



SYMPOSIUM

How Song Experience Affects Female Mate-Choice, Male Song, and Monoaminergic Activity in the Auditory Telencephalon in Lincoln's Sparrows

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Synopsis A sexual signal can indicate not only the signaler's attractiveness as a potential mate but also the signaler's competitiveness relative to rivals. As the attractiveness or competitiveness of the prevailing signaling environment increases, individuals prospecting for mates should change their choice threshold, whereas competing individuals should shift resources toward elevating their own competitiveness. Previous studies show that experimental elevations of song competition increase male competitive behavior in Lincoln's sparrows (*Melospiza lincolnii*) and European starlings (*Sturnus vulgaris*). Through a series of experimental manipulations using laboratory-housed Lincoln's sparrows, we have also discovered that females change the strength of their song preferences depending on the attractiveness of the song environment to which they have recently been exposed; compared to a less-attractive environment, a highly-attractive environment elevates the threshold for releasing phonotaxis behavior toward male song. These behavioral adjustments are associated with changes in forebrain monoaminergic activity that are triggered by experimental manipulations of the quality of the song environment. Findings from these studies suggest possible neural mechanisms for the regulation of adaptive behavioral plasticity associated with dynamic sexual signaling environments.

Introduction

Sexual signaling systems can play pivotal roles in evolutionary processes. They can drive the evolution of elaborate traits and influence the genetic constitution of offspring and the parental effects they experience (Andersson 1994). No understanding of sexual signaling in animals is complete without an understanding of the neural mechanisms that give rise to signal production, signal reception, and plasticity in both (Phelps et al. 2006).

The nervous system performs two tasks in response to a biologically relevant stimulus, such as a sexual signal. It effects a behavioral response and, in some situations, it encodes a memory, which, together with other memories, may be retrieved later for adaptively modifying responses either to another iteration of the stimulus or to a new one (Kandel et al. 2012). Sexual signaling presents a useful system

for studying this two-part function of the nervous system in an ecological context; individual receivers make reproductive decisions based on a stimulus (the sexual signal), and they also remember the stimulus, together with other stimuli, to modify future responses to such signals. For example, the representation of a male mouse's pheromones may stimulate lordosis in a female receiver (DiBenedictis et al. 2012) but also may be stored as a memory later retrieved to modify solicitation or social behavior during future encounters with that or other males (Roberts et al. 2010).

Sexual signals can serve as indicators of the signaler's quality, broadly defined as the signaler's traits most relevant to the receiver's reproductive potential. Thus, by extension, sexual signals themselves can be evaluated in terms of their quality and indicate not only the signaler's attractiveness to opposite-sex

individuals, which may be prospective mates, but also the signaler's competitiveness to same-sex individuals, which may be rivals. In short, for both male and female receivers, a single sexual signal can release behavior, can be either positive or negative in its valence (depending on whether the sexes of the signaler and receiver are the same or different), and can be encoded in memory for the adaptive modification of future responses to new signals.

We have been using the Lincoln's sparrow (*Melospiza lincolni*) for examining how variation in the quality of sexual signals with which an individual has experience changes the brain and behavior. Specifically, a representative sample of signals from multiple individuals should indicate the prevailing quality of individuals against which a rival must compete (Sockman et al. 2009; Bailey et al. 2010; DiRienzo et al. 2012) or from which a prospective mate must choose (Real 1990; Gibson and Langen 1996; Bateman et al. 2001; Bateson and Healy 2005; Collins et al. 2006; Sockman 2007; Fowler-Finn and Rodríguez 2012). This, we predict, allows the receiver to make adaptive adjustments to its own behavior accordingly (Fawcett et al. 2014; Kelley and Kelley 2014). As the attractiveness or competitiveness of this prevailing signaling environment increases, prospective mates should change their choice threshold, and competing rivals should shift resources toward elevating their own competitiveness.

