Shared neural substrates for song discrimination in parental and parasitic songbirds

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ABSTRACT

In many social animals, early exposure to conspecific stimuli is critical for the development of accurate species recognition. Obligate brood parasitic songbirds, however, forego parental care and young are raised by heterospecific hosts in the absence of conspecific stimuli. Having evolved from non-parasitic, parental ancestors, how brood parasites recognize their own species remains unclear. In parental songbirds (e.g. zebra finch *Taeniopygia guttata*), the primary and secondary auditory forebrain areas are known to be critical in the differential processing of conspecific vs. heterospecific songs. Here we demonstrate that the same auditory brain regions underlie song discrimination in adult brood parasitic pin-tailed whydahs (*Vidua macroura*), a close relative of the zebra finch lineage. Similar to zebra finches, whydahs showed stronger behavioral responses during conspecific vs heterospecific song and tone pips as well as increased neural responses within the auditory forebrain, as measured by both functional magnetic resonance imaging (fMRI) and by immediate early gene (IEG) expression. Given parallel behavioral and neuroanatomical patterns of song discrimination, our results suggest that the evolutionary transition to brood parasitism from parental songbirds likely involved an "evolutionary tinkering" of existing proximate mechanisms, rather than the wholesale reworking of the neural substrates of species recognition.

Key words: Auditory cortex; birdsong; brood parasite; oscines; species recognition; zebra finch

INTRODUCTION

The recognition of conspecifics (species recognition) is essential for diverse functions in animals, including flock formation, foraging, and sexual reproduction. For most social vertebrates, species recognition depends on early exposure to conspecific stimuli [15], where sensory perceptual systems engage in heightened levels of neural plasticity during sensitive periods that subsequently guide both neural response selectivity and behavioral decisions through adulthood [17]. Given the lasting effects of

experience-dependent plasticity on species recognition, it is unclear how associated neural circuits evolve to produce dramatically novel phenotypes [26].

For example, many of the vocalizations, behaviors, and mate choice decisions of songbirds are learned from conspecific referents (e.g. parents, siblings) early in ontogeny [2]. Obligate avian brood parasites, however, lay their eggs in the nests of heterospecifics and thus, juvenile parasites are typically raised without exposure to conspecific stimuli. This reproductive strategy has evolved within at least seven independent lineages in birds, including twice in songbirds, each time from a non-parasitic, parental ancestor [33]. Yet, whether the transition to a parasitic reproductive strategy was a result of relatively small changes ("evolutionary tinkering" [18]) or substantial physiological shifts remains largely unknown, as previous comparative work on brood parasite neurobiology has focused mostly on gross neuroanatomical differences associated with spatial information processing between parasitic and parental lineages of songbirds [29, 30].

In general, neurobiological research using a variety of methodologies including immediate early gene expression [25], electrophysiology [16], and functional magnetic resonance imaging [27], on parental songbirds including the model species zebra finch *Taeniopygia guttata*, finds the primary (field L) and secondary auditory forebrain regions (CMM (caudomedial mesopallium), and NCM (caudomedial nidopallium)) to be critical in the differential processing of auditory input from conspecific vs. heterospecific songs. Furthermore, non-parasitic songbirds raised by heterospecifics exhibit signatures of neural activation within the same telencephalic regions in response to heterospecific songs [12, 40], providing evidence for this region's involvement in auditory memory, retrieval, and species recognition [3]. While the auditory forebrain appears anatomically conserved among bird species, studies of some songbirds [1] and non-songbird species [35] were unable to identify signatures of differential neural activation within this region in response to conspecific vs. heterospecific vocalizations. This disparity in observed (lack of) neural responses may reflect functional variability among species.

Here we studied the pin-tailed whydah *Vidua macroura*, an obligate brood parasite and member of the sister family to parental estrildid finches (including zebra finches) to address whether the same auditory brain regions underlie song discrimination in brood parasites and parental songbirds. By comparing our novel data with published information on the zebra finch, we aimed to assess whether behavioral responses [6], patterns of neural activation [27], and immediate early gene expression [25] in response to conspecific vs. heterospecific song and synthetic pure tone stimuli are broadly conserved across parasitic and non-parasitic taxa.

