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

Susan M. Lyons1, Michaël Beaulieu1,† and Keith W. Sockman1,2

1Department of Biology, and 2Curriculum in Neurobiology, University of North Carolina, Chapel Hill, NC 27599-3280, USA

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 lincolnii) 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 [15], 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 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.

(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 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.

Acknowledgements. The USFWS, USDA, Colorado Division of Wildlife and UNC IACUC each granted the relevant permissions to conduct this study. We thank Daniel Bobrowski, Emma Johnson, Caroline Jordan and Alex Rohila for bird collection; Jonathan Hootman for bird care and Rob Aldredge, Donna Maney and Haven Wiley for comments on the manuscript.

Funding statement. Supported in part by NINDS R01 NS055125 to K.W.S.
References