Although both male and female receivers should show adaptive plasticity in their response to sexual signals (Alonzo and Sinervo 2001; Ah-King and Gowaty 2016), we do not know the extent to which the signaling environment shapes this plasticity and how receivers' brains integrate cues regarding the prevailing signaling environment to flexibly orchestrate adaptive changes in behavior (Sockman et al. 2002, 2005; Cousillas et al. 2006; George and Cousillas 2013; Weitekamp and Hofmann 2014). To investigate this, one needs a suitable study system, one with a well-characterized sexual signal to which both sexes show adaptive behavioral responses in natural conditions, in which the signal is easily manipulated in an experimental fashion, in which the prevailing signaling environment is known to change, and in which one can readily examine its neural underpinnings.

Lincoln's sparrow song system

In songbirds, a male's song can advertise his quality not only to prospective mates but also to rival males (Searcy and Yasukawa 1996; Searcy and Beecher 2009). In our research on the Lincoln's sparrow,

we have found a compelling system for the study of adaptive plasticity in response to a performance-based sexual signal and a means for examining the neural basis for this plasticity. Performance-based sexual signals are appropriate for these investigations because they may be constrained either by physiology or morphology, and they often reflect a male's developmental history, skill, and vigor (Podos 1997; Nowicki et al. 1998; Ballentine 2009; Byers et al. 2010). Therefore, the quality of performance-based signals can vary spatially or temporally, based on the composition and condition of signalers in a population at any given time (Sockman 2009; Byers et al. 2010). Samples of performance-based signals should indicate to a male or female receiver the prevailing quality of signalers in a population (Gibson and Langen 1996; Sockman 2009; Bailey et al. 2010).

Lincoln's sparrows are migratory songbirds that winter in Mexico and the southern US and breed during summer months in either high altitude or high latitude wet meadows of the United States and Canada (Ammon 1995). After arriving on breeding grounds in May, males sing prolifically during early daylight hours (Beaulieu and Sockman 2012). Their songs are complex (Cicero and Benowitz-Fredericks 2000) and characterized typically by having between one and six (usually three or four) trills (Sockman 2009), defined as song components in which a syllable is rapidly repeated multiple times (Podos 1997). Trills are characteristic of the songs of many songbirds, but in particular the Emberizid sparrows (Catchpole and Slater 1995; Podos 1997), of which the Lincoln's sparrow is a member. Such trills may be the basis for performance-based signals in which an individual could advertise his quality through his ability to perform a difficult vocal maneuver (Podos 1996, 1997; Podos et al. 1999; Ballentine 2009; Byers et al. 2010). In order to produce a change in sound frequency, the songbird's vocal tract must undergo a conformational change in the skeletal and muscular components that form the vocal tract (Hoese et al. 2000; Riede et al. 2006). The larger that frequency change is (i.e., the larger the trill's frequency bandwidth), the larger the conformational change, which necessarily trades off with the speed over which the frequency change can occur (i.e., the number of syllables per second, or trill rate). The trill has been hypothesized as a means for advertising one's ability to perform difficult vocal behavior (Vehrencamp 2000; Podos and Nowicki 2004; Byers et al. 2010; Moseley et al. 2013; Podos et al. 2016). Researchers have been able to capture this trade-off by measuring the

relationship between maximum frequency bandwidth and trill rate (Podos et al. 2009; Wilson et al. 2014), the relationship between intersyllable gap duration and intersyllable frequency shift (Geberzahn and Aubin 2014), and frequency excursion, or total frequency modulation over time (Podos et al. 2016).

The trills of Lincoln's sparrows indeed seem to reflect this trade-off, as indicated by the triangular-shaped distribution of frequency bandwidth plotted against trill rate (Sockman 2009). At the highest trill rates, only the lowest bandwidths are possible, whereas at the highest bandwidths, only the lowest trill rates are possible. There are two ways of estimating the strength of this trade-off. One can estimate the pareto frontier (upper boundary) for values in this bivariate space, such that it represents an approximation of the theoretical maximum performance of bandwidth given the trill rate (Podos 1997). Alternatively, one can derive a quantile regression line that estimates the relationship between trill rate and frequency bandwidth for trills in the upper percentile of the frequency bandwidth distribution. This latter approach provides a more conservative estimate of the trade-off (Wilson et al. 2014). In Lincoln's sparrows, there is a negative trade-off between frequency bandwidth and trill rate using either the upper bound regression or quantile regression (Podos 1997; Sockman 2009; Lyons et al. 2014; Wilson et al. 2014). After calculating the relationship using either method, one can calculate the orthogonal distance of any point in the bivariate plot to the regression line. This distance provides a dimensionless estimate of an individual trill's performance level, whereby the higher (less negative) the value, the higher the performance. Moreover, one can digitally manipulate the performance of individual trills within songs to experimentally evaluate the role of this sexual signal in driving receiver responses (Caro et al. 2010; Lyons et al. 2014).

