



Research

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Animal behaviour

Contrast influences female attraction to performance-based sexual signals in a songbird

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Animals do not make decisions in a bubble but often refer to previous experience when discriminating between options. Contrast effects occur when the value of a stimulus affects the response to another value of the stimulus, and the changes in value and response are in the same direction. Although contrast effects appear irrational, they could benefit decision makers when there is spatial or temporal variation and autocorrelation in the value of stimuli that elicit decisions. Here, we examined whether contrasts influence female evaluation of male performance-based sexual signals. We exposed female Lincoln's sparrows (*Melospiza lincolni*) to one week of songs that we had experimentally reduced or elevated in performance, followed by a novel song of intermediate performance. We found that high-performance songs were more attractive to females than low-performance songs. Moreover, the intermediate songs were more attractive following exposure to low- than to high-performance songs. These results indicate that contrast can influence evaluation of performance-based sexual stimuli. By examining contrast effects in the ecologically relevant context of mate choice for performance, we can better understand both the adaptive value of comparative evaluation as well as the mechanisms that underlie variation in mate choice and sexual selection.

1. Introduction

Individuals often enhance or reduce their response to a stimulus depending on whether they previously experienced similar stimuli of lesser or greater value, respectively. These contrast effects appear irrational under the view that decisions should be path independent, such that the value of past stimuli is irrelevant to current decision-making [1]. However, contrast effects appear to be taxonomically widespread and occur for a variety of stimuli [2,3]. Determining how contrasts influence behaviours directly relevant to the natural history of organisms may elucidate the ecological rationality of contrast effects [1,4]. Mate choice often involves comparison of multiple mates and a resultant choice, based at least in part on perceptions of mate attractiveness [5]. Previous studies indicate that contrasts can influence perception of mate attractiveness, which could have major fitness implications for mate choice (e.g. [6], reviewed in [4,7]).

In this study, we tested the hypothesis that the attractiveness of a performance-based sexual signal depends on its contrast with recently experienced signals. Performance-based traits are typically under positive directional selection [8] and may convey information about vigour and skill [9,10], suggesting they can be important in assessment of prospective mates. Owing to a biomechanical constraint of the vocal tract, the performance of trilled syllables in the songs of many songbird species reflects a trade-off between maximizing the rate of syllable repetition and maximizing the frequency bandwidth of those syllables [9,11]. Trill performance varies within and between males [11,12], and in several species

females prefer high-performance trills in mate-choice contexts [9,13]. In Lincoln's sparrows (*Melospiza lincolnii*), females prefer songs with high-performance trills [13], and there is annual variation in a population's mean level of trill performance [12]. For females experiencing such variation in trill performance, a contrast effect could be adaptive as it would allow females to adjust their threshold of acceptance for trill performance relative to the current availability of high-performance trills [14]. We predicted that if contrasts influence female evaluation of male trill performance, females accustomed to low-performance trills would find a novel song with trills of intermediate performance more attractive than would females accustomed to high-performance trills.

2. Material and methods

In July 2010, we collected 8-day-old Lincoln's sparrow chicks near Molas Pass, CO, USA (37.74° N, 107.69° W) and reared them in outdoor aviaries at the University of North Carolina (Chapel Hill, NC, USA) [13,15]. Starting March 2012, we moved 12 females indoors into individual cages on a 16 L:8 D photoperiod for 21 days to drive them into a reproductive-like state [16].

(a) Song exposure

We randomly assigned 12 females to exposure to either high-performance or low-performance songs (six females per treatment). We created these treatments from 18 songs (three recorded from each of six males) by cutting 15 ms of silence from the inter-syllable space of each trill in each song for the high-performance treatment and pasting it into the corresponding inter-syllable space of each song's digital copy for the low-performance treatment (figure 1; electronic supplementary material).

