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Female Songbirds: The unsung drivers of courtship behavior and its neural substrates

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ABSTRACT

Songbirds hold a prominent role in the fields of neurobiology, evolution, and social behavior. Many of these fields have assumed that females lacked the ability to produce song and have therefore treated song as a male-specific behavior. Consequently, much of our understanding regarding the evolution and neural control of song behavior has been driven by these assumptions. Here we review literature from diverse fields to provide a broader perspective of the role of females in vocal communication and courtship. Recent evidence indicates that song evolved in both males and females and instances of female song are still common. The specialized neural circuit known as the "song system," which is necessary for singing in males, is also present in females, including those that do not sing, implying broader functions that include evaluating male song and controlling courtship behavior. In addition to having flexible, individualized preferences, females actively shape their social network through their interactions with males, females, and juveniles. We suggest that by developing more accurate hypotheses concerning the role of females we may better understand the evolution and neural mechanisms of song production and courtship behavior.

1. Introduction

Songbirds (birds of the group Passeri) have been central to ecological and evolutionary thought for centuries and are one of the few groups of animals with learned vocalizations (alongside humans and a few others (Nowicki and Searcy, 2014; Nottebohm, 1972). The identification of a specialized neural circuit for song production (often called the "song system") has made songbirds an important model for the study of vocal learning (Brainard and Doupe, 2013; Doupe and Kuhl, 1999) and motor control (Suthers and Margoliash, 2002). Throughout the history of songbird research, particularly amongst neurobiologists, much of the focus has been on active signalling by males. Females, in contrast, were viewed primarily as signal receivers and choosers. (Nottebohm and Arnold, 1976; Searcy and Andersson, 1986). This view has likely biased the study of courtship behavior and its neural bases to overlook the importance and complexity of female behavior (Jennions and Petrie, 1997), beyond its established role of driving evolution through mate-choice (Trivers, 1972). Increasing evidence suggests that female song is much more prevalent than once believed (Langmore, 2000; Riebel et al., 2005; Odom et al., 2014). This has far-reaching implications for how we understand the evolutionary origins of the avian communication system, even for species where female song has been lost (Price, 2015; Riebel, 2016). Here we review literature from various disciplines, focusing on the active role *non-singing* females play in mating interactions, the putative neural circuits that support and modulate these communicative behaviors, and the role that female behavior plays in driving social interaction.

2. The evolution of female choice

Females generally must invest more in their own offspring than males (Trivers, 1972) and therefore have strong incentives for selectivity in their mating choices. Assuming females can choose with whom they mate, these choices become a strong selective factor on males, driving male characteristics within the population in the direction of female preferences. This simple model was proposed by Darwin and more rigorously developed by Fisher as a mechanism to explain traits which otherwise appeared maladaptive under natural selection (Darwin, 1859; Fisher, 1930). In songbirds, female mating preferences for particular variants of male song (e.g. trill length, frequency modulation, etc.) are well documented (Searcy and Andersson, 1986; Vallet and Kreutzer, 1995; Woolley and Doupe, 2008; Suthers et al., 2012),

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and female selection of song quality is one of the classical examples of female choice and sexual selection (Andersson, 1994; Bateson, 1983).

While this model is appealing in its simplicity, it fails to capture the interactive nature of courtship or the full scope of female behavior beyond choosing the suitor with the best displays. While the selective pressure of female mate choice certainly drives male phenotypes over generations, females can also instantaneously alter male behavior through active feedback (West and King, 1988). In addition, males bear significant costs in reproduction (e.g. parental care, STD exposure, male–male competition, risk of predation, etc.) and male preference therefore acts as an important selective force on females (Amundsen, 2000; Hill, 1993). Finally, females often display behaviors unrelated to courtship, competing for territory and resources with both males and other females (Hobson and Sealy, 1990; Rosvall, 2011; Johnson, 1988). Given these complexities, precise identification of courtship behavior is challenging and models of female choice must account for the extent and diversity of female behavior.

Careful study of female mate choice reveals that female assessment strategies are often plastic and influenced by a diverse set of variables. In addition to song, females attend to a range of features, including male coloration (Hill, 1991), active courtship displays (Borgia, 1995), territory (Alatalo et al., 1986) (reviewed in Jennions and Petrie, 1997), and even observed interactions between other males and females (King et al., 2003). Their preferences do not necessarily remain constant across, or even within, individuals, with females often exhibiting a range of individual (Holveck and Riebel, 2010), plastic (Freed-Brown and White, 2009; West and King, 1988a,b; Maguire et al., 2013) preferences, which they act upon to shape and attain their desired mating outcomes (West and King, 1988a,b; Maguire et al., 2013). Given these complications, it is perhaps unsurprising that little is known regarding the mechanisms underlying female song preference and response, particularly in comparison to our understanding of song production in males. However, recent studies continue to clarify the role of females in song interactions.

2.1. A broader picture of song evolution in males and females

Birdsong is defined as a complex, learned signal, generally used to attract mates and compete with rivals. Based on comparative phylogenetics, birdsong evolved in the tropics and was present in both males and females (Fig. 1) (Odom et al., 2014; Webb et al., 2016). This contradicts the long-held idea that song evolved as a uniquely male trait (Darwin, 1859; Andersson, 1994), and that instances of female song are rare and derived. While the prevalence of female song does not necessarily contradict the hypothesis that song is a sexually selected male ornament–given that traits selected in males can easily persist in females–it does indicate that our understanding concerning the emergence of song may be incomplete.

Females in the majority of species of passeri sing (Webb et al., 2016) and many of them produce song for courtship and competition (Langmore, 1998). Song production was even shown to increase in females experimentally subjected to heightened female–female competition (Hobson and Sealy, 1990; Langmore, 1998), in one case surpassing the song rate of males (Illes and Yunes-Jimenez, 2009). However, it appears that female song is reduced in many species, having been secondarily lost. In some this loss can be complete, as it is in the zebra finch, which is the best studied model of song production. In many other species, female song is either significantly reduced compared to males (as in canaries (MacDougall-Shackleton and Ball, 1999) or produced at very low volumes, with these female "quiet songs" often going unnoticed (Dabelsteen et al., 1998). The loss of song appears to correlate with dispersal into temperate regions, and is perhaps a response to different environmental pressures (nest competition, predation, etc.) favoring more furtive females, as argued by Wallace (Wallace, 1891). In New World Blackbirds (Icteridae), for example, parsimony estimates suggest that song has been lost or reduced multiple times in females, correlating with migration to temperate climates (Price et al., 2009). Interestingly, this suggests that sexual dimorphism may be the result of female-specific adaptations to reduce ostentatious signals rather than male-specific adaptations to produce them (Price, 2015).