In the Lincoln's sparrow, we have conducted experiments in the laboratory and the field using playbacks of such digitally manipulated songs (Caro et al. 2010; Lyons et al. 2014) (Fig. 1). After digitally cutting 15 ms of silence from the intersyllabic space of a trill's syllables, we paste that 15 ms silence into the corresponding intersyllabic space of an otherwise identical digital copy of the song to produce two identical songs, one with low trill performance (i.e., one with 15 ms silence added to the intersyllabic space) and another with high trill performance (i.e., one with 15 ms silence removed from the intersyllabic space). Importantly, following this manipulation, the songs are still within the natural range of Lincoln's sparrows' songs, both in terms of trill rate

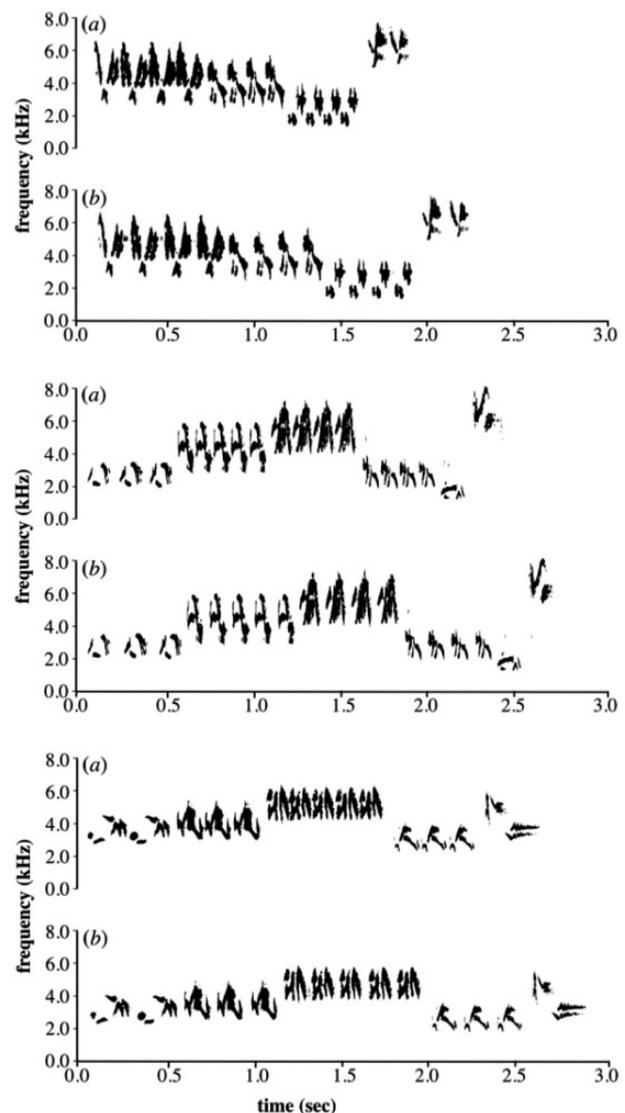


Fig. 1 Exemplars of three treatment songs that were recorded from wild, free-ranging Lincoln's sparrows (*Melospiza lincolni*) and digitally manipulated to be (a) high performance and (b) low performance by removing 15 ms silence between the intersyllabic space of each trill of one digital copy of the song and pasting it in the corresponding space of the other copy of the song. Modified from Lyons and Sockman (2017).

and trill performance, and using either the upper bound regression or quantile regression method (Caro et al. 2010; Lyons et al. 2014; Lyons and Sockman 2017). When wild, free-ranging male Lincoln's sparrows are exposed to playbacks of songs manipulated to have high trill performance, they respond more aggressively than they do when they are exposed to the same songs manipulated to have low trill performance, thus establishing the behavioral relevance to males of variation in trill performance (S. M. Lyons et al., unpublished data).