We exposed females to treatment songs using eight sound-attenuation chambers (58 × 41 × 36 cm; Industrial Acoustics Company, New York, NY, USA), each containing a functioning speaker at one end and a non-functioning speaker at the other end (Pioneer Corp. TS-G1040R). We balanced the side with the functioning speaker across treatments. We attached each speaker to a mono-block amplifier (Audiosource Amp 5.1A, Portland, OR, USA) that we interfaced (M-Audio Delta 1010, Irwindale, CA, USA) to a central computer (Apple Inc., Cupertino, CA, USA) broadcasting the high- and low-performance songs to their respective chambers. We placed the chambers in one room and assigned individual females to chambers such that the chambers of one treatment were spatially interspersed with those of the other treatment.

Each morning for seven days, we exposed females to 6 h of the treatment songs. An individual song lasts 2–3 s, and we played one every 10 s for 20 min periods interspersed with 10 min of silence. The order of songs was random, except that we played all three songs from a single male before moving on to playbacks from another randomly drawn male. On the eighth morning, instead of treatment songs, we exposed all females from both treatments to the same novel song, repeated every 10 s. We selected the song based on its mean trill performance, which was between that of the low- and high-performance treatments (i.e. intermediate performance).

Ten days after exposure to the intermediate-performance song, we repeated the experiment in a second round using the same females in their same chambers, but we exposed them to the opposite treatment and a new, novel intermediate-performance song on the eighth day. Because we had only eight chambers, we split each round between two sessions.

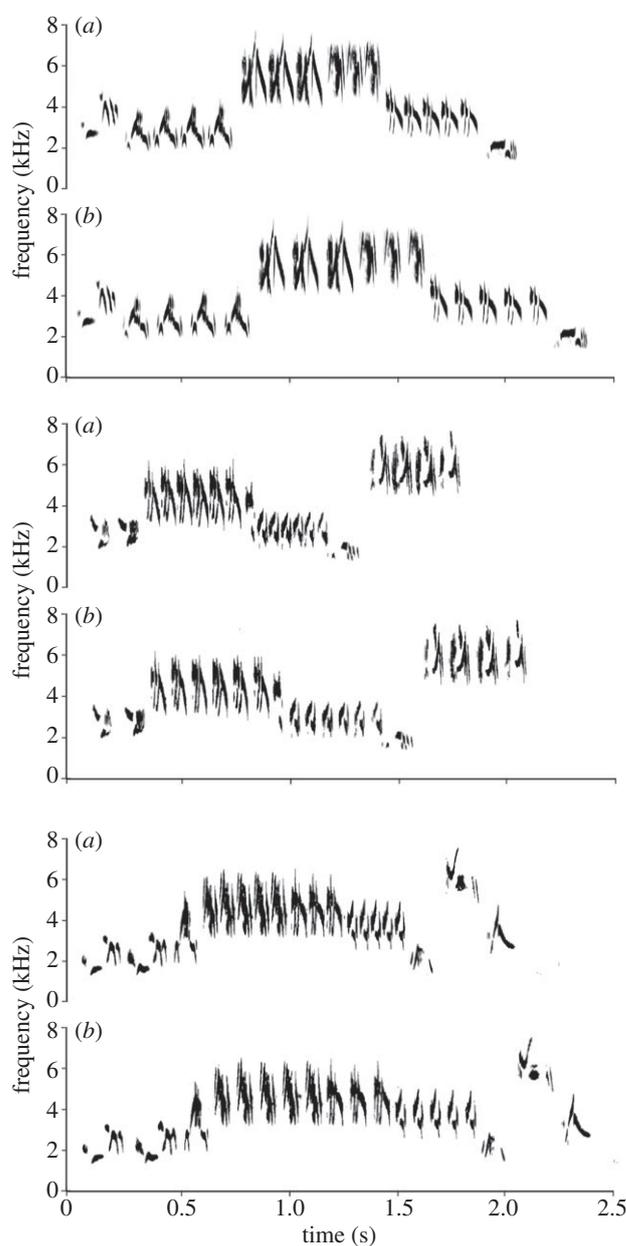


Figure 1. Spectrograms of three exemplars of the 18 treatment songs manipulated for the (a) high-performance and (b) low-performance treatments.

