Animal Behaviour 86 (2013) 1131–1137

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Does true syntax or simple auditory object support the role of skylark song dialect?

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ARTICLE INFO

Article history:
Received 9 July 2013
Initial acceptance 20 August 2013
Final acceptance 3 September 2013
Available online 9 October 2013
MS. number: 13-00572

Keywords:
Alauda arvensis
dialect
playback experiment
skylark
songbird
temporal ordering

Parallels between birdsong and human language are numerous and include particular temporal arrangements of acoustic units and the existence of dialects. In animal communication, modifications of the temporal ordering of existing acoustic units have rarely been clearly linked with changes in information content, particularly in a natural environment. Here, we show that the organization of birdsong units ('syllables') in sequences supports interindividual relationships within skylark communities. We manipulated the temporal arrangement of song dialect variants ('shared phrases') in the skylark, *Alauda arvensis*, a songbird with a very large repertoire of syllables and complex song. When tested with playback experiments performed in the field, skylarks were able to perceive subtle differences in the ordering of syllables. Modifications of the syllable ordering within shared phrases changed the information content from 'group member' to 'unfamiliar individual' and induced more aggressive reactions than shared phrases with a preserved syllable arrangement. Shared phrases often varied between individuals in the number of successive repetitions of similar syllable types, but were very consistent in terms of syllable type ordering. Our results indicate that skylarks rely not simply on the composition in syllable types of shared phrases to recognize group members, but on syllable type ordering. Shared phrases could be perceived by birds as 'auditory objects' embedded within songs. Alternatively, birds might identify incorrect phrases using grammatical rules governing the succession of syllables composing the phrases shared by their group. The presence of between-individual variation in phrase length, associated with consistent syllable type ordering revealed by our analysis, suggests that the latter hypothesis is more likely. Our results show that birds perceive disruptions in the natural temporal pattern of song units, and that this temporal pattern is behaviourally salient and carries information.

Striking genetic, neural and behavioural similarities exist between vocal learning in birds and human infants. This includes innate predispositions to learn species-specific signals, a sensitive period in early life and a memorization phase followed by a motor phase of production. It also includes the necessity for auditory feedback during the memorization phase, complex neural substrates and a role of social interactions (Doupe & Kuhl 1999; Beecher & Burt 2004; Beecher & Brenowitz 2005; Nottebohm 2005; Bolhuis et al. 2010). As a consequence of vocal learning, birdsong is characterized, like human language, by geographical variation in element composition called 'dialects' (Catchpole & Slater 1995). Furthermore, the songs are computational, that is, they consist of discrete song units, named syllables, organized in a particular temporal arrangement, in a similar way to how phonemes are organized in a particular order to form words ('phonology'; Yip 2006). This temporal arrangement of elements into larger units in birds has been termed 'phonological syntax' (Marler 1977).

A poorly explored parallel between human language and birdsong is the importance of the ordering of syllables composing natural songs for their information content. Are birds able to distinguish and react to sequences composed of syllables in an incorrect order, and is the organization of syllables crucial for the behaviourally relevant information carried by songs? There is evidence in primates that adding a particular suffix before an alarm call (Zuberbühler 2002; Ouattara et al. 2009a) or combining calls (Arnold & Zuberbühler 2006; Ouattara et al. 2009b) changes the meaning of the sequence. In swamp sparrows, *Melospiza georgiana*, adding an extra note at a particular position within a sequence of three notes constituting a syllable, which transformed the syllable of a dialect area to the syllable characteristic of another dialect area, triggered more aggressive responses in males than unmodified song (Balaban 1988). However, in birds, as in other species

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0003-3472/$38.00
http://dx.doi.org/10.1016/j.anbehav.2013.09.019

producing complex vocalizations, modifications of the temporal arrangements of existing discrete acoustic units ('broken syntax'; e.g. changing 'a b c d e' into 'b d e c a') have all been shown to induce a similar response to unmodified vocalizations, or to decrease or suppress the response, but never to increase it (Becker 1982; Mitani & Marler 1989; Holland et al. 2000; Nowicki et al. 2001; Clucas et al. 2004; Gentner 2008; Dahlin & Wright 2012). Any change in response indicates that the syntax modification is perceived by the animals. Yet, a suppression of response or decrease in response could potentially indicate that the broken syntax signal is not fully recognized as a conspecific signal, and is perceived as 'unnatural' and therefore irrelevant. By contrast, an increase in response would provide clear evidence that the temporal arrangement modification has triggered a change in information content.

