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Neural mechanisms of auditory species recognition in birds

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ABSTRACT

Auditory communication in humans and other animals frequently takes place in noisy environments with many co-occurring signallers. Receivers are thus challenged to rapidly recognize salient auditory signals and filter out irrelevant sounds. Most bird species produce a variety of complex vocalizations that function to communicate with other members of their own species and behavioural evidence broadly supports preferences for conspecific over heterospecific sounds (auditory species recognition). However, it remains unclear whether such

auditory signals are categorically recognized by the sensory and central nervous system. Here, we review 53 published studies that compare avian neural responses between conspecific *versus* heterospecific vocalizations. Irrespective of the techniques used to characterize neural activity, distinct nuclei of the auditory forebrain are consistently shown to be repeatedly conspecific selective across taxa, even in response to unfamiliar individuals with distinct acoustic properties. Yet, species-specific neural discrimination is not a stereotyped auditory response, but is modulated according to its salience depending, for example, on ontogenetic exposure to conspecific *versus* heterospecific stimuli. Neuromodulators, in particular norepinephrine, may mediate species recognition by regulating the accuracy of neuronal coding for salient conspecific stimuli. Our review lends strong support for neural structures that categorically recognize conspecific signals despite the highly variable physical properties of the stimulus. The available data are in support of a 'perceptual filter'-based mechanism to determine the saliency of the signal, in that species identity and social experience combine to influence the neural processing of species-specific auditory stimuli. Finally, we present hypotheses and their testable predictions, to propose next steps in species-recognition research into the emerging model of the neural conceptual construct in avian auditory recognition.

CONTENTS

I. INTRODUCTION

Nearly all birds produce auditory signals for communication, which range from simple

calls to complex songs. These have a variety of functions, the most common and well studied

being courtship and territory defence. Other social functions of vocalizations include competition,

foraging, and predator avoidance (Kroodsma & Byers, 1991). One obstacle imposed on all

signallers is that their vocalizations must transmit through the environment and reach the

intended receiver (Brumm, 2004). Signals may become muddled in noisy environments where

many avian species are trying to communicate simultaneously, thus birds often need to be able to

discriminate conspecific vocalizations from those of heterospecifics in order to communicate

effectively (Bee & Micheyl, 2008).

For most avian species, the perception and discrimination of conspecific vocalizations is

experience dependent and learned early in life for the purpose of producing song (Doupe & Kuhl,

1999; Brenowitz & Beecher, 2005) or for developing song preferences for mate choice (Lauay *et

al.*, 2004). Species also may have experience-independent preferences for conspecific song that

are seemingly innate (Marler, 1997; Braaten & Reynolds, 1999). Additionally, birds can utilize salient heterospecific stimuli for eavesdropping and predator avoidance (Magrath *et al.*, 2015). The perception of species-specific vocalizations has profound evolutionary consequences, including effects on reproduction isolation and speciation (Ratcliffe & Grant, 1985; Seddon, 2005; Freeman, Montgomery & Schluter, 2017). Consequently, it has been of interest to researchers to determine the sensory, perceptual, neural, and cognitive bases for the recognition of conspecific auditory signals in birds.

Here we review studies that have utilized a conspecific *versus* heterospecific vocalization paradigm to investigate neural mechanisms of avian auditory species recognition. Our aim is to decipher where in the brain species-specific stimuli are discriminated and recognized. The review highlights how recognition supports a model of categorical representation of conspecific stimuli in the auditory nervous system of birds. Furthermore, this review contributes to understanding how the mechanisms of the vertebrate nervous system process and encode salient stimulus classes and categories, which remains a crucial, yet largely unresolved, question in neuroscience.

II. NEURAL RESPONSES TO SPECIES-SPECIFIC SOUNDS

We identified 53 studies, representing 21 focal bird species, in which direct and/or indirect metrics of neural activity levels were compared between responses to conspecific or heterospecific sounds (Table 1). Of these, 41 (77%) studies reported one or more comparisons

with statistically greater neural activity in response to conspecific auditory stimuli (Table 1). Given the major types of neurobiological (song-learning oscines *versus* non-song learning taxa) and developmental (altricial *versus* precocial) variation across avian taxa, we broke down these categories further. Accordingly, 78% of song-learning species *versus* 75% of non-song learning species showed neural response selectivity for conspecific over heterospecific stimuli and each of the three studies investigating precocial species found conspecific selectivity.

(1) Techniques used in auditory recognition studies

Neurobiologists have employed several techniques to compare neural responses between conspecific and heterospecific sounds in birds (Table 1), each with advantages and disadvantages regarding the type and accuracy of the data that can be collected (e.g. Boynton, 2011; Van Ruijssevelt *et al.*, 2018). Regarding real-time *in situ* neuronal responses, for example, studies using electrophysiology have recorded conspecific-selective firing patterns from individual neurons at the microsecond scale (Chew *et al.*, 1995; Chew, Vicario & Nottebohm, 1996; Woolley, Hauber & Theunissen, 2010; Hauber *et al.*, 2013; Smulders & Jarvis, 2013). Brain imaging, such as functional magnetic resonance imaging (fMRI) and positron emission tomography (PET), also showed that conspecific sounds evoke greater neural activity at a stimulus-length (several seconds) time scale, when compared to sequential playbacks of heterospecific sounds (Poirier *et al.*, 2009; Louder *et al.*, 2016; Lattin, Stabile & Carson, 2017). Furthermore, genes that are induced in response to regulatory signals from external stimuli,

known as immediate early genes (IEGs), can be used to infer the intensity of neural activity across a longer time scale of continued exposure to stimuli, ranging from minutes to hours. For example, the numbers of neurons that express ZENK (an acronym for the homologous genes: *zif268*, *EGR-1*, *NGFI-A*, and *krox24*), selectively increase in response to conspecific *versus* heterospecific auditory stimuli (Mello, Vicario & Clayton, 1992). Likewise, other IEGs, including *FOS* (also known as *c-Fos*) and *Arc*, have also been found to exhibit conspecific-selectivity in the auditory forebrain of birds (Bailey & Wade, 2003; Velho *et al.*, 2005). Finally, behavioural preferences of female zebra finches (*Taeniopygia guttata*) for conspecific *versus* heterospecific songs was eliminated by lesioning of the caudomedial mesopallium (CMM) (MacDougall-Shackleton, Hulse & Ball, 1998).

Nonetheless, several studies also reported a lack of statistically significant species-specific neural responses in the auditory forebrain. For example, conspecific calls induced greater ZENK production relative to silent controls in the caudomedial nidopallium (NCM) and CMM of ring doves (*Streptopelia risoria*), but not greater than compared to song presentations of zebra finch (Terpstra *et al.*, 2005). Similarly, *ZENK* expression was greater in the auditory forebrain (CMM, NCM and field L combined) of embryonic zebra finches in response to conspecific song than silence, but not significantly different relative to two different heterospecific song playbacks) (Rivera *et al.*, 2019). In male adult zebra finches, both conspecific and heterospecific songs induced greater neural firing rates within the NCM when compared to pure tones and bursts of white noise, but there were no statistical differences in

either the mean or the population distribution of electrophysiological responses to conspecific *versus* heterospecific stimuli (Stripling, Volman & Clayton, 1997). Furthermore, *ZENK* induction was not significantly different between putatively non-learned calls of conspecific and heterospecific species in the CMM and NCM of both black-capped chickadees (*Poecile atricapillus*; Avey *et al.*, 2014) and zebra finches (Scully *et al.*, 2017).

