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Research report

Dopaminergic neurons are preferentially responsive to advertisement calls and co-active with social behavior network nuclei in sneaker male midshipman fish

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HIGHLIGHTS

- TH-ir neurons in TPp and VM-VL are preferentially responsive to advertisement calls.
- No single brain region discriminates advertisement from agonistic vocalizations.
- Co-activation among TH-ir and SBN nuclei differ as a function of acoustic treatment.

ARTICLE INFO

ABSTRACT

Vocal species use acoustic signals to facilitate diverse behaviors such as mate attraction and territorial defense. However, little is known regarding the neural substrates that interpret such divergent conspecific signals. Using the plainfin midshipman fish model, we tested whether specific catecholaminergic (i.e., dopaminergic and noradrenergic) nuclei and nodes of the social behavior network (SBN) are differentially responsive following exposure to playbacks of divergent social signals in sneaker males. We chose sneaker (type II) males since they attempt to steal fertilizations from territorial type I males who use an advertisement call (hum) to attract females yet are also subjected to vocal agonistic behavior (grunts) by type I males. We demonstrate that induction of cFos (an immediate early gene product and proxy for neural activation) in two forebrain dopaminergic nuclei is greater in sneaker males exposed to hums but not grunts compared to ambient noise, suggesting hums preferentially activate these nuclei, further asserting dopamine as an important regulator of social-acoustic behaviors. Moreover, acoustic exposure to social signals with divergent salience engendered contrasting shifts in functional connectivity between dopaminergic nuclei and nodes of the SBN, supporting the idea that interactions between these two circuits may underlie adaptive decision-making related to intraspecific male competition.

1. Introduction

The ability to evaluate the salience of social-acoustic signals in order to engender context-sensitive behavioral responses is essential for mating in songbirds (Schlinger and Brenowitz, 2002), anurans (Kelley, 2004), and some teleost fishes (Bass and McKibben, 2003; Fine and Parmentier, 2015). Various forms of vertebrate sociality, including but not limited to intraspecific vocal communication, are mediated by an evolutionarily conserved and reciprocally coupled array of hormone-sensitive nuclei within the basal forebrain and midbrain termed the "social behavior network" (SBN) (Goodson, 2005; Goodson and Kabelik, 2009; Goodson and Kingsbury, 2013; Newman, 1999). Catecholamines, which include dopamine and noradrenaline, are thought to play an important role in affecting the salience of conspecific social-acoustic stimuli (Maney, 2013; Maney and Rodriguez-Saltos, 2016). However, little is understood with regard to how these neurochemicals work jointly with the SBN to generate appropriate behavioral responses to sensory input. This paucity of functional data provides an incentive to further clarify the role that catecholaminergic nuclei play in directing and executing adaptive behavioral responses to salient environmental opportunities or challenges (e.g., deciding to approach potential spawning opportunities or flee from aversive agonistic signals).

The plainfin midshipman fish, *Porichthys notatus*, provides a remarkable opportunity to investigate neural mechanisms underlying the perception of social-acoustic signals because production and recognition of such information is fundamental to their reproductive success. There are two distinct male sexual phenotypes with corresponding alternative reproductive tactics: type I males are the aggressive, territorial morph which court females into their nests by emitting multi-harmonic advertisement calls or "hums", while type II males sneak-spawn in competition with larger type Is. Importantly, type II males are also the recipient of physical and vocal agonistic behavior (e.g., grunts) by type I males (Brantley and Bass, 1994). A number of studies have demonstrated that type II males are more similar to females than to type I males in a suite of traits (morphological, hormonal, behavioral) (Bass, 1996; Bass and Forlano, 2008a; Bass and Remage-Healey, 2008; Feng and Bass, 2017). All three reproductive morphs (type I, type II, female) are capable of producing short-duration broadband agonistic "grunts" which are sonically distinct from hums (Bass and McKibben, 2003; Brantley and Bass, 1994; McKibben and Bass, 1998). However, type I males are known to exclusively produce "grunt trains", being defined as a rapid succession of single grunts at intervals of about 400 ms (Bass et al., 1999). It has also been established that the auditory systems of all three morphs are seasonally plastic, adapting to detect the dominant harmonic components of type I male advertisement calls and broadband agonistic calls during the breeding season (Bhandiwad et al., 2017; Forlano et al., 2015b; Rohmann and Bass, 2011; Sisneros and Bass, 2003). These adaptations are presumably vital in shallow water acoustic environments for conspecific detection and localization, mate choice decisions, and intraspecific male competition (Sisneros, 2009a, 2009b). Key components of the neural circuitry underlying vocal-acoustic behavior in midshipman receive catecholaminergic input, overlap with the SBN, and are conserved across vertebrate taxa (Forlano et al., 2014; Goebrecht et al., 2014; Goodson, 2005; Goodson and Bass, 2002; Goodson and Kingsbury, 2013). Moreover, vocalization is thought to have first arisen in teleost fishes (Bass et al., 2008b), contextualizing midshipman sociality as an archetypal observable condition for vocal-acoustic communication in vertebrates.

By double-labeling tyrosine hydroxylase (TH; rate-limiting enzyme in catecholamine synthesis) immunoreactive (-ir) neurons with cFos (an immediate early gene product used as a proxy for neural activation), it was determined that type I male midshipman exposed to the advertisement hums of other males had significantly more TH-ir neurons expressing cFos-ir within the dopaminergic periventricular nucleus of the posterior tuberculum (TPp; putative mammalian A11 homologue;

Table 1
Catecholaminergic (TH-ir), social behavior network (SBN), and auditory (CPc) nuclei matched with their corresponding putative mammalian homologues.