Assessing the relevance of variation in trill performance to females is more difficult, as females

tend to be furtive and difficult to observe freely behaving in the wild. Thus, we used laboratory experiments to examine the effect of variation in trill performance on females. Specifically, using similar digital manipulations of the songs' trill performances, we discovered that females preferentially approach speakers playing the high-performance versions of songs compared to those playing the low-performance versions of the same songs (Caro et al. 2010). In short, our field experiments on wild male Lincoln's sparrows and our laboratory experiments on wild female Lincoln's sparrows reveal that variation in trill performance is behaviorally relevant to receivers of both sexes, as has been shown for other species (Ballentine et al. 2004; Illes et al. 2006; Moseley et al. 2013; Goodwin and Podos 2014). Elevating trill performance in songs causes elevated aggression in male receivers and more strongly attracts female receivers.

Song experience changes behavioral responses to song

As indicated above, female Lincoln's sparrows prefer songs with high-performance trills over those with low-performance trills. But to what extent might they be flexible in this preference? For example, would females forgo mate choice and therefore mating if, for some reason, none of the males produced song with high-performance trills during a breeding season? This would seem maladaptive because adults face an annual mortality rate of ~50% (K. W. Sockman, personal observation) and therefore may not have a future opportunity to choose a mate and reproduce. Interestingly, female Lincoln's sparrows may be faced with such a conundrum. We discovered significant between-year variation in the average trill performance produced by males in the population (Sockman 2009; Lyons 2016), suggesting that in some years, either the males' songs do not rise to the level of performance to attract females or that females might modulate their threshold of acceptance.

We examined the possibility that females modulate their threshold for attraction to a song, depending on their recent experiences. We digitally manipulated 3 songs recorded from each of six males to form two treatment levels, one with 18 songs of high trill performance and one with the same 18 songs but of low trill performance (Lyons et al. 2014) (Fig. 1). We assigned females to one of the two treatments and, during the first 5 hours every morning for a week, we played their assigned songs in semi-random order while recording their

proximity to the speaker with a video camera. Our goal was to manipulate the females' perception of the typical quality of male songs in an effort to examine whether it influences their attraction to a novel song of intermediate performance. Thus, on the eighth day we no longer exposed the females to these manipulated songs and instead recorded their proximity to the speaker playing novel song chosen explicitly for its level of trill performance, which was intermediate to that of the low and high treatment groups. Thus, females were provided with a week-long exposure to an experimentally induced low-performance or high-performance song environment before they were assessed for their attraction to a single, novel intermediate-performance song. Following this procedure, we housed them with no playbacks for another week before switching each female to the alternate treatment and repeating the above procedures, choosing a second, novel, intermediate-performance song at the end. Results from this study provide support for the idea that females change the behavioral threshold for attraction to a song based on its performance (Real 1990; Collins et al. 2006; Sockman 2007). Specifically, after experiencing songs with low-performance trills for a week, females showed stronger attraction to the song with intermediate trill performance than they did after experiencing songs with high-performance trills for a week (Lyons et al. 2014) (Fig. 2).

Sewall et al. (2010) have conducted similar work on Lincoln's sparrows using males as the subjects and showed that, as receivers, males, like females, respond to variation in song quality with lasting shifts in their behavioral phenotype. The way in which they approached this question for male receivers differed somewhat from the way in which we approached it for female receivers. For males, instead of digitally manipulating songs, they selected natural songs based on trill performance and other traits. They exposed laboratory-housed males for a week to songs that were naturally high in trill performance (and also long in duration and having more syllables and phrases) or naturally low in trill performance (and also short in duration and having fewer syllables and phrases). Males respond to song by counter-singing. Thus, for the week-long song exposure they collected audio recordings of the male subjects. They discovered that males sang more in response to the high-quality (high trill performance, long duration, high syllable and phrase-count) song playbacks than in response to the low-quality song playbacks. On the eighth day, they continued to collect audio recording of the male

