

Neural orchestration of mate-choice plasticity in songbirds

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Abstract Females may choose between prospective mates based on signals that reflect male quality. In songbirds, variation in male song can be such a signal. Females can adjust their choosiness according to the prevalence of preferred song, presumably because environmental variation can influence the availability of preferred phenotypes. Studies using induction of the immediate early gene ZENK (also called zif-268, egr-1, NGFI-A, and Krox-24) as an indicator of neuronal activity have revealed that the caudomedial mesopallium (CMM) and caudomedial nidopallium (NCM) of the female auditory forebrain are sensitive to song quality and respond proportionally to the strength of the female's choosiness. In European starlings (*Sturnus vulgaris*), long songs are preferred by females and induce higher ZENK expression in the CMM and NCM compared to short songs. Experimentally reducing the perceived prevalence of long songs in the environment reduces this forebrain sensitivity to song length, raising the possibility that the songbird auditory forebrain integrates information about the social environment that enables the female to adjust her choosiness according to the availability of preferred phenotypes. In some songbird species, the noradrenergic system modulates mate-choice behavior, modulates song-induced auditory forebrain activity, and itself is modulated by the prevailing song environment, suggesting a possible role for this system in mediating the effects of social environment on forebrain and behavioral

sensitivity to mate-choice cues. The presence of such a system would seem beneficial when the availability of preferred mates varies.

Keywords European starling · Immediate early gene · Mate-choice · Neuroplasticity · Norepinephrine · ZENK

Introduction

Mate-choice is among the most important decisions a sexually reproducing organism can make, because it affects the genetic constitution of the offspring and, in some species, the quality and quantity of parental care. Females may make mate-choice decisions based on variation among males in traits that reflect male quality (e.g., Hill 1991; Nowicki et al. 2000; Duffy and Ball 2002), which can be influenced by genetic and environmental factors (Anderson 1994; Gil and Gahr 2002). As the physical or ecological environment changes temporally or spatially, the mean perceived quality of prospective mates from which females choose may change due to changes in the distribution or abundance of preferred traits that are constrained by the environment. Therefore, females should possess the plasticity to adjust choosiness according to the unpredictable availability of preferred traits (Ball et al. 2006). Female songbirds assess the quality of prospective mates and choose between them based in part on variation in their courtship songs (Searcy and Yasukawa 1996; Gil and Gahr 2002). Here, I review what we currently know regarding how the female songbird brain integrates information about the distribution and abundance of male song traits and precipitates the programs that culminate in choosiness adjusted to this prevailing song environment.

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Song variation as a mate-choice cue

Within many songbird species, there is considerable variation between the song complexity, song performance, song length, or song type (e.g., dialect) of different males. Females attend to this between-male variation in song because it may reflect constraints males faced during development (Nowicki et al. 1998, 2000, 2002a, 2002b; Buchanan et al. 2003, 2004; Nowicki and Searcy 2004) and thus serve as an honest signal of male quality. In wild, free-living European starlings (*Sturnus vulgaris*), for example, male mating success and female choice and reproductive success are associated with the length of the male's song (Eens et al. 1991; Mountjoy and Lemon 1996; Eens 1997), and, in lab contexts mimicking natural mate-choice situations, female starlings demonstrate robust preferences for long songs over short songs (Gentner and Hulse 2000). In male European starlings, song length positively correlates with immunocompetence (Duffy and Ball 2002), which itself is likely influenced by developmental constraints. Thus, this long-song preference results in the female's affiliation with and choice of mates of higher immunocompetence and higher quality in general (for a review of male song, female preferences, and neural responses to song exposure and song production in European starlings, see Ball et al. 2006).

Modulation of mate-choice decisions by the song environment

Females will likely face variation in the perceived proportion of preferred traits being expressed (i.e., variation in the prevailing song environment) because resources (Johnson and Geupel 1996), habitat-effects on signal degradation (Blumenrath and Dabelsteen 2004), and the degree to which costs of song production (Eberhardt 1994; Catchpole and Slater 1995; Oberweger and Goller 2001; Gil and Gahr 2002; Thomas et al. 2003; Ward et al. 2003) constrain song signaling can vary between and within populations both seasonally and between years. Using mate-sampling experience with these variable population-densities of song traits—a process requiring the neural integration of the local song environment prior to breeding—females should express some plasticity in the phenotypic threshold they set for their mate-choice decision (Wiegmann et al. 1996; Jennions and Petrie 1997; Badyaev and Qvarnström 2002). In the absence of this plasticity, they may spend periods without mating due to the inability of some males to meet their high demands for song quality (Ball et al. 2006).