Brain area	Putative mammalian homologue
TH-ir	
Vp	Extended central amygdala/bed nucleus of stria terminalis[1,5,6,8,9]
VM-VL	Dopaminergic A13[10,12]
TPp	Dopaminergic A11[10,12]
LC	Noradrenergic A6[9,10]
SBN/Auditory	
Vv*	Septum[1,5,6,8,11]
Vs*	Extended central amygdala/bed nucleus of stria terminalis[1,5,6,8]
AT*	Ventromedial hypothalamus (in part)[2,3,5]
CPc*	Medial geniculate nucleus[7]
PAG*	Periaqueductal/central gray[3,4,5]

 * Confirmed to receive auditory input in midshipman fish (Bass et al., 2000; Goodson and Bass, 2002).
 [1] (Bruce and Braford, 2009).
 [2] (Forlano et al., 2005).
 [3] (Goodson, 2005).
 [4] (Goodson and Bass, 2002).
 [5] (Goodson and Kingsbury, 2013).
 [6] (Maximino et al., 2013).
 [7] (Mueller, 2012).
 [8] (Northcutt, 1995).
 [9] (Smeets and González, 2000).
 [10] (Tay et al., 2011).
 [11] (Wullimann and Mueller, 2004).
 [12] (Yamamoto and Vernier, 2011).

see Table 1 and Forlano et al., 2017) and noradrenergic locus coeruleus (LC) (Petersen et al., 2013). A more recent study showed that activation of TH-ir neurons in the TPp and ventromedial-ventrolateral thalamic nuclei (VM-VL; putative mammalian A13 homologue; see Table 1 and Forlano et al., 2017) were significantly correlated with the amount of time females spent attending to simulated type I male advertisement calls (Forlano et al., 2017). While these findings suggest that certain catecholaminergic nuclei are generally engaged by conspecific advertisement calls (likely playing a role in appetitive sexual behavior), it is unknown whether specific subpopulations of TH-ir neurons are differentially responsive to advertisement or agonistic vocal-acoustic signals, and whether this divergent feedback modulates the execution of adaptive behavioral responses.

The goal of this study was to characterize the neural responses of type II "sneaker" males during exposure to divergent social-acoustic signals (i.e., hums and grunts produced by type I males) (see Fig. 1). Type II males were chosen as subjects of focus because they attempt to steal fertilizations from territorial type I males who use hums to attract females yet are also subjected to vocal agonistic behavior (grunts) by type I males. Quantification of cFos-ir nuclei in TH-ir neurons were carried out in the dopaminergic postcommissural (Vp) division of the ventral telencephalon, VM-VL, TPp, and noradrenergic LC. cFos-ir neurons were also quantified in components of the midshipman SBN/vocal-acoustic pathway (Goodson, 2005) which express robust TH-ir innervation, including the ventral (Vv) and supracommisural (Vs) divisions of the ventral telencephalon, anterior tuberal nucleus of the hypothalamus (AT), auditory-recipient compact division of the central posterior thalamus (CPc), and the midbrain periaqueductal grey (PAG) (Forlano et al., 2014; Goodson, 2005; Goodson and Kingsbury, 2013; Kittelberger and Bass, 2013). Rooted in the notion that catecholaminergic signaling may encode positive or negative valence of social stimuli (Goodson and Kingsbury, 2013; Horvitz, 2000; Schultz et al., 1997; Wightman and Robinson, 2002), it was hypothesized that specific populations of TH-ir neurons would exhibit differential responsivity to the acoustic exposure of courtship versus agonistic social-acoustic signals. Based on previous findings in midshipman (Forlano et al., 2017;
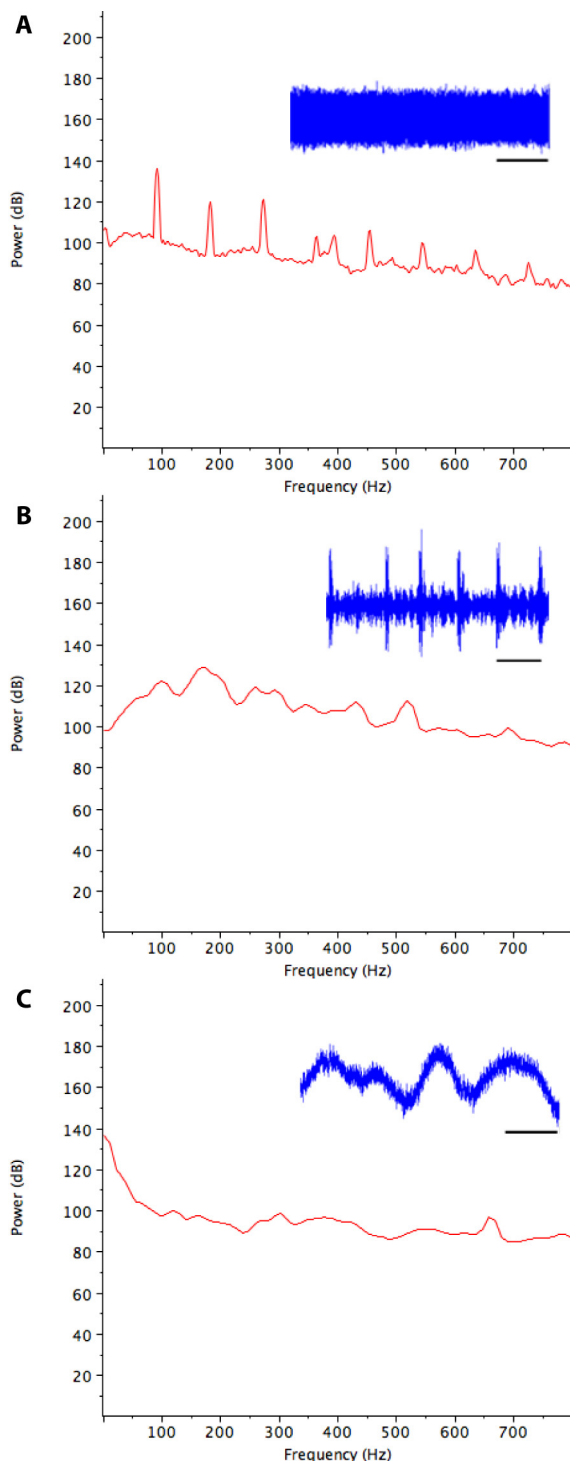
Fig. 1. Visualization of the three acoustic treatments used in this study. Representative power spectra (red) and waveform insets (blue) from field-recorded hums (A), grunts (B), and a recording of ambient background noise that was made by placing a hydrophone in the center of the testing cage (C). Hamming window, 3171 samples, 18.1 Hz bandwidth with 50% overlap. Bars = 100 ms.