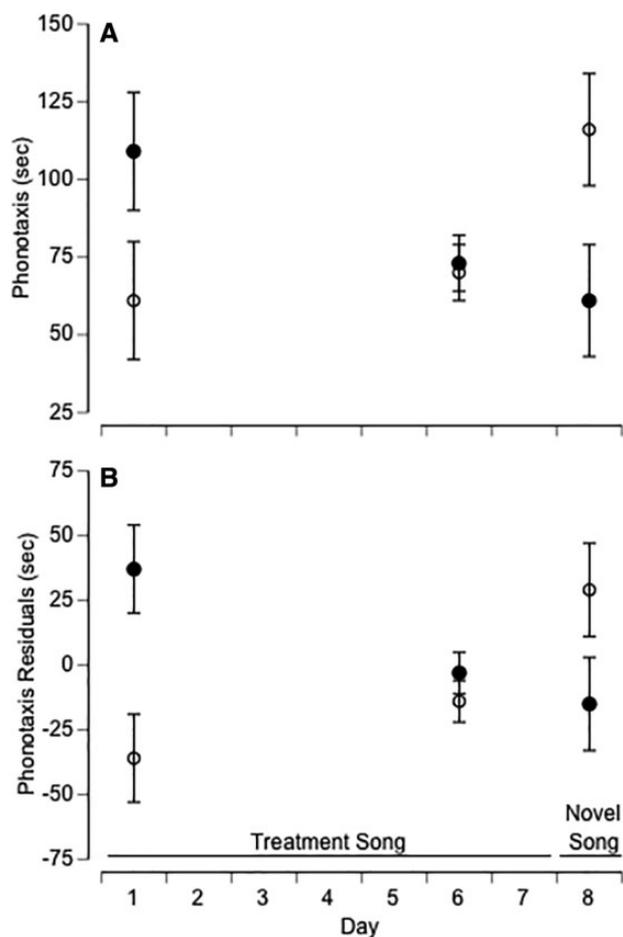


Fig. 2 Mean (\pm SEM) (A) phonotaxis time and (B) residuals of phonotaxis time (controlling for cage side-bias) of female Lincoln's sparrows (*Melospiza lincolni*) exposed to low- (open symbols) or high-performance (black symbols) songs, during exposure to treatment songs (Days 1 and 6) and to novel intermediate-performance song (Day 8). Note that symbol shading refers only to variation in the treatment songs to which individuals were exposed during the first 7 days. All individuals were under the same song exposure during the 8th day of novel song. Modified from Lyons et al. (2014).

subjects, but they provided no playback. The male Lincoln's sparrow subjects retained their song-response difference even in the absence of playback; males that had just experienced a week of high-quality songs continued to sing more than males that had just experienced a week of low-quality songs. These findings indicate that the quality of the prevailing song environment not only triggers a change in behavior in real time but also effects a longer-term shift in behavioral phenotype that lasts at least a day following cessation of the playback treatment (Sewall et al. 2010). Thus, both male and female receivers are sensitive to trill performance or other aspects of song quality, and they fundamentally change their behavior in the longer term in response to these different song environments. The next

question we began to address, then, was how the brain might be orchestrating such behavioral plasticity.

Forebrain monoaminergic responses to the sexual signaling environment

For most behaviors that are complex, the search for neural mechanisms is also complex. Fortunately, a history of research on songbird song processing and the roles of neuromodulators has guided our research on the neural basis for sexual signaling and mate-choice plasticity in Lincoln's sparrows.

Song quality in the social environment could have long- and short-term influences on social behavior by changing regions of the brain that perceive and process information about song (Weitekamp and Hofmann 2014). Therefore, in studying the mechanisms underlying plasticity in sexual signaling and mate choice in Lincoln's sparrows, we concentrated our efforts on examining the auditory sensory system. In particular, we focused on areas called the caudomedial mesopallium (CMM) and caudomedial nidopallium (NCM), which, together, are considered analogous to the mammalian secondary auditory cortex, and we will refer to them together as the auditory telencephalon (or auditory forebrain) (Vates et al. 1996; Jarvis 2004; Pinaud and Terleph 2008).

