available at www.sciencedirect.com

ScienceDirect

www.elsevier.com/locate/brainres

BRAIN RESEARCH

Research report

Selective behavioral responses to male song are affected by the dopamine agonist GBR-12909 in female European starlings (*Sturnus vulgaris*)

*Benjamin A. Pawlisch, Lauren V. Riters**

Department of Zoology, University of Wisconsin, Madison, USA

ARTICLE INFO

Article history:
Accepted 6 July 2010
Available online 12 July 2010

Keywords:
Song discrimination
Mate choice
GBR-12909
Birdsong
Incentive motivation
Playback
Sexual behavior
Proceptivity

ABSTRACT

Female songbirds use attributes of male song to select mates. Different types of male song differ in incentive value (or the ability to attract females). Dopamine plays a role in incentive value and reward; however, little is known about its role in selective female behavioral responses to male courtship signals. We examined the effects of the indirect dopamine agonist (dopamine reuptake inhibitor) GBR-12909 on female songbird responses to male song stimuli. Female European starlings were played recordings of long starling song (presumed high incentive value), short starling song (presumed lower incentive value), or purple martin song (lowest incentive value). Vehicle-treated females investigated nest boxes playing starling song more than purple martin song. However, GBR-12909 disrupted preferential responses to the starling song stimuli. GBR-12909 also increased cFOS immunolabeling in the ventromedial nucleus of the hypothalamus (VMH) at the same dose that disrupted female selective responses to male starling song. The results suggest that dopamine receptors play an important role in female selective responses to biologically meaningful stimuli and that the VMH may be influenced by dopamine to alter female responses to male song.

Published by Elsevier B.V.

1. Introduction

Vocal communication plays an important role in social interactions in many animal species. In seasonally breeding songbirds, male song during the breeding season functions primarily to attract mates and to defend territories (Zeigler and Marler, 2008). Female songbirds respond selectively to attributes of male song and approach or display copulation solicitation in response to particular songs (Searcy and Yasukawa, 1996). Both the function of vocal communication and the neural regulation of vocal production have been well-studied in songbirds (Zeigler and Marler, 2008). Progress also has been made in understanding the neural basis of auditory processing of song (Zeigler and Marler, 2008); however, less is known about neural systems regulating the motivation for females to respond to male song.

A stimulus, such as male song, that activates approach behaviors is considered an incentive (Berridge and Robinson, 1998; Berridge, 2004; Ikemoto and Panksepp, 1999); thus, female approach responses to distinct male songs can be

* *Corresponding author*. Department of Zoology, 361 Birge Hall, 430 Lincoln Drive, University of Wisconsin, Madison, WI 53706, USA. Fax: +1 608 265 6320.
E-mail address: LVRiters@wisc.edu (L.V. Riters).
URL: http://www.wisc.edu/zoology/faculty/fac/Rit/Rit.html (L.V. Riters).

0006-8993/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.brainres.2010.07.003

considered a reflection of incentive motivation. The catecholamine dopamine (DA), acting in part within the mesolimbic system, which includes projections from the ventral tegmental area (VTA) to the nucleus accumbens (Ac), has been implicated in reward (Ikemoto and Panksepp, 1999; Wise, 2002). Recently, a growing body of data suggests that, rather than underlying reward per se, DA is involved in motivated responses to incentively-salient or rewarding stimuli, such as food or a conspecific of the opposite sex (Berridge and Robinson, 1998; Ikemoto and Panksepp, 1999; Kelley and Berridge, 2002). Although not as extensively studied, DA activity within the incertohypothalamic system, which includes projections from the zona incerta to the medial preoptic nucleus (referred to as POM in birds), is implicated in sexual behavior and motivation (Hull et al., 1995, 1999; Moses et al., 1995; Panzica et al., 1996; Pfaus and Phillips, 1991).