Table 2
Summary statistics for morphometric data.

Acoustic Treatment	Hum, n = 9	Grunt, n = 8	Ambient, n = 7
	Range (mean ± s.d.)	Range (mean ± s.d.)	Range (mean ± s.d.)
Standard length (cm)	7.4–9.1 (8.2 ± 0.5)	8.1–10.5 (8.7 ± 0.8)	7.6–9.2 (8.3 ± 0.6)
Body mass (g)	5.0–9.9 (7.2 ± 1.6)	6.3–16.1 (8.8 ± 3.4)	6.3–10 (7.7 ± 1.5)
Gonad weight (g)	0.2–1.6 (0.8 ± 0.4)	0.4–2.1 (1.0 ± 0.5)	0.1–1.1 (0.6 ± 0.4)
GSI (%)	3.8–18.6 (11.8 ± 4.1)	5.4–18.9 (12.4 ± 4.6)	1.3–13.5 (7.9 ± 5.4)

was used to statistically compare random permutations of correlation coefficient matrices formed among network nodes, thereby testing for differences in functional connectivity between treatments.

2. Results

Morphological analyses were performed on all fish used in this study. See Table 2 for a complete breakdown of standard length (SL), body mass (BM), gonad weight (GW), and gonadosomatic index (GSI). There were no differences in body metrics between type II males exposed to the three acoustic treatments (one-way ANOVA, p > 0.1 in all cases).

2.1. Activation of TH-ir neurons

There was no effect of sound stimulus on %TH + cFos-ir in Vp ($H_2 = 2.514$, p = 0.297) (Fig. 2B). Kruskal-Wallis tests showed an overall significant effect of sound stimulus on %TH + cFos-ir activity in VM-VL ($H_2 = 8.01$, p = 0.012) (Fig. 2D) and TPp ($H_2 = 8.795$, p = 0.008) (Fig. 2F). Dunn's multiple comparison tests revealed significant differences between hum and ambient noise in VM-VL (p = 0.019; Hum Mean Rank = 14.88; Ambient Mean Rank = 6.167) and TPp (p = 0.011; Hum Mean Rank = 16.17; Ambient Mean Rank = 6.714). There was no effect of sound stimulus on %TH + cFos-ir in LC ($H_2 = 0.092$, p = 0.955) (Fig. 2H).

Importantly, results of one-way ANOVA showed no differences in the total number of TH-ir neurons (exclusive of cFos-ir) between treatments in Vp (Hum: 116.6 ± 36.1, Grunt: 112.3 ± 44.1, Ambient: 105.5 ± 31.7; p > 0.8), VM-VL (Hum: 347 ± 40.3, Grunt: 325.5 ± 94.1, Ambient: 346.7 ± 65.9; p > 0.8), TPp (Hum: 182.3 ± 81.5, Grunt: 175.2 ± 53.22, Ambient: 214.3 ± 29.8; p > 0.4), or LC (Hum: 37.1 ± 10.1, Grunt: 34.1 ± 7.2, Ambient: 38.1 ± 6.6; p > 0.6).

2.2. Activation of SBN and auditory nuclei

Exposure to social-acoustic signals did not have a significant effect on cFos-ir/section in Vv ($H_2 = 0.526$, p = 0.782) (Fig. 3B), Vs ($H_2 = 0$, p > 0.9) (Fig. 3D), AT ($H_2 = 2.277$, p = 0.332) (Fig. 3F), CPc ($H_2 = 1.011$, p = 0.603) (Fig. 3H), or PAG ($H_2 = 1.941$, p = 0.379) (Fig. 3J).

2.3. Co-activation of TH-ir neurons with SBN nuclei

Finally, pairwise Spearman correlation matrices were constructed to elucidate differences in co-activity between TH-ir and SBN nuclei in type II males exposed to advertisement hums, agonistic grunts, or ambient noise. Each acoustic treatment had correspondingly different sets of significant correlations among network nodes (Hum = 9, Grunt = 1, Ambient = 1), supporting distinct patterns of co-activation underlying