(2) Species-specific stimuli

Studies have used a variety of species to serve as exemplar heterospecific stimuli. Thus, neural response selectivity could depend purely on the acoustic dis/similarities between conspecific and heterospecific sounds used as stimuli (Mendelson *et al.*, 2016). However, IEG activation in red-winged blackbirds (*Agelaius phoeniceus*) did not reflect acoustic similarities between the call used as the conspecific stimulus *versus* heterospecific stimulus calls of two different species (Lynch, Louder & Hauber, 2018). Similarly, Hauber *et al*. (2013) found the neural firing rates of zebra finches responded at similarly lower levels to the heterospecific songs of Bengalese finch (*Lonchura striata domestica*) and Parson's finch (*Poephila cincta*) *versus* conspecific songs, and Poirier *et al*. (2009) found greater neural responses in zebra finches upon hearing conspecific songs *versus* multiple exemplars of canary (*Serinus canaria domestica*) and European starling (*Sturnus vulgaris*) songs, despite the contrasting acoustic structures of each set of heterospecific stimuli. Taken together, these results support a model of neural activation to represent stimulus-dependent neural selectivity of specific content of the playback types (e.g.

conspecific *versus* heterospecific), rather than the acoustic contrasts between stimulus sounds (Lynch *et al.*, 2018).

ZENK protein regulation is strongly implicated in long-term neuronal changes, and likely in the formation of memories (Bolhuis *et al.*, 2000; Gobes, Zandbergen & Bolhuis, 2010). Therefore, it is possible that the lack of observed conspecific-selective ZENK induction in response to hearing non-learned calls in both black-capped chickadees (Avey *et al.*, 2014) and zebra finches (Scully *et al.*, 2017) reflects a lack of stimulus-induced neuroplasticity rather than a lack of discrimination between conspecific and heterospcific stimuli that share acoustic similarities.

The number of representative stimuli can influence the interpretation of neural responses. In particular, studies using playbacks of a single heterospecific stimulus have been argued to represent a potential confound of pseudoreplication, or an inappropriate sample size for the hypothesis being tested (Kroodsma, 1989). Indeed, many of the studies reviewed used a single heterospecific exemplar for comparison (Table 1). However, given that studies regularly report an increase in neural responses for conspecific over heterospecific stimuli, irrespective of the technique or heterospecific species used, there is overall support for neural species recognition.

III. NEURAL REGIONS INVOLVED IN SPECIES-SPECIFIC DISCRIMINATION
(1) Auditory pathway

Birds and mammals have relatively similar auditory pathways (Vates *et al.*, 1996; Jarvis *et al.*, 2005). Sounds are transduced into neural signals by hair cells in the ear that synapse onto sensory neurons, which then transmit from the cochlea to the midbrain and thalamic auditory nuclei (Theunissen *et al.*, 2006). The thalamic nuclei then project to primary auditory regions (nucleus Field L in birds; layer 4 of the auditory cortex in mammals), which in turn project to secondary auditory nuclei (CMM and NCM in birds). Like the mammalian primary auditory regions, Field L is tonotopically organized such that neurons that respond to specific frequencies are spatially arranged in neighbouring areas. The avian auditory regions are also hierarchically interconnected, analogous to the microcircuitry of the six-layered mammalian neocortex (Calabrese & Woolley, 2015). Additionally, these secondary auditory nuclei in birds appear homologous to the belt auditory cortex in mammals and Wernicke's region in humans (Meliza & Margoliash, 2012).

Several different techniques have demonstrated the role of the avian auditory forebrain in differential processing of acoustic stimuli from different species, even when presenting sounds produced by unfamiliar individuals. Studies using electrophysiology have recorded conspecific-selective greater firing for neurons within Field L (Woolley *et al.*, 2010; Hauber *et al.*, 2013), as well as in the NCM and CMM (Chew *et al.*, 1995, 1996; Smulders & Jarvis, 2013). fMRI and PET showed that conspecific sounds evoke greater neural activity when compared to heterospecific sounds (Poirier *et al.*, 2009; Louder *et al.*, 2016; Lattin *et al.*, 2017). Furthermore, the numbers of neurons that express IEGs such as *ZENK*, *c-FOS* and *Arc* selectively increase in

response to conspecific *versus* heterospecific auditory stimuli in the NCM and CMM of birds (Mello *et al.*, 1992; Bailey & Wade, 2003; Velho *et al.*, 2005). Importantly, however, IEG studies using *ZENK* or *c-FOS* have not been able to analyse gene-expression patterns in field L, and although another IEG (*DUSP1*) is expressed in field L, it has not yet been used in conspecific *versus* heterospecific listening tasks (Horita *et al.*, 2010). Finally, behavioural preferences of female zebra finches for conspecific *versus* heterospecific songs were eliminated by lesioning of the CMM (MacDougall-Shackleton *et al.*, 1998). Therefore, evidence supports secondary auditory areas as the site of integration amongst these different categories of avian auditory signals.

Conspecific-selective neural activation was found simultaneously in both the NCM and CMM in several studies (e.g. Mello *et al.*, 1992; Hernandez & MacDougall-Shackleton, 2004; Farrell *et al.*, 2015), suggestive of parallel neural substrates for the representation of species-typical sounds. However, the two regions may have functional differences for the various types of auditory signals encountered by an individual based on context, including sex (Bolhuis & Gahr, 2006) and prior experience (Lynch *et al.*, 2017, 2018). Accordingly, young males of the brood-parasitic brown-headed cowbird (*Molothrus ater*), a species that lacks parental care and relies on a foster species to raise their offspring, exhibited increased *ZENK* induction within the CMM following exposure to familiar songs, regardless of whether the recently exposed song was conspecific or heterospecific (Lynch *et al.*, 2017). In the brains of immature male red-winged blackbirds, a non-parasitic parental species closely related to cowbirds, playbacks also evoke

conspecific selectivity for familiar non-learned female chatter calls in the CMM but not in the

NCM (Lynch *et al.*, 2018). By contrast, young male cowbirds showed conspecific-selective

ZENK expression within the NCM, but not the CMM, for a conspecific female non-learned call,

the chatter (Lynch *et al.*, 2017), suggesting that the chatter call is a species-specific password to

cue species recognition in juvenile brood parasites (Hauber, Russo & Sherman, 2001). Further

demonstrating the importance of the NCM for species recognition, females of the closely related

and occasionally hybridizing California quail (*Callipepla californica*) and Gambel's quail (*C.*

gambelii) both had greater neural responses to conspecific *versus* heterospecific non-learned

calls in the NCM (Gee, Tomaszycki & Adkins-Regan, 2009). Thus, the available evidence

suggests that the NCM may contribute to auditory species recognition through experience-

independent neural responses, whereas the CMM may primarily respond to learned auditory

signals (Gentner & Margoliash, 2003).