While female song remains more prevalent than widely believed, particularly in the tropics, large radiations of Passerida (in which female song is commonly reduced or absent) and a temperate bias in bird observations have facilitated the belief that learned vocalization is a uniquely male trait (Fig. 1). This, in turn, made it natural to conclude that birdsong was a male ornament driven by sexual selection. Given our current understanding of the role of song in females, it may be beneficial to revisit this assumption. It is possible song evolved through alternative evolutionary incentives, perhaps being adaptive in both males and females.

One alternative theory is that learned vocalizations provide benefits by enabling increased social complexity (Freeberg et al., 2012; Nowicki and Searcy, 2014). Empirically, vocal learning appears primarily in highly social species (humans, dolphins, bats, songbirds, etc.) and likely allows for a greater complexity–and therefore variety–in the types of vocal signals that can be produced. While this variety could simply be the signal preferred by females, it could also provide social benefits allowing for a greater ability to navigate (and benefit from) social interactions. In the case of songbirds, it is important to note that social complexity does not necessarily imply gregariousness. While many species do live in hierarchical communities (e.g. icterids, corvids and various species of finches; reviewed in (Emery et al., 2007; Silk et al., 2014)), many species are highly territorial to the point of being solitary (Lack, 1968). That said, complexity can exist even in individual (particularly repeated) interactions. Social monogamy, for example, which is common across many bird species, requires increased complexity of interactions (Emery et al., 2007; Freeberg et al., 2012) and territoriality, which is itself a social structure, requires individuals to properly interact with neighbors over the course of repeated interactions. Further study is needed to understand how these interactions are mediated by song learning and to what extent they influence fitness.

Experimental observations have confirmed a relationship between sociality and fitness in at least some songbirds. In a communal species of cowbird, prosocial birds do better in breeding tournaments (Gersick et al., 2012) and sociability correlates with reproductive performance (Kohn et al., 2013; White et al., 2010). In this lineage, song likely was influenced by a need to navigate a complex social landscape. While social navigation is unlikely to be the only adaptive feature of birdsong, it could have been a key component of song evolution, and it highlights the need to account for the broad function of song and the many likely factors that shape it.

2.2. The neurobiology of song

In most songbirds, vocal learning can be divided into two, often-overlapping phases: a sensory learning phase and a motor phase. The song must first be memorized from a tutor or peers and then must be produced in a way that matches the acquired song template. This process requires a specialized neural circuit known as the "song system" (Fig. 3). In practice, this neural circuit can be broken down into three distinct functional modules: an auditory module handling higher order representations of sound (Vates et al., 1996), a brainstem module that drives the muscles necessary for respiration and vocal control (Wild, 2008), and a vocal-motor module that links the two together (Nottebohm et al., 1976). There is an additional module, known as the anterior forebrain pathway, which is necessary for dopamine-dependent reinforcement-learning during song acquisition and maintenance (Brainard and Doupe, 2013; Fee and Goldberg, 2011). In most species, female song regions are reduced in size compared to males and the volume of these regions (mostly) correlates with song production in their respective species (MacDougall-Shackleton and Ball, 1999; Ball, 2016). Surprisingly, however, these regions persist in non-singing

