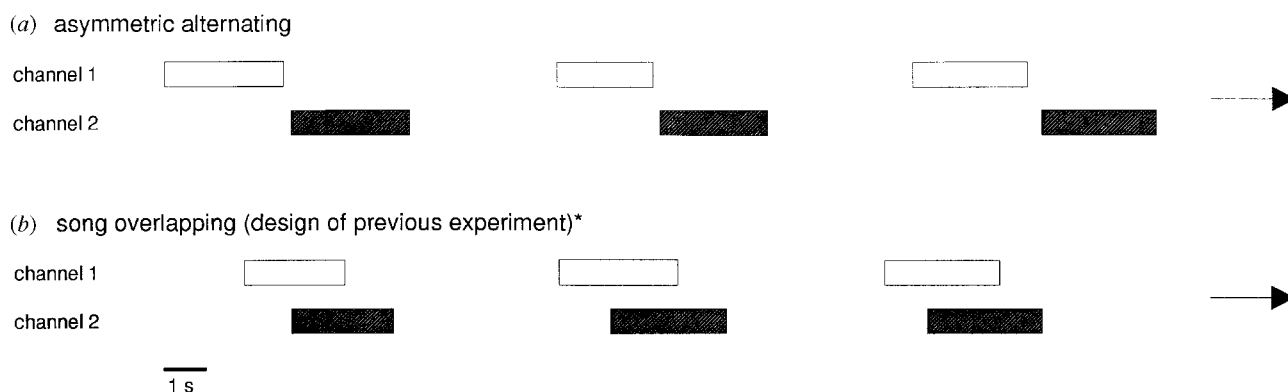


Figure 2. Symbolized succession of songs on the two channels (a) in this experiment and for comparison (b) in the previous experiment with song overlapping (Naguib & Todt 1997). Open bars represent songs on channel 1 and hatched bars represent songs on channel 2, respectively. Song lengths were variable.

channel of a Sony TC-D5 tape recorder. On the other channel we recorded additional information on the subjects' behaviour with a Sony ECM-959DT microphone.

After each experiment we repeated the first minute of the previous playback, but only with the loudspeaker connected that the subject had not approached at first or at which it was not singing currently. This playback was used to make sure that both loudspeakers were placed inside the territory. It further tested if any discrimination between loudspeakers would persist when songs of only one of the presumed rivals was played. For subjects that had approached first the loudspeaker broadcasting the preceding songs, we thus broadcast 1 min of the following songs (from the same loudspeaker and location as before). For those subjects that first had approached the loudspeaker broadcasting the following songs we broadcast the previously preceding songs.

(iii) Measures of response and statistical analysis

Measures of response were based on subjects' location and singing activity. We recorded responses for 12.5 min (2.5 min playback plus the subsequent 10 min) and assigned responses to the loudspeaker closest to a subject's position. We excluded two trials from the analysis since the subjects either did not respond at all or responded to only one loudspeaker.

The direction of initial response was tested first by using a binomial test. Because additional measures of response correlated with each other ($r = 0.47$ to $r = 0.96$), we used a principal component analysis with six measures of response, separated for each subject and loudspeaker, as variables (SPSS 6.1.2 for Windows[®], unrotated factor solution). The data set appeared to be suited for such an analysis (Kaiser–Meyer–Olkin measure of sampling adequacy 0.69, Bartlett test of sphericity = 234.61, $p < 0.001$).

Response measures and their loadings on the first principal component were (i) closest approach to each loudspeaker (-0.855); (ii) latency to approach each loudspeaker (-0.783); (iii) number of songs sung within 10 m of each loudspeaker (0.858); (iv) number of songs sung within 5 m of each loudspeaker (0.852); (v) time spent within 5 m of each loudspeaker (0.815); and (vi) time spent singing within 10 m of each loudspeaker (0.909).