Not only is there evidence for functional differences between the NCM and CMM, but

there is also some support for hemispheric lateralization in the processing of species-specific

vocalizations. The left hemisphere of the auditory forebrain and the dorsal part of the lateral

mesencephalic nucleus (MLd) exhibited greater conspecific selectivity in the blood oxygen

level-dependent (BOLD) response in male zebra finches (Poirier *et al.*, 2009). Furthermore, the

left hemisphere processes sounds according to their acoustic category (combinations of features

that differentiate conspecific *versus* heterospecific song; Yang & Vicario, 2015) as well as

conspecific song *versus* acoustically matched synthetic noises (Hauber *et al.*, 2007) and tutor

versus unfamiliar conspecific songs (Moorman *et al.*, 2012). These results are particularly intriguing as left hemisphere biases are also thought to be responsible for the perception of species-specific vocalizations in primates and language processing in humans (Frost *et al.*, 1999). However, some avian studies using *ZENK* expression to evaluate neural activity find no species-specific treatment effect of vocalizations between hemispheres (Avey *et al.*, 2011). More research in this area could benefit our understanding of the role of the laterality of neural substrates in the evolution of conspecific auditory perception.

(2) Sensory-motor vocal nuclei

The circuitry of vocal nuclei in the songbird brain comprises two pathways, a motor pathway critical for normal song production, and the anterior forebrain pathway which is necessary for song acquisition (Bolhuis & Gahr, 2006). The motor pathway consists of the high vocal centre (HVC), which projects to the robust nucleus of the arcopallium (RA), then to the tracheosyringeal portion of the hypoglossal nucleus (nXIIts), and out to the syrinx. The HVC is also part of the anterior forebrain, although in this pathway the HVC projects to Area X, which has further connections to the nucleus dorsolateralis anterior, pars medialis (DLM) and lateral portion of the magnocellular nucleus of the anterior nidopallium (lMAN), forming a feedback loop which projects back to the RA from the lMAN, again connecting the two pathways. These pathways subserving the production and learning of song and are unique to songbirds (Gahr, 2000), parrots (Jarvis & Mello, 2000) and hummingbirds (Jarvis *et al.*, 2000; Gahr, 2000), as

evidenced by the lack of these forebrain nuclei in non song-learning avian lineages (but see Liu *et al.*, 2013). It is therefore unsurprising that the vocal motor circuitry nuclei have also been studied to determine their role, if any, in the perception of conspecific *versus* heterospecific vocalizations in song-learning species (mostly songbirds). Single-unit neuron recordings in the HVC, for example, show no differences in response to conspecific and heterospecific songs in both white-crowned sparrows *Zonotrichia leucophrys* (Whaling *et al.*, 1997) and swamp sparrows *Melospiza georgiana* (Mooney, Hoese & Nowicki, 2001). Multiunit recordings in the HVC of juvenile male zebra finches likewise show similar responses to conspecific (non-tutor) and heterospecific songs (Nick & Konishi, 2005). Analogous behavioural findings were shown in female zebra finches, which maintained their preference for conspecific song after the HVC was lesioned (MacDougall-Shackleton *et al.*, 1998). HVC-lesioned female brown-headed cowbirds lost some behavioural selectivity for the quality of conspecific male songs and did not respond to heterospecific songs (Maguire, Schmidt & White, 2013).

However, some studies also suggest that the HVC is critically involved in species recognition. Lesions to the HVC of female canaries disrupted behavioural preferences for conspecific song and resulted in a similar number of copulation solicitation displays to heterospecific song (Brenowitz, 1991; Del Negro *et al.*, 1998). In female European starlings, HVC volume was positively correlated with a bird's preference for conspecific song in an operant conditioning task (Farrell *et al.*, 2015). The HVC has also been implicated in associating specific songs with a referent, therefore, lesions of the HVC may have affected the ability

recognize the relevance of the stimuli and not the ability to discriminate between species-specific songs *per se* (Gentner *et al.*, 2000). The species-level discrepancy in the role of the HVC in conspecific recognition may be due to differences in female singing ability between the focal study species. Specifically, evidence for conspecific recognition in the HVC has only been found in European starlings and canaries, both of which exhibit female song production. Additionally, researchers have used vocalizations from a variety of species for heterospecific stimuli (see Table 1), which may result in inconsistencies across some studies (e.g. MacDougall-Shackleton *et al.*, 1998). With expanding knowledge of the presence and function of female song (Langmore, 1998; Odom & Benedict, 2018), including its ancestral state across songbirds (Odom *et al.*, 2014), the scope for further comparative work on the evolutionary role of female HVC-mediated species-discrimination is prime for future research.

Avian responses to conspecific *versus* heterospecific stimuli in Area X and lMAN have been studied almost exclusively in zebra finches. Single-unit recordings in Area X and lMAN have found no selectivity for conspecific over heterospecific song (Solis & Doupe, 1997; Rosen & Mooney, 2000). Male zebra finches trained to discriminate between conspecific and heterospecific song were unaffected by lesions to Area X or lMAN, suggesting that these nuclei are not involved in conspecific recognition (Scharff, Nottebohm & Cynx, 1998). Interestingly, the area surrounding Area X, known as the medial striatum (MSt), exhibited induction of IEGs in young zebra finches after listening to conspecifics but not to heterospecifics (Bailey & Wade, 2006). Similarly, HVC projections to Area X in zebra finches strongly expressed the cAMP

response element binding (CREB) protein after the bird listened to conspecific song (Sakaguchi *et al.*, 1999); CREB is necessary for the formation of long-term memories. Taken together, these studies suggest that while Area X and lMAN may not be involved in conspecific recognition, the neurons projecting to and surrounding Area X are involved with discriminating and learning conspecific vocalizations. Unfortunately, zebra finches have been the dominant species used in these studies and, like auditory-species-recognition studies, focusing on the HVC, differing results were found in female canaries, where deficits in the bird's ability to discriminate between previously learned acoustic stimuli of different species were shown after lesioning in lMAN (Burt *et al.*, 2000). Whether this is due to differences in female singing ability between these species or seasonally open-ended *versus* closed-ended learning remains unclear, and emphasizes the need for more study species to be tested on these brain regions to tease apart such discrepancies.

(3) Additional neural regions with auditory responsiveness

Outside of the *sensu stricto* song-learning and production circuitry, several additional forebrain regions have been examined for possible conspecific selectivity. In one study (Bailey & Wade, 2003), the hippocampus (HP) of day 30 post-hatching male and female zebra finches was found to exhibit conspecific over heterospecific selectivity for *ZENK* and *FOS* expression, respectively. This same FOS expression was seen in adult females as well, in both the HP and the parahippocampal area (AHP) (Bailey, Rosebush & Wade, 2002). Collectively, these studies

suggest that the HP is involved in the learning and recognition of species-specific vocalizations, yet the underlying neural functional and anatomical connectivities remain unknown. Additionally, examination of single-unit auditory responses in the nucleus taeniae of the amygdala (TnA) and surrounding areas in Bengalese finches found no evidence for conspecific selectivity; indicating that the amygdala may not be involved in species recognition (Fujii, Ikebuchi & Okanoya, 2016). Finally, in a recent study, the caudocentral nidopallium was found to play a role in the processing of courtship signals in female zebra finches using both fMRI and IEG approaches (Van Ruijssevelt *et al.*, 2018). This latter study also highlights both the need for additional whole-brain surveys and scans to identify specific regions and functional connectivity between them in the auditory processing of salient vocalizations in birds, and the general pattern, also illustrated above, that there is a strong confluence of different neurofunctional techniques, from lesioning to IEG, PET, and fMRI to neurophysiology, in identifying the same brain regions underlying auditory response selectivity in the avian brain (e.g. Louder *et al.*, 2016).