(b) Behavioural assay

One computer-driven (Dell Optiplex 990 running Multicam Surveillance software; Ingram Technologies, Price, UT, USA) video camera (B/W CCD Camera, Super Circuits, Austin, TX, USA) per chamber enabled us to record phonotaxis behaviour on treatment days 1 and 6 and during intermediate song exposure (day 8). We quantified the time females spent in the half of the cage nearest the active speaker for 3 min before (baseline) and the first 3 min during (phonotaxis) song exposure [13,15].

(c) Analyses

We performed analyses using linear mixed-effects models (lme, R package nlme) or linear models in R [17]. Phonotaxis time was the dependent variable, song treatment the predictor and baseline association time was a covariate to control for cage-side bias. On days 6 and 8, we nested round within individual as a random intercept. We did not include random effects for

day 1, because on this day, we failed to record behaviour for all birds during round one and for one bird during round two.

3. Results

On the first day of song treatment, females were more attracted to high-performance songs than low-performance songs ($t = 2.99$, d.f. = 8, $p = 0.017$). When we assayed females' behaviour five days later, we no longer found an effect of song treatment ($t = 0.14$, d.f. = 10, $p > 0.2$), suggesting females had habituated to these stimuli. However, on day 8, females were more attracted to the novel intermediate-performance song following exposure to the low- than to the high-performance treatment ($t = 2.50$, d.f. = 10, $p = 0.031$, figure 2).

4. Discussion

Our study demonstrated a contrast effect in attraction to a performance-based sexual signal. We found that novel intermediate-performance birdsong was more attractive to females following exposure to low- than to high-performance song treatments. Contrast effects occurring in the context of feeding are predicted to be adaptive if there is autocorrelated variation in the quality of the environment [18]. Similarly, contrast effects occurring in the context of mate choice may be adaptive when there is autocorrelated variation in availability of high-performance sexual signals. Average trill performance of a population of Lincoln's sparrows varies annually [12], suggesting that females who are not flexible in the performance threshold that they accept from a potential mate might forego mating during years when high-performance trills are rare [14,19–21]. The contrast effect we demonstrated would provide a mechanism for such flexibility.

Most studies of the contrast effect show evidence for only a negative contrast effect (reduced response to the test stimulus following exposure to a higher-valued stimulus, relative to controls). However, theory predicts that contrasts should be both positive and negative [18]. In this study, we were not able to determine whether the contrast effect was positive, negative or both. To determine the direction of the effect, one would need also to expose females to intermediate-performance versions of the treatment songs to control for overall attractiveness of the novel songs. However, we had no such control nor any pre-conceived expectations of the overall attractiveness of the novel, intermediate-performance songs, as Lincoln's sparrows' songs vary in many aspects other than performance, and these aspects can also influence songs' attractiveness [13]. Instead, we predicted only that intermediate-performance song would be more attractive after exposure to low-performance songs than after exposure to high-performance songs. Our results were in line with this prediction.

Contrast effects often occur when reward value is different from the anticipated value, suggesting that reward reinforcement underlies the contrast effect [2]. In songbirds, it is probable that song in general does hold reward value for females [22], raising the possibility that motivation and reward expectation could explain the observed contrast effect. However, non-rewarding sensory stimuli can also elicit similar perceptual contrasts [3]. Studies in European starlings (*Sturnus vulgaris*) suggest that the quality