We then used the scores on the first principal component as a composite measure of response for further analysis. The first principal component had an eigenvalue of 4.29 and explained 72% of variance in the data. We then used the scores on the first principal component in an asymptotic Wilcoxon matched-pairs signed-ranks test (Siegel & Castellan 1988; Mundry & Fischer

1998). In addition, we measured the number of songs that were overlapped by the playback. Potential effects of the number of subjects' songs overlapped by a loudspeaker on the overall strength of response at that loudspeaker were tested by using a linear regression.

To analyse differences in singing activity at the active and silent loudspeaker in the 'post-playback' with one loudspeaker, we calculated a preference score ranging from 1 to -1 ((songs at the 'active' loudspeaker' – songs at the 'silent' loudspeaker) / (songs at the 'active' loudspeaker' + songs at the 'silent' loudspeaker)). A score of 1 indicates that subjects sang exclusively at the 'active' loudspeaker, and a score of -1 indicates that subjects sang exclusively at the silent loudspeaker. The scores were then tested for statistical significance with an asymptotic Mann–Whitney U -test.

3. RESULTS

Twelve subjects first approached the loudspeaker from which the preceding songs were broadcast, and five subjects first approached the loudspeaker from which the following songs were broadcast (binomial test, two-tailed: $p > 0.1$). Sixteen subjects sang their first, longer singing bouts of more than five songs at the side of the loudspeaker that broadcast the preceding songs, whereas only one subject sang its first bout at the side of the loudspeaker that broadcast the following song (binomial test, two-tailed: $p < 0.001$).

Also, pairwise comparisons with the scores on the first principal component as a composite measure of response indicated significantly stronger responses at the loudspeaker from which the preceding songs were broadcast (Wilcoxon matched-pairs signed-ranks test, two-tailed: $z = -1.97$, $n = 17$, $p < 0.05$). All measures of response showed a stronger response at the side of the loudspeaker from which the preceding songs were broadcast than at the side of the loudspeaker from which the following songs were broadcast (figure 3). Subjects approached the loudspeaker to which they flew first after latencies of 52 ± 12 s (mean \pm s.e.), therefore after they had heard several songs from both loudspeakers. The intensity of response at a loudspeaker showed no significant relation to the number of its songs that overlapped the subject's songs (linear regression, loudspeaker that broadcast the preceding songs, $r^2 = 0.04$, $n = 17$; loudspeaker that broadcast the following songs, $r^2 = 0.004$, $n = 17$), although subjects

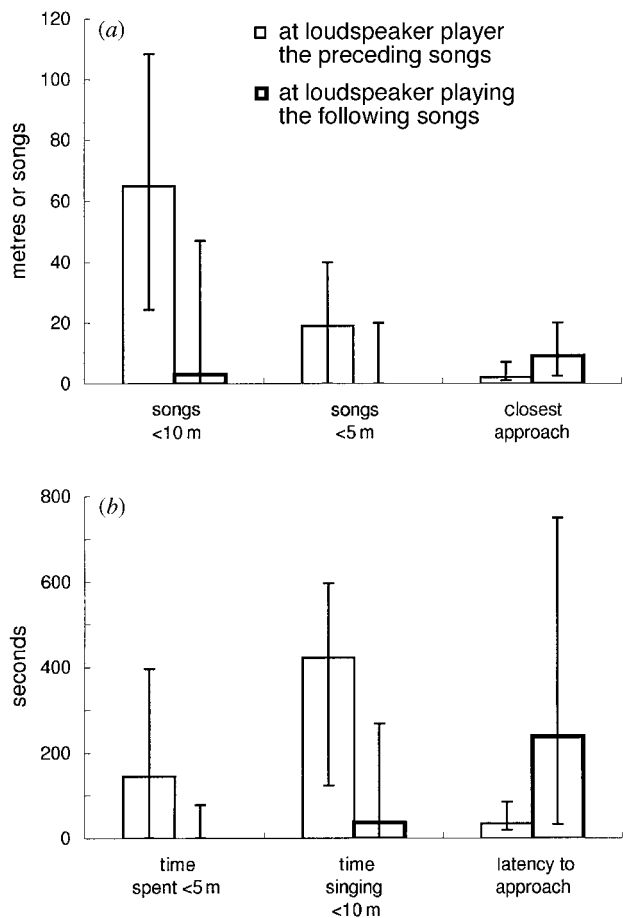


Figure 3. Medians and first and third quartiles of measures of response.

tended to respond less when they were overlapped more (figure 4).