Petersen et al., 2013), it was predicted that dopaminergic neurons in VM-VL and TPp would show an increased response to hums, but not grunts. Furthermore, it was hypothesized that exposure to divergent social-acoustic signals would result in distinct patterns of brain activation across TH-ir (Vp, VM-VL, TPp, LC), SBN (Vv, Vs, AT, PAG) and auditory (CPc) nuclei, and the Quadratic Assignment Procedure (QAP)
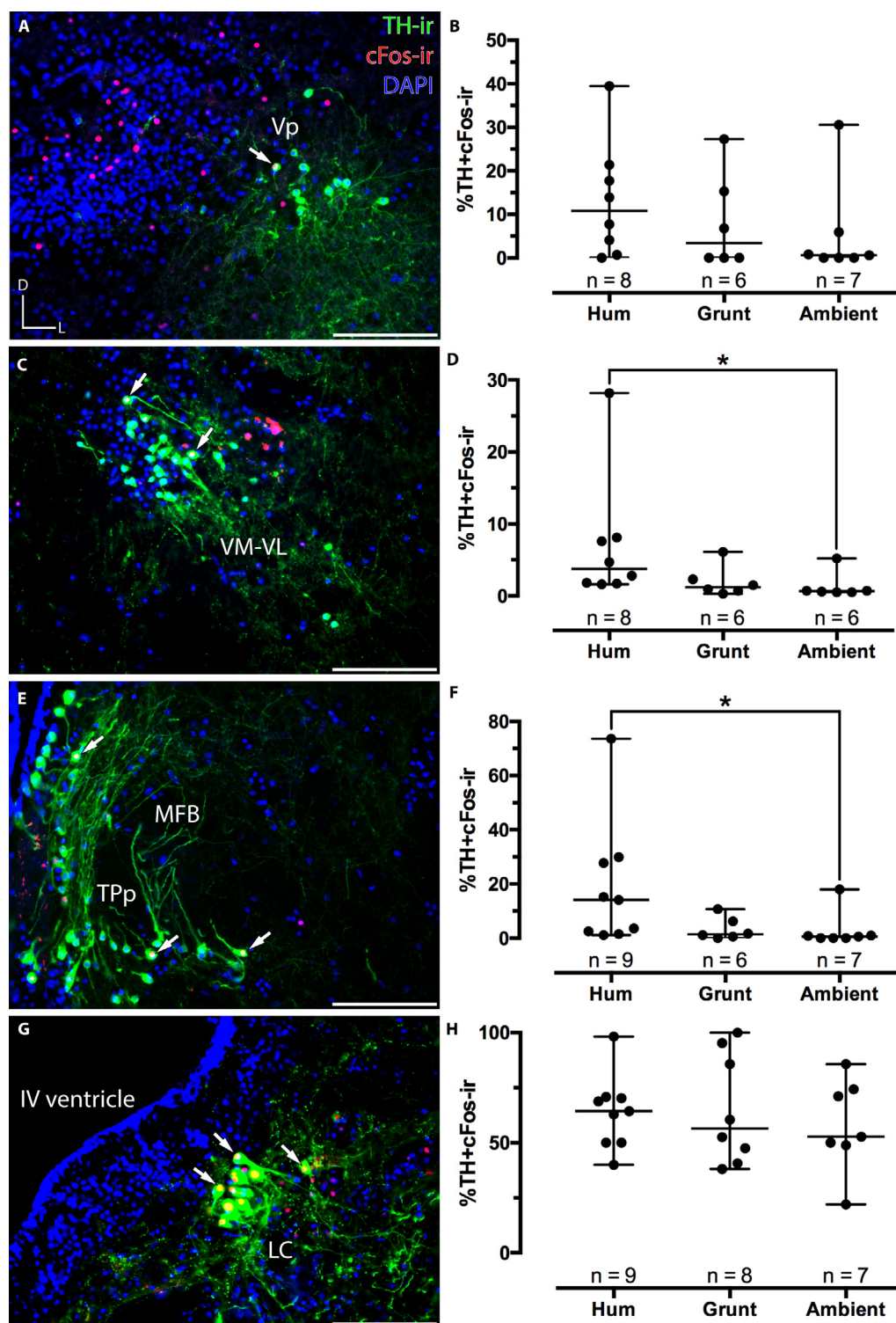
Fig. 2. cFos-ir colocalization with catecholaminergic (TH-ir) neurons. Arrows indicate cFos-ir (red) colocalized to TH-ir (green) neurons within the postcommissural nucleus of the ventral telencephalon (Vp) (A), ventromedial and ventrolateral thalamic (VM-VL) nuclei (C), periventricular posterior tuberculum (TPp) (E), and locus coeruleus (LC) (G) in type II males exposed to advertisement hums, agonistic grunts, or ambient noise. Compass in the bottom left corner of (A) represents the dorsal (D) and lateral (L) orientation for each image. Scale bars = 100 μm. Scatter dot plots in (B, D, F, H) represent median ± range of %TH + cFos-ir per animal. *p = 0.019 in (D) and *p = 0.011 in (F) using Dunn's multiple comparison test.

the processing of divergent social-acoustic signals (Tables 3–5).

Results of QAP tests detected no similarity in patterns of brain activation between hums and grunts (r = 0.169, p = 0.202), hums and ambient noise (r = 0.366, p = 0.064), or grunts and ambient noise (r = 0.104, p = 0.314), providing evidence for differential brain activation patterns for each stimulus (Fig. 4).