METHODS

(a) Behavioral responses to auditory stimuli

Commercially sourced adult pin-tailed whydahs (n = 4 males, 4 females) were housed in the Hunter College Animal Facility in groups containing a male and female whydah with a pair (male and female) of zebra finches in each cage on a 12:12 L:D light cycle with food and water provided ad libitum.

For experimental playback sessions, two whydah subjects previously housed together (one male, one female) were moved to an observation cage (65“x21”x34” cage soundproofed with studio foam) in a separate room from the colony, and left to acclimate overnight. Cardboard visors as well as a curtain were installed on and around the cage to minimize potentially confounding visual input. Placement of food, water, and perches was symmetrical across the lengthwise midline to minimize side bias. The following morning, the two birds were presented with playback stimuli, comprising 4-second clips played every 15 seconds over a three minute period. The playback stimuli consisted of eight songs of different conspecifics, 8 songs of zebra finches, sourced from Macaulay Library (Cornell Lab of Ornithology, Ithaca, NY, USA), and synthetic pure tones designed to mimic the power-spectrum, amplitude and spectral modulation in zebra finch songs (tone pips, sourced directly from [13]). To eliminate background noise, songs were processed through a high-pass filter set to 500Hz using Raven software (Cornell University, Ithaca, NY, USA), and the peak amplitude was standardized using Audacity.

The playback volume was adjusted to be 74 dB SPL at 1.5m distance from the speaker, which was the same as the sound pressure measured in our captive colony at the same distance. The order of playback stimuli was randomly selected prior to experimental trials. Alternative playback trials were continued following a ten-minute silent period between presentations. Each three minute presentation was recorded with a wide-angle webcam for analysis. A behavior was defined by us based on an a priori criterion to be a "response" to the stimulus if it occurred during the four-second playback clip or within three seconds of its end. Response types recorded from both subjects were aerial turns (defined as an oppositional change of direction midflight), crosses (defined as crossing the length-wise midline of the cage), and vocalizations. Immediately following the conclusion of the experimental session, the pair was returned to their permanent housing and the experimental cage was cleaned and food and water replenished for the next male/female whydah pair. For statistical analyses, we performed repeated measures ANOVA for the vocalizations and movements (turns and crosses combined) of each individual and included song stimuli type and sex as explanatory variables. We used a Tukey adjustment for comparisons of responses among stimuli.

(b) Functional magnetic resonance imaging (fMRI)

Whydahs of either sex (n = 5 males, 4 females; the same individuals and housed as above) were placed in a 7.0 Tesla Avance III Biospec 70/30 USR small animal MRI system (Bruker Biospin MRI, Inc., Billerica, MA) equipped with a 12 cm diameter, 450 mT/m amplitude and 4500 T/m/s slew rate actively shielded gradient subsystem with integrated shim capability. A customized 20 mm diameter litzcage coil with holes at the position of the ears (Doty Scientific) was used for transmission and reception of the MR signal, as well as for head fixation. Birds were lightly anesthetized with Diazepam (0.05 ml) injected into the leg muscles, targeting a concentration of 7.5 mg/kg body weight [37, 38]. Birds were immobilized by wrapping them in soft tissue paper and placing them within plastic holders within a radiofrequency coil

and equipped with custom headphones to deliver song playback. The RF coil was placed in an RF shield (Doty Scientific) and the RF shield into a layer of acoustical rubber for sound isolation. To further reduce ambient scanner noise, the scanner's helium compressor was switched off during the auditory fMRI runs. A heated water circulated warming blanket was used to keep the bird's temperature as measured under the wing at approximately 39^{o} C. Respiration was monitored with a pneumatic pillow sensor under the bird. Both temperature and respiration trends were visualized during the experiments (Small Animal Instruments, Inc.).