We examined the role of the temporal ordering of syllables within songs in a species with a very large repertoire (>100 syllables) and complex songs, the skylark, *Alauda arvensis*, in its natural habitat. Male skylarks produce one of the longest and most complex songs among oscines (Briefer et al. 2010a). In this species, during the breeding season, pairs settle in adjacent territories of about 1 ha each. Because of the heterogeneity of the habitat, birds are gathered in small groups (range 5–19 males per group; Briefer et al. 2008a, b) separated from other groups by unsuitable habitat. Within each group, males ('neighbours') remain in their territory to breed and forage at short distances from their nest (Donald 2004). They defend these stable territories by producing long and continuous songs to deter intruders. In these songs, species identity is encoded in temporal parameters, and particularly in the rhythm (Aubin & Brémond 1983). A mean duration of 150 s that can be extended to more than 40 min, and a repertoire size of more than 300 different syllables, provides skylark song with a huge potential for variation in temporal arrangement (Aubin 1982; Briefer et al. 2008a, 2010a). When boundaries between territories are stable in the middle of the breeding season, neighbours establish 'dear-enemies' relationships (Temeles 1994), reacting weakly to a territory intrusion by their familiar neighbours and aggressively to an intrusion by unfamiliar individuals established in other distant groups ('strangers'; Briefer et al. 2008b).

Recently, we showed that neighbouring males share many syllables (on average 83% of the syllable repertoire, corresponding to about 269 types of syllable) and many sequences of syllables, named phrases (on average 71% of the sequence repertoire, or 44% of the total song duration, corresponding to about 91 types of sequences), in their songs. Phrases shared by neighbours differ from nonshared sequences by having shorter intersyllable intervals and fewer repetitions of syllables (Briefer et al. 2008a). Males identify and recognize these particular phrases to achieve neighbour–stranger discrimination, indicating that shared phrases support a group signature and serve as a basis for the dear-enemy effect (Briefer et al. 2008a). These phrases might also allow recognition of distant neighbours within the same dialect area. Indeed, adjacent and distant neighbours (established two to three territories away) within a group share a similar number of syllables and phrases in their songs (Briefer et al. 2010b). Two-by-two comparisons showed that pairs of neighbours share 216 syllable types and 59 different sequences on average, compared to 105 syllable types and only 0.5 sequences for pairs of strangers. Furthermore, phrases shared by at least two neighbours in a group are never found in the songs of strangers. Between two distinct groups, phrases may thus be composed of a few similar syllable types, but not with the same phonology, making the temporal arrangement of syllables constituting one group signature unique (Briefer et al. 2008a).

In this study, we assessed between-individual variation and complexity of sequential arrangements of syllables within shared phrases and, using playback experiments, we tested the hypothesis that these sequential arrangements are crucial for group recognition. We predicted that, if birds rely on single syllables composing the shared phrases to identify group members, they should react in a similar way to phrases containing syllables in their natural order as they do to phrases in which the phonological syntax has been modified. Conversely, if birds perceive shared phrases as 'auditory objects' (i.e. a set of acoustic events that can be perceived as a whole; Gentner 2008), or if they rely on the temporal ordering of syllables composing shared phrases (i.e. on the phonological syntax), they should not be able to recognize shared phrases with syllables presented in a modified order (i.e. with broken syntax) and therefore react as if these sequences were produced by a stranger.

METHODS

Study Area, Subjects and Song Recordings

We carried out our recordings for the song analysis and our playback experiment in the fields surrounding the University of Paris South, France. The songs for the analysis had been recorded, as part of a previous study (Briefer et al. 2010a), in four locations (i.e. four groups) during the breeding season in 2005 from the middle of February to the end of March. In total, the songs of 11 territorial males were analysed. The playback experiment was carried out in three additional locations (i.e. three groups) during two successive breeding seasons in 2007 and 2008. Playbacks were conducted in May, when territory borders are stable and males consider their neighbours as 'dear enemies' (Briefer et al. 2008b). In total, we tested 17 territorial males. Within a group, males are established in adjoining and stable territories of about 1 ha and are referred to as 'neighbours'. The total number of neighbours (group size) within each of the seven groups of our study was 10.43 ± 1.13 (mean $\pm$ SE; range 7–15 territorial males). We refer to males from two different locations situated at least 2 km apart as 'strangers' (Briefer et al. 2008a, 2010a). We estimated the territory boundaries of the studied birds after numerous observations of the birds' movements at different times of day, and recorded GPS coordinates at the centre of each territory (Garmin GPSMAP 76S). We recorded several songs per individual between 0900 and 1200 hours Eastern Daylight Time using a Marantz PMD 690 numeric recorder (sampling rate: 48 kHz) connected to a Sennheiser ME 64 K6 omnidirectional microphone (frequency response: 30 Hz to 20 kHz $\pm$ 1 dB) mounted on a Telinga Universal parabola (diameter: 50 cm). Song files were transferred to a computer and high-pass filtered (cutoff frequency: 1600 Hz) to remove background noise. We used Avisoft SASLab pro version 4.31 software (Avisoft Bioacoustics, Berlin, Germany) and Seewave (Sueur et al. 2008) for subsequent analyses and for the preparation of songs played back.

Song Analysis

We carried out a song analysis on 100.03 ± 0.02 s of continuous song per individual ($N = 11$) to measure between-individual variation in syllable number (i.e. total number of syllables) and in syllable type ordering (i.e. how the different types of syllable, which are characterized by different overall frequency modulation shapes, are temporally ordered) within shared phrases. Then, we measured the complexity of shared phrases, by calculating the number of different shared phrases per group and the number, the diversity and the organization of syllables within these phrases.

Shared phrases used in this study had been previously identified, as part of another study (Briefer et al. 2010a), by labelling all