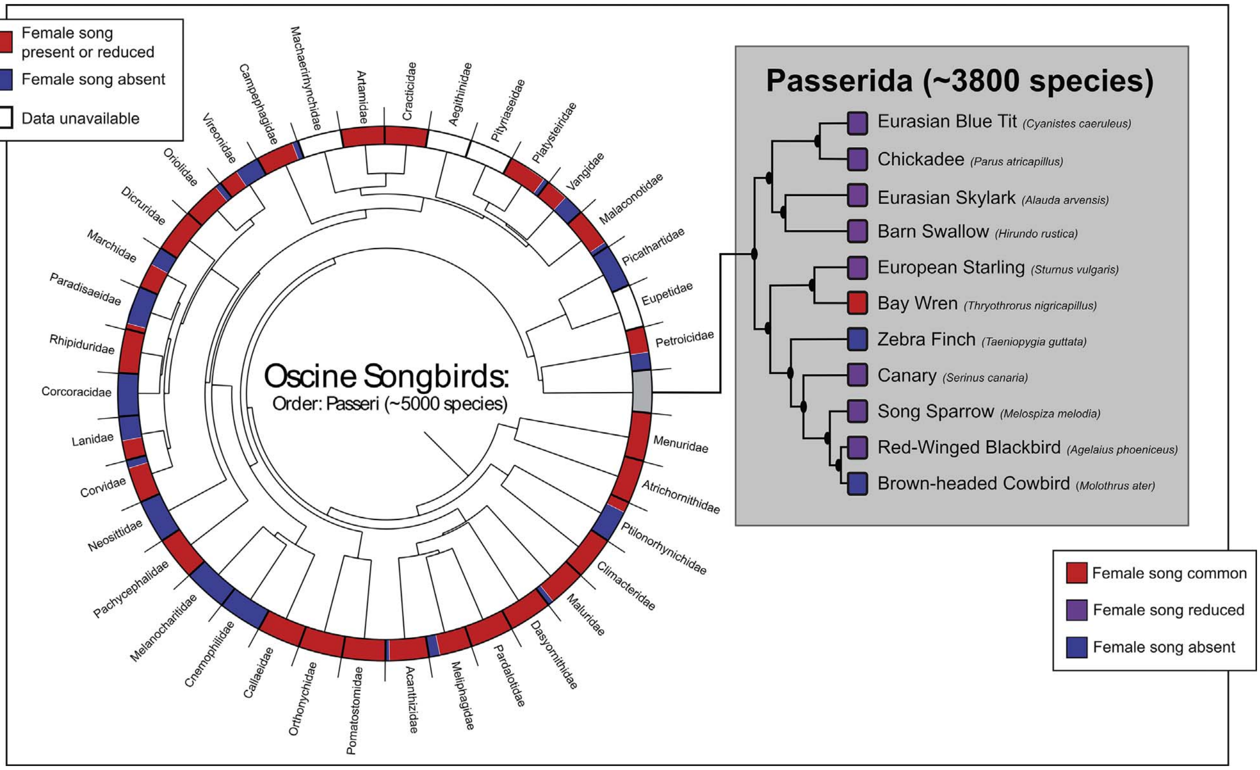

Fig 1. Phylogenetic comparison of singing in male and female songbirds.
This phylogenetic tree illustrates the distribution of female song production across songbirds. While the common assumption is that female song is exceptionally rare, phylogenetic reconstruction demonstrates that female song is the ancestral trait. *Left*, Wedges correspond to the percentage of species, per family, that exhibit some degree of female song (red, percent present, blue, percent absent). In the original phylogenetic analysis by Odom et al. (2014), the presence of song in both sexes was found to be the most likely ancestral condition. In 71% of all oscine species for which data was available (excluding the parvorder passerida, see below), females exhibit some degree of song production, albeit reduced. Despite the prevalence of female song, observational biases in the birds surveyed and prior expectations likely facilitated the idea that only males sang. *Right*, the parvorder Passerida includes roughly two-thirds of songbird species, but as the most recent radiation, contributes less than 1% toward the ancestral reconstruction, and was thus excluded from the analysis by Odom et al. In the majority of commonly studied songbird species, female song is absent or dramatically reduced, particularly in temperate regions. In many cases, where female song is present, it is significantly quieter than male song, and may often go unnoticed (Dabelsteen et al., 1998). More recently Webb et al. (2016) performed an expanded analysis, including passerida, and reported female song in 64% of oscine species surveyed. Note that species count per family is not represented here, see Odom et al., 2014 for original figure and data. Song levels for the Eurasian blue tit and chickadee, Eurasian skylark, barn swallow, and song swallow based on (Hinde 1952; Cresswell 1994; Samuel, 1971; Arcese et al., 1988) respectively; all others from (MacDougall-Shackleton and Ball, 1999). Phylogeny was constructed using BirdTree.org (Jetz et al., 2012), based on (Hackett et al., 2008).

females. Some have suggested that these regions are vestigial in females (Wade and Arnold, 2004), or the result of developmental constraints (Arnold and Gorski, 1984). Increasing evidence, however, suggests that these views are incorrect and that the “song system” plays a significant role in non-singing females to control behavioral features that can range from call timing (Benichov et al., 2016) to control of copulatory behavior (see below).

Given the shared common evolutionary history and the similar requirement for song recognition (e.g. identification of their pair mate’s song) followed by context appropriate motor action (O’Loghlen and Rothstein, 2004; Vignal et al., 2008), it is perhaps not surprising that females, including non-singing females, possess a “song system” that might help them establish song selectivity within the context of courtship behavior. Given such a system, we might predict the development of female song responses to be similar to the development of song in males, including the necessity for social context during preference learning, some degree of malleability during early life, and some degree of preference crystallization after sexual maturity.

2.3. Non-singing females signal preference with posture

For non-singing females, the correct motor response to song often manifests itself as postural motion–although non-learned female vocal responses are also important signals (Benichov et al., 2016; Freed-Brown and White, 2009). Female responses to song can be measured to test song perception. Females can signal preference by their willingness to approach rather than flee male courtship, and various studies have measured female affinity for different signals (Lauay et al., 2004; Remage-Healey et al., 2010). There also seems to exist a variety of more subtle motor cues that signal female preference, such as the wingstrokes reported by West and King, but these behaviors have proven difficult to study (West and King, 1988a,b). In many species, females produce a dramatic posture in response to preferred male song, called the copulation solicitation display (CSD). This posture both solicits and facilitates the act of copulation. Immediately following the initiation of CSD, the male mounts the female and copulation is accomplished through contact between the male and female cloacae.

When housed in sound isolation chambers, females of some species produce CSD in response to recordings of male song, provided they are in breeding condition. In such species CSD can be used to test female preference for song stimuli (King and West, 1977; Searcy, 1981). This protocol can be expanded to create a more detailed representation of song selectivity. While individual responses are variable, when a large set of different songs are presented over several days, female preference can be measured by quantifying the frequency with which they produce CSD to the various male songs (Fig. 2) (Maguire et al., 2013).

3. Social malleability of female song preferences

Female preferences have typically been considered a means for females to select quality males based either on direct benefits (e.g. territory, parental care, nest defense) or indirect benefits (i.e. good genes

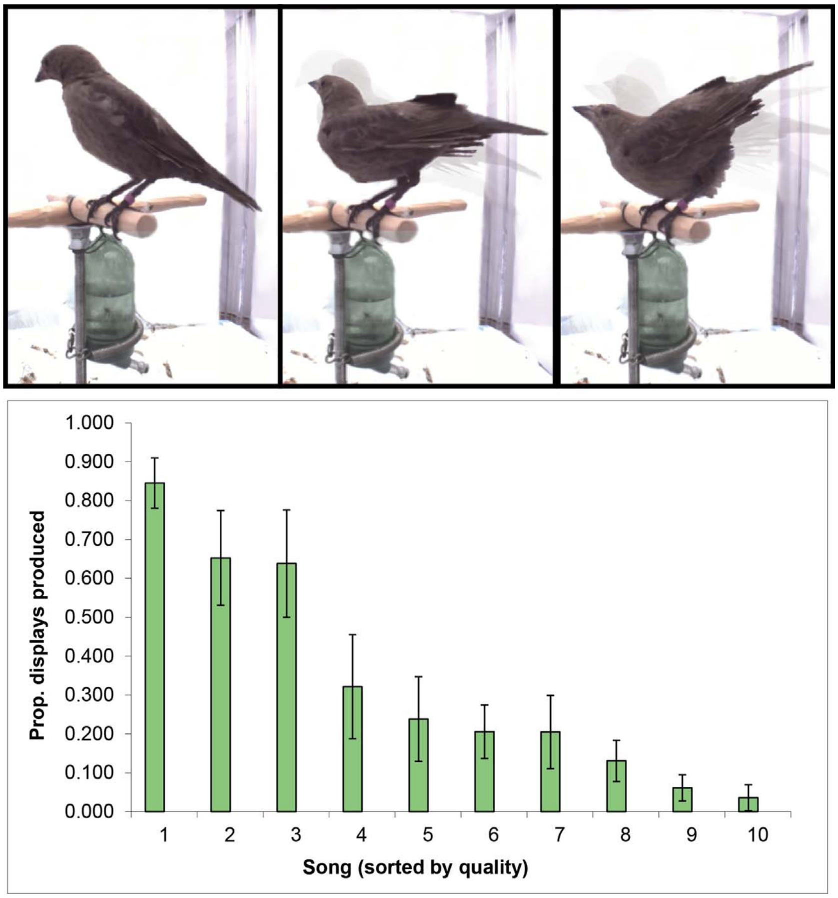

Fig. 2. Song selectivity of the copulation solicitation display.
The copulation solicitation display (CSD) signals female willingness to mate and enables copulation. When housed in sound proof chambers, female cowbirds produce CSD in response to playback of male song. This behavior can be used as a bioassay for female song preference *Top,* Copulation solicitation display in a cowbird. During CSD, the female arches her back to raise her torso, and spreads the posterior feathers to expose the cloaca. *Bottom,* Females produce CSD more frequently for some songs than others. The rate at which females produce CSD reveals preference for each song. Here, the averaged responsiveness of 8 females for ten different male songs is shown, sorted by quality. While individual variation exists, there is broad consensus concerning song quality (see Maguire et al., 2013).