Each run corresponded to eight repetitions of each of stimulus blocks (including eight different individuals' whydah songs and zebra finch songs, respectively, sourced as above), with each block containing eight samples of a 4 s stimulus each followed by six samples of 4 s of silence each. Therefore, each of the 24 blocks lasted 56 s. The order of the stimuli was quasi-randomized for each bird, ensuring that all transitions between stimuli occurred the same number of times.

After initial calibration and localizer scans for functional imaging, seven gradient echo EPI image slices of 1.1 mm thickness (including a gap of 0.1 mm between slices) were acquired sagittally with the fourth slice centered on the sagittal brain mid-plane. We used gradient-echo [4, 36] rather than spin-echo methods [27] due to its higher BOLD contrast-to-noise ratio [28]. The echo time was TE = 16 ms, the repeat time TR = 4 s, and the matrix size = 64 × 64, defining an in-plane spatial resolution of 0.22 × 0.27 mm (overall voxel size = 0.0594 mm^3). We obtained 336 volumes over the course of 22.4 minutes. The sound level was optimized during pilot experiments on zebra finches. Stimuli were played by Matlab. For anatomical reference, a high-resolution RARE scan was acquired, using the same slice prescription as the EPI scan.

Preprocessing was performed as follows: File conversion from DICOM to NIfTI-format with dcm2niigui, motion correction and spatial smoothing with a Gaussian kernel of full-width-half-maximum = 0.5 mm with AFNI [7]. A general linear model was defined with AFNI using the 3dDeconvolve

command applied to the preprocessed functional MRI data with a repeat time of 4 s, an orthogonal polynomial of degree eight for detrending, block design functions defined by 0's and 1's. Only mean intensity and volume blood oxygenation level dependent (BOLD) clusters located on or near the auditory forebrain (inclusive of field L, CMM, and NCM) were taken into account for statistical analysis and bird activation clusters was defined by using the 3dclust procedure of AFNI, with a threshold value of z = 3.5. This z-value corresponds to a p-value of $5*10^{-4}$ (uncorrected), which, depending on the activation, approximately corresponds to a false discovery rate of p(FDR) < 0.01 as determined by AFNI. Measurements were normalized by the average for each individual. We used repeated measures ANOVA to compare normalized volume and mean BOLD activation in response to song stimuli type with Tukey adjusted p-values for comparisons among stimuli.

(c) Immediate early gene expression (IEG)

Commercially sourced adult whydahs (a separate stock from above) were placed individually in sound attenuating chambers and kept overnight (as described in [21]). Speakers within each sound chamber were adjusted to ensure consistent sound pressure (~65 dB). After exposure (30 min) to conspecific (n = one male and one female subject) or heterospecific zebra finch (n = two male and one female subjects) song playback, individuals were sacrificed, and the left hemisphere extracted, flash frozen, sectioned to 12µm in a cryostat, and stored at −80°C until use. We performed in situ hybridization with ZENK (also known as: zif268, egr-1, ngfi-a, krox24) antisense riboprobes as described previously [22]. ZENK is an IEG known to be selectively responsive to conspecific song within the auditory forebrain and associated with neuroplasticity [25]. We used the zebra finch atlas (http://www.zebrafinchatlas.org) to locate known areas of the auditory forebrain, and quantified the number of labelled cells within the entire NCM and CM with ImageJ (http://imagej.nih.gov/ij/) and the binary threshold and ‘analyze particles’ functions to generate a density value for each subject and brain nucleus. We used an ANOVA to compare the mean

densities of ZENK expressing cells within CM and NCM (field L is known not to express ZENK [25]) between treatments.

RESULTS

(a) Behavioral response to auditory stimulus

Auditory stimuli significantly influenced vocal behaviors in adult whydahs (repeated ANOVA: $F_{2,12} = 7.36$, $p = 0.009$; Fig. 1b), where vocal responses were greater for conspecific song playback (mean = 6.23 ± 3.90 SE) vs. zebra finch (mean = 1.16 ± 2.03 SE) ($t = 3.02$, $p = 0.03$) and tone pips (mean = 1.91 ± 1.59 SE) ($t = 3.56$, $p = 0.01$). There was no statistical difference in vocal responses between zebra finch and tone pips ($t = 0.60$, $p = 0.86$). We did not observe a sex difference for vocal responses ($F_{1,6} = 1.19$, $p = 0.32$), or a significant effect of auditory stimuli on movement metrics ($F_{2,12} = 0.95$, $p = 0.41$).