Over 20 years of research have shed considerable light on the role of the auditory telencephalon in songbird song processing. Electrophysiological and immediate-early gene studies have revealed the auditory telencephalon's high-order processing capabilities (Mello et al. 1992; Chew et al. 1995; Stripling et al. 1997; Ribeiro et al. 1998; Sen et al. 2001). This region appears responsible for experience-dependent processing of conspecific song (Bolhuis et al. 2000; Sockman et al. 2002, 2005; Gentner and Margoliash 2003; Gentner et al. 2004; Sockman and Ball 2009), and for processing female and male responses to variation in conspecific song (Gentner et al. 2001, 2004; Sockman 2007). Thus, the songbird auditory telencephalon may help regulate behavioral plasticity in response to experience with high-order acoustic features such as trill performance.

The songbird auditory telencephalon is innervated by monoaminergic inputs (Mello et al. 1998; Appeltants et al. 2001; Kubikova et al. 2010; Matragnano et al. 2011; 2012a, 2012b), which regulate aspects of attention and perception (Oades 1985; Maney 2013; Ikeda et al. 2015), and which might facilitate integration of the social environment within

the songbird brain (Castelino and Schmidt 2010; Kubikova and Kostal 2010). Central monoamines have a host of neuromodulatory effects, including changes in behavioral motivation and reward processing often ascribed to dopamine action (Berridge and Robinson 1998; Maney 2013; Riters et al. 2014), changes in alertness and concentration associated with norepinephrine signaling (Oades 1985; Aston-Jones and Cohen 2005; Sara 2009; Castelino and Schmidt 2010), and changes in sensory processing associated with serotonin action (Hurley et al. 2004; Hurley and Hall 2011). Many effects of monoamines are tied to environmental context and individual experience (Berridge and Waterhouse 2003; Hurley et al. 2004; Castelino and Schmidt 2010; Hurley and Hall 2011), and monoamines modulate neuroplasticity in response to auditory signals (Bao et al. 2001; Hurley and Hall 2011; Velho et al. 2012; Ikeda et al. 2015). In addition, previous studies have found that exposure to more salient stimuli, such as songs compared to tones (Matragrano et al. 2012b), or more attractive song compared to less attractive song (Sockman and Salvante 2008; Salvante et al. 2009; Sewall et al. 2013) generally increases monoaminergic activity in the auditory telencephalon of male and female songbirds. Thus, monoamines likely play a role in experience-dependent plasticity in sexual signaling and mate choice (Lynch and Ball 2008; Lynch et al. 2008; Castelino and Schmidt 2010). In an effort to examine the potential role of monoamines in this experience-dependent plasticity, Sockman and colleagues have been quantifying the effects of variation in trill performance on dopamine, norepinephrine, serotonin, and their primary metabolites using high-pressure liquid chromatography with electrochemical detection (Sockman and Salvante 2008; Salvante et al. 2009; Sewall et al. 2013; Lyons and Sockman 2017).

As described above, variation in song trill performance over seven days drives long-term behavioral shifts in both females and males. Thus, whatever neural processes change the brain to effect this behavioral change must occur during the seven-day period of song exposure. In fact, we observe significant effects on monoaminergic activity in the Lincoln's sparrow auditory telencephalon that depend on the trill performance of song an individual experienced over just a single morning (Lyons and Sockman 2017). Specifically, we digitally manipulated Lincoln's sparrow songs to be of either high or low trill performance and then exposed males and females to one 5-hr morning of song before removing brains and collecting tissue punches from the auditory telencephalon (Sewall et al. 2013).

