



CrossMark
click for updates

Research

Cite this article: Lyons SM, Beaulieu M, Sockman KW. 2014 Contrast influences female attraction to performance-based sexual signals in a songbird. *Biol. Lett.* **10**: 20140588. <http://dx.doi.org/10.1098/rsbl.2014.0588>

Received: 24 July 2014

Accepted: 23 September 2014

Subject Areas:

behaviour, cognition, evolution

Keywords:

contrast effect, comparative evaluation, mate choice, birdsong, Lincoln's sparrow (*Melospiza lincolni*), trill performance

Authors for correspondence:

Susan M. Lyons

e-mail: lyonssm@live.unc.edu

Keith W. Sockman

e-mail: kws@unc.edu

[†]Present address: Zoological Institute and Museum, University of Greifswald, Johann-Sebastian Bach Str. 11/12, 17489 Greifswald, Germany.

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2014.0588> or via <http://rsbl.royalsocietypublishing.org>.

Animal behaviour

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

Susan M. Lyons¹, Michaël Beaulieu^{1,†} and Keith W. Sockman^{1,2}

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 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.

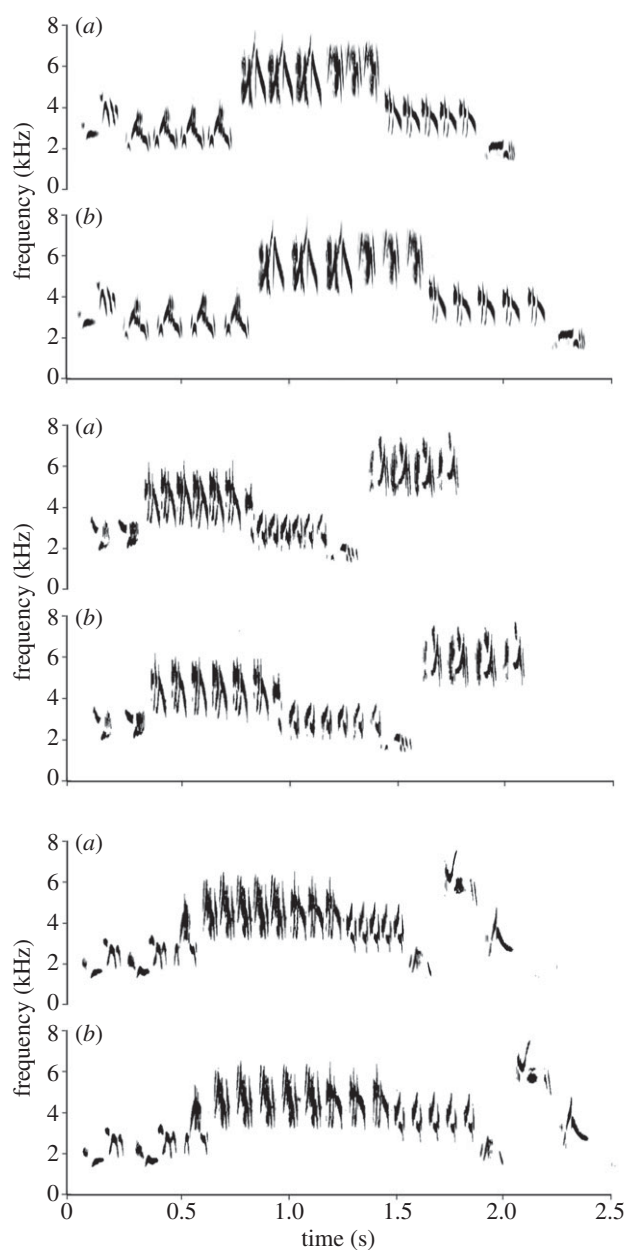


Figure 1. Spectrograms of three exemplars of the 18 treatment songs manipulated for the (a) high-performance and (b) low-performance treatments.

(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

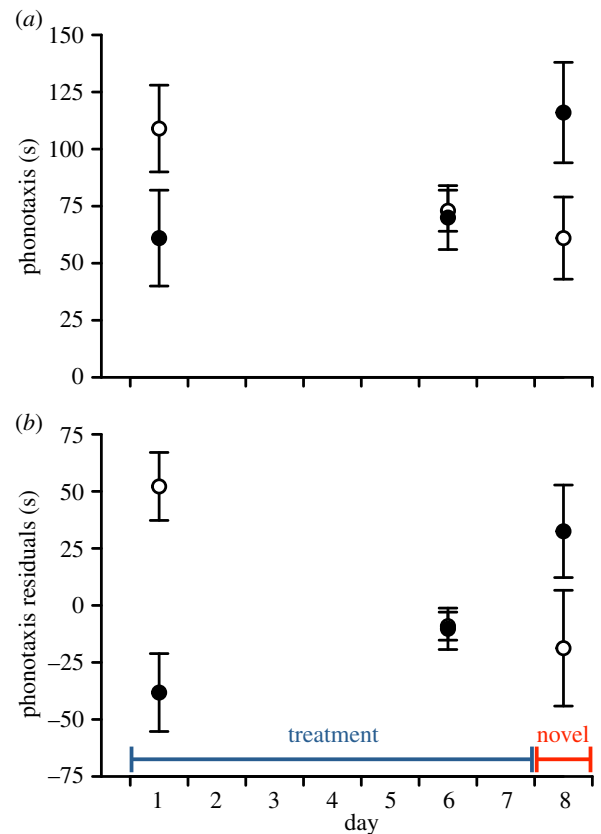


Figure 2. Mean (\pm s.e.m.) (a) phonotaxis time and (b) residuals of phonotaxis time (controlling for cage-side bias) of female Lincoln's sparrows exposed to high- (open symbols) or low-performance (solid symbols) songs, during exposure to treatment songs (days 1 through 7) and to novel intermediate-performance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

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 Rohtla 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.