IV. RECOGNITION OF SPECIES-SPECIFIC SOUNDS

Discrimination between sounds does not necessarily reflect the subject's recognition of the auditory stimuli. Indeed, recognition requires a predictable response to a stimulus – typically a previously experienced and remembered stimulus (Mendelson *et al.*, 2016). Below we review the literature to identify the role of previous experience in neural responses to species-specific stimuli.

(1) Auditory experience with conspecifics

The plasticity of neural responses to species-specific sounds demonstrates that discrimination in the auditory forebrain is not merely a sensory or auditory response, but rather that the neural processing of stimuli is based on the relevance of the auditory signal to the receiver. In the short-term, neurons habituate to repeated exposure to the same stimuli as each repeated presentation provides less information, such that repeated presentations of heterospecific songs cause neurons within the auditory forebrain to habituate much more rapidly compared to repeated exposure to conspecific songs (Smulders & Jarvis, 2013). Heterospecific-induced cellular habituation also lasts for a shorter duration (Chew *et al.*, 1995, 1996). After experience with conspecific tutors, a small subset of NCM neurons exhibit highly selective auditory responses to the tutor song, but not to songs of other conspecifics or heterospecifics (Yanagihara & Yazaki-Sugiyama, 2016). These findings are consistent with a pattern that perceptual filters developed during ontogenetic exposure to conspecific vocalizations mediate short-term habituation responses.

Social experiences with conspecifics can dramatically influence long-term preferences for conspecific sounds. For many so-called 'closed-ended' or 'age-limited learning' species, auditory learning generally occurs during a relatively brief period early in life (Brenowitz & Beecher, 2005). For example, in superb fairy-wrens (*Malurus cyaneus*), embryos are exposed to and learn maternal incubation calls and incorporate these calls into their begging calls upon

hatching (Colombelli-Négrel *et al.*, 2012). Juvenile zebra finches, which are fed by their parents until ~30 days post-hatching, already exhibit neural selectivity within the NCM for conspecific sounds as early as post-hatch day 20 (Stripling, Kruse & Clayton, 2001). However, at this age, baseline *ZENK* expression is constitutively high within the NCM, such that there are no detectable differences between conspecific and silent control treatments (Stripling *et al.*, 2001). The period of high overall expression of *ZENK*, and other song-responsive genes (London *et al.*, 2009), observed in young birds may represent the sensitive period for learning, where selectivity for vocalizations remains relatively indiscriminate, followed by the fine-tuning of an auditory recognition system. Accordingly, the electrophysiological rate of habituation in juveniles was notably lower than in adults (Stripling *et al.*, 2001). As baseline expression of *ZENK* declines, differential expression of conspecific *versus* heterospecific sounds begins to develop by day 30 (Stripling *et al.*, 2001; Bailey & Wade, 2003). Therefore, as the sensitive period closes and existing memories become stabilized, low baseline *ZENK* expression in adults potentially represents a limitation of synaptic modification in response to novel salient contexts (Clayton, 2000). Some bird species are capable of learning to produce new songs prior to each reproductive season or at any point during their life, known as 'open-ended learners' (Brenowitz & Beecher, 2005). Although early experiences can influence behavioural conspecific preferences in some open-ended learners (Nagle & Kreutzer, 1997), how early-life experiences influence auditory species recognition in these taxa remains unclear.

There is some evidence that the development of auditory species recognition differs between the sexes, much as there is sex dimorphism in the development of song production between the sexes in species where females also sing (Yamaguchi, 2001). At day 30, male zebra finches show conspecific selectivity for ZENK-positive cells within the NCM, CMM, and HP (Bailey & Wade, 2003). However, densities of FOS-immunoreactive neurons are similar in response to conspecific and heterospecific songs in males (Bailey & Wade, 2003). Yet, this pattern is reversed in day 30 females where the densities of FOS-positive neurons, but not ZENK, are increased for conspecific *versus* heterospecific songs (Bailey & Wade, 2003). These sex-specific differences for *FOS* and *ZENK* induction are not observed by post-hatch day 45 (Bailey & Wade, 2005). Furthermore, female, but not male, California and Gambel's quail had greater conspecific call-based induction of *ZENK* (Gee *et al.*, 2009). The rearing of California and Gambel's quail, which have non-learned vocalizations, in a mixed-species flock did not affect the neural responses to conspecific *versus* heterospecific vocalizations (Gee *et al.*, 2009).

(2) Species-specific predispositions for conspecific vocalizations

Behavioural preferences for conspecific sounds often appear independent of prior experience with conspecific vocalizations (Wheatcroft & Qvarnström, 2015). Several studies have found conspecific-induced neural activity in birds raised in isolation from particular conspecific vocalizations. Female zebra finches that lacked exposure to male songs have greater neural firing rates in Field L for conspecific male songs *versus* the songs of closely related

heterospecifics (Hauber *et al.*, 2013) and greater *ZENK* induction in the auditory forebrain (Diez, Cui & MacDougall-Shackleton, 2018). Field L neurons also fire specifically to silent intervals within the zebra finch song, regardless of whether zebra finches were raised with conspecifics, heterospecifics (Bengalese finch), or in isolation (Araki, Bandi & Yazaki-Sugiyama, 2016). Male zebra finches produce typical gaps within their song even after being raised with heterospecifics or in isolation (Araki *et al.*, 2016). Some neurons in the HVC of white-crowned sparrows were found to respond preferentially to segments of conspecific song, such as whistles or trills, regardless of rearing with conspecifics or in isolation (Whaling *et al.*, 1997). Chickens (*Gallus gallus domesticus*) and Japanese quail (*Coturnix japonica*) reared without experience with conspecific vocalizations exhibited greater *ZENK* induction across the whole brain in response to conspecific *versus* heterospecific calls, but not statistically so in any specific region (Long *et al.*, 2002). Predispositions for conspecific vocalizations were further demonstrated to mediate behavioural preferences by transplanting developing neural tubes between quails and chickens (Long, Kennedy & Balaban, 2001). Quail chimeras with chicken neural structures behaviorally preferred chicken vocalizations and *vice versa*, clearly demonstrating that neural structures mediate predispositions for conspecific sounds (Long *et al.*, 2001).

Predispositions for conspecific sounds may also depend on early auditory experiences. Female zebra finches tutored by isolated song did not exhibit conspecific selectivity when comparing wild-type *versus* heterospecific song, but rather displayed increased *ZENK* responses to the particular songs they were tutored with (Diez *et al.*, 2018). By contrast, female zebra

finches raised without exposure to any male songs show behavioural preferences for (Braaten & Reynolds, 1999) and consistently greater neuronal spike rates to conspecific over heterospecific songs (Hauber *et al.*, 2013).