In females, we discovered that, relative to the low-performance treatment, the high-performance treatment reduced concentrations of serotonin in the CMM, concentrations of the primary serotonin metabolite in the NCM, and concentrations of both norepinephrine and its primary metabolite in the NCM (Lyons and Sockman 2017) (Fig. 3). Both serotonin and norepinephrine help modulate auditory processing. In mammals, serotonin modulates the auditory system's responses to complex auditory signals (Hurley et al. 2004). In the songbird NCM, norepinephrine sharpens the response to and encoding accuracy of auditory signals. Thus, the finding that both norepinephrine and serotonin activity in the auditory telencephalon differed between the treatments suggests that just one morning (five hours) of exposure to songs that differ in trill performance may be effective at modulating auditory processing in the female auditory telencephalon. Furthermore, these findings raise the hypothesis that either norepinephrine or serotonin in the auditory telencephalon contributes to the differences in phonotaxis behavior observed in females after one week of exposure to songs that differ in trill performance.

Interestingly, the direction of song quality's effect on auditory monoamines after one morning of exposure to high quality songs is opposite the direction of the effect after one week of exposure. After one morning of exposure, monoaminergic activity was lower in female Lincoln sparrows exposed to high-quality (high-performance) songs compared to low-quality songs. In previous studies that exposed female European starlings to one week of high- or low-quality songs, monoaminergic activity was higher in females exposed to high-quality songs compared to low-quality songs. After one week of song exposure, monoamine and metabolite levels may reflect longer-term tonic changes to baseline monoaminergic activity, whereas after one morning of song exposure, monoamine and metabolite levels may reflect more immediate, phasic responses to the song stimuli.

In contrast to the findings that exposure to 5 h of high- or low-performance songs affected monoamines in the auditory telencephalon of female Lincoln's sparrows, in males we observed no such treatment effects on monoaminergic activity in either auditory region (Fig. 3), perhaps because variation in the quality of song males experience causes long-term changes in behavior through other systems, for example through motor or motivational systems (Sewall et al. 2010; Maney and Goodson 2011; Rosvall et al. 2012) or because the monoaminergic

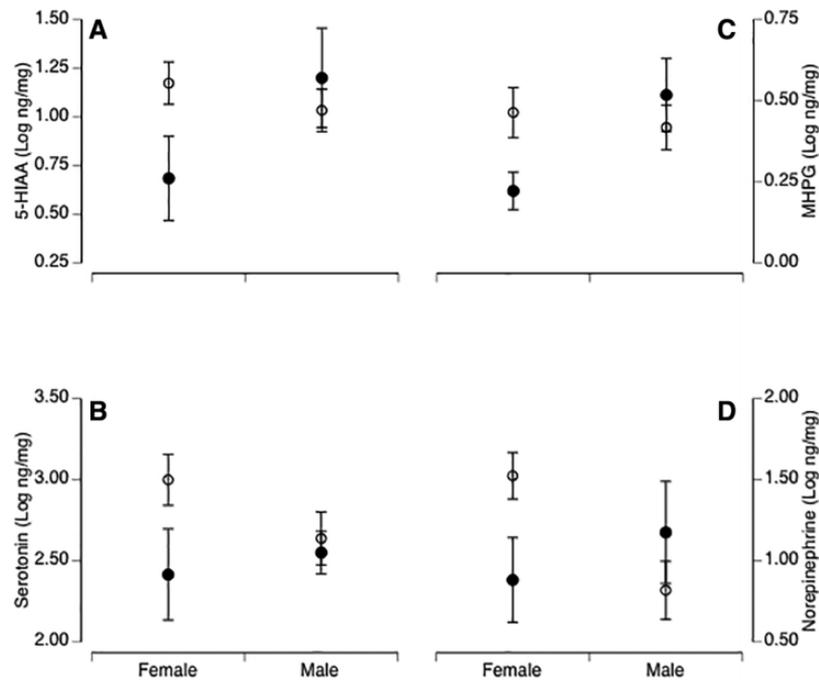


Fig. 3 Effects of sex, the experimental treatment, and their interaction on the concentration (mean \pm SEM) of (A) serotonin metabolite (5-HIAA) in the caudomedial nidopallium, (B) serotonin in the caudomedial mesopallium, (C) norepinephrine metabolite (MHPG) in the caudomedial nidopallium and (D) norepinephrine in the caudomedial nidopallium, in Lincoln's sparrows (*Melospiza lincolnii*). The experimental treatment involved the digital manipulation of the trills in playback songs to be of either low (open symbols) or high (black symbols) performance. Modified from Lyons and Sockman (2017).

response in males occurs over a different time period than females (Sewall et al. 2013).