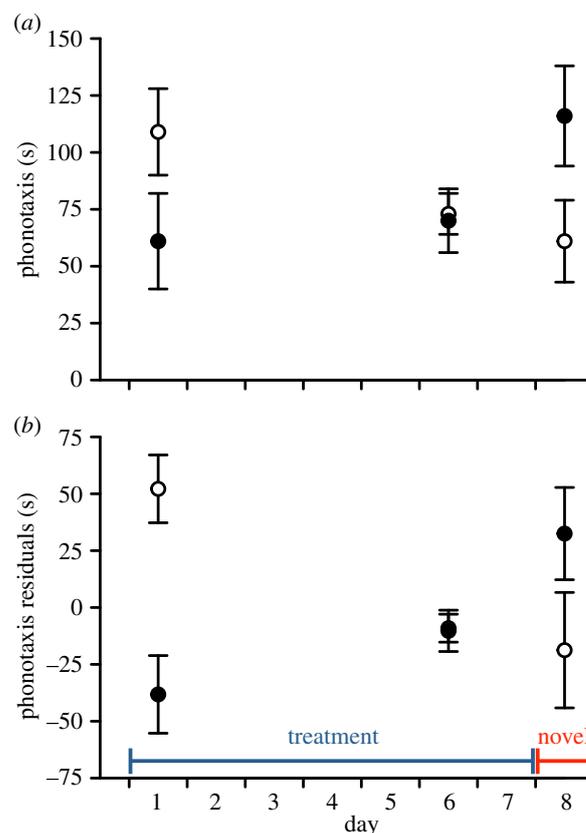


Figure 2. Mean (\pm s.e.m.) (a) phonotaxis time and (b) residuals of phonotaxis time (controlling for cage-side bias) of female Lincoln's sparrows exposed to high- (open symbols) or low-performance (solid symbols) songs, during exposure to treatment songs (days 1 through 7) and to novel intermediate-performance song (day 8). (Online version in colour.)

of previously heard song modulates the auditory forebrain's sensitivity to song quality [23], and it is tempting to speculate that neuroplasticity in the auditory forebrain mediates the effect of contrast on female responses to male song [20]. Therefore, perceptual as well as motivational factors may mediate female response to change in trill performance.

If rational choice requires path independence, females should respond to the novel song without regard to previous song experience [1]. However, the effect of contrasts in this study supports the hypothesis that females assign a relative value rather than an absolute value to male traits when choosing a mate [4]. Mate choice can strongly contribute to fitness and can play a role in speciation [5], and the contrast effect may underlie much of the observed variation in mate choice [4]. Understanding how contrasts can influence mate choice provides further insight into the fitness consequences of this possibly widespread phenomenon.

Data accessibility. The dataset supporting this article has been uploaded as part of the electronic supplementary material.

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ELECTRONIC SUPPLEMENTARY MATERIAL

Quantifying and digital manipulation of trill performance

A trill is a rapidly repeated syllable in a song. Trill performance defines the relationship between the rate with which the individual syllables of a trill are produced and the frequency bandwidth of those syllables. Current hypotheses suggest that variation in trill performance results from a biomechanical constraint between producing syllables that span a broad frequency bandwidth and producing syllables that are rapidly repeated [1, 2]. High performance trills maximize both trill rate and frequency bandwidth.

From 2005-2011 at Molas Pass, CO, we recorded 6,866 Lincoln's sparrow songs as described in [3]. For each of the more than 20,000 trills in these songs, we determined trill rate and frequency bandwidth using the software Raven Pro (v. 1.5, Cornell Laboratory of Ornithology, Ithaca, NY, USA). Specifically, the software calculates the duration and frequency bandwidth of the middle 90% of sound energy of the area of the trill we specified, which, for each trill, was all except the final syllable. Excluding the final syllable circumvents the problem of uncertainty in where a trill ends and the next phrase of the song begins. We then calculated trill rate as 1 less than the number of syllables in the trill divided by the duration described above (in sec).

We next plotted each trill's frequency bandwidth against the trill rate (Figure S1). This plot followed a triangular distribution of points, suggesting a trade-off between trill rate and frequency bandwidth because only low frequency bandwidths occurred at the highest trill rates and only low trill rates occurred at the highest frequency bandwidths [1-3]. From this plot we calculated the regression line at the 95th percentile as an estimate for the upper boundary of the relationship between frequency bandwidth and trill rate [2]. The slope of this line was significantly negative ($t_{23,271} = 10.99$, $p < 0.001$). The formula for the line was:

$$y = -0.021x + 2.224$$

We then determined each trill's performance as the orthogonal distance of the trill from the 95th percentile regression line, using the slope and y-intercept for the 95th percentile regression indicated above and the bandwidth and trill rate values of each trill in the following formula:

$$\frac{(0.021 \times \text{trill rate}) + \text{bandwidth} - 2.224}{\sqrt{0.021^2 + 1}}$$

Trills that fell farther below the regression line had more negative trill performance values and indicated a poorer trill performance. From our field

recordings, the range of trill rate was 2.12 to 39.75 syllables/sec and the range of trill performance was -1.73 to 1.25.