(Andersson, 1994)). In comparison to male variation, little attention has been given to how song preferences may vary across or within individuals: if female song preferences evolved to obtain a single best mate, and if each female could obtain the same optimal male, preferences need not vary. However, investigations across a wide variety of species have documented extensive variation in female preferences (Jennions and Petrie, 1997). One important driver of preference variation is the social interaction with conspecifics.

In females, adult preferences are influenced by a range of social experiences throughout life, beginning with very early (even prenatal) social conditions (Laland, 1994; Payne et al., 2000; Cate and Bateson, 1988; Cate et al., 1993). For example, in brood parasitic village indigobirds (*Vidua chalybeata*), both males and females imprint on the song of their individual foster parents. Adult males produce songs similar to their foster parents and females come to prefer such songs (Payne et al., 2000). In addition to imprinting, females are affected by experiences that occur throughout development (Dooling, 1982; Riebel, 2000; Riebel, 2003; Woolley and Doupe, 2008; White, 2004; Adkins-Regan and Krakauer, 2000). In zebra finches raised without exposure to adult male song, for example, females develop a range of abnormal preferences that include preference for same-sex partners over partners of the opposite-sex (Adkins-Regan and Krakauer, 2000).

Female preference is also subject to experiences occurring near mating events, as demonstrated in the (non-songbird) Japanese quail, where females show enhanced preferences for males seen mating with other females (Westneat et al., 2000; White, 2004; White and Galef, 1999). Similar results were observed in zebra finches (Swaddle et al., 2005) and cowbirds (Freed-Brown and White, 2009). Preferences can be further altered by individual physiological conditions (Holveck and Riebel, 2010) or recent exposure to males of differing quality (Lyons et al., 2014). Taken together, these effects indicate that female preference is plastic and subject to both developmental imprinting and individual learning. Establishing this plasticity likely requires a complex interaction of physiological and neural systems which are adjusted based on individual experience over a variety of time scales.

3.1. Cowbirds as a model system

While female preference has been studied in a variety of songbirds and other systems (reviewed in Jennions and Petrie, 1997; Cotton et al., 2006), we will focus here primarily on the body of research concerning malleability of preference in the brown-headed cowbird (*Molothrus ater*). Cowbirds have been the subject of extensive studies of how social experiences influence mate preferences. At first, this species may seem an unlikely model for this purpose because cowbirds are obligate brood parasites (that is, they lay their eggs in the nests of other birds, who raise the cowbird hatchlings themselves) and therefore they lack normal opportunities for sexual imprinting. However, extensive examination has shown that cowbirds require social experiences to develop appropriate communication and social skills just as other birds do. Given their abundance, ease of capture, and their ability to live and breed in captivity without stress, cowbirds serve as an excellent model system for studying the formation of preference in a controlled setting.

Based on their unique life history, cowbirds were presumed to be a prime example of species with genetic, non-malleable preferences, providing females the ability to locate and mate with male cowbirds without requiring imprinting (Mayr, 1974). Indeed, early examinations of female cowbird preferences supported this idea, with young female cowbirds expressing species-typical preferences in their first breeding season regardless of prior exposure to males (or lack thereof) (King and West, 1977, 1983b). The same females also showed high levels of concordance in their preferences for variants of cowbird song. That is, all females responded in similar patterns to song presentations. Early attempts to modify these preferences failed. For example, exposing