Future directions

The work on Lincoln's sparrows that is described above provides insights into the ecological, behavioral, and neural bases for plasticity in sexual signaling and mate choice. However, future work on this or other species could benefit from focus on the most pressing questions. From an ultimate, evolutionary perspective, we still do not fully understand the adaptive basis for this behavioral plasticity in sexual signaling. It is intuitive that females adjust their song-quality threshold for mate choice according to the prevailing quality of the song environment, but whether such adjustments benefit fitness remains to be determined. Similarly, the fact that variation in the quality of song males experience affects their own singing effort raises questions about the adaptive significance of this plasticity and also whether or not singing effort trades off with responses in some other behavioral or physiological system (Gil and Gahr 2002). For example, if elevating singing effort is energetically costly (e.g., Ward and Slater 2005), what system might be down regulated to offset such a cost?

From an ecological perspective, the fact that the quality of the prevailing song environment varies annually is of considerable interest. Presumably this annual variation reflects some annual variation in ecological conditions, such as climate, habitat maturation, or food conditions (Sockman 2009), and, if so, what specific ecological parameters are driving annual variation in song quality and how?

From a behavioral perspective, it would be interesting to examine the various time-periods over which song experience drives behavioral plasticity. Our experiments focused on a week-long experience, but can individuals assess the song environment more rapidly and show similar behavioral plasticity after shorter periods of song experience? In addition, it would be interesting to determine the extent to which song experience during other life stages plays a role, in particular the developmental stage when individuals are learning song (Podos 1996; Podos et al. 1999, 2009). We have begun to explore this question by exposing juvenile males to experiences with digitally manipulated low- and high-performance song, and results show that this juvenile experience affects their own trill performance later, as adults, when they are performing their own sexual signaling (S. M. Lyons and K. W. Sockman, unpublished data). On another front, although trill performance as an indicator of

skill makes sense, it is not clear why this particular skill should be an indicator of male quality more broadly and therefore why receivers should show strong responses to variation in trill performance.

Perhaps in greatest need of future research concerns the neural basis for this behavioral plasticity. As described above, variation in trill performance affects monoaminergic activity in the auditory forebrain, but does this monoaminergic activity have anything to do with the neuroplasticity that underlies the behavioral plasticity we demonstrated? Experiments that involve controlled manipulations of that monoaminergic activity could help to answer this question.

Of course, these specific studies on Lincoln's sparrows have broader implications for research in other systems that addresses sexual signalling, plasticity, and their underlying neural regulation. Of particular interest would be research examining the extent to which there exists population-wide temporal (annual) or spatial variation in the quality of male sexual signals. In other words, how often and in what other systems are females tasked with adjusting their threshold for acceptance of a courting male? Annual variation in the mean quality of sexual signals was a surprising discovery in Lincoln's sparrows (Sockman 2009), and it may turn out to be the norm after careful investigation elsewhere.

Of considerable interest would be to understand the neural mechanisms underlying plasticity in signaling and mate choice broadly (Sockman 2007). Are there mechanisms common to vertebrates and other animals, and, if so, what are they and to what extent does monoaminergic signaling play any role? As described here, we have been exploring the role of sensory processing, but mate choice involves other neural systems as well, such as motivational and motor systems, raising the possibility that other aspects of brain function are important in plasticity in signaling and mate choice.

Regardless of the many avenues that we have yet to pursue, we believe that this Lincoln's sparrow system has already contributed to a broader understanding of how experience with a sexual signal can affect key neuromodulatory systems and change behavior in response to the signal. The future studies described above, as well as others, will undoubtedly continue to change the way we understand behavioral plasticity and the brain in natural systems and under relevant ecological contexts.

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