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In Focus

Featured Articles in This Month's *Animal Behaviour*

Song Syllable Order Matters to Skylarks

In the last 50 years experimental behavioural studies have demonstrated fascinating parallels between human language and animal communication across different taxa. Birdsong is a particularly good model for such studies. First, like human language, birdsong is subject to vocal learning in early life and, as a consequence, song composition has geographical variants called 'dialects' similar to the variants in human language. Second, birdsong consists of the arrangement of discrete units, called syllables, similarly to the way human language is made up of words formed by the order of phonemes. An important but poorly explored parallel is whether the particular arrangement of syllables in birdsong carries information content. This is a possibility explored by Elodie Briefer (Université Paris-Sud, France and ETH Zürich, Switzerland), Fanny Rybak and Thierry Aubin (Université Paris-Sud and CNRS, Orsay, France) in the present issue (pp. ?–?).

In a properly controlled experiment in which songs with broken syllable order would be played back to birds, an increase in the response would indicate that birds can perceive the change in syllable order (or syntax) and demonstrate that syllable arrangement carries information content. By contrast, no change or a decrease in the response could be interpreted in several ways. It could mean that the broken syntax is not recognized and therefore carries no information or simply that it is perceived as 'unnatural' and is therefore ignored. Earlier studies have shown that transforming a syllable from one dialect into a syllable from another dialect by adding an extra note triggers more aggressive response than the unmodified song. However, all earlier experiments involving broken syntax manipulations have shown no change or a decrease in the response compared to unmodified vocalizations.

Briefer and coauthors chose skylarks as their experimental species because the repertoire of these birds consists of more than 300 syllables and their song is long and complex (Fig. 1). The study was carried out in the skylarks' natural habitat. During the breeding season skylark pairs in adjacent territories form small groups separated from other groups by unsuitable habitat. Males deter intruders with a continuous song, which lasts on average 150 s but could be more than 40 min long. They react weakly to intrusions from neighbouring males and much more aggressively to 'strangers' from distant groups. Earlier work by the authors had established that neighbouring males share on average 83% of their syllable repertoire and 71% of their phrase (that is a sequence of syllables) repertoire, and that it is these shared phrases that help males discriminate neighbours from strangers. In the present study the authors used playback experiments to test the hypothesis that the sequential arrangement of syllables within shared phrases contains the crucial information enabling such discrimination. To study the sequential arrangement of syllables within shared phrases, the authors analysed the songs of 11 males from four groups (one continuous song per male). For each of the 11 songs, the authors carried out a sophisticated analysis to measure between-individual variation in syllable number and syllable type ordering, the number of shared phrases per group and the number, diversity and organization of syllables within these phrases.

To test the importance of syllable order for neighbour–stranger discrimination, the authors tested 17 males from three groups with playback recordings of the natural and artificially modified songs of six males from other groups ('strangers'; i.e. males whose locations were at least 2 km apart). Briefer and coauthors compared the responses of the tested birds to the following three treatments: (1) a natural song of a stranger, (2) a chimeric song (the same stranger song but with 30% of it replaced by artificially inserted shared phrases from the group of the tested subject) and (3) chimeric modified song (the same chimeric song but with a randomly changed order of the syllables forming the artificially inserted shared phrases). Each of the tested subjects underwent each treatment in a random order with a minimum of 10 min between successive treatments and within the same day to control for any change in the environment. Each of the responses of each of the tested birds was scored over 180 s according to five different measures and the combination of these measures was used for analysis.

Intriguingly, the analysis of the songs shows that, although the variation among individual skylarks in the length and composition of shared phrases is large, syllable type ordering is very consistent. The comparison between the responses of the tested birds to the three playback treatments reveals that skylarks reacted significantly more strongly to stranger songs and chimeric modified songs than to chimeric songs, with no difference in their reaction between stranger and chimeric modified songs. This clearly demonstrates that skylarks responded with increased aggressiveness to the same chimeric song when the order of the syllables in the shared phrase was randomized. This shows that the change in the order of the syllables changed the information content from one indicating a group member to one indicating a stranger.

One possible interpretation of these intriguing results is that shared phrases are perceived by skylarks as a whole, in other words as 'auditory objects' embedded in the song. An alternative interpretation is that instead of perceiving them as a whole, skylarks use syntactical grammatical rules about the order of syllables in a phrase. Given that the results from this study demonstrated a very consistent ordering of shared phrases between birds even though phrase length varied greatly, the interpretation involving simple grammatical rules is the more plausible.

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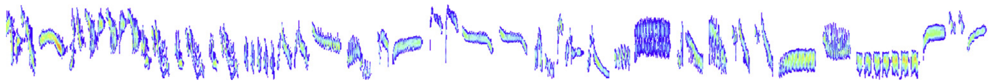

Figure 1. A spectrogram of a natural skylark song showing clearly the order and different characteristics of the song's component acoustic units (or 'syllables'). Photo: Elodie Briefer.