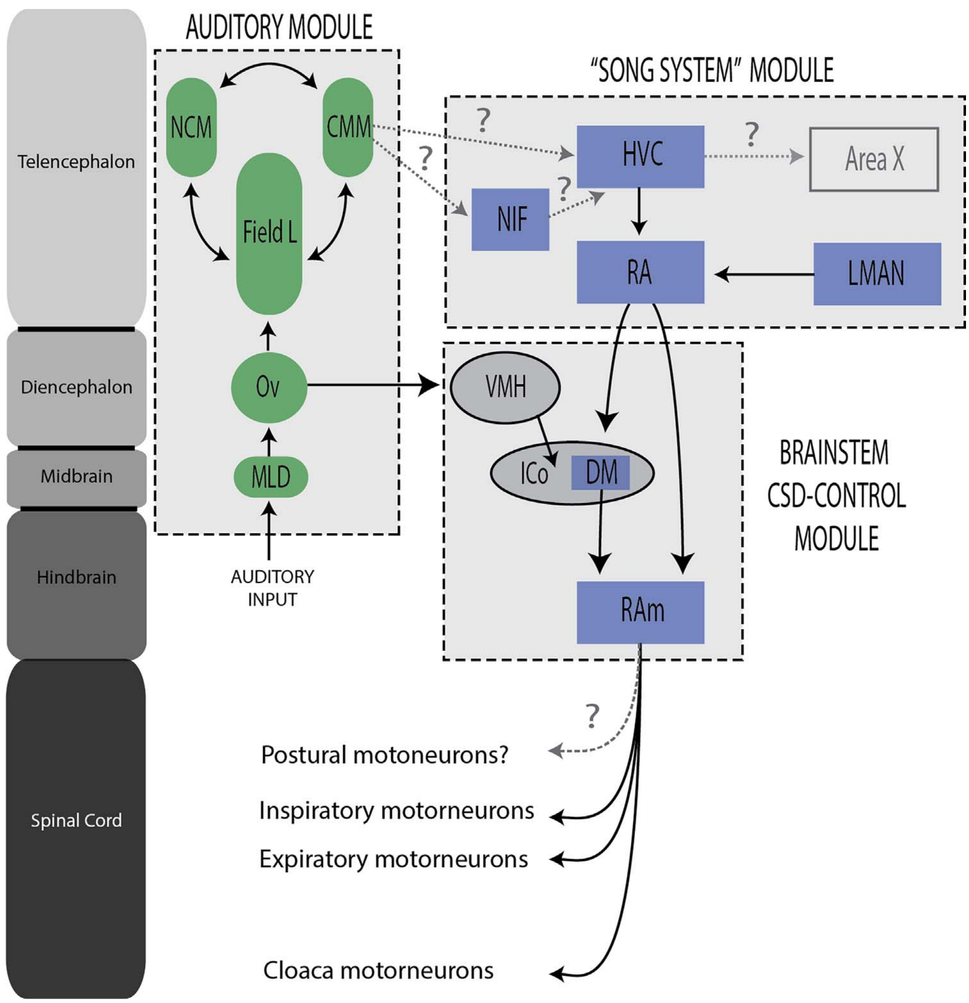

Fig. 3. Putative neural circuit for CSD production and modulation.
This schematic figure highlights the major brain areas hypothesized to be involved in the production and modulation of response selectivity for CSD in a female songbird. Copulatory posture is thought to be driven by circuits in the brainstem (brainstem CSD-control module) which directly innervate spinal motoneurons, such as those of the cloaca, which are presumed to be active during CSD. Projection onto postural motoneurons has yet to be determined. Activation of this brainstem circuit is hypothesized to be made possible by indirect input from auditory thalamus (nucleus Ovoidalis, Ov) to the midbrain area DM (equivalent to lateral or ventrolateral PAG in mammals). DM and medullary nucleus RAm (homologous to nucleus Retroambiguus (NRA) in mammals) are each highly innervated by RA which is necessary for controlling spectrotemporal features of song in singing birds. RA is innervated by HVC and LMAN, two areas known to be critical in sing production and learning; together they form a neural module that is hypothesized to link brainstem circuits for CSD production with higher-order auditory areas, such as NCM and CMM, which are specialized for encoding salient features of male song. Abbreviations are as follows: *Auditory Module* – MLD, dorsal lateral nucleus of the mesencephalon; Ov, nucleus ovoidalis; Field L; NCM, Caudal medial nidopallium; CMM, Caudal medial mesopallium; *"Song System" Module* – NIf, interfacial nucleus of the nidopallium; HVC (used as a proper noun); Area X; LMAN, lateral magnocellular nucleus of the anterior nidopallium; RA, Robust nucleus of the arcopallium. *Brainstem Module* – VMH, Ventromedial nucleus of the hypothalamus; ICo, nucleus intercollicularis; DM, dorsomedial nucleus of the intercollicular complex; RAm, nucleus retroambigualis.

females in sound chambers to songs from males with a different dialect failed to change their preferences (King and West, 1977, 1983b; West and King, 1988a,b).

3.2. Malleability of female choice

The first piece of evidence of malleability in preferences appeared in playback tests, in which male song quality is judged by its ability to produce CSD in females housed in sound attenuation chambers (King and West, 1977). In these experiments, a song's attractiveness depended on the other songs in the series being played. A song might elicit very few CSDs when played with other, highly attractive songs, but that same song elicits high levels of CSD when grouped with less attractive songs (King and West, 1983b; King et al., 1981). A song's ability to elicit CSD therefore is relative to the songs around it, demonstrating that female preference for a male is relative to her exposure to the songs of other males.

Social experiments further reveal malleability of preference. Juvenile females raised in social groups with adult females (i.e. without males) have broad song preferences and show little concordance (King et al., 2003; West et al., 2006; White et al., 2006). This contrasts with isolate females which, as mentioned, agree on song quality. This suggests that juveniles are learning song preferences by observing other females. We might expect preference learning to produce greater concordance rather than greater diversity; however, just as in vocal learning, preference learning causes a greater range of complexity beyond what would otherwise be innate, genetic traits.

This preference learning can be studied experimentally by providing artificial social feedback. Adult females typically produce chatter calls in response to their pair mate's song. When females housed in aviaries are presented with a series of novel male songs paired with chatter calls immediately prior to the breeding season, then tested for preference during the breeding season, they produce CSD more frequently in response to those songs compared to females that are presented the same songs without paired chatter (Freed-Brown and White, 2009). These experiments suggest that chatter calls help account for the variation in preference learning previously observed in females, biasing them towards the song of successfully paired males.

As shown, when song preferences are examined with respect to the social system in which mate selection occurs, it is clear that preferences are plastic rather than fixed. It is important to note that malleability of female preference is not limited to cowbirds, and has been demonstrated in other species of songbirds (Riebel, 2000; Riebel and Slater, 1998) and non-songbirds (White and Galef, 1999). Females appear to integrate song quality with other characteristics–including coloration, male postural displays, male–male or male-female interactions, song performance, and endurance (Rothstein et al., 1988; White, 2004; White et al., 2010; O'Loghlen and Rothstein, 2004; Byers et al., 2010; Ronald et al., 2017; Hebets and Papaj, 2005). This plasticity has implications for both the mechanisms underlying CSD reactivity as well as the evolution of female choice. From a mechanistic perspective, these results imply that a wide variety of inputs mediate CSD reactivity and that reactivity changes across circumstances and experience. To modulate CSD in such a way likely requires a neural circuit that can integrate many inputs which converge onto a dedicated brainstem circuit for the production of the copulatory response.

4. A putative neural circuit for CSD production and mate choice

The neural mechanisms that underlie CSD production and its selectivity in female songbirds have not been studied in a rigorous fashion and as such the precise neural circuitry for this behavior remains poorly understood. Given the similarity of CSD behavior to the lordosis response in mammals, there is a strong likelihood that homologous circuits in the brainstem and spinal cord are engaged during CSD behavior. Furthermore, because CSD is a hormonally-dependent behavior that can be driven by song, selectivity of this behavior likely requires higher-order auditory processing linked to a neural system that connects directly to brainstem networks that control CSD. The song system is a strong candidate circuit for connecting auditory forebrain circuits to the brainstem (Fig. 3). Experimental evidence supports a fundamental role of this circuit, showing that lesions of key song system nuclei in the forebrain modulate CSD selectivity in response to song. Below, we describe anatomical and physiological evidence to support the existence of a dedicated circuit for CSD production and modulation in the female songbird that is analogous to known circuits controlling posture in other animals.

4.1. A brainstem circuit for producing the copulation solicitation display

The females of several common species of mammals (including cats, rats and monkeys) demonstrate lordosis in reproductive contexts. Lordosis is an extensor, dorsiflexed body posture–often accompanied by other species-specific behaviors–that solicits and facilitates mounting and insemination by the male. The neural control of lordosis was systematically investigated in the rat by Pfaff and colleagues from the 1970′s onwards (Pfaff et al., 1994). The ventromedial nucleus of the hypothalamus (VMH) and certain parts of the periaqueductal gray (PAG) of the midbrain were shown to be key nuclei for lordosis production (Flanagan-Cato, 2011). Electrical stimulation of VMH or the implantation of estradiol in VMH elicits lordosis in rats (Pfaff and Sakuma, 1979; Rubin and Barfield, 1980), and similar effects occur following stimulation in the PAG (Ogawa et al., 1991). This similarity is not surprising because VMH projects to those parts of PAG that, when stimulated, elicit lordosis (Krieger et al., 1979; Veening et al., 1991; Canteras et al., 1994). The subsequent components of a pathway linking the PAG with final common path neurons for lordosis have been somewhat controversial (Kow and Pfaff, 1998). A lordosis pathway has been identified in cats, rats and monkeys by Holstege and his colleagues (Vanderhorst and Holstege, 1995, 1996) as proceeding from the PAG to a nucleus in the caudal medulla known as nucleus retroambiguus (NRA) (Gerrits and Holstege, 1996; Holstege et al., 1997; Vanderhorst et al., 2000). Neurons in this nucleus possess a rhythmic discharge in phase with expiration and project to spinal motoneurons innervating internal intercostal and abdominal expiratory muscles (Holstege, 1989; Ezure, 1990). However, other targets of NRA were found to include lumbosacral motoneurons innervating pelvic floor motoneurons and motoneurons in Onuf's nucleus that innervate the urethral and anal sphincters (Holstege and Tan, 1987; Gerrits and Holstege, 1999; Gerrits et al., 2000; Vanderhorst and Holstege, 1997). The implication, therefore, is that NRA is not only involved in the control of the expiratory phase of respiration, which is the basis of vocalization (Holstege, 1989), but is also involved in the control of reproductive behavior in mammals (Kirkwood and Ford, 2004; Boers et al., 2005). In the latter NRA has spinal projections that target motoneurons that innervate the varied muscles that are active in lordosis (Pfaff et al., 1978; Vanderhorst and Holstege, 1995, 1996).