Regarding network centrality, exposure to divergent acoustic stimuli evoked differential recruitment patterns of TH-ir and SBN nuclei: Vp and TPp received more connections following exposure to hums, Vv and AT received the most connections in the grunt-exposed group, and
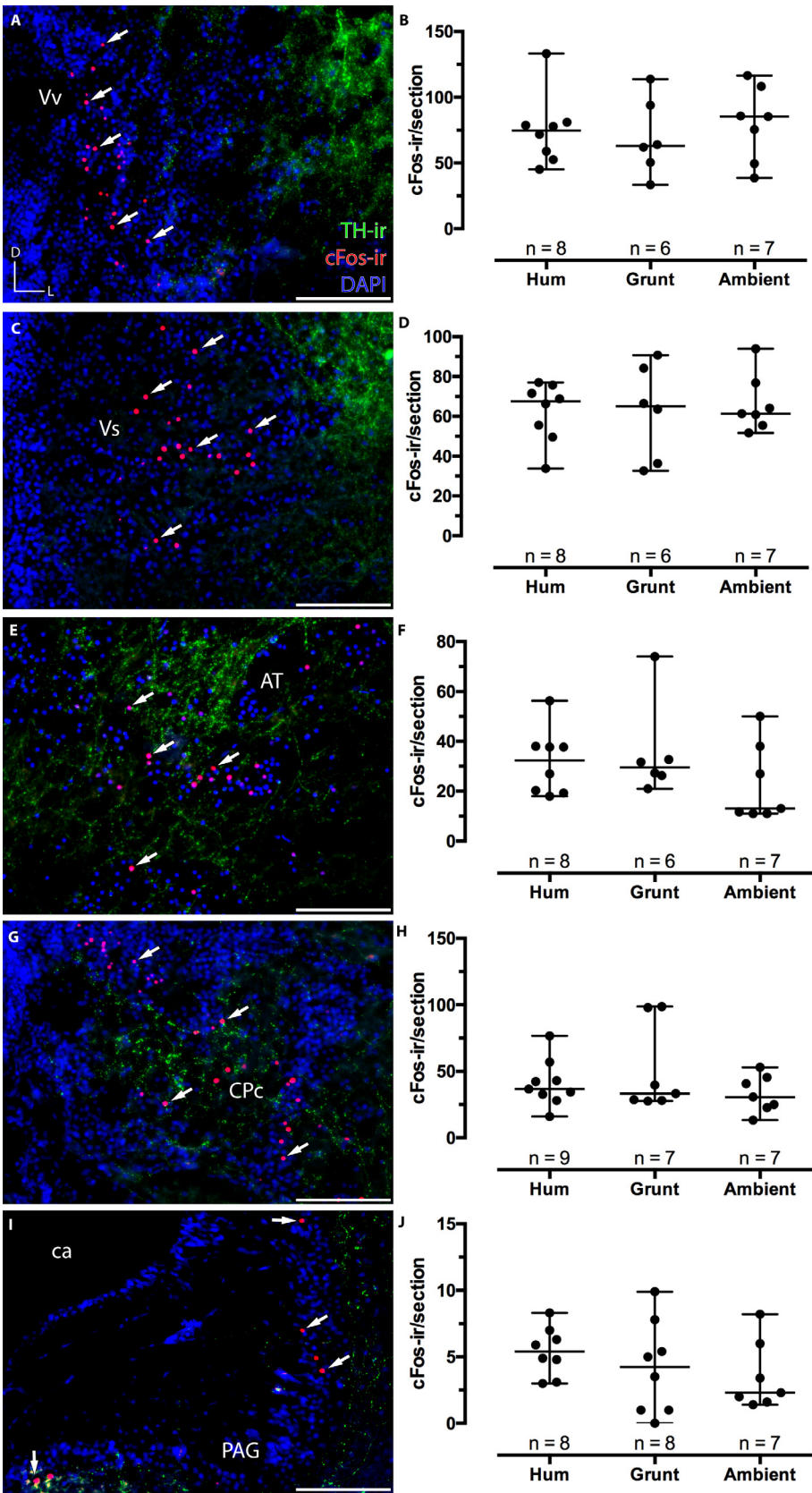
Fig. 3. cFos response to social-acoustic signals in SBN nuclei. Representative images of cFos-ir neurons (red) within the ventral (Vv) (A) and supracommissural (Vs) (C) nuclei of the ventral telencephalon, anterior tuberal nucleus of the hypothalamus (AT) (E), compact division of the central posterior nucleus of the thalamus (CPc) (G), and periaqueductal grey (PAG) (I) in type II males exposed to advertisement hums, agonistic grunts, or ambient noise. Compass in the bottom left corner of (A) represents the dorsal (D) and lateral (L) orientation for each image. Scale bars = 100 µm. ca = cerebral aqueduct. Scatter dot plots in (B, D, F, H, J) represent median ± range of cFos-ir/section per animal.

VM-VL, TPp, and Vv showed the highest recruitment after exposure to ambient noise (Table 6). While the grunt matrix generated the largest overall network density (Table 6), there were no significant differences in density between hums and grunts (t = 1.7164, p = 0.0812), hums and ambient noise (t = 0.1142, p = 0.9092) or grunts and ambient noise (t = 1.8, p = 0.0686) (Table 6).

Table 3
Correlation matrix between TH-ir and SBN nuclei during exposure to hums.

		TH + cFos				cFos			
		Vp	VM-VL	TPp	LC	Vv	Vs	AT	CPc
TH + cFos									
VM-VL	rho	**0.810**							
	p	**0.022**							
	n	8							
TPp	rho	**0.881**	**0.833**						
	p	**0.007**	**0.015**						
	n	8	8						
LC	rho	−0.286	−0.381	−0.167					
	p	0.501	0.360	0.667					
	n	8	8	9					
cFos									
Vv	rho	**0.833**	0.690	**0.857**	−0.071				
	p	**0.015**	0.069	**0.011**	0.882				
	n	8	8	8	8				
Vs	rho	**0.833**	0.500	0.571	−0.238	0.548			
	p	**0.015**	0.216	0.151	0.582	0.171			
	n	8	8	8	8	8			
AT	rho	0.072	−0.096	0.287	0.587	0.395	−0.228		
	p	0.872	0.825	0.487	0.134	0.335	0.589		
	n	8	8	8	8	8	8		
CPc	rho	−0.667	**−0.905**	**−0.700**	0.527	−0.429	−0.476	0.359	
	p	0.083	**0.005**	**0.043**†	0.149	0.299	0.243	0.381	
	n	8	8	9	9	8	8	8	
PAG	rho	**0.786**	**0.786**	**0.810**	−0.299	**0.893**	0.393	0.321	−0.476
	p	**0.048**†	**0.048**†	**0.022**	0.470	**0.012**	0.396	0.498	0.243
	n	7	7	8	8	7	7	7	8

Bold values indicate significant correlation at p < 0.05.
† Indicates loss of significance after adjustment for multiple comparisons.

Table 4
Correlation matrix between TH-ir and SBN nuclei during exposure to grunts.

		TH + cFos				cFos			
		Vp	VM-VL	TPp	LC	Vv	Vs	AT	CPc
TH + cFos									
VM-VL	rho	0.410							
	p	0.500							
	n	5							
TPp	rho	0.462	0.486						
	p	0.433	0.356						
	n	5	6						
LC	rho	−0.152	−0.200	−0.029					
	p	0.833	0.714	1.000					
	n	6	6	6					
cFos									
Vv	rho	0.395	**1.000**	0.700	0.143				
	p	0.450	**0.017**	0.233	0.803				
	n	6	5	5	6				
Vs	rho	0.516	0.500	−0.100	0.314	0.600			
	p	0.333	0.450	0.950	0.564	0.242			
	n	6	5	5	6	6			
AT	rho	0.667	0.829	0.486	−0.086	0.900	0.800		
	p	0.267	0.058	0.356	0.919	0.083	0.133		
	n	5	6	6	6	5	5		
CPc	rho	0.030	0.086	0.257	0.679	0.486	0.771	0.429	
	p	1.000	0.919	0.658	0.110	0.356	0.103	0.419	
	n	6	6	6	7	6	6	6	
PAG	rho	−0.273	0.486	0.314	0.527	0.543	0.429	0.371	0.721
	p	0.617	0.356	0.564	0.184	0.297	0.419	0.497	0.079
	n	6	6	6	8	6	6	6	7

Bold value indicates significant correlation at p < 0.05.