(3) Molecular modulation of conspecific selectivity

Chemical messengers such as neuromodulators exert broad influences on social decisions, and therefore are predicted to play a significant role in the processing of species-specific sounds. Hypothalamic and mesolimbic reward systems synthesise and release neuromodulators that target sensory systems as well as cognitive and motivational processes. Well-known neuromodulators of the avian auditory forebrain include catecholamines (norepinephrine and dopamine) as well as steroids such as oestradiol (Maney, 2013). Norepinephrine plays a significant neuromodulatory role during the reception of conspecific *versus* heterospecifc songs in female canaries (Lynch & Ball, 2008) and starlings (Pawlisch, Stevenson & Riters, 2011). Within the NCM, norepinephrine enhances auditory detection and coding accuracy of individual neurons for conspecific, but not heterospecific sounds (Ikeda *et al.*, 2015). Thus, not only do these neuromodulators have a robust influence on components of reproduction decision-making such as sexual motivation and cognitive processes such as attention, arousal and memory, they also have a profound effect on sensory processing, especially in auditory forebrain regions (Maney, 2013). Similarly, the steroid hormone oestradiol serves a necessary role in auditory processing and memory formation of conspecific, but not heterospecific songs (Yoder, Lu &

Vicario, 2012; Yoder *et al.*, 2015). Oestradiol increases spike rates for conspecific, but not heterospecific, song exposure in male zebra finches (Remage-Healey *et al.*, 2010) and induces detectable differences in conspecific-selective brain responses in female house sparrow *Passer domesticus* (Lattin *et al.*, 2017). By targeting brain regions in the social decision-making network (O'Connell & Hofmann, 2012), as well as sensory regions, these hormones and neuromodulators transform passive listeners into active responders that are able to minimize errors in their responses to signals.

Conspecific sounds have an incentive salience, and this increases during the breeding season when preference for conspecific vocalizations is both rewarding and adaptive for breeding success. In turn, seasonal increases in steroids may modulate the incentive salience of conspecific vocalizations by upregulating monoamine synthesis (reviewed in Brenowitz & Remage-Healey, 2016). Birds often increase their song production during the breeding season in order to attract mates and defend territories, so many studies have examined the influence of seasonality on modulation of species selectivity. For example, during the breeding season, black-capped chickadees showed conspecific selectivity for *ZENK* induction in the NCM, but this disappeared during the non-breeding season (Phillmore, Veysey & Roach, 2011).

Through endocrine mechanisms stress early in life can also impact selectivity for conspecific vocalizations during adulthood. Female song sparrows (*Melospiza melodia*) that received food-restricted or corticosterone treatments did not show species-specific *ZENK* induction in the auditory forebrain upon exposure to conspecific and heterospecific songs

(Schmidt *et al.*, 2013). Similarly, female European starlings that were subjected to reductions in food availability for the first few months of life displayed muted behavioural preferences and ZENK expression for conspecific *versus* heterospecific songs as compared to the control treatment (Farrell *et al.*, 2015).

(4) Auditory experience with heterospecifics

Many environmental sounds provide little valuable information to the receiver. To process the barrage of irrelevant sounds efficiently, auditory neurons can be inhibited or suppressed *via* sensory gating (Cromwell *et al.*, 2008). Whether sensory gating is used in the auditory forebrain in response to heterospecific stimuli (Hoke, Ryan & Wilczynski, 2010) remains unclear. A comparison of neurotranscriptomic responses in female zebra finches indicated that different neural mechanisms are induced upon hearing either conspecific or Bengalese finch songs (Louder, Hauber & Balakrishnan, 2018). At least one gene known to be associated with sensory gating, the alpha 3 subunit member of nicotinic cholinergic receptors (*CHRNA3*), was differentially expressed in response to hearing Bengalese finch song (Louder *et al.*, 2018). By contrast, birds raised experimentally with Bengalese finch male tutors did not exhibit the down-regulation of *CHRNA3* (Louder *et al.*, 2018). This suggests that the reduced neural responses typically observed from heterospecific stimuli are a result of inhibition in the auditory forebrain, rather than a lack of excitation.

However, not all sounds produced by heterospecifics are irrelevant. Valuable information can be gleaned from heterospecific signals, such as predator identity and foraging locations; indeed, some heterospecific mobbing calls are learned by other species (Magrath *et al.*, 2015). Both conspecific and heterospecific songs were found to induce reproductive development (follicular growth) in canaries, suggesting that songs of other distantly related species (song sparrow) may signal the onset of the breeding season (Bentley *et al.*, 2000). In song-mimetic species, males sing complex songs that are made up of heterospecific songs, yet females correctly choose conspecifics, rather than mimics as mates (Eda-Fujiwara, Satoh & Miyamoto, 2006). Therefore, neural responses to auditory stimuli can represent biological relevance, regardless of the species producing the sound. *ZENK* expression in the CMM and NCM of two closely related species, black-capped chickadee and mountain chickadee (*Poecile gambeli*), was similar in response to calls of the predatory saw-whet owl (*Aegolius acadicus*) and to saw-whet owl-specific referential alarm calls of conspecific and heterospecific chickadees (Avey *et al.*, 2011). Interestingly, *ZENK* expression was also greater in response to saw-whet owl calls *versus* vocalizations of the predatory great-horned owl (*Bubo virginianus*), although the latter is a species considered 'non-threatening' as its typical prey items are much larger than chickadees (Avey *et al.*, 2011). Furthermore, the chickadees' response patterns appear to be experience-dependent, as hand-reared birds that lacked experience with the predatory saw-whet owls had significantly less *ZENK* expression in response to the owl calls when compared to wild-sourced, and presumably predator-exposed, birds (Avey *et al.*, 2011).

Exposure to heterospecifics during sensitive periods can clearly impact behavioural and neural responses. Juvenile birds experimentally cross-fostered into the care of other species tend to adopt the behaviours and mate-choice preferences of their foster parents. This mis-imprinting on the heterospecific phenotype demonstrates that many of the salient auditory features are learned early in life. Female zebra finches raised with Bengalese finches as foster parents exhibited similar spike rates in Field L neurons for unfamiliar songs of the foster species as in conspecifics, but lower in response to unfamiliar Parson's finch song, a different heterospecific species unfamiliar in the captive setting (Hauber *et al.*, 2013). Similarly, the spike-pattern-based information-coding capacity of single field L neurons was shown to be different between control and cross-fostered male zebra finches in response to unfamiliar conspecific over heterospecific songs (Woolley *et al.*, 2010). *ZENK* expression in response to conspecific calls for black-capped chickadees reared with heterospecifics was intermediate between birds reared with conspecifics and birds reared in isolation (Hahn *et al.*, 2015). This demonstrates that experience with conspecific adults (or adult vocalizations) is important for neuronal activation, but experience with heterospecific adults (or adult vocalizations) can also lead to increased activation relative to social isolation (Hahn *et al.*, 2015).

V. CATEGORIZATION OF SPECIES-SPECIFIC SOUNDS

Although extensive behavioural evidence exists for auditory species recognition and preferences for conspecific vocalizations, it remains unclear whether such auditory signals are

categorically recognized and/or classified by the sensory and central nervous system (Mendelson & Shaw, 2012). Various avian species can show clear behavioural evidence of categorization of conspecific *versus* unfamiliar heterospecific sounds (Dooling *et al.*, 1992); it is plausible that conspecific vocalizations are recognized as a categorically distinct class in the brains of birds (Hausberger & Cousillas, 1995). Alternatively, organisms may either only recognize and respond to phenotypes, and not conceptualize groups of individuals, or recognize conspecifics as a subset of mate and other social-choice-relevant decisions (Mendelson & Shaw, 2012).

To be clear, categorization, in which a subject assigns two or more stimuli to a common set differs from categorical perception, or the perception of distinct categories from a trait that varies along a continuum. For example, male swamp sparrows appear to categorically perceive components of a continuously variable conspecific song (Nelson & Marler, 1989). This is reflected in their neuronal responses, which exhibit distinct changes along the variation in note duration (Prather *et al.*, 2009).