Several species exhibit this type of frequency-dependent mate-choice behavior. For instance, female white-crowned sparrows (*Zonotrichia leucophrys*) normally prefer their

natal song dialect. However, if they experience a more prevalent foreign dialect during preceding months, females exhibit no choice-bias toward either song type (MacDougall-Shackleton et al. 2001). This suggests that when the prevailing song environment is lacking in the preferred song type, females adjust the threshold for choosing a male as a mate. Female cowbirds (*Molothrus ater*) (Freeberg et al. 1999) and canaries (*Serinus canaria*) (Nagle and Kreutzer 1997) also exhibit choice biases toward the preferred male song-type when it is prevalent but not when the less-preferred song-type is prevalent. In fact, frequency-dependent mate-choice plasticity even occurs in arthropods (van Gossum et al. 2001; Hebets 2003), suggesting how taxonomically widespread this phenomenon may be.

Neural integration of mate-choice cues

In the songbird brain, the caudomedial mesopallium (CMM) and caudomedial nidopallium (NCM) are central to the high-order acoustic processing of conspecific song and possess reciprocal, ipsilateral connections (Vates et al. 1996). One hallmark of these areas that enabled the discovery of their important roles is their stimulus-specific expression of immediate early genes (IEGs) (Clayton 2000; Mello 2002; Bolhuis and Eda-Fujiwara 2003; Mello 2004; Ball et al. 2006). In the white-crowned sparrow, CMM and NCM expression of the IEG ZENK (the avian homolog of and an acronym for zif-268, egr-1, NGFI-A, and Krox-24) is greater in females exposed to the preferred local dialect than in those exposed to the less preferred foreign dialect (Maney et al. 2003). ZENK induction in both the CMM and NCM positively correlates with the level of sexual receptivity to a particular song type (Maney et al. 2003). Female European starlings, which prefer long song over short song, have greater ZENK induction in the CMM and NCM in response to long songs than in response to short songs, even when the total song exposure is held constant (Sockman et al. 2002). Male canaries (*Serinus canaria*) sometimes produce song elements known as “sexy” syllables, which are characterized by their complex spectrotemporal structure, rapid frequency modulation over a wide bandwidth, and high repetition rate (Vallet et al. 1998). Female canaries express stronger sexual displays (Vallet et al. 1998) and higher levels of ZENK in the auditory forebrain (Leitner et al. 2005) in response to songs with “sexy” syllables than to songs without such syllables. Females of the non-oscine budgerigar also show a similar auditory forebrain sensitivity toward more complex male budgerigar song (Eda-Fujiwara et al. 2003). These studies raise the hypothesis that auditory processing in the CMM and NCM is associated with the decision of mate-choice in female oscine and possibly some non-oscine birds.

If the female’s forebrain ZENK-response reflects the strength of her choice toward a particular song phenotype, as it does in the white-crowned sparrow, then one means by which the brain might enable the modulation of choice according to the prevailing song environment is by making the forebrain ZENK-response sensitive to song type after experience with the preferred song type but less sensitive to song type after experience with the less-preferred song type. Recently, my colleagues and I found evidence for such a neural system mediated by induction of ZENK (Sockman et al. 2002, 2005). In these studies, we exposed pairs of female European starlings to one week of either long or short male song played 5.5 h/day. We then exposed each female of each pair to 30 min of either novel long- or novel short-songs and quantified forebrain ZENK expression. We found that, in both the CMM and NCM, the ZENK response-bias toward the long-song stimulus occurred after recent experience with long but not short songs (Fig. 1). Thus, song environment modulates this measure of forebrain sensitivity to a preferred trait. These findings also demonstrate a previously unknown type of adult neuroplasticity. Because stimulus songs were always novel, neural responses to the stimuli were modulated by experience with the *category* of stimulus to which they are sensitive, not by experience with the stimulus itself.