Like mammals, birds have a caudal medullary nucleus (called nucleus retroambigualis, or RAm) whose neurons discharge rhythmically in phase with expiration and whose spinal projections target motoneurons innervating muscles involved in expiration (Wild 1993a,b; Wild 1994; Wild et al., 2009). Because almost all vocalizations are produced during expiration, and the expiratory muscles are instrumental to the compression of the air sacs that produces the expiratory air flow correlated with syllabic production (Hartley, 1990), it follows that RAm likely plays a key role in song and call production, in addition to its vital role in respiration – although recordings from RAm during singing or calling are not yet available.

Similarities of respiratory-vocal control in birds and mammals extend beyond RAm, particularly in the midbrain, where birds have an area, known as DM (dorsomedial nucleus of the intercollicular complex), that is considered equivalent to the lateral or ventrolateral parts of the periaqueductal gray (PAG) of mammals (Kingsbury et al., 2012; Wild et al., 1997). In both birds and mammals, electrical or chemical stimulation of these nuclei drives call-like vocalizations while lesions produce muteness, and tracer injections label downstream projections to vocal motoneurons and respiratory premotor neurons (Davis et al., 1996; Wild et al., 1997).

This lordosis behavior is analogous to CSD in birds. Like NRA in mammals, RAm in both Japanese quail and canaries projects to sacral motoneurons innervating the cloacal sphincter muscle (Wild and Balthazart, 2013; Wild and Botelho, 2015), which in quail is known to be involved in copulation, as well as in voiding (Seiwert and Adkins-Regan, 1998); but whether RAm also projects to spinal motoneurons innervating other muscles involved in CSD is as yet unknown, partly because the identity of these muscles is unclear (Pfaff et al., 1978). It is possible that RAm's projection on cloacal sphincter motoneurons serves an anti-incontinence function during the elevated intra-abdominal pressures associated with singing. Although the sphincter muscle did not appear to contract rhythmically during quiet respiration in anesthetized canaries (Wild, unpublished observations), the transverse cloacal muscle is active during respiration in pigeons (Baumel et al., 1990). Whether this muscle is active during CSD in a manner that is uncoupled from breathing remains to be determined.

4.2. The "song system" as higher-order circuit for modulating CSD choice preference

Like many brainstem motor circuits that control behavior (Roh et al., 2011), the brainstem circuit that controls the copulatory display receives input from higher-order structures that presumably serve to modulate its function in a way that ensures context specificity. Remarkably, RAm, which serves as the presumptive premotor coordination structure for the complex postural response that makes up CSD (Kirkwood and Ford, 2004; Boers et al., 2005), receives heavy innervation from nucleus RA, a prominent nucleus in male songbirds that is necessary for the production of learned vocalizations (Wild, 1993a,b; Vicario, 1991). Because some of the anatomical projections to and from RA were originally identified in the canary, a species where the female sings, it was assumed that this circuit was used primarily for song production (Nottebohm et al., 1982). This assumption was strengthened by the observation that the size of RA and other forebrain nuclei involved in song control was almost always correlated with singing frequency (reviewed in Ball, 2016). However, these song control areas and their anatomical projections persist in females that do not sing (Tobari et al., 2006; Wild et al., 2001), suggesting that RA and associated areas might be involved in behaviors other than song production.

Recent evidence suggests that RA projections onto RAm could regulate precise timing during complex call interactions. In zebra finches (in which females do not produce song), lesions of RA have a profound impact on call timing in both males and females–without disrupting the acoustic properties of the call (Benichov et al., 2016). This indicates that RA, in addition to controlling song in the male, plays a key role in controlling call timing in both male and female zebra finches.

In addition to controlling call timing, we propose that RA may have an additional role in regulating copulatory behavior. While a direct role of RA has never been demonstrated, several studies have shown that lesions of nucleus HVC, which projects directly to RA in male and female songbirds, significantly affect copulatory display. Interestingly, lesions do not affect the behavior itself, but rather its selectivity (Brenowitz, 1991; Del Negro et al., 1998; Maguire et al., 2013; Halle et al., 2002). The female cowbird (which does not produce song) is a striking example of this phenomenon (Maguire et al., 2013). As mentioned, female cowbirds exhibit a high degree of selectivity in their postural response to song and lesions targeting HVC (Maguire et al., 2013) cause a complete loss of this selectivity, inducing the female to produce CSD with similar frequency for every song. Because these lesions do not produce observable changes to the display itself, these and other findings suggest that HVC, and possibly RA, are involved in behavioral selectivity rather than actual instantiation of the behavior.

In male songbirds, the nuclei required for song are anatomically well defined and therefore easily identified on Nissl stained slides. In females, especially in species that do not sing, these nuclei are typically smaller and more difficult to identify using these same histological techniques. Nevertheless, nuclei RA and HVC are clearly identifiable when viewed with fluorescent retrograde tracers (Messier, Wild, Perkes and Schmidt, Unp. Obs.). Injection of RA with these same tracers also labels nucleus LMAN, which in males serves as the primary connection to RA from a specialized basal ganglia circuit known as the anterior forebrain pathway (AFP), which provides an indirect link between HVC to RA and is necessary for song learning and maintenance. What role LMAN might play in courtship behavior and CSD selectivity is still unknown. Intriguingly, a positive correlation has been shown between LMAN size and degree of selectivity in CSD production in female cowbirds (Hamilton et al., 1997). How LMAN connects to the rest of the AFP remains to be shown.

4.3. Auditory forebrain circuits for modulating CSD choice preference and plasticity

Unlike lordosis, which requires activation of somatosensory inputs (typically by rubbing the animal's flanks), the CSD response in songbirds can be elicited by auditory stimulation alone (King and West, 1977; Catchpole et al., 1986; Vallet and Kreutzer, 1995). Although CSD activation during normal courtship is likely also modulated by visual cues, much can be understood regarding the selectivity and mechanisms of CSD production by understanding how auditory stimulation modulates this sexual response.