(b) Functional magnetic resonance imaging (fMRI)

Within the auditory forebrain, we detected a significant effect of auditory stimuli on the normalized volume of BOLD activation (repeated ANOVA: $F_{2,14} = 13.72$, $p < 0.001$; Fig. 2b). There was a greater normalized volume of BOLD activation in response to conspecific song (mean = 1.55 ± 0.42 SE) vs. zebra finch (mean = 0.91 ± 0.43 SE) ($t = 3.28$, $p = 0.01$) and tone pips (mean = 0.53 ± 0.35 SE) ($t = 5.18$, $p < 0.001$). There was no statistical difference in the volume of BOLD activation among zebra finch and tone pips ($t = 1.90$, $p = 0.08$). The normalized mean intensity of bold activation was not significantly greater ($F_{2,14} = 1.71$, $p = 0.21$) in response to conspecific song (mean = 1.16 ± 0.19 SE) vs. zebra finch (mean = 0.95 ± 0.40 SE) or tone pips (mean = 0.88 ± 0.38 SE). Sex was not found to be a significant predictor for either response variable (both $p > 0.69$).

(c) Immediate early gene expression (IEG)

The type of auditory stimulus significantly influenced the densities of ZENK-expressing cells, in which the number of cells was significantly greater in conspecific (mean = 285.12 ± 30.06 SE) vs. heterospecific song (mean = 85.97 ± 10.65 SE) (ANOVA: $t = 5.94$, $p < 0.001$; Fig. 2d). No difference was detected between CMM and NCM ($t = 0.90$, $p = 0.40$).

DISCUSSION

Conspecific songs trigger greater behavioral responses and generate increased neural activity metrics relative to heterospecific songs, as tracked by BOLD levels and induction of ZENK, within the auditory forebrain of adult brood parasitic songbirds. These results are consistent with previous studies of the closely related, non-parasitic parental songbird, the zebra finch, in which the auditory forebrain has been found critical to the differential processing of auditory inputs from conspecific vs. heterospecific song using a variety of neural response metrics, including neurophysiology [16, 40] as well as the methods utilized in this study: ZENK [25] and fMRI [27].

A major challenge associated with brood parasitism is the need to avoid mis-imprinting on host song. Juvenile non-parasitic songbirds experimentally cross-fostered into heterospecific nests generally imprint on the foster parents; adopting the behaviors and mate choices preferences, including the production and preference of songs, from the foster species [34]. As an exception to this rule, species recognition in brood parasites was once considered completely innate [8]. More recent behavioral tests have revealed that vocalizations and mate choice decisions are driven by both predisposed biases and learning [9, 14, 32], as found in non-parasitic songbirds [39]. One possibility is that accommodating this developmental challenge in brood parasitic life histories required major alterations in neural processing, for example, as observed in vocal learning and non-learning bird groups [3, 19]. Our results, however, are suggestive of evolutionarily conserved higher-order processing within the auditory forebrain for parasitic songbirds.

Although our experiments were performed with adult brood parasites, our results indicate that relatively small changes within the existing auditory system contributed to a substantial behavioral adaptation. Therefore, selective pressures throughout the evolution of brood parasitism have likely resulted in modifications to existing neural architecture that enable parasites to avoid imprinting solely on the host's phenotype, while also recognizing conspecifics [11, 31]. Developmental delays in the onset of the sensitive periods for song learning until after conspecific flocking has begun, or the enhancement of innate predispositions for conspecific song (e.g. neural selectivity) could generate a stable mechanism for song-based species recognition with relatively minor changes to the auditory forebrain.