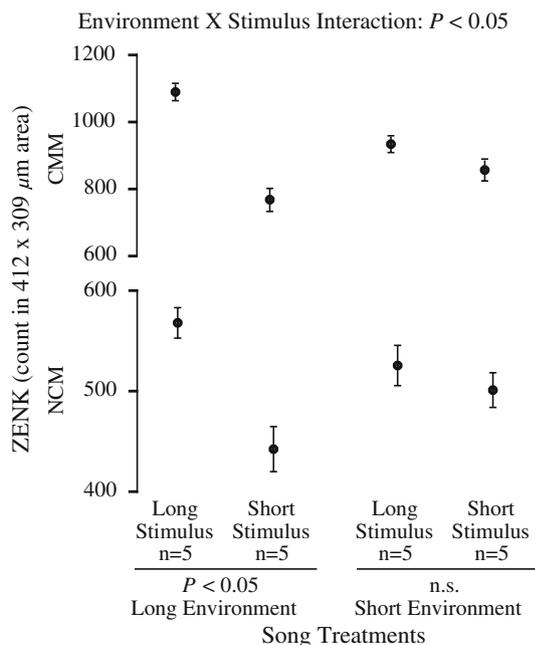


Fig. 1 Modulation of forebrain (CMM and NCM) sensitivity to song length by the prevailing song environment. Forebrain sensitivity is measured as the difference between ZENK induction (mean ± SE) in response to the preferred long song and ZENK induction in response to the less-preferred short song. Forebrain sensitivity is greater when the prevailing song environment is long song than when it is short song. Modified from Sockman et al. (2002) with permission

In some cases, habituation processes might explain reduced neural (Mello et al. 1995) and behavioral (Searcy 1992) responses to song, but they could not explain the results shown in Fig. 1. That is, the song sets used in this experiment retained across treatments their categorical distinctions (long or short), while they varied across treatments in their spectro-temporal features. Although it might still be possible for females to habituate to song features shared across males or treatments, feature sharing between experience and stimulus songs in our experiment would be greatest for treatment combinations of the same category (long experience with novel long stimulus or short experience with novel short stimulus). However, the lowest and highest responses occurred when treatment combinations were, respectively, different and the same in category, exactly the opposite pattern predicted by habituation processes. Thus, these neural responses illustrate a perceptual sensitivity that would require cognitive processes beyond simple habituation (Sockman et al. 2002, 2005). Further, these findings raise the possibility that as the prevalence of the less-preferred trait-type increases, neural sensitivity for discriminating between preferred and less preferred traits decreases (Fig. 2). The question now is: how does the prevailing song environment modulate the sensitivity of the female auditory forebrain to song type?

Noradrenergic integration of the song environment

The forebrain neurons of most sensory systems exhibit some form of experience-dependent representational plasticity (Gilbert et al. 2001; Calford 2002), and in the mammalian auditory system, this plasticity is linked to the

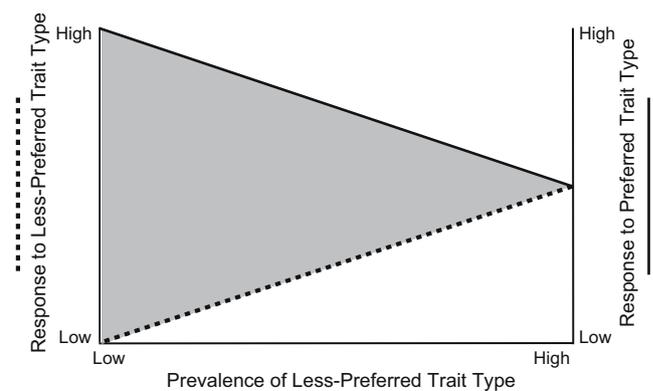


Fig. 2 Hypothesis that forebrain sensitivity to mate-choice cues (width of gray shaded region) varies with social environment. In the European starling, the social environment could vary in the perceived prevalence of preferred or less-preferred male trait-types in the population (x axis). Forebrain sensitivity to mate-choice cues is measured by ZENK induction in response to preferred mate-choice cues (solid line: response to long songs) relative to less-preferred mate-choice cues (dotted line: response to short songs)

activation of catecholaminergic neurotransmitter systems (Bao et al. 2001). It has been suggested that one of these catecholaminergic systems, the noradrenergic system, controls forebrain plasticity by directly modulating IEGs known to play a role in this plasticity (Cirelli et al. 1996; Yamada et al. 1999; Cirelli and Tononi 2004; Castelino and Ball 2005). In the songbird HVC (Dave et al. 1998) and nucleus interfascialis of the midpallium (Cardin and Schmidt 2004), norepinephrine secretion regulates state-dependent responses to song. In the rat (Cirelli and Tononi 2004) and songbird (Castelino and Ball 2005), chemical lesion of noradrenergic input to the forebrain with *N*-(2-chloroethyl)-*N*-ethyl-2-bromobenzylamine (DSP-4) reveals that noradrenergic projections mediate context- or state-dependent forebrain ZENK expression.

