



Developmental stress impairs a female songbird's behavioural and neural response to a sexually selected signal



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Birdsong is a complex, learned vocalization that is strongly shaped by early developmental conditions. In males, stressful early-life conditions are known to have adverse effects on the development of song and its supporting neural structures (i.e. the song-control system). Conversely, how developmental stress affects female song preferences and brain development is understudied. We subjected female European starlings, *Sturnus vulgaris*, to an unpredictable food stressor through the first few months of life. As adults, we first assessed females' song preferences using an operant-conditioning task in a (1) conspecific versus heterospecific song comparison and (2) short- versus long-bout starling song comparison. Then, we measured the immediate-early gene (*Zenk*) response in auditory forebrain areas when birds were listening to either conspecific song or heterospecific song and quantified the volumes of song-control brain regions. We observed that females reared in control conditions showed a significant behavioural preference for conspecific song (over heterospecific song), whereas females reared in food-restricted conditions did not. Although individual females showed clear preferences for either short- or long-bout starling song, the direction of this preference was not consistent between birds. Control females had significantly more *Zenk* induction in auditory forebrain areas than food-restricted females when listening to conspecific song. Heterospecific song playback resulted in significantly less *Zenk* induction than conspecific song playback, with no difference between treatment groups. Across the song-control regions measured, we observed no significant differences in volumes between the treatment groups. However, we did find that the volume of the song-control region HVC was positively related to the strength of preference that females displayed in the conspecific versus heterospecific operant preference test. Thus, early-life stressors known to affect male song and brain development have similar effects on female behaviour and neural response to song stimuli.

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Birdsong is a sexually selected signal that has been researched extensively because of its conspicuous nature. Variation in male song can be explained, in part, by the quality of the environment in which a male is reared: males reared in stressful environments are unable to devote as many resources to the costly development of the neural structures that enable song learning, ultimately affecting the quality of the song phenotype produced in adulthood (Nowicki, Peters, & Podos, 1998; Nowicki, Searcy, & Peters, 2002). However, the effects of early-life stress on a female's ability to perceive male

song is of equal importance to understanding the evolution of sexually selected traits, and yet is understudied in songbirds (Cotton, Small, & Pomiankowski, 2006).

In songbirds, the quality of a male's song (e.g. repertoire size, song bout length) can reflect other aspects of male condition (Searcy & Andersson, 1986). In European starlings, *Sturnus vulgaris*, male song quality is positively associated with spatial learning, social rank and immune function (Buchanan, Spencer, Goldsmith, & Catchpole, 2003; Duffy & Ball, 2002; Farrell, Weaver, An, & Macdougall-Shackleton, 2011; Spencer, Buchanan, Goldsmith, & Catchpole, 2004). Females that mate with males that possess a high-quality song may be receiving direct/indirect benefits by doing so (Searcy, 1992b) and therefore a female must be sensitive to variation in song quality. Although the adverse effects of developmental stress on male song are well documented (see Spencer &

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MacDougall-Shackleton, 2011), the effects of such stress on female song preferences are mixed. Female zebra finches, *Taeniopygia guttata*, raised in large broods had weaker absolute song preferences (Riebel, Naguib, & Gil, 2009), and females that experienced a nutritional stressor were less active in mate choice trials (Woodgate et al., 2011), yet compared to their control siblings, they preferred songs of equal complexity when sung by unfamiliar singers (Woodgate et al., 2011). In another study, female zebra finches raised in large broods preferred the songs of males raised in similar stressful conditions, suggesting an assortative mating strategy based on developmental experience (Holveck & Riebel, 2010). Female song sparrows, *Melospiza melodia*, raised in control conditions were more active when listening to conspecific song than when listening to heterospecific song, but this difference was reduced in females exposed to different developmental stressors (food restriction or exogenous corticosterone treatment; Schmidt, McCallum, MacDougall-Shackleton, & MacDougall-Shackleton, 2013). Interestingly, there was no difference between stressed and control females in a high- versus low-quality conspecific comparison (Schmidt, McCallum, et al., 2013). With only data from two species, more experimental studies are necessary before general conclusions can be made about how developmental stress affects female song preferences and ultimately mate choice decisions.

Male song is adversely affected by developmental stress partly because it hinders neural development of the song-control system (HVC; robust nucleus of the arcopallium, RA; Area X; reviewed in Spencer & MacDougall-Shackleton, 2011). Female songbirds also have a song-control system, albeit reduced in size (MacDougall-Shackleton & Ball, 1999), which may be necessary for the perception of song. Partial lesions to HVC in canaries, *Serinus canaria domestica*, disrupts song preferences (Brenowitz, 1991; Del Negro, Gahr, Leboucher, & Kreutzer, 1998), and the size of HVC in canaries and starlings is related positively to the strength of preference towards sexually stimulating songs (Leitner & Catchpole, 2002; Ritters & Teague, 2003). However, little is known about the effects of developmental stress on the female song-control system. Preliminary work with female song sparrows found that juveniles exposed to early nutritional stress had smaller HVC volume, but this effect was not found in adult females that were subjected to either a nutritional stress or exogenous corticosterone treatment in early development (MacDonald, Kempster, Zanette, & MacDougall-Shackleton, 2006; Schmidt, McCallum, et al., 2013). These results suggest that HVC may exhibit catch-up growth following an early-life stress, but more work in additional species is needed to substantiate this claim.