Both male and female songbirds have sophisticated auditory systems that allow for precise discrimination between complex acoustic signals–corresponding to their complex and sophisticated vocal communication system. At least three separate auditory streams have been identified that project to auditory forebrain areas capable of processing higher-order auditory signals (Wild and Farabaugh, 1996; Coleman et al., 2007; Vates et al., 1996). Two of these pathways, the lemniscal and nucleus basalis pathways, might contribute to auditory selectivity of CSD but neither are directly connected to brains regions directly involved in vocal communication. A third pathway (Fig. 3) can be defined as ascending through nucleus MLd (central nucleus of the inferior colliculus in mammals) to nucleus ovoidalis (auditory thalamus) and then to an auditory complex in the forebrain known as Field L. From Field L, auditory projections in male songbirds eventually reach nuclei of the song control system, such as HVC, through a number of reciprocally connected auditory forebrain areas, including NCM, CMM and NIf (Theunissen et al., 2008). Although a direct projection from auditory forebrain areas to HVC has yet to be shown in females that do not sing, there do not appear to be major anatomical differences in auditory forebrain circuits between male and female songbirds. Overall physiological properties in the auditory forebrain also seem to be mostly similar across sexes (Theunissen et al., 2008) even though specific auditory tuning properties can be significantly different between males and females (Yoder et al., 2015; Brenowitz and Remage-Healey, 2016).

There is considerable evidence that variation in song complexity signals male fitness, and that female auditory tuning is sensitive to these differences. In canaries, for example, females produce copulatory displays more readily in response to certain, particularly complex male song elements (Vallet and Kreutzer, 1995; Suthers et al., 2012; King and West, 1983a). Acoustically, these song elements, known as "sexy syllables," optimize the trade-off between trill rate and frequency bandwidth (Podos et al., 2004). Vocal performance in swamp swallows (measured as a function of this optimization), was shown to be correlated with male age and size (Ballentine et al., 2004), suggesting these elements are a true signal of male quality. Physiologically, it appears these syllables can only be produced through rapid switching between the left and right syrinx (Suthers et al., 2012), explaining their difficulty and why females would be sensitive to these signals.

Although the mechanism by which the auditory stimulus (i.e. song) triggers CSD is not known, it is likely the range and speed of frequency and amplitude modulation present in many of the syllables that trigger CSD behavior require the type of high-level auditory processing that is present in forebrain auditory areas (Theunissen et al., 2008; Comins and Gentner. 2014; Del Negro et al., 2000). Where such processing occurs is unclear, but NCM and CMM are strong candidates given that both encode behaviorally relevant features of song (Prather, 2013; Comins and Gentner, 2014). NCM is likely to be an interesting area for further study because it encodes song memories (Phan et al., 2006; London and Clayton, 2008; Gobes and Bolhuis, 2007) and shows strong selectivity for song (Terleph et al., 2007; Thompson and Gentner, 2010) that can be modulated by locally synthesized estrogen (Remage-Healey et al., 2010; Krentzel and Remage-Healey, 2015). Further support for NCM comes from recent finding that its inactivation decreases song and mate choice discrimination in female zebra finches (Tomaszycki and Blaine, 2014).

While the effect of NCM inactivation on CSD production and selectivity is not known, the observation that HVC lesions cause a decrease in selectivity, but not in the actual generation of the behavior, suggests that song can drive CSD directly, independent of the auditory forebrain. Consistent with this idea, recent anatomical findings have shown a projection from the thalamic auditory nucleus ovoidalis (Ov) to the ventromedial nucleus of the hypothalamus (VMH; (Wild, 2017)). The VMH is necessary for eliciting the lordosis response in mammals and likely plays a significant role in CSD production (Gibson and Cheng, 1979) via its projections to the midbrain intercollicular (ICo) nucleus (Wild and Balthazart, 2013; Wild, 2017), an area that surrounds nucleus DM (equivalent to the lateral or ventrolateral parts of the mammalian PAG). How projections from the ICo might reach a pathway for CSD is presently unclear but the link could possibly be mediated via overlapping dendritic fields between the ICo and nucleus DM.

5. Discussion

Females have unique evolutionary pressures that encourage nuanced song preferences, which are individually variable and subject to a number of social factors. Mounting evidence points to the "song system" as a putative circuit for female courtship interactions where selectivity of female mating posture can be modulated by the same brain regions that drive song production in the male. While we have focused on CSD selectivity, these brain regions impact a range of behaviors in both male and females, including call timing (Benichov et al., 2016), species recognition (Brenowitz, 1991), sex identification (Vicario et al., 2001) and sociality (Hamilton et al., 1997). The body of evidence suggests that the "song system" might be better understood as a circuit that controls a suite of social behaviors, integrating a variety of sensory inputs and higher order representations (such as song memory and social standing) to ensure the correct selection of social responses. This system appears to have evolved functions in both males and females and continues to be active in a range of social behaviors including, but not limited to, song production. While many unknowns remain, these facts have important implications for 1) the evolution of vocal learning and sociality, 2) our understanding of courtship