1. Fawcett TW, Fallenstein B, Higginson AD, Houston AI, Mallpress DE, Trimmer PC, McNamara JM. 2014 The evolution of decision rules in complex environments. *Trends Cogn. Sci.* **18**, 153–161. (doi:10.1016/j.tics.2013.12.012)
2. Flaherty CF. 1996 *Incentive relativity*. New York, NY: Cambridge University Press.
3. Kelley LA, Kelley JL. 2014 Animal visual illusion and confusion: the importance of a perceptual perspective. *Behav. Ecol.* **25**, 450–463. (doi:10.1093/beheco/art118)
4. Bateson M, Healy SD. 2005 Comparative evaluation and its implications for mate choice. *Trends Ecol. Evol.* **20**, 659–664. (doi:10.1016/j.tree.2005.08.013)
5. Andersson MB. 1994 *Sexual selection*. Princeton, NJ: Princeton University Press.
6. Bateman PW, Gilson LN, Ferguson JWH. 2001 Male size and sequential mate preference in the cricket *Gryllus bimaculatus*. *Anim. Behav.* **61**, 631–637. (doi:10.1006/anbe.2000.1617)
7. Gibson RM, Langen TA. 1996 How do animals choose their mates? *Trends Ecol. Evol.* **11**, 468–470. (doi:10.1016/0169-5347(96)10050-1)
8. Irschick DJ, Meyers JJ, Husak JF, Le Galliard J. 2008 How does selection operate on whole-organism functional performance capacities? A review and synthesis. *Evol. Ecol. Res.* **10**, 177–196.
9. Byers J, Hebets E, Podos J. 2010 Female mate choice based upon male motor performance. *Anim. Behav.* **79**, 771–778. (doi:10.1016/j.anbehav.2010.01.009)
10. Barske J, Schlinger BA, Wikelski M, Fusani L. 2011 Female choice for male motor skills. *Proc. R. Soc. B* **278**, 3523–3528. (doi:10.1098/rspb.2011.0382)
11. Wilson DR, Bitton PP, Podos J, Mennill DJ. 2014 Uneven sampling and the analysis of vocal performance constraints. *Am. Nat.* **183**, 214–228. (doi:10.1086/674379)
12. Sockman KW. 2009 Annual variation in vocal performance and its relationship with bill morphology in Lincoln's sparrows, *Melospiza lincolni*. *Anim. Behav.* **77**, 663–671. (doi:10.1016/j.anbehav.2008.11.016)
13. Caro SP, Sewall KB, Salvante KG, Sockman KW. 2010 Female Lincoln's sparrows modulate their behavior in response to variation in male song quality. *Behav. Ecol.* **21**, 562–569. (doi:10.1093/beheco/arq022)
14. Collins EJ, McNamara JM, Ramsey DM. 2006 Learning rules for optimal selection in a varying environment: mate choice revisited. *Behav. Ecol.* **17**, 799–809. (doi:10.1093/beheco/arl008)
15. Beaulieu M, Sockman KW. 2012 Song in the cold is 'hot': memory of and preference for sexual signals perceived under thermal challenge. *Biol. Lett.* **8**, 751–753. (doi:10.1098/rsbl.2012.0481)
16. Nicholls TJ, Goldsmith AR, Dawson A. 1988 Photorefractoriness in birds and comparison with mammals. *Physiol. Rev.* **68**, 133–176.
17. Pinheiro J, Bates D, DebRoy S, Sarkar D. 2014 nlme: linear and nonlinear mixed effects models. *R package v. 3.1-117*.
18. McNamara JM, Fawcett TW, Houston AI. 2013 An adaptive response to uncertainty generates positive and negative contrast effects. *Science* **340**, 1084–1086. (doi:10.1126/science.1230599)
19. Real L. 1990 Search theory and mate choice. I. Models of single-sex discrimination. *Am. Nat.* **136**, 376–405. (doi:10.1086/285103)
20. Sockman KW. 2007 Neural orchestration of mate-choice plasticity in songbirds. *J. Ornithol.* **148**, 225–230. (doi:10.1007/s10336-007-0151-3)
21. Fowler-Finn KD, Rodríguez RL. 2012 Experience-mediated plasticity in mate preferences: mating assurance in a variable environment. *Evolution* **66**, 459–468. (doi:10.1111/j.1558-5646.2011.01446.x)
22. Maney DL. 2013 The incentive salience of courtship vocalizations: hormone-mediated 'wanting' in the auditory system. *Hearing Res.* **305**, 19–30. (doi:10.1016/j.heares.2013.04.011)
23. Sockman KW, Gentner TQ, Ball GF. 2002 Recent experience modulates forebrain gene-expression in response to mate-choice cues in European starlings. *Proc. R. Soc. Lond. B* **269**, 2479–2485. (doi:10.1098/rspb.2002.2180)