3. Discussion

This study provides insight into the neural responses of type II "sneaker" male midshipman to divergent social-acoustic signals. Results show that hums, but not grunts, preferentially activated two distinct dopaminergic nuclei in the forebrain. These cell populations could play an important role in differentiating an advertisement call from an agonistic signal (Goodson and Kingsbury, 2013; O'Connell and Hofmann, 2011), and may therefore be involved in the decision to approach potential spawning opportunities. Reproductive type I males

Table 5
Correlation matrix between TH-ir and SBN nuclei during exposure to ambient noise.

		TH + cFos				cFos			
		Vp	VM-VL	TPp	LC	Vv	Vs	AT	CPc
TH + cFos									
VM-VL	rho	0.188							
	p	0.817							
	n	6							
TPp	rho	0.038	**0.985**						
	p	0.971	**0.006**						
	n	7	6						
LC	rho	−0.778	0.353	0.334					
	p	0.057	0.522	0.471					
	n	7	6	7					
cFos									
Vv	rho	0.519	**0.883**	0.593	0.000				
	p	0.245	**0.044†**	0.179	1.037				
	n	7	6	7	7				
Vs	rho	−0.037	0.618	0.704	0.464	0.429			
	p	0.969	0.244	0.105	0.302	0.354			
	n	7	6	7	7	7			
AT	rho	−0.393	−0.045	0.019	0.396	−0.450	−0.126		
	p	0.370	0.939	0.990	0.378	0.311	0.793		
	n	7	6	7	7	7	7		
CPc	rho	−0.408	0.353	0.185	0.714	0.393	0.107	0.198	
	p	0.371	0.522	0.719	0.088	0.396	0.840	0.667	
	n	7	6	7	7	7	7	7	
PAG	rho	−0.074	0.530	0.556	0.143	0.464	0.321	−0.595	0.071
	p	0.893	0.311	0.212	0.783	0.302	0.498	0.173	0.906
	n	7	6	7	7	7	7	7	7

Bold values indicate significant correlation at $p < 0.05$.
† Indicates loss of significance after adjustment for multiple comparisons.
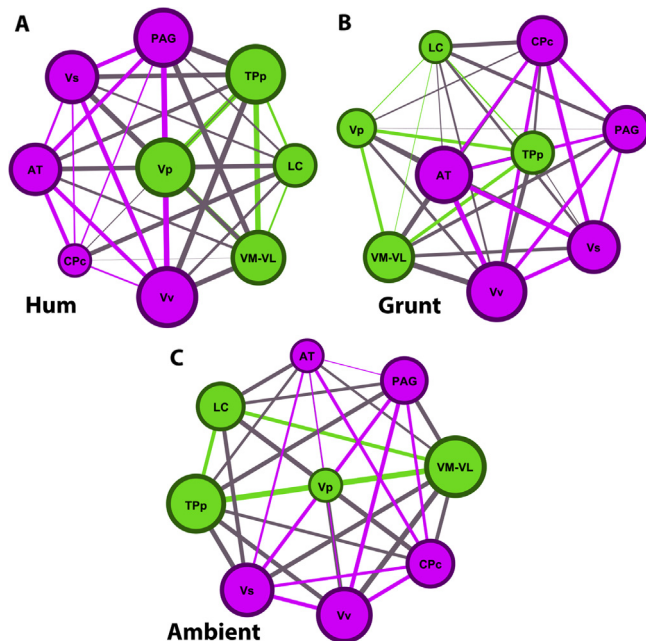

Fig. 4. Networks formed among TH-ir and SBN nuclei. Sociograms representing correlations between TH-ir (green) and SBN (magenta) nuclei in type II males exposed to hums (A), grunts (B), or ambient noise (C) using cFos-ir as a marker of neural activation. The size of the node indicates its average weighted degree of centrality, and line size indicates the strength of the connection between nodes (e.g., rho values, see Tables 3–5).

often produce trains of broadband, short-duration (50–200 ms) grunts to obviate potential nest interlopers (Brantley and Bass, 1994). Grunt trains have a repetition rate of about 2.5 Hz with grunt intervals of approximately 400 ms (Bass et al., 1999). In contrast, the hum is a long-duration, multiharmonic signal with a fundamental frequency that

ranges from 80 to 102 Hz (Bass et al., 1999). The several prominent harmonics contained within the hum range up to 400 Hz with additional lower amplitude harmonics at ≥800 Hz (Bass et al., 1999). While we did not find any one nucleus to be differentially responsive between hums and grunts (e.g., the functional localization hypothesis; see below), it was determined that exposure to divergent acoustic stimuli evoked shifts in functional connectivity between dopaminergic nuclei and SBN nodes, suggesting that these circuits do indeed form a comprehensive network that could underlie the systemization of auditory sensitivity and social decision-making.

Results of the current study revealed two dopaminergic nuclei in the forebrain (VM-VL, TPp) which were preferentially responsive to advertisement hums. While VM-VL and TPp are putative homologues of the mammalian A13 and A11 dopamine groups respectively, these nuclei are not well understood in the context of social behavior (Goodson and Kingsbury, 2013; Yamamoto and Vernier, 2011). In the context of signal recognition and preference, type II males have been observed to exhibit positive phonotaxis to the playback of simulated hums (McKibben and Bass, 1998). It has been shown that the peripheral auditory system of reproductive type II males can encode frequencies ≥165 Hz, encompassing the dominant higher frequency components of type I male vocalizations, including hums (Bhandiwad et al., 2017). Under conditions of midshipman sociality, the hum could be considered a signal of high incentive salience (Maney, 2013; Maney and Rodriguez-Saltos, 2016), as it is both necessary and sufficient to induce positive phonotaxis in gravid females (Bass and McKibben, 2003; Forlano et al., 2017; McKibben and Bass, 1998; Zeddies et al., 2010). The primary components of the mesolimbic dopamine system in mammals are the ventral tegmental area (VTA) and nucleus accumbens, and it has been proposed that these nuclei mediate approach-avoidance behaviors (see Goodson and Kingsbury, 2013). Importantly, teleosts do not exhibit any midbrain dopamine neurons, thereby excluding them from possessing an equivalent "mesolimbic" dopamine system all together (Yamamoto and Vernier, 2011). However, behavioral functions that would depend on VTA-derived dopamine in mammals and birds may instead rely on

Table 6
Characterization of the SBN for each acoustic treatment using cFos-ir induction as a marker of neuronal activity.