Studies of the avian auditory system in response to conspecific *versus* heterospecific stimuli support a conceptual construct model for auditory species recognition rather than recognition as a subset of mate and other social-choice-relevant decisions (*sensu* Mendelson & Shaw, 2012). Our review demonstrates that birds predictably exhibit discriminatory neural responses towards conspecific over heterospecific stimuli, even without prior experience with conspecifics. Conspecific-selective neural activation is observed for both learned and non-learned vocalizations, between and within sexes, and throughout ontogeny. Neural activity is

modulated by the perceived salience of the sound, in which auditory relevance reflects the individual experiences (e.g. sensitive periods, recent exposure to individuals) and evolutionary properties (preexisting biases). Furthermore, unfamiliar conspecific sounds almost always induce greater neural responses relative to unfamiliar heterospecific sounds, especially in the primary and secondary auditory regions rather than in the sensory-motor nuclei (Table 1).

Taken together, birds appear to engage a conceptual construct for categorizing conspecific *versus* heterospecific vocalizations, shaped by predispositions of their own species vocalizations that is further built upon using recent and ontogenetic experiences (Fig. 1). This is evidenced by predictable behavioural and neural responses to conspecific vocalizations, including to novel stimuli of their own species. Furthermore, behavioural and neural responses to salient heterospecific sounds indicate that the conceptual-construct model for auditory species recognition extends beyond conspecific sounds and encompasses other sensory modalities. Thus, the available evidence supports a conceptual auditory species recognition model, such that different types of conspecific sounds are initially preferred, categorically recognized through additional experience, and ultimately grouped based on shared stimulus-class properties.

VI. FUTURE DIRECTIONS: HYPOTHESES AND THEIR PREDICTIONS

The studies reviewed here represent foundational work for developing further studies, experiments, and theory in avian acoustic processing and species recognition research. Below we

discuss three hypotheses, and their testable predictions, regarding the neural concept of species recognition.

(1) Stimuli from different modalities are integrated into a species-specific neural representation

Humans perceive objects *via* multiple interacting sensory modalities, and one sensory modality (e.g. auditory) may even trigger another (e.g. visual) in a mental representation (reviewed in Nanay, 2017). Yet it remains unclear whether non-human organisms merely respond to phenotypes, failing to integrate different traits and sensory modalities to conceptualize groups of individuals (Mendelson & Shaw, 2012). Our review of avian auditory species recognition supports the species-based categorization of different classes of vocalizations, and we predict that birds and other taxa may also integrate visual, olfactory and tactile cues into a species-specific neural construct. Although this will be difficult to test, experimental multimodal stimulus presentations in fMRI, and cross-modal recognition paradigms will be suitable to determine whether multiple sensory modalities interact to form neural representations of conspecifics in non-human animals.

(2) Species-specific passwords induce neural plasticity and auditory imprinting

Our review demonstrates that neural selectivity is biased towards conspecific auditory sounds, irrespective of auditory experience. However, it remains unclear how non-learned

predispositions interact with auditory learning. Brood-parasitic birds, which lay their eggs in the nests of other species and are raised in the absence of social experience with conspecifics, are illustrative of an interaction between auditory experience and predispositions (Hauber *et al*., 2001). As in other songbirds, the development of male courtship song displays for brood-parasitic songbird lineages such as the cowbirds (*Molothrus* spp.) and parasitic finches (*Vidua* spp.) are largely experience-dependent (King & West, 1983; Payne, Payne & Woods, 1998). The brood-parasitic pin-tailed whydah (*Vidua macroura*) is closely related to the estrildid lineage of non-parasitic finches that includes zebra finches, and shares with them neuroanatomical substrates of conspecific selectivity in the auditory forebrain as measured by fMRI and *ZENK* mRNA expression (Louder *et al.*, 2016). How then do brood parasites avoid mis-imprinting on heterospecifics, and recognize their own species-specific songs? It is possible that the sensitive period for auditory learning is delayed until brood parasites join social groups (O'Loghlen & Rothstein, 1993; Brenowitz & Beecher, 2005). However, this does not explain how the bird recognizes the conspecifics in the first place. Thus, predispositions for conspecific auditory signals are likely to initiate species recognition in brood parasites (Hauber *et al.*, 2001). In cowbirds, evidence points to the female chatter call as the specific cue for conspecific recognition (the password hypothesis: Hauber *et al.*, 2001; Lynch *et al.*, 2017). We predict that the chatter call not only serves as a cue for species recognition in cowbirds, but also directly mediates subsequent motor and perceptual learning of additional male vocalizations. Following the password hypothesis, upon hearing the chatter call, the auditory forebrain of young cowbirds

would enter a state of enhanced neural plasticity, facilitating auditory learning and potentially vocal learning in males. Finally, we predict that the use of passwords and other, lock-and-key type, mechanisms for the activation of sensitive-period-based learning, was co-opted from ancestral taxa which displayed predispositions for components of conspecific vocalizations, such as the introductory whistle in the white-crowned sparrow (Whaling *et al.*, 1997) and golden-crowned sparrow (*Zonotrichia atricapilla*) (Hudson & Shizuka, 2017).

(3) Species-specific predispositions can evolve from experience-dependent neural selectivity

Predispositions for conspecific vocalizations play an important role in the production and perception of avian conspecific vocalizations (Marler, 1997; Wheatcroft & Qvarnström, 2015). How predispositions for conspecific stimuli evolve remains unknown. Genomic mutations may change the neural substrates, resulting in altered preexisting biases. Alternatively, predispositions could theoretically evolve through the genomic canalization of experience-dependent preferences (Robinson & Barron, 2017). Following the 'plasticity-first hypothesis' (reviewed in Levis & Pfennig, 2016), preferences for a vocalization that increases fitness could be favoured *via* natural selection to transfer from a dependence on learning of the preference to experience-independent mechanisms. Given that epigenetic processes, such as DNA methylation, histone modification, and non-coding RNA, facilitate neural plasticity by changing gene regulation and not DNA sequences, it is possible that evolutionary changes in predispositions are a result of modifications in epigenetic mechanisms (Robinson & Barron, 2017). However, the molecular mechanisms for

transgenerational epigenetic inheritance remain unclear (Bohacek & Mansuy, 2017). A comparison of DNA methylation sites that putatively regulate androgen receptor expression were correlated with differences in singing complexity between domesticated and wild populations of Bengalese finch (Wada *et al.*, 2013). Although this study illustrates the potential association between methylation and behavioural evolution in songbirds, it remains unclear whether experience-dependent processes were involved with the putative epigenetic-mediated evolution. Thus, similar comparisons of epigenetics and gene expression between populations or species that differ in plasticity of conspecific preferences would help to advance understanding of how auditory predispositions evolve.

VII. CONCLUSIONS

(1) Irrespective of the research techniques used, the avian auditory forebrain generally discriminates conspecific from heterospecific auditory signals.

(2) Neural discrimination of conspecific stimuli is modulated according to its salience. Genetic predispositions and social experience, including ontogenetic exposure to conspecifics, combine to influence the neural processing of auditory stimuli.

(3) Neuromodulators, and in particular norepinephrine, may mediate species recognition by regulating the accuracy of neuronal coding for salient conspecific stimuli.