In the post-playback tests with one loudspeaker, all subjects approached the active loudspeaker and on average sang more near this loudspeaker than near the silent loudspeaker. However, the preference to sing at the active loudspeaker tended to be stronger in those subjects to which we played the previously preceding songs (index = 0.98 ± 0.02 , $n = 4$) than in those subjects to which we broadcast the previously following songs (index = 0.33 ± 0.21 , $n = 13$), although this difference was not significant (Mann-Whitney U -test, two-tailed, $z = -1.29$, $p > 0.1$).

4. DISCUSSION

The results indicate that male territorial nightingales discriminated between the two rivals simulated by the asymmetrical vocal interaction near their territorial boundary. Almost all subjects sang their first singing bout at the side of the loudspeaker that broadcast the preceding songs, and subjects responded significantly more to this loudspeaker compared with the loudspeaker that broadcast the following songs. This preference for the loudspeaker that broadcast the preceding songs clearly contrasts with stronger responses to the overlapper (non-preceding songs) in our previous experiment (Naguib & Todt 1997). These contrasting responses rule out the idea that birds used one single proximate cue, such as to approach the first- or last-heard stimulus. In contrast to

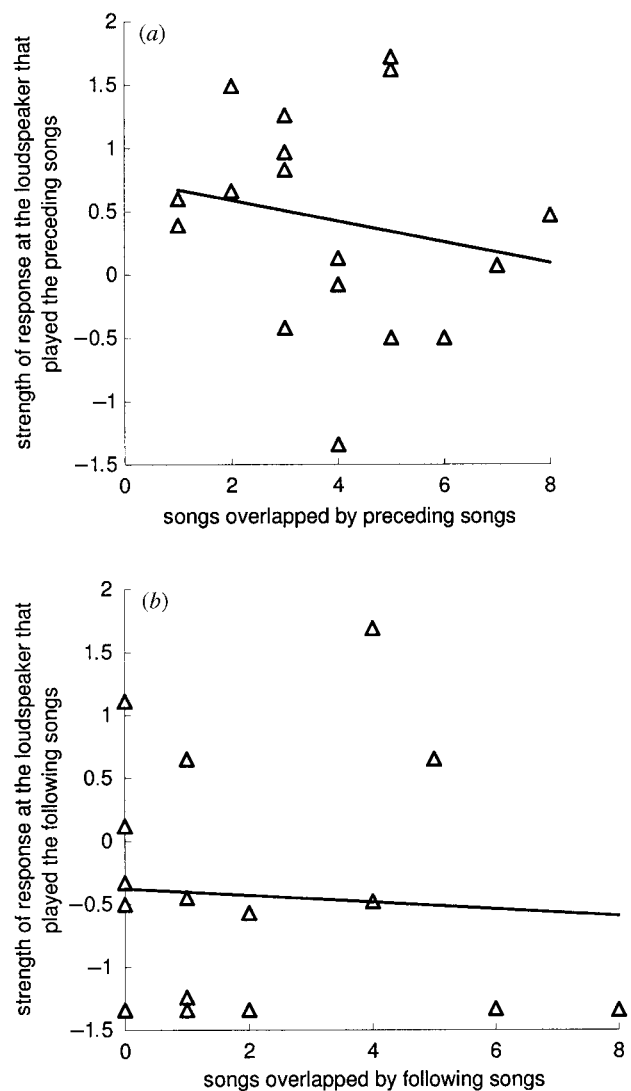


Figure 4. Linear regression of the intensity of response (measured as scores on the first principal component) at (a) the loudspeaker that broadcast the preceding songs (leader), and (b) the loudspeaker that broadcast the following songs (follower) on the number of songs that were overlapped by songs of the respective loudspeaker.