		Hum	Grunt	Ambient
Density Eigenvalue		0.227	0.403	0.213
	TH + cFos			
	Vp	**0.413**	0.240	0.024
	VM-VL	0.397	0.387	**0.496**
	TPp	**0.402**	0.270	**0.461**
	LC	−0.163	0.108	0.228
	cFos			
	Vv	0.372	**0.452**	**0.417**
	Vs	0.302	0.367	0.376
	AT	0.020	**0.435**	−0.115
	CPc	−0.338	0.305	0.219
	PAG	0.373	0.295	0.336

Reported values correspond to network cohesion (density) and centrality (eigenvalue) of each brain region. Bold eigenvalues indicate high levels of centrality (> 0.4) among network nodes.

dopaminergic input from other classically defined basal forebrain nuclei in teleosts (e.g., A13 and A11) (Tay et al., 2011). Therefore, dopamine neurons in VM-VL and TPp may serve a role that is at least functionally analogous to the VTA in amniotes (Forlano et al., 2017, 2014; Goodson and Kingsbury, 2013; Salamone and Correa, 2012).

To date, there is a notable deficiency of investigations into patterns of brain activation following playbacks of multiple conspecific social-acoustic signals with divergent behavioral relevance. Previous studies in anurans and songbirds have demonstrated that specific brain regions discriminate between conspecific and heterospecific social-acoustic stimuli, thereby conferring an adaptive advantage to the individual (e.g., females localizing appropriate mates, or juvenile male songbirds choosing appropriate tutors during vocal learning). For example, using the immediate early gene ZENK as a marker for neural activation, it was shown that intrahypothalamic connectivity in túngara frogs shifted as a function of the behavioral relevance of social-acoustic stimuli (Hoke et al., 2005). Furthermore, ZENK response was greater in the caudomedial neostriatum (NCM) of zebra finches and canaries exposed to conspecific compared to heterospecific song (Mello et al., 1992), and cFos response in the A8-A11 midbrain dopamine neurons of zebra finches differentiated conspecific from heterospecific sociosexual stimuli (Bharati and Goodson, 2006; Mello et al., 1992). A recent playback study in female midshipman showed greater cFos induction at the level of the auditory midbrain in response to conspecific vocalizations compared with ambient noise, and greater activation in response to conspecific vocalizations compared with both heterospecific calls and ambient noise in the forebrain (auditory thalamus and hypothalamus), indicating that higher-order processing plays an essential role in the discrimination of complex social signals in teleosts (Mohr et al., 2018). While the current study did not find cFos induction in one particular brain region to discriminate between playbacks of conspecific hums or grunts, exposure to acoustic treatments with divergent salience did produce distinct patterns of functional connectivity among TH-ir and SBN nuclei (Tables 3–5; Fig. 4). These findings support the idea that the SBN relies on integration across various nodes of the network in lieu of regional specialization of specific nuclei (Goodson, 2005; Newman, 1999; O'Connell and Hofmann, 2011). For example, a human fMRI study showed that functional connectivity between the amygdala and hippocampus shifted with regard to the emotional valence of visual stimuli in a contextual memory task (Smith et al., 2006). In Japanese macaques, unilateral lesions of the left (but not the right) auditory cortex resulted in a temporary impairment in the ability to discriminate conspecific "coo" vocalizations, but not other types of auditory stimuli (Hefner and Heffner, 1986), providing support for wide-scale neural specialization in vocal recognition. Thus, the results of this study support the hypothesis that functional connectivity of catecholamine

neuromodulators with the conserved SBN can integrate variable social signals into diverse brain patterning and subsequent behaviors (Goodson, 2005; Goodson and Kingsbury, 2013; Newman, 1999; O'Connell and Hofmann, 2011).

Correlation matrices were constructed to visualize co-activation of TH-ir nuclei with SBN nodes, and to resolve shifts in functional connectivity attributed to the behavioral relevance of the acoustic stimulus. After adjusting p-values to account for multiple comparisons, 4 out of 15 significant correlations did not remain as such (see Tables 3–5). However, those higher p-values (e.g., ≥0.0433) which were no longer significant after correction may in fact be attributed to low power due to small sample size rather than being random and spurious (Nakagawa, 2004). The hum-exposed group showed the largest number of significant correlations between TH-ir nuclei and SBN nodes. All three dopaminergic nuclei of interest (Vp, VM-VL, TPp) were co-active after exposure to hums, suggesting that these groups form a circuit which may be important in processing the incentive salience of advertisement signals (Table 3). Following the same treatment, dopaminergic activity in Vp was correlated with cFos induction in Vv and Vs (Table 3), suggesting that exposure to advertisement signals may trigger local dopamine release in the ventral forebrain, thereby affecting responsivity of putative amygdalar/septal homologues (see Table 1 and Forlano et al., 2017). Structural connectivity between TPp and Vv was initially established in zebrafish, and activity in both nuclei were correlated during exposure to hums (Table 3), providing evidence for an ascending dopaminergic system emanating from the diencephalon (Rink and Wullimann, 2001). Moreover, co-activation of TPp with PAG in type II males that were exposed to hums (Table 3) corroborates previously established reciprocal anatomical connectivity in midshipman, as both nuclei are directly implicated in vocal-acoustic behavior (Forlano et al., 2014; Goodson and Bass, 2002; Kittelberger and Bass, 2013). The grunt (Table 4) and ambient noise (Table 5) matrices showed the fewest number of significant correlations, indicating minimal interaction (see below) between TH-ir and SBN nuclei in the absence of advertisement signals.