In addition to the song-control system, auditory forebrain nuclei (caudomedial mesopallium, CMM; caudomedial nidopallium, NCM) that project to song-control nuclei are necessary for recognizing and processing song (Bolhuis & Gahr, 2006; Vates, Broome, Mello, & Nottebohm, 1996). In zebra finches, lesioning of the CMM disrupts song preferences, yet lesioning of the HVC does not (MacDougall-Shackleton, Hulse, & Ball, 1998). In response to playback stimuli, the neural response within these areas can be measured by assessing expression of the immediate-early gene *Zenk* (an acronym of *zif-268*, *erg-1*, *NGFI-A* and *Krox-24*), which is a transcriptional regulator (Mello, Vicario, & Clayton, 1992). *Zenk* expression is greatest when birds are listening to conspecific song, decreases when listening to heterospecific song, and is minimal in response to tonal stimuli (Mello et al., 1992). Furthermore, levels of *Zenk* correspond to the sexual potency of an auditory stimulus (Maney, MacDougall-Shackleton, MacDougall-Shackleton, Ball, & Hahn, 2003) and are therefore a powerful tool to quantify song preferences in addition to behavioural measures. In starlings, behavioural measures of preference show that females prefer to

listen to longer song bouts over shorter song bouts and that these behavioural preferences are reflected in the *Zenk* response in NCM: females that heard long song bouts had more *Zenk* immunoreactivity than females that heard short song bouts (Gentner, Hulse, Duffy, & Ball, 2001). More recently, *Zenk* immunoreactivity was quantified in females whose early developmental backgrounds were known: song sparrows that were unstressed had significantly more cells expressing *Zenk* immunoreactivity in auditory nuclei CMM and NCM when listening to playbacks of conspecific versus heterospecific song in adulthood, yet the amount of *Zenk* induction was equal across both playback conditions for developmentally stressed females (Schmidt, McCallum, et al., 2013).

Using both behavioural and neural measures of song preference (volumetric analysis of song-control nuclei and *Zenk* immunoreactivity within auditory forebrain regions) within the same individual provides a powerful method to observe how early developmental stress shapes female song preferences. We examined how developmental stress affects female starlings using both these methods. Starlings are an excellent species in which to address these questions for numerous reasons. First, the results from studies of captive and free-living starlings clearly demonstrate that females have a robust preference for male conspecific song, particularly for bouts of song that are long in duration (e.g. Mountjoy & Lemon, 1991, 1996). In addition, song quality is clearly related to reproductive success in this species: males that sing longer song bouts acquire mates faster, their female partners lay clutches sooner and they have larger clutches (Eens, Pinxten, & Verheyen, 1991; Mountjoy & Lemon, 1996). Females are sensitive to variation in male song quality, as measured in choice tests (Gentner & Hulse, 2000) and based on the amount of *Zenk* induction to playbacks of conspecific songs of long and short duration (Gentner et al., 2001; Sockman, Gentner, & Ball, 2002). Finally, experiencing stressful food restriction in early development has known effects on song behaviour and other cognitive abilities in starlings (Buchanan et al., 2003; Farrell et al., 2011; Spencer et al., 2004).

In our study, we manipulated early developmental conditions through an unpredictable food supply paradigm. After the developmental treatment ceased, we measured females' preferences for songs several months later using an operant-conditioning paradigm in two comparisons: (1) conspecific versus heterospecific (canary) song and (2) short versus long bouts of conspecific songs. After behavioural testing was complete, we then played either conspecific or heterospecific songs to birds prior to quantifying the *Zenk* response within the auditory forebrain regions of CMM and NCM. We also measured the volumes of three song-control nuclei (HVC, RA, Area X) in relation to overall telencephalon volume and compared HVC size to the strength of preferences as measured in the operant-conditioning tasks. We hypothesized that females raised in stressful early-life environments would show weaker behavioural and neural responses towards sexually potent signals compared to their control counterparts. Moreover, these weaker responses could be correlated with song-control system volumes and we hypothesized that females with larger HVC volume would, regardless of early-life conditions, show the strongest preferences for sexually relevant songs.

METHODS

Study Subjects and Developmental Treatment

In May–June 2012, we captured European starlings as nestlings from around London, Ontario (42°98'N, 81°25'W). Nestlings were

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