the experiment we presented here, in the previous experiment subjects responded less to the speaker that broadcast the preceding song. Differences in response, which are context dependent in reaction to preceding or non-preceding songs (following as well as overlapping songs), suggest that the responses are not an incidental consequence of attention to the first- or last-heard stimulus but probably reflect adaptive strategies. This argument is important to consider because attention to a last-heard stimulus is presumably under selection in other contexts, such as, for instance, in avoidance of predators. This provides strong evidence that responses either to the last or to the first songs are functionally relevant to the context studied.

(a) *Functional implications of leading in an interaction*

The results suggest that singers that are leading in an interaction are perceived as being more salient and presumably more threatening. The stronger responses to

the leader are in line with interpretations of observational studies that suggest that leader–follower relations in the timing of songs during alternated singing may reflect a sort of dominance–subordination relation (Smith & Norman 1979; Popp 1989). In line with these observational studies our results indicate that the timing of songs does carry important information, even when there is no acoustic overlap, as shown earlier (Todt 1981; Hultsch & Todt 1982; Wolffgramm & Todt 1982; Brindley 1991; Nielsen & Vehrencamp 1995; Dabelsteen *et al.* 1996, 1997; Naguib 1999). Leading during alternating singing might reflect a higher status because the timing of songs here is relatively independent from that of the counterpart. Followers, in contrast, adjust their songs to those of their counterpart in a much more immediate and discernible manner. In addition, one functionally important consequence of these two singing strategies is the likelihood of being overlapped. Starting a song immediately after the counterpart has terminated a song reduces the probability of being overlapped by a subsequent song. Thus, leading and following might reflect differences between singers on a different level than does song overlapping. Overlapping appears to be an active signal by the more aroused or dominant singer. Leader–follower relations, in contrast, result from the supposedly more defensive or more threatened singer adjusting its timing of songs in close relation to the other singer. Thus, song overlapping and leader–follower relations during song alternation seem to reflect different properties of the relations between two singers. Because overlapping is a more active signal compared to leading, we assume that overlapping is more of an immediate threat. Leader–follower relations may possibly reflect relationships between singers that are more established.

(b) *Relevance for additional listeners*

There is increasing experimental evidence that songbirds extract information from vocal interactions between other males (McGregor *et al.* 1997; Naguib & Todt 1997; Todt & Naguib 1999). Listening to interactions of others provides considerable potential for acquiring information. Floaters could use such information to find out which territory holders within an area are the weakest or the least prone to escalate a territorial interaction. Females might also extract information on relative differences among males by listening to their interactions. In doing so, they will not need to sample directly each male individually. Differences among males that become evident during their interactions could then play an important role in female choice (Searcy & Yasukawa 1996). So far as we are aware, such arguments have been applied primarily to lekking species (Wiley 1991), but less so to territorial songbirds (e.g. Todt 1981; McGregor & Dabelsteen 1996). Individuals that have obtained information on rivals' differences by attending to their interactions still have to decide how to respond. The kind of response will clearly depend on the context and the urgency of a response. In the territorial intrusions we simulated here, they may first deal with the more threatening intruder. However, birds interact in a wide range of contexts, so that the ability to obtain information from others' interactions and to process this information has much wider implications than just in the context studied here.

The timing of song onset is highly variable and can thus potentially carry more detailed information on relations between interacting individuals than assessed to date (Todt & Naguib 1999). Gathering information from others' interactions in general might not only be used in immediate decisions such as those examined here. It is likely that such information can be accumulated over time by attending to different kinds of interactions between different neighbours. Such information may enable the animal to assess its social position and that of others relative to each other. These considerations suggest that integrating information from several features of others' interactions may be of high value for subsequent social encounters.

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