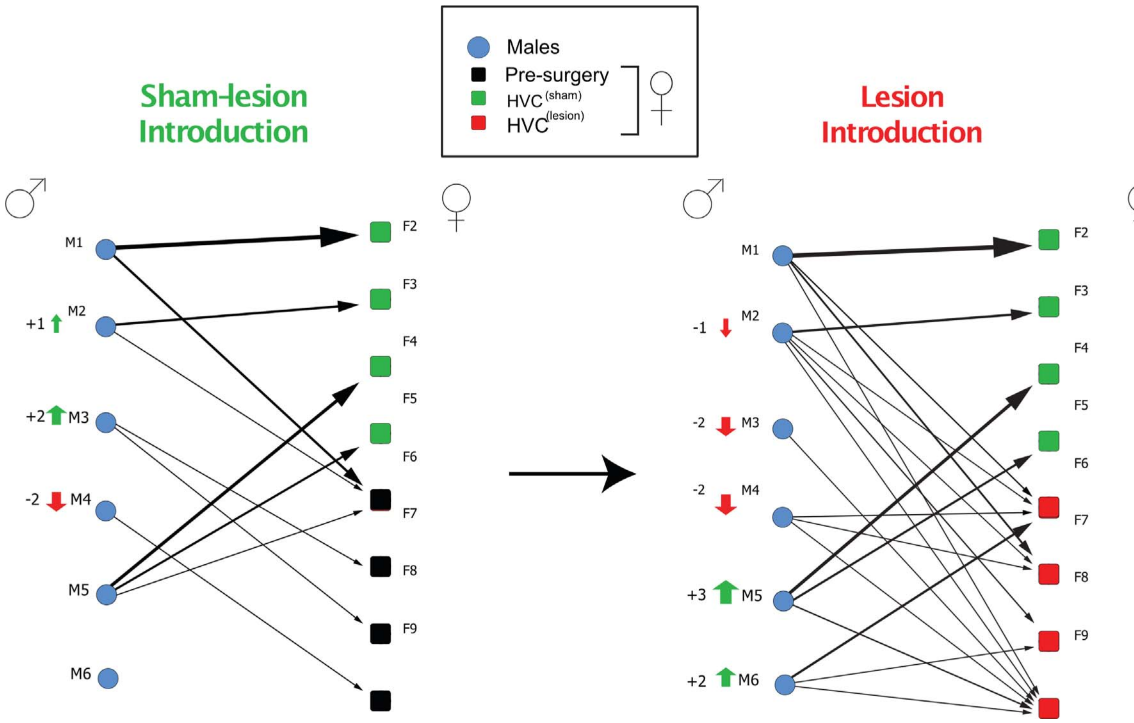

Fig. 4. Lesioned to song regions females disrupt selectivity and social interactions.
This plot depicts changes in song behavior following introduction of lesioned females (red, right) versus sham-lesioned females (green, left). Brown-headed cowbirds housed together during the breeding season show pair bonding behavior as measured by the pattern of directed singing by males (blue circles) to their consort female(s) (squares). Females were removed from the aviary and received ibotenic lesions targeted at HVC. Following recovery, females were reintroduced to the aviary (right panel; red squares) and song interactions were recorded. Black arrows represent female-directed male song, where thickness corresponds to song frequency. Male hierarchy (determined by male–male counter singing) is noted, including the change following introduction (direction and magnitude indicated by red and green arrows). Lesioned females received song from increased numbers of males–compared to both themselves prior to surgery and to shame-lesioned females (right panel; green squares). Introduction of lesioned females also disrupted male hierarchies while increasing female chatter in non-lesioned birds. (Male-male song and female chatter not shown here, see Maguire et al., 2013).

behavior, and 3) our assumptions within the field of birdsong neurobiology.

5.1. A broader picture of songbird evolution

The prevalence of female song across oscine families, along with the varied functions of so-called song nuclei, even in non-singing females, indicate that our understanding of the origin of learned song is incomplete. Rather than acting as a dedicated circuit for producing song and signaling male quality, the evidence surveyed in this article suggest that it should be viewed as a central circuit for navigating a range of complex social interactions of which song production is the most obvious and easily studied component. It remains possible that learned vocalizations emerged as a response to female preference for complex signals. However, it seems likely that a variety of preferences and socially mediated selection shaped the evolution of courtship behavior, including birdsong and the associated neural structures.

Many songbird species exhibit social hierarchies (King et al., 1981; Dufty, 1986) and the navigation of these complex environments, i.e. correctly responding to varied social stimuli, could itself be an important selective trait. In one particularly salient example, cowbird males appear to reduce their song quality to match their position in hierarchies (King et al., 1981). Male cowbirds raised without social feedback produce more potent songs than socially reared males (as measured by playback studies), but typically are unsuccessful in aviaries, largely due to social antagonism by other males. While theoretically more potent songs provide isolate males with better mating opportunities, their inability to correctly interact with other males results in violent confrontations, while socially reared males are capable of navigating a dominance hierarchy without injury. In this example, song production is intrinsically linked with social interactions, suggesting that song learning is tightly coupled to social learning.

Although there are multiple examples of highly social songbirds, many species have comparatively simple social networks, including those of several basal families of songbirds in which territoriality limits the number and frequency of interactions (Lack, 1968). The degree to which social complexity is a selective force unto itself in these birds (either through territorial interactions or through maintenance of pair bonds) is not well understood. Laboratory research has a natural bias towards communal birds (e.g. zebra finches, cowbirds), which can be housed in large numbers and easily studied in captivity. While these examples are compelling, these species might represent extreme examples in terms of evolution and social complexity. In free living, non-communal species it is more difficult to quantify the extent or the importance of social interactions. Future research into the selective impact of sociality in these species will help to establish to what degree the development of learned vocalizations was driven by selection for social complexity.

In this paper, we have argued that selection for social complexity was–if not the original cause of–likely a factor in the evolution of vocal learning. Communication is, by definition, social and song is a central component of songbird communication. It is difficult therefore to separate the evolution of song learning from accompanying social complexity. As mentioned, females across a range of species show preferences for complex vocalizations and it is generally accepted that a preference for complex displays (either through sensory bias or as a true signal of quality) could lead to the emergence of vocal learning. Learned vocalizations could then facilitate the complex social organizations that we observe. It is also possible that selective forces favoring social complexity drove the evolution of complex vocalizations (in both males and females) and simultaneously favored a female preference for vocal complexity in males (which would reinforce this complexity through sexual selection for male phenotypes). Distinguishing between these two hypotheses requires detailed examination of preference and the selective impact of sociality across various clades of oscine and suboscine songbirds. Regardless of the ultimate cause, the involvement of bird song in social navigation highlights the role that neural structures linked to song likely play in courtship, preference, and social behavior in general.

5.2. The neural correlates of courtship

The female songbird offers unparalleled opportunities for understanding mate preference and courtship. At the behavior level, the copulation solicitation display offers a quantifiable measurement of female preference that can be manipulated by both acoustic and hormonal manipulations. At the circuit level, the "song system" provides an appealing target for investigating the neural mechanisms underlying courtship behavior. An example of the richness of this model system is apparent in the changes in behavior observed when female cowbirds are reintroduced into the aviary following small lesions targeted to the song system (Maguire et al., 2013). In addition to the loss of CSD selectivity to song, these females fail to form normal pair bonds, instead receiving song from a variety of males (Fig. 4). This behavior in turn alters both male–male interactions and the behavior of resident control females. In many cases, low-ranking males increase the frequency of song challenges to dominant males and resident females increase the frequency with which they produce chatter calls.

Together with previous evidence showing that females can shape male song (King and West, 1977,1983b; West and King, 1988a,b) and female preference (Freed-Brown and White, 2009), these results emphasize females' central role at many levels of social behavior. They also highlight that a neural circuit previously thought to be inactive in females can modify mating behavior with population-level implications. Female songbirds thus provide exciting opportunities to investigate behavior at a neural, individual, and population level to reveal the mechanisms underlying complex social systems.

6. Conclusion

We have argued that across the fields of songbird research, we must modify our assumptions regarding the evolution and function of birdsong. While the ability to reduce a complex system to a tractable model is central to scientific investigation, and rewards from increased complexity of models diminish rapidly, it is abundantly clear that female songbirds have functional neural pathways and relevant social behaviors that impact a broad range of social interactions. A failure to acknowledge these realities and revisit biased assumptions increases the risk of overlooking or misinterpreting key features of the evolution of vocal communication, social behavior, and neural circuit function.

Conflicts of interest

None.

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