(4) Most heterospecific sounds are relatively unimportant, and likely filtered in the brain *via* sensory gating. Salient heterospecific sounds, as determined by exposure to predators or heterospecific tutors during ontogeny, are recognized in the auditory forebrain.

(5) Neural activation for salient signals, despite the highly variable physical properties of species-specific vocalizations, demonstrates that birds categorically recognize sounds.

(6) Our review highlights how avian species recognition represents a powerful system to understand the mechanisms of perceptual filters that bias attention towards salient vocalizations (Fig. 1). Furthermore, our review contributes to understanding the general mechanisms of the ability of the vertebrate nervous system to recognize and encode complex auditory objects; which remains a largely unresolved question in neuroscience.

VIII. ACKNOWLEDGEMENTS

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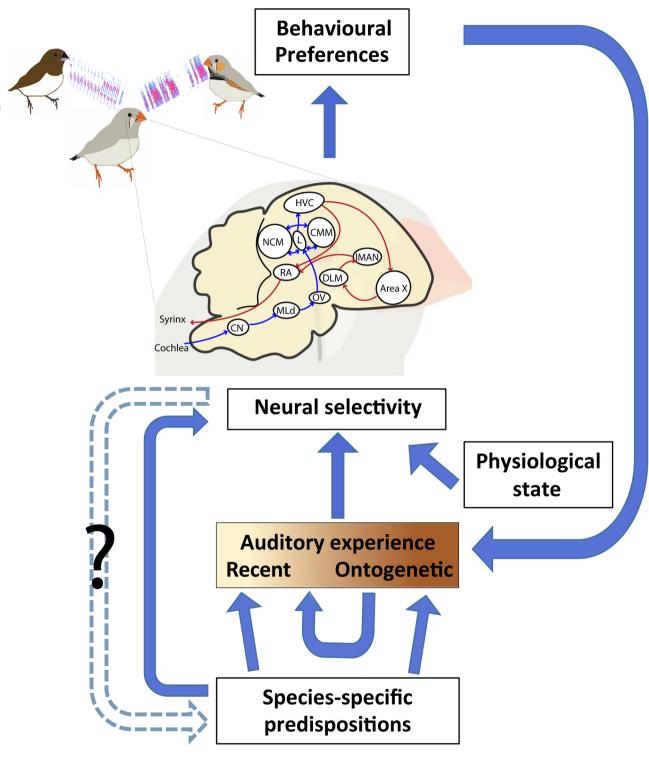
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Figure Legend

Fig. 1. A conceptual diagram that depicts influences on auditory species recognition *via* neural selectivity in the auditory forebrain. We use an oscine, song-learner's brain to depict both auditory (blue lines) and vocal-motor (red lines) neural pathways. Conspecific and heterospecific sounds are processed in the auditory forebrain, in which neural selectivity is determined by the physiological state (e.g. breeding condition, stress), non-learned biases for specific auditory stimuli (species-specific predispositions), and past auditory experiences (recent and during ontogeny). In turn, the behavioural preferences (e.g. tutor learning, mate choice) affect the auditory experiences of the individual. Experience-dependent neural selectivity may evolve into species-specific predispositions following the plasticity-first evolution hypothesis (*via* epigenetic mechanisms). CMM, caudomedial mesopallium; CN, cochlear nucleus; DLM, dorsal lateral nucleus of the medial thalamus; HVC, high vocal centre; L, Field L; lMAN, lateral portion of the magnocellular nucleus of the anterior nidopallium; MLd, lateral mesencephalic nucleus; NCM, caudomedial nidopallium; OV, ovoidalis; RA, robust nucleus of the arcopallium.

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Table 1. Summary of avian studies that compare neural responses between conspecific *versus* heterospecific vocalizations. Studies with one or more significant differences in neural response selectivity for conspecific *versus* heterospecific stimuli are identified in the conspecific selectivity column. Altricial species (development column) are abbreviated as (A) and precocial species as (P); fMRI, functional magnetic resonance imaging; IEG, immediate early gene; PET, positron emission tomography; RNA-seq, RNA sequencing. Brain areas are abbreviated as: CMM, caudomedial mesopallium; HP, hippocampus; HVC, high vocal centre; ICo, nucleus intercollicularis; lMAN, lateral portion of the magnocellular nucleus of the anterior nidopallium; MLd, lateral mesencephalic nucleus; MSt, medial striatum; NCM, caudomedial nidopallium; RA, robust nucleus of the arcopallium; TnA = nucleus taeniae of the amygdala.

Species name	Vocal learner (development)	Experience/source	Sex	Method	Heterospecific stimuli	Regions	Conspecific selectivity	Reference
Bengalese finch (*Lonchura striata domestica*)	Yes (A)	Captive colony	Both	Electrophysiology	Zebra finch	TnA	No	Fujii *et al.* (2016)
Black-capped chickadee (*Poecile atricapillus*)	Yes (A)	Wild	Male	IEGs (immunohistochemistry)	Chestnut-backed chickadee, tufted titmouse, zebra finch	NCM; CMM	No	Avey *et al.* (2014)
Black-capped chickadee (*Poecile atricapillus*)	Yes (A)	Wild	Male	IEGs (immunohistochemistry)	Song sparrow	NCM; CMM	Yes	Phillmore *et al.* (2011)
Black-capped chickadee (*Poecile atricapillus*);	Yes (A)	Wild, hand-raised	Both	IEGs (immunohistochemistry)	Mountain chickadee, saw-whet owl, great-	NCM; CMM	Yes	Avey *et al.* (2011)

					horned owl, red-breasted nuthatch, black-capped chickadee			
mountain chickadee (*P. gambeli*)								
Brown-headed cowbird (*Molothrus ater*)	Yes (A)	Wild	Male	IEGs (immunohistochemistry)	Mourning dove	NCM; CMM	Yes	Lynch *et al.* (2017)
Brown-headed cowbird (*Molothrus ater*)	Yes (A)	Wild	Both	Lesioning	American redstart, Bell's vireo, yellow warbler, song sparrow, red-winged blackbird, barn swallow	HVC	Yes	Maguire *et al.* (2013)
California quail (*Callipepla californica*); Gambel's quail (*C. gambelii*)	No (P)	Commercial, isolation	Both	IEGs (immunohistochemistry)	Gambel's quail; California quail	Auditory forebrain; MLd, TnA, Ico	Yes	Gee *et al.* (2009)
Canary (*Serinus canaria domestica*)	Yes (A)	Captive colony	Female	Lesioning	White-crowned sparrow	HVC	Yes	Brenowitz (1991)
Canary (*Serinus canaria domestica*)	Yes (A)	Captive colony	Female	Lesioning	Song sparrow	lMAN	Yes	Burt *et al.* (2000)
Canary (*Serinus canaria domestica*)	Yes (A)	Captive colony	Female	Lesioning	Greenfinch	HVC	Yes	Del Negro *et al.* (1998)
Canary (*Serinus canaria domestica*)	Yes (A)	Commercial	Female	IEGs (immunohistochemistry)	Cassin's finch	NCM; CMM	Yes	Lynch & Ball (2008)
Chicken (*Gallus gallus domesticus*); Japanese quail	No (P)	Isolation	Both	Neural transplant	Japanese quail; chicken	Midbrain; diencephalon; forebrain	Yes	Long *et al.* (2001)

