



Early-life stress affects the behavioural and neural response of female song sparrows to conspecific song

Kim L. Schmidt^{a,b,*}, Erin S. McCallum^{c,1}, Elizabeth A. MacDougall-Shackleton^a,
Scott A. MacDougall-Shackleton^{a,b,c}

^a Department of Biology, University of Western Ontario, London, ON, Canada

^b Advanced Facility for Avian Research, University of Western Ontario, London, ON, Canada

^c Department of Psychology, University of Western Ontario, London, ON, Canada

ARTICLE INFO

Article history:

Received 2 October 2012
Initial acceptance 6 December 2012
Final acceptance 16 January 2013
Available online 7 March 2013
MS. number: A12-00761R

Keywords:

birdsong
caudomedial mesopallium
caudomedial nidopallium
CMM
developmental stress
HVC
Melospiza melodia
NCM
RA
song preference

In songbirds, both song production and song preferences may be influenced by early-life experience. Early-life stress impairs development of the song-control brain regions and permanently affects male song production. However, few studies have examined the effects of early-life stress on female song preferences or the brains of female songbirds. We exposed female song sparrows, *Melospiza melodia*, to stressors (food restriction or exogenous corticosterone treatment) early in development. When birds were adults, we determined the effects of the stressors on: (1) the behavioural response to high-complexity versus low complexity-songs as well as to conspecific versus heterospecific songs; (2) the volume of song-control brain regions; and (3) the immediate early gene (*Zenk*) response in auditory forebrain regions following exposure to either conspecific or heterospecific song. We found no significant effect of developmental stress on the strength of the behavioural response to high- versus low-complexity song, but control females showed more selectivity in their behavioural response to conspecific versus heterospecific song when compared with food-restricted or corticosterone-treated birds. We observed no effect of either stressor on volume of the song-control nuclei. Control females exposed to conspecific song had more *Zenk*-immunoreactive cells in the auditory brain regions than control females exposed to heterospecific song. In contrast, food-restricted and corticosterone-treated females did not have more *Zenk*-immunoreactive cells after exposure to conspecific song. These results show that stressors known to affect male song production might also affect neural processing of song by females, and their subsequent behavioural response to song.

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Stress experienced early in life can alter brain development, leading to long-term effects on cognition and behaviour in many vertebrate species (Welberg & Seckl 2001). In songbirds, developmental stress can have persistent effects on multiple aspects of cognition and behaviour, including spatial learning (Farrell et al. 2011), social dominance and neophobia (Spencer & Verhulst 2007). In addition, a variety of early-life stressors can impair development of the brain regions that are important for song learning and production and affect adult song production (Nowicki et al. 1998). For example, food restriction affects growth of the song nucleus HVC in zebra finches, *Taeniopygia guttata* (Buchanan et al. 2004) and song sparrows, *Melospiza melodia* (MacDonald et al. 2006). Male zebra finches exposed to early-life food restriction or

treatment with the glucocorticoid hormone corticosterone (CORT) also sing songs that are shorter and less complex (Spencer et al. 2003). Swamp sparrows, *Melospiza georgiana*, exposed to food restriction early in life produce poorer copies of their tutor's song compared with males exposed to control conditions (Nowicki et al. 2002a). As song is a sexually selected trait that is important for attracting mates and/or intermale aggression in many species (Collins 2004), the effects of early-life stress on song-control nuclei and subsequent song production could have important fitness consequences for songbirds.

In most species of songbird that breed in the temperate zone, males sing much more than females, if females sing at all. However, even if females do not produce song, they may attend to a variety of features of male songs when selecting mates (Nowicki & Searcy 2005). For example, females may prefer songs that are more complex (Reid et al. 2004), that are more similar to those of their natal population (MacDougall-Shackleton et al. 2001) or that were more accurately learned from a tutor (Nowicki et al. 2002b). Although there is now substantial evidence that developmental stressors can

* Correspondence: K. L. Schmidt, Department of Biology, Advanced Facility for Avian Research, University of Western Ontario, London, ON N6A 5B8, Canada.

E-mail address: kschmi5@uwo.ca (K. L. Schmidt).

¹ Present address: E. S. McCallum, Department of Psychology, Neuroscience and Behaviour, McMaster University, Hamilton, ON L8S 4L8, Canada.

have long-term effects on song learning and production in males (reviewed in MacDougall-Shackleton & Spencer 2012), few studies have examined the effects of developmental stress on female song preferences. However, in some species (including song sparrows; Hernandez et al. 2009), exposure to songs during development affects female song preference in adulthood, indicating that females learn or memorize songs they later prefer. Therefore, as early-life stress has been shown to affect song learning in males, it is possible that early-life stress may affect learned female song preferences. So far, studies testing this hypothesis have found mixed results. In one study, female zebra finches reared in experimentally enlarged broods (and presumably exposed to developmental stress) had weaker preferences than did control females when choosing between two unfamiliar songs (Riebel et al. 2009). Interestingly, another study of zebra finches found that females reared in large broods preferred the songs of males reared in similar conditions, whereas females reared in small broods preferred songs of males from small broods, potentially resulting in assortative mating (Holveck & Riebel 2010). These results suggest that early-life stress may affect both the strength and direction of female song preferences. However, there appears to be no effect of early-life food restriction on the preference for high-complexity songs in zebra finches (Woodgate et al. 2011). Therefore, the effects of developmental stress on female preference may depend on the type of stressor, as well as the particular aspect of song being tested.