Recent evidence implicates a role for the noradrenergic system specifically when it comes to the mediation of mate-choice decisions based on song variation in songbirds. The auditory forebrain of songbirds is richly innervated with noradrenergic input, much of which probably arises from the avian homolog of the locus coeruleus (Mello et al. 1998; Ribeiro and Mello 2000; Appeltants et al. 2001, 2004). This system comes in close contact with song-responsive neurons in the auditory forebrain, and interference of noradrenergic signaling by alpha-adrenergic receptor blockade abolishes song-induced ZENK induction in the NCM of zebra finches (Ribeiro and Mello 2000). DSP-4 lesion of forebrain noradrenergic projections in female canaries reduces their mate-choice bias toward the preferred male song when compared to control-lesioned females (Appeltants et al. 2002). Because both forebrain sensitivity and this behavior can arise from experience with a particular song environment, and because both are altered by manipulating some aspect of noradrenergic signaling in this area, the intuitive hypothesis is that information about the song environment is integrated by a socially sensitive noradrenergic system, which innervates the forebrain and influences its sensitivity to song type.

The mechanism by which the prevailing song environment might modulate noradrenergic activity in the auditory forebrain is not clear, but representations of the song environment may feed either directly or indirectly into the locus coeruleus or the auditory forebrain and exert effects on norepinephrine secretion. The locus coeruleus receives input from many forebrain, midbrain, and hindbrain structures, including the amygdala, hypothalamus, and raphe nuclei, each of which might be modulated by the song environment due to their auditory responses (Berridge and Waterhouse 2003). Noradrenergic activity could then change in several ways. For example, noradrenergic axons might change in their connectivity with the forebrain. Alternatively, axonal connections may not change, but biochemical changes within noradrenergic cell bodies or

axons could affect norepinephrine secretion. My colleague and I have recently collected some evidence that song environment can modulate noradrenergic activity in the songbird forebrain (Sockman KW, Salvante KG, unpublished data). We exposed individual female starlings to one week of either long or short song (5.5 h/day), using a protocol similar to that described above (Sockman et al. 2002). Then, blind to the treatment of each female, we assessed by immunocytochemistry the presence in the auditory forebrain of immunoreactivity for dopamine beta-hydroxylase (DBH-ir), the enzyme that synthesizes norepinephrine from dopamine (Cooper et al. 2003). With higher norepinephrine secretion rates in the auditory forebrain predicted under the long-song environment, one would expect higher rates of norepinephrine synthesis to keep pace and thus higher DBH-ir in the auditory forebrain. This is exactly what we found (Sockman KW, Salvante KG, unpublished data). We did not find evidence that the song environment affected DBH-ir in the stratum cellulare internum or stratum cellulare externum, regions that are not expected to change in DBH-ir. Thus, the effects of the prevailing song environment on DBH-ir are at least somewhat specific to the auditory forebrain. However, presuming that the DBH specificity of the antibody is high, DBH-ir may be, at best, a proxy for norepinephrine synthesis. Still, the DBH-ir results are consistent with the prediction that the prevailing song environment modifies some aspect of the forebrain noradrenergic system in female starlings, such as norepinephrine secretion. We are now conducting studies aimed at more precisely characterizing the effects of song environment on forebrain norepinephrine secretion, forebrain sensitivity to song type, and mate-choice decisions. Due to the role mate-choice plays in the process of sexual selection and the role of sexual selection in the evolution of sexual traits and in speciation as a whole (Andersson 1994), research in this area may help to reveal part of a mechanistic basis for a number of evolutionary processes.

Broader implications

In the recent past, one might have assumed that the integration of social information prior to decision-making is so complex that understanding its neural architecture might extend beyond the province of modern neuroscience (Insel and Fernald 2004). However, progress has been made on how the vertebrate brain processes social cues during decision-making tasks and what implications variation in neural processing might have for the causes, consequences, prevention, and treatment of several human behavioral disorders (Adolphs 1999, 2001, 2003; Blakemore and Frith 2004; Ferguson and Bargh 2004; Insel and Fernald 2004).

As research progresses, the need for invasive, manipulative approaches and therefore the need to use vertebrate models amenable to these approaches has increased. Considerable advances have occurred in our understanding of the neural mechanisms for social cognition and behavior in a variety of species (Insel and Fernald 2004; Jarvis 2004), and these advances help us to better understand how the human brain processes social cues due to the importance of social behavior in most vertebrates, and the fact that many of the perceptual mechanisms are likely to be highly conserved across diverse species. Science benefits from model systems in which the natural history of the social behavior is well characterized, in which the social environment is easily controlled and manipulated in an experimental context, in which a clear decision-making task can be measured efficiently and precisely as a dependent outcome of social processing, and in which the neural basis for integrating social information and for precipitating the motor outcomes are well understood. Research on the song biology of songbirds exemplifies such a system with which we can begin to answer questions about the underlying neuroplasticity of socially modulated decision-making processes, how they are influenced at the level of the single cell by neuromodulatory systems, and how this, in turn, has shaped the evolution of social behavior.

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