(*Coturnix coturnix japonica*)								
Chicken (*Gallus gallus domesticus*); Japanese quail (*Coturnix coturnix japonica*)	No (P)	Isolation	Both	IEGs (*in situ* hybridization)	Japanese quail; chicken	Whole brain	Yes	Long *et al.* (2002)
European starling (*Sturnus vulgaris*)	Yes (A)	Wild	Female	IEGs (immunohistochemistry)	Canary	NCM; CMM	Yes	Farrell *et al.* (2015)
European starling (*Sturnus vulgaris*)	Yes (A)	Wild	Female	Infusion	Purple martin	Whole brain	Yes	Pawlisch *et al.* (2011)
House finch (*Haemorhous mexicanus*)	Yes (A)	Wild	Female	IEGs (immunohistochemistry)	White-crowned sparrow	NCM; CMM	Yes	Hernandez *et al.* (2004)
House sparrow (*Passer domesticus*)	Yes (A)	Wild	Female	PET	White-throated sparrow	Whole brain	Yes	Lattin *et al.* (2017)
Pin-tailed whydah (*Vidua macroura*)	Yes (A)	Commercial	Both	fMRI; IEGs (*in situ* hybridization)	Zebra finch	NCM; CMM	Yes	Louder *et al.* (2016)
Red-winged Blackbird (*Agelaius phoeniceus*)	Yes (A)	Wild	Male	IEGs (immunohistochemistry)	Brown-headed cowbird, mourning dove	NCM; CMM	Yes	Lynch *et al.* (2018)
Ring dove (*Streptopelia risoria*)	No (A)	Commercial	Female	IEGs (immunohistochemistry)	Zebra finch	NCM; CMM; HP	No	Terpstra *et al.* (2005)
Song sparrow (*Melospiza melodia*)	Yes (A)	Wild	Female	IEGs (immunohistochemistry)	White-crowned sparrow	NCM; CMM	Yes	Schmidt *et al.* (2013)

Swamp sparrow (*Melospiza georgiana*)	Yes (A)	Wild	Male	Electrophysiology	Song sparrow	HVC	Yes	Mooney *et al.* (2001)
White-crowned Sparrow (*Zonotrichia leucophrys*)	Yes (A)	Wild, hand-raised	Both	Electrophysiology	Song sparrow	HVC; neostriatum below HVC	No	Whaling *et al.* (1997)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony, cross-fostered	Male	Electrophysiology	Bengalese finch	Field L	Yes	Araki *et al.* (2016)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony	Both	IEGs (immunohistochemistry)	American robin, Baird's sparrow, Bell's vireo, Cassin's finch, Connecticut warbler, marsh wren, Scott's oriole, summer tanager, western meadowlark, white-breasted nuthatch	NCM; CMM; HP	Yes	Bailey & Wade (2003)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony	Both	IEGs (immunohistochemistry)	American robin, Baird's sparrow, Bell's vireo, Cassin's finch, Connecticut warbler, marsh wren, Scott's oriole, summer tanager, western meadowlark, white-breasted nuthatch	NCM; CMM; HP	Yes	Bailey & Wade (2005)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony	Male	IEGs (immunohistochemistry)	American robin, Baird's sparrow, Bell's vireo, Cassin's finch, Connecticut warbler, marsh	Area X, MSt	Yes	Bailey & Wade (2006)

					wren, Scott's oriole, summer tanager, western meadowlark, white-breasted nuthatch			
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony	Male	Electrophysiology	Canary	NCM	Yes	Chew *et al.* (1995)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony	Both	Electrophysiology	Bengalese finch, canary, silverbill, human	NCM	Yes	Chew *et al.* (1996)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony, cross-fostered, isolation	Female	IEGs (immunohistochemistry)	Bengalese finch	NCM; CMM	Yes	Diez *et al.* (2018)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony, cross-fostered, isolation	Female	Electrophysiology	Bengalese finch, Parson's finch	Field L	Yes	Hauber *et al.* (2013)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony	Female	Electrophysiology	Bengalese finch	NCM	Yes	Ikeda *et al.* (2015)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony	Female	RNA-seq	Bengalese finch	Auditory forebrain	Yes	Louder *et al.* (2018)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony	Female	Lesioning	European nightingale	HVC; CMM	Yes	MacDougall-Shackleton *et al.* (1998)
Zebra finch (*Taeniopygia guttata*); canary (*Serinus canaria*	Yes (A)	Commercial	Male	IEGs (*in situ* hybridization)	Canary; zebra finch	NCM; CMM	Yes	Mello *et al.* (1992)

domestica)

Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony, cross-fostered	Male	Electrophysiology	Bengalese finch	HVC	No	Nick & Konishi (2005)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony	Male	fMRI	Canary, European starling	HVC, RA, Area X, lMAN, MLd, Field L, CMM, NCM	Yes	Poirier *et al.* (2009)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony	Male	Electrophysiology	Bengalese finch	NCM	No	Remage-Healey *et al.* (2010)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony, song-playback tutored	Both (embryos)	IEGs (*in situ* hybridization)	Bengalese finch, pin-tailed whydah	Auditory forebrain	No	Rivera *et al*. (2019)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony	Male	Electrophysiology	Bengalese finch	lMAN	No	Rosen & Mooney (2000)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Commercial	Male	IEGs (immunohistochemistry)	Canary	HVC; Area X	Yes	Sakaguchi *et al.* (1999)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony	Male	Lesioning	Canary	Area X; lMAN	No	Scharff *et al*. (1998)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Commercial	Both	IEGs (immunohistochemistry)	Black-capped chickadee, tufted titmouse, American goldfinch	NCM; CMM	No	Scully *et al.* (2017)
Zebra finch (*Taeniopygia*	Yes (A)	Captive colony	Female	Electrophysiology	Bengalese finch	Field L; NCM; CMM	Yes	Smulders & Jarvis (2013)

guttata)

Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony	Male	Electrophysiology	Bengalese finch	Area X; lMAN	No	Solis & Doupe (1997)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony	Male	Electrophysiology	White-crowned sparrow	NCM	No	Stripling *et al*. (1997)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony	Both	Electrophysiology	White-crowned sparrow	NCM	Yes	Stripling *et al*. (2001)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony	Both	IEGs (*in situ* hybridization)	Canary	NCM; CMM	Yes	Velho *et al*. (2005)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Captive colony, song-playback	Male	Electrophysiology	Canary	NCM	Yes	Yang & Vicario (2015)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Commercial	Male	Electrophysiology	Canary	NCM	Yes	Yoder *et al*. (2012)
Zebra finch (*Taeniopygia guttata*)	Yes (A)	Isolation	Female	Electrophysiology	Canary	NCM	Yes	Yoder *et al*. (2015)
Zebra finch (*Taeniopygia guttata*)*;* Bengalese finch (*Lonchura striata domestica*)	Yes (A)	Captive colony, cross-fostered	Male	Electrophysiology	Bengalese finch; zebra finch	MLd; Field L	Yes	Woolley *et al*. (2010)

| Zebra finch (*Taeniopygia guttata*) | Yes (A) | Captive colony, cross-fostered | Male | Electrophysiology | Bengalese finch | NCM | Yes | Yanagihara & Yazaki-Sugiyama (2016) |