Despite a growing body of evidence implicating developmental stress in adult song preferences, the neural bases underlying these effects are unclear. Two descending pathways of song control nuclei have been identified as important for song learning and production (Margoliash 1997). The development of two nuclei in particular, HVC and the robust nucleus of the arcopallium (RA), may be impaired in individuals exposed to early-life stress (Nowicki et al. 2002a; Buchanan et al. 2004). These two nuclei are important for the learning or production of song in males. However, studies investigating the role of the song-control nuclei in the formation or maintenance of female song preferences have found conflicting results. For example, female canaries, *Serinus canaria domestica*, that are better able to discriminate between songs of different quality have a larger HVC (Leitner & Catchpole 2002), and lesions of HVC disrupt normal song preferences in this species (Brenowitz 1991). However, in female zebra finches, lesions of HVC had no effect on the preference for conspecific song over heterospecific song (MacDougall-Shackleton et al. 1998a).

In addition to the song-control nuclei, a series of auditory regions in the forebrain connect the general auditory area, field L, to the song-control system (Vates et al. 1996). In contrast to studies investigating the role of the song-control nuclei, there is strong evidence that the auditory forebrain is important for song discrimination and the formation and maintenance of song preferences. For example, lesions to one of these regions, the caudomedial mesopallium (CMM) impair the preference of female zebra finches for conspecific over heterospecific song (MacDougall-Shackleton et al. 1998a). In addition, these regions, including CMM and the caudomedial nidopallium (NCM), exhibit enhanced induction of the immediate early gene *Zenk* (an acronym for *Zif-268*, *Egr-1*, *NGFIA* and *Krox-24*) when birds hear song but not when they produce song (Jarvis & Nottebohm 1997). The *Zenk* gene encodes a protein (referred to here as *Zenk*), which is a transcription factor mediating the effects of growth factors and other signals on membrane depolarization. *Zenk* has been widely used in songbirds to investigate the neural response to song presentation (Tischmeyer & Grimm 1999; Hernandez et al. 2008). For example, *Zenk* induction is increased in male zebra finches and canaries exposed to conspecific song compared with males exposed to silence, a pure tone or heterospecific song (Mello & Clayton 1994).

In addition, female white-crowned sparrows, *Zonotrichia leucophrys*, show higher *Zenk* induction in CMM and NCM in response to their local song dialect compared with a foreign dialect, and also show a stronger behavioural response to the local dialect (Maney et al. 2003). Moreover, individual variation in *Zenk* induction was correlated to levels of courtship behaviour in this study (Maney et al. 2003). To date, no studies have determined the effects of early-life stress on *Zenk* induction in the auditory forebrain regions of the songbird brain. Thus, the hypothesis that changes in the behavioural response to song are mediated by changes in the neural responsiveness of the auditory forebrain regions to song presentation remains an open question.

In the current study we examined the long-term effects of developmental stressors (either food restriction or exogenous CORT treatment) on: (1) the behavioural response to high-complexity versus low-complexity songs, and to conspecific versus heterospecific songs; (2) the volume of the song-control nuclei HVC and RA; and (3) the number of cells that were immunoreactive for the immediate early gene *Zenk* in CMM and NCM following exposure to conspecific or heterospecific song in female song sparrows. In song sparrows only males sing and a bird typically sings 5–12 unique song types (Pfaff et al. 2007). In addition, song sparrows are closed-ended song learners, meaning that males do not alter their song repertoires in adulthood (Nordby et al. 2002). Female song sparrows show a preference for high-complexity song bouts in laboratory studies (Searcy 1984). In addition, the preference of female song sparrows for locally typical song is influenced by sensory experience early in life (Hernandez et al. 2009), suggesting that the formation of song preferences may be susceptible to variation in the early-rearing environment in this species. To our knowledge, this is the first study to examine the long-term effects of chronic early-life stress on induction of an immediate early gene in the brain of any species.

METHODS

Study Subjects and Experimental Treatments

All animal procedures followed guidelines set by the University of Western Ontario and the Canadian Council on Animal Care, and were approved by our institutional Animal Use Subcommittee (protocol 2007-089). The birds in this study were used in a previous study examining the effects of early-life food restriction and CORT treatment on growth and metabolic rates; rearing conditions and experimental treatments are described in detail elsewhere (Schmidt et al. 2012a). Briefly, song sparrow nests were located near Newboro, ON, Canada (44°38'N, 76°20'W) during May and June 2010. Sex was determined by polymerase chain reaction (PCR) amplification of genes located on the sex chromosomes (Griffiths et al. 1998). A total of 22 female nestlings (control: $N = 7$; food restriction: $N = 7$; CORT: $N = 8$; Table 1) from 12 broods were used in the current study. Of these, 19 were brought into captivity at 3 days of age (d3), two were brought in at d4 and one at about d7 (mean \pm SE = 3.27 ± 0.19 days).

Table 1
Samples sizes for the three treatment groups

Treatment	Sample size	Killed after exposure to conspecific song	Killed after exposure to heterospecific song	Age at start of tutoring (days)
Control	7	4	3	20.7 \pm 2.77
Food restriction	7	4	3	18 \pm 2.4
Corticosterone	8	3	5	16.1 \pm 2.45

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