Using these field recordings, we selected from each of six different males three songs each consisting of four trills with similar mean trill rates and performances. Using Raven Pro, we generated two identical digital copies of each song. From one copy, we cut 15 ms of silence between each syllable of each trill and pasted it into the corresponding inter-syllable space in the other copy, effectively reducing trill rate and therefore trill performance in one copy (low performance) and increasing trill rate and therefore trill performance in the other (high performance). Manipulated songs significantly differed from each other in mean trill rate and performance and fell within the natural range of variation in trill rate and performance recorded for our study population (Table S1).

For the eighth day of song exposure (exposure to intermediate song), we selected two songs from each of two different males that were not used for the treatment songs and were of intermediate trill performance (song 1: trill rate mean \pm SEM: 8.75 ± 0.72 ; trill performance mean \pm SEM: -0.76 ± 0.11 ; song 2: trill rate mean \pm SEM: 9.17 ± 0.83 ; trill performance mean \pm SEM: -0.75 ± 0.11).

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Table ESM 1. Mean trill rate and trill performance of songs digitally manipulated to be of high and low trill performance. Trill performance is a relative measure determined by the distance of the trill from the regression line at the 95th percentile of a bivariate plot of trill frequency bandwidth (kHz) regressed on trill rate (syllables/sec).

	N	High (mean ± SEM)	Low (mean ± SEM)	t*	p
Trill rate	18	11.08 ± 0.34	9.97 ± 0.29	8.366	<0.001
Trill performance	18	-0.74 ± 0.02	-0.77 ± 0.02	5.74	<0.001

* From paired t-test

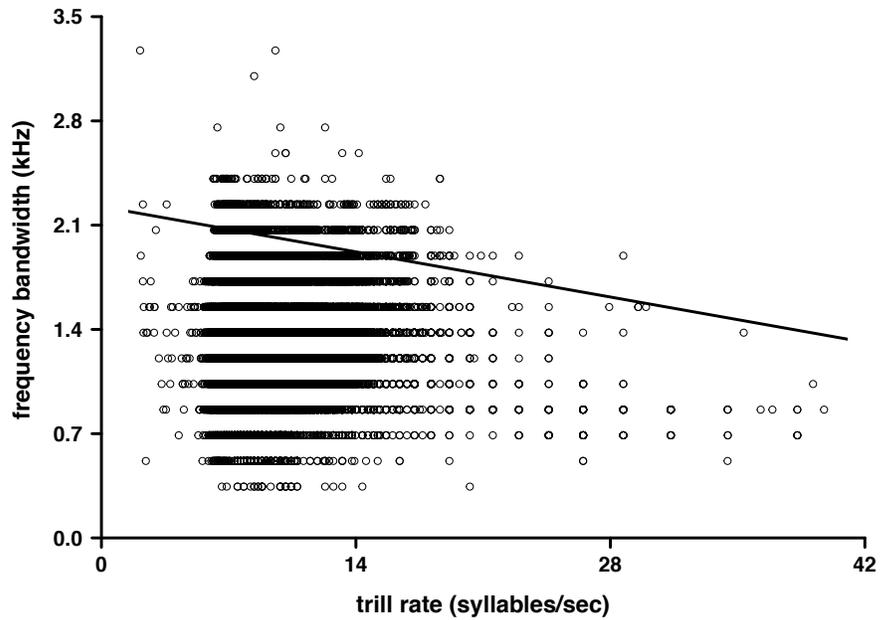


Figure ESM 1. Frequency bandwidth as a function of trill rate for over 20,000 trills recorded from Lincoln's sparrows at Molas Pass, CO from 2005 – 2011. Line is a 95th percentile regression. Each trill's performance was calculated as its orthogonal distance below the regression line, with more negative values corresponding to lower trill performance.