Future studies where the chimeric modified songs involve different levels of modification, from the permutation or deletion of just a few syllables to a change in the ordering of all the syllables in a phrase, could establish the minimum length of component features in a song that skylarks can perceive as relevant in a neighbour–stranger discrimination. The ability of skylarks to use syntactical grammatical rules could be tested using operant conditioning whereby individuals are trained to discriminate between synthetic strings of syllables.

The study by Briefer and coauthors demonstrates that the skylark is a very promising model for experimental studies using a natural communication context to test hypotheses about language-like communication in nonhuman animals.

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A Scented Mental Education

Although Frederic's love affairs all ended with disillusionment in Flaubert's 'Sentimental Education', butterflies do learn to choose the right mate. In fact, learning conspecific signals is important for mate choice in a wide variety of taxa. From birds to butterflies, young females exposed to courtship signals as juveniles will show preference for those same cues as adults. But male courtship displays often involve signals in several different modalities. In this issue, Erica Westerman and Antónia Monteiro, now at the University of Chicago and National University of Singapore, respectively (pp. xx–xx) ask just what information these different components might mean to females. Multimodal signals might convey either redundant information, each signal thus reinforcing the display making it more attractive, or different information. They might, for example, help to differentiate between conspecifics and heterospecifics. Multimodal signals might affect preference learning in one of two ways, based on these two hypotheses. If the former were the case, the two signals should have an additive effect on preference learning. Alternatively, if multiple signals convey different messages, they may have different effects on learning, with some signals either enhancing or reducing learning in a positive or negative way.

The subtropical African butterfly *Bicyclus anynana* (Fig. 2) has two UV-reflective eyespots on the dorsal forewings of males that have been shown to be important in female mate choice. Females also pay attention to male sex pheromones when picking mates. These butterflies are seasonally polymorphic and often live in sympatry with multiple other species in the clade. These factors suggest that learning the correct courtship signal would be important but that learning should be constrained so that they do not use inappropriate models. Since sex pheromones are often species specific in Lepidoptera, Westerman and Monteiro hypothesized that these pheromones may serve either to enhance or to restrict the learning of the visual courtship signals in *B. anynana*.

Male and female pupae were sexed and isolated visually and olfactorily. When adult males emerged, their odour was altered by painting over the pheromone-producing organ on their wings. Controls were sham painted. Their wing patterns were similarly altered by painting out the UV-reflective spots, painting over them with UV-reflective paint or adding two more UV-reflective spots between the natural ones creating males with zero, two or four spots. (Westerman had previously demonstrated that females exposed to males with no pheromone manipulation but with either two or four spots learned to favour the visual signals they had been exposed to but had no preference between males with two or no spots, Westerman, Hodgins-Davis, Dinwiddie, & Monteiro, 2012.) On the morning of their emergence, virgin females were either kept completely isolated (naïve females) or exposed to males with zero, two or four spots and with altered pheromones. When they were 3 days old, females were given a choice between two virgin males with altered wing patterns and natural odour.

Naïve females found males with manipulated odour unattractive and chose control males more often than those with their pheromone-producing organ blocked. Naïve females also tended to prefer the wild-type two-spot males to four-spot males. However, females that had been exposed to the males with the wrong, unattractive odour (both those with the organ blocked and those sham blocked) and to the enhanced four-spot males did not learn the preference for them over the wild-type males as naïve females did. They also learned to avoid the wild-type two-spot males when previously exposed to unattractive males with two spots, mating preferentially with enhanced four-spot males. Naïve females did not discriminate between males with two or zero spots. There was also no effect of early exposure to males with manipulated odour of either type; females did not learn to discriminate between zero and two spots. Westerman and Monteiro also recorded the behaviour of the males during the training period and found that the only behaviour that correlated with preferential learning was the percentage of time the male spent walking. Male models that

Figure 2. A male and female *Bicyclus anynana* eye to eye. Photo: William Piel.

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spent more time walking, rather than flying, fluttering or courting, reduced the ability of the females to learn, probably because by doing so they exposed the females less to the unattractive odour and the visual cue.

For these butterflies, the development of the preferred visual cue is influenced by the species-specific pheromone that accompanies the visual cue during early exposure. In this experiment, with the wrong pheromone cue, females learned to avoid the wild-type visual signal or, if exposed to the enhanced cue, did not learn to prefer it. These results suggest that the olfactory cue is guiding the learning for a preference of the visual signal, which supports the hypothesis that these two courtship signals convey different meanings or have different functions. This study highlights the potential for multimodal signals to have complex functions in the development of preference for sexually selected traits.

Michelle Pellissier Scott
Executive Editor

Reference

Westerman, E., Hodgins-Davis, A., Dinwiddie, A., & Monteiro, A. (2012). Biased learning affects mate choice in a butterfly. *Proceedings of the National Academy of Sciences of the United States of America, 109*, 10948–10953.