Although multiple studies demonstrate that DA facilitates sexual motivation in male birds and mammals (Ikemoto and Panksepp, 1999; Pfaus and Phillips, 1991; Rauceo et al., 2008; Sasaki et al., 2006; Schroeder and Riters, 2006; van Furth et al., 1995), studies in females yield contradictory results. In female rats, peripherally-administered DA receptor agonists inhibit sexual responses to males as reflected in a reduction in lordosis behavior (Eliasson and Meyerson, 1976; Ellingsen and Agmo, 2004; Everitt et al., 1974; Guarraci and Clark, 2003). In a study in female rats specifically examining sexual-incentive motivation in the context of mate choice, injections of the DA agonist apomorphine also decreased approach responses to males and additionally disrupted preferential responses to intact over castrated males (Ellingsen and Agmo, 2004). In contrast to the effects of peripheral DA manipulations, microdialysis in female rats demonstrated that DA is elevated within specific brain regions (e.g., the preoptic area and the nucleus accumbens) in association with sexual activity (Matuszewich et al., 2000; Mermelstein and Becker, 1995; Pfaus et al., 1995). Futhermore, DA infused into the preoptic area, VTA, or ventromedial nucleus of the hypothalamus (VMH) stimulated lordosis in female rats (Apostolakis et al., 1996; Foreman and Moss, 1979; Petralia and Frye, 2006).

The role of DA in sexual-incentive motivation has not been well-studied in female songbirds, but a study of peripheral administration of DA agonists and antagonists is consistent with peripheral administration studies of DA agonists and antagonists in rodents. In female European starlings (*Sturnus vulgaris*), peripheral injections of a DA receptor agonist decreased female approach responses and interactions with a nest box from which male starling courtship song was played; whereas, a DA receptor antagonist increased approach responses and interactions with a nest box broadcasting song (Riters et al., 2007). These data suggest DA can inhibit female responses to male courtship song, a stimulus normally of high incentive value.

It is unknown where DA is acting to influence female responses to male courtship song. It may be that DA is acting within mesolimbic and incertohypothalamic systems. DA, DA synthetic enzymes, or receptors are dense within VMH, POM, Ac, and VTA (Appeltants et al., 2001; Bharati and Goodson, 2006; Bottjer, 1993; Mello et al., 1998; Riters and Ball, 2002). Studies in female birds show each of these regions has steroid receptors and is activated during sexual behavior (Japanese quail (Meddle et al., 1999), ring doves (Belle and Lea, 2001; Belle et al., 2003; Gibson and Cheng, 1979)). In estradiol-treated female white-throated sparrows, playback of male song as compared to playback of artificial tones increased immediate early gene activity in VMH, POM, and VTA (Maney et al., 2008). Furthermore, playback of male courtship song in estradiol-treated female starlings reduced the density of phosphorylated tyrosine hydroxylase (a marker of catecholamine synthesis) in VMH (Riters et al., 2007). The precise location of Ac in songbirds has yet to be identified. Recently in male zebra finches, playback of various song stimuli did not alter DA or its metabolites in one proposed location for Ac (Svec et al., 2009); however, this study measured a more rostral region than we examine here and did not distinguish between possible Ac shell and core regions (Balint and Csillag, 2007). Thus, additional study of avian Ac is warranted. These past studies suggest the possibility that DA activity within VMH, POM, VTA, or Ac may regulate female responses to male song.

The goal of the present study was to begin to characterize a role for DA in incentively-motivated responses to song in female European starlings. Unlike some commonly studied songbird species, female starlings do not show copulation solicitation displays in response to playback of male song. Instead, approach responses to nest boxes broadcasting male song provide an effective measure for assessing female responses to song stimuli (Riters and Pawlisch, 2007). In female starlings, variation in male song bout length is a strong predictor of mate choice (Eens et al., 1991; Eens, 1997), with females tending to prefer males singing longer songs. Furthermore, female starlings have been found to spend more time on perches triggering playback of longer compared to shorter bouts of male starling song (Gentner and Hulse, 2000). We examined the effects of peripheral administration of the DA reuptake inhibitor GBR-12909, which functions as an indirect DA receptor agonist, on female responses to song stimuli designed to differ in incentive value. After GBR-12909 peripheral administration, female approach responses were measured during playback of long starling song (presumed high incentive value for a sexually-motivated female), short starling song (presumed lower incentive value), or purple martin (*Progne subis*) song (presumed lowest incentive value). Movements throughout the cage (landings on any perch in the experimental cage) and feeding and drinking were also quantified to further test the motor effects of the drug. Finally, after completion of behavioral tests, GBR-12909-induced immediate early gene immunolabeling for cFOS was performed to identify brain areas influenced by DA manipulations that may underlie behavioral effects of the drug.

2. Results

One of the 16 female subjects was removed from analysis of the behavior after a toe injury interfered with perching behavior during the first few observation periods. Data from this female were included in the analysis of drug effects on cFOS immunolabeling. Comparisons of behavioral responses to short and long male song after vehicle treatment revealed no significant differences for any of the behavioral responses measured ($p>0.05$ for all comparisons). Therefore, mean behavioral