Our approaches here focused on the auditory forebrain and did not assess differential activation among additional nuclei within the auditory system or in other brain regions of the whydahs. Thus it is possible that other brain regions also contribute to song discrimination. For example, the sensorimotor nucleus HVC (proper name), may also contribute to song discrimination in the canary *Serinus canaria* [5], but see [24]. Likewise, the lateral dorsal mesencephalon (MLd) and nucleus ovoidalis (Ov), which provide ascending projections to the auditory forebrain, may also facilitate higher-order processing that enables conspecific song discrimination [27]. However, without further examination in parental songbirds for neurophysiological responses to conspecific song discrimination among nuclei within the primary auditory pathway, our hypotheses were restricted to the auditory forebrain.

Comparative investigations of conspecific song discrimination, as documented by ZENK expression in the auditory forebrain, have found widely contrasting responses between species. Where conspecific songs induce greater ZENK expression for zebra finches and canaries, black-capped chickadees, *Poecile atricapillus* did not differ in response to conspecific vs. heterospecific calls with similar acoustic characteristics [1]. Similarly, in non-songbird species, ZENK induction within the auditory forebrain has produced conflicting results: ring doves (*Streptopelia risoria*) had greater ZENK expression in conspecific calls vs. silence, but not vs. zebra finch songs [35]; conspecific calls induced greater ZENK

across the whole brain in domestic chickens (*Gallus gallus dom*.) and Japanese quails (*Coturnix coturnix jap*.), but not in any specific area [23]; and female, but not male, California and Gambel's quails (*Callipepla californica* and *C. gambelii*) exhibited greater ZENK expression within the NCM in response to conspecific vs. heterospecific calls [10]. Therefore, the variation in responses of the auditory forebrain may represent evolutionary differentiation in function. Although the study duration under light anesthesia (fMRI) and sample size considerations for destructive sampling (IEG) inhibited our ability to compare the responses of whydahs to numerous species' songs or the responses of other species to whydah songs, our use of eight different conspecific and heterospecific songs, as well as synthetic pure tones, provides robust support for the involvement of the auditory forebrain in the recognition of conspecific songs in pin-tailed whydahs. Further comparative studies of responses to conspecific vs. heterospecific vocalization will help elucidate the function of the auditory forebrain in songbirds, including the role of species recognition, auditory memory retrieval and song production.

Homologous neuroanatomical regions that are recognizable across taxa demonstrate that the songbird nervous system's functional architecture remains relatively conserved [19]. Yet, modifications to structure or function facilitate species-specific behavioral evolution [20]. Here we suggest that the auditory forebrain is functionally homologous among parental and parasitic songbirds. Therefore, the evolutionary transition from a parental reproductive strategy to brood parasitism for Viduid finches is consistent with changes to existing neural mechanisms–"evolutionary tinkering" [18]–rather than wholesale reworking of neural substrates for species recognition in songbirds.

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255 **FIGURE LEGENDS**

256 Figure 1. (a) Examples of spectrograms from songs of pin-tailed whydah (CON), zebra finch (HET) and
257 tone pips (TONE). (b) Individual adult female (grey) and male (black) whydah vocal responses to auditory
258 stimuli (within three seconds).

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261 Figure 2. (a) Anatomical scans (sagittal) depicting mean BOLD response to conspecific, heterospecific
262 song and tone pips from fMRI data within auditory forebrain for an adult whydah (color bar indicates
263 corresponding t values). (b) Individual adult female (grey) and male (black) BOLD response (normalized
264 volume in auditory forebrain) to conspecific and heterospecific songs and tone pips. (c) Examples of in
265 situ hybridization of ZENK from auditory forebrain sections of individuals exposed to conspecific or
266 heterospecific song. (d) Comparison of mean ZENK-expressing cell densities in NCM and CM of adult
267 whydahs exposed to conspecific (dark grey) or heterospecific song (light grey) playbacks (± SE).

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Figure 1

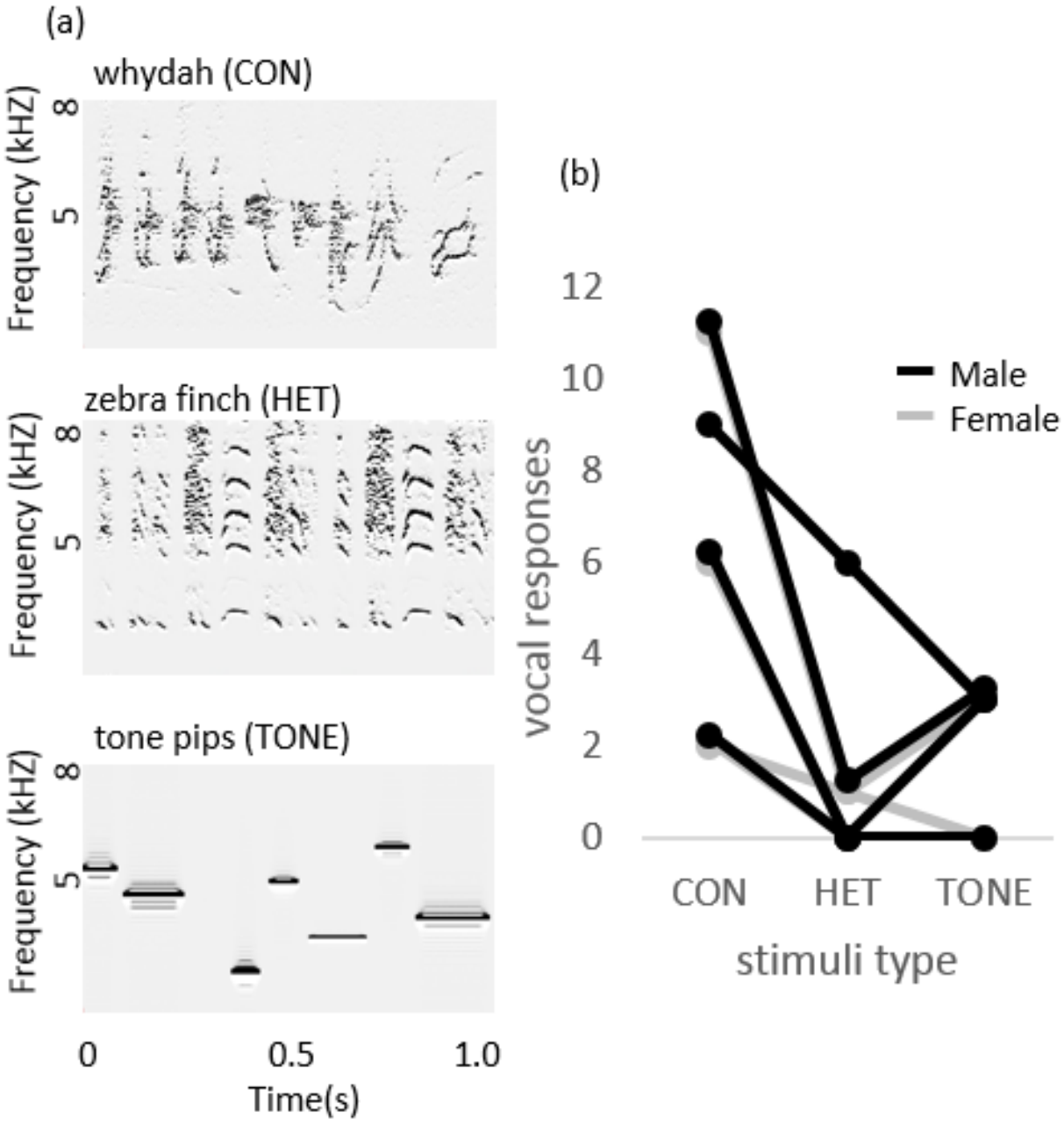
(a)
whydah (CON)
zebra finch (HET)
tone pips (TONE)
Frequency (kHZ)
8
5
0
0.5
1.0
Time(s)
(b)
vocal responses
12
10
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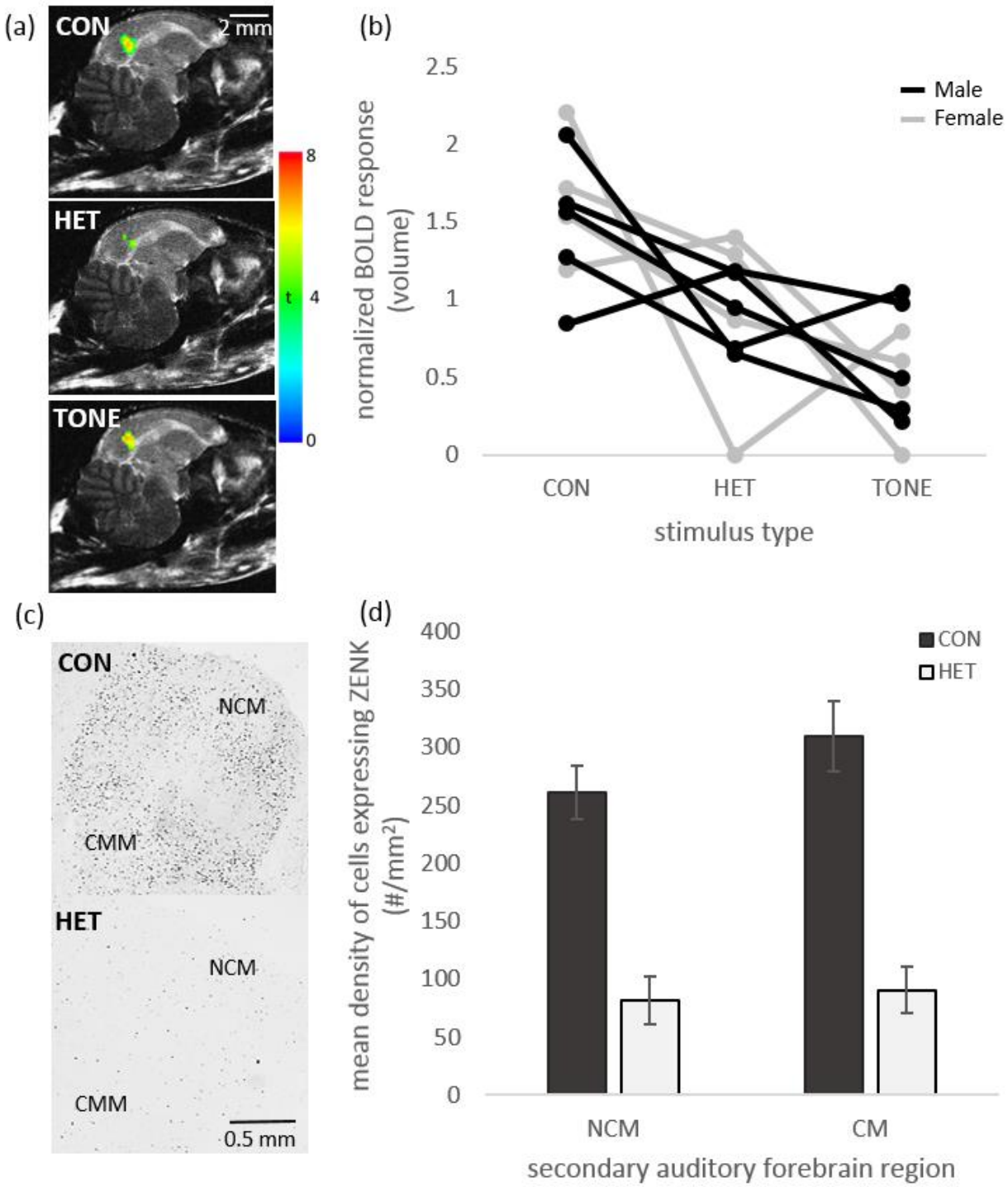
Figure 2


(a)
CON
2 mm
HET
TONE
8
t
4
0
(b)
normalized BOLD response (volume)
2.5
2
1.5
1
0.5
0
Male
Female
CON
HET
TONE
stimulus type
(c)
CON
NCM
CMM
HET
NCM
CMM
0.5 mm
(d)
mean density of cells expressing ZENK (#/mm²)
400
350
300
250
200
150
100
50
0
CON
HET
NCM
CM
secondary auditory forebrain region