Following exposure to hums, TH-ir activity in Vp and TPp displayed the highest network centrality scores. This, along with the finding that TPp TH-ir activity was greater in the same acoustic treatment suggests that the presence of advertisement hums promotes the phasic release of dopamine in the forebrain. It has been suggested that behaviorally relevant stimuli produce transient activation of dopaminergic neurons to trigger the phasic or volumetric component of dopamine release, which is thought to be involved in reward and appetitive arousal processes (Alcaro and Panksepp, 2011; Grace, 1991). Neuroanatomical evidence suggests that TPp TH-ir neurons receive auditory input via the PAG (Kittelberger and Bass, 2013), innervate both the central and peripheral auditory system (Forlano et al., 2014; Perelmuter and Forlano, 2017), as well as limbic forebrain and spinal cord (Tay et al., 2011), and thus are ideally situated to integrate sensory responsivity with behavioral output (Forlano et al., 2017; Forlano and Sisneros, 2016). After exposure to ambient noise, TPp, VM-VL, and Vv showed the highest network centrality scores. The high degree of network centrality coupled with low TH-ir activity observed in TPp and VM-VL under control condition could represent tonic release of dopamine in the forebrain in the absence of social-acoustic signals, possibly serving to strengthen the internal motivational signal-to-noise ratio within neural networks and promote active engagement with the environment (Alcaro et al., 2007). In contrast to phasic dopamine release, tonic release may regulate intensity of the phasic response via its effect on extracellular dopamine levels, effectively setting the background level of autoreceptor and postsynaptic receptor stimulation and sensitivity of the network to dopamine at these areas (Grace, 1991). However, further molecular investigations are necessary to determine expression patterns of various dopamine receptor subtypes to help elucidate dopamine mechanisms of action in midshipman TH-ir and SBN nuclei. The high centrality of Vv and AT in the grunt-exposed network may represent differential

processing related to the social relevance of the signal (Goodson, 2005; Goodson and Kingsbury, 2013; Hoke et al., 2005; Maney, 2013), considering both nuclei and/or their putative mammalian homologies (septal and ventromedial hypothalamus, respectively; see Table 1) are implicated in regulating stress sensitivity, sexual behavior, and aggression (O'Connell and Hofmann, 2011; Vindas et al., 2014).

Unlike type I males, which showed significant cFos induction in LC TH-ir noradrenergic neurons after exposure to advertisement hums (Petersen et al., 2013), the current study did not find a significant effect of sound stimulus on LC activity. In the present study, cFos induction in LC TH-ir neurons was 68.7% higher than seen in type I males subjected to the same ambient noise treatment (Petersen et al., 2013) (Table S1A). These results imply that type II males are in a generally higher state of arousal at night during the reproductive season, which may be a necessary adaptation for their reproductive tactic and survival. We also found no effect of sound stimulus on cFos induction in CPc or AT in type II males, whereas significant differences were found in both nuclei between hum and ambient noise in type I males (Petersen et al., 2013) and in females (Mohr et al., 2018). Compared to the hum-exposed type II males in the current study, cFos induction was over 50% higher in CPc and AT in type I males that heard hums (Table S1B). Both CPc and AT and are reciprocally connected and receive significant TH-ir innervation (Forlano et al., 2014; Goodson and Bass, 2002). Therefore, the non-discriminatory responses of LC, CPc and AT to various social acoustic cues in type II males suggests intrasexual divergence in social behavioral processing (e.g., advertisement hums could be perceived as social challenges by type I males vs. potential spawning opportunities by type II males).

In conclusion, it was determined that cFos induction in two distinct populations of forebrain dopaminergic neurons were higher in type II "sneaker" males exposed to hums compared to those subjected to ambient background noise, suggesting that these nuclei are preferentially responsive to advertisement calls compared to agonistic grunts, thereby reinforcing dopamine as an important neuromodulator of positive valence in social-acoustic driven behaviors. Moreover, playbacks of social-acoustic signals with divergent salience elicited distinctive shifts in correlated activity between dopaminergic nuclei and components of the SBN, supporting the notion that adaptive behaviors (e.g., conspecific detection and localization, mate choice decisions, and intraspecific male competition) are an emergent property of the interactions between these two circuits.

4. Experimental procedure

4.1. Ethics statement

All experimental animal procedures performed in this study were approved by the Institute for Animal Care and Use Committee of the University of California, Davis (Protocol Number: 15977), and CUNY Brooklyn College (Protocol Number: 260). Animals were collected from the field under California Department of Fish and Game Permit 802021-01.

4.2. Animals

Twenty-four type II male plainfin midshipman fish were collected at morning low tides from intertidal nesting sites near Marshall, CA in Tomales Bay during the summer breeding season. Fish were maintained in large, same-morph communal tanks at natural ambient temperatures (11.5–14.3 °C) at the University of California Bodega Marine Laboratory (BML) until playback experiments were conducted within 24–72 h post-capture.

4.3. Playback experiment

All tests were conducted at BML in an outdoor, cylindrical concrete tank (4 m diameter, 0.75 m depth) at night between 2200 and 0200 h. A UW-30 underwater speaker (Telex Communications, Burnsville, MN, USA) was suspended from a wooden beam in the center of the tank and positioned 10 cm above the tank floor. Individual fish were randomly assigned to an acoustic treatment and placed in a 30-cm diameter plastic mesh cylinder cage in the tank at a fixed distance from the underwater sound source so that average peak-to-peak sound level was approximately 130 dB (re: 1 μPa) at the center of the cage when the sound stimulus was turned on. These sound levels are consistent with the sound pressure levels of advertisement hums produced by type I males recorded near their nests (Bass and Clark, 2003). Sound levels were calibrated and measured nightly using a mini-hydrophone (model 8103, Brüel and Kjaer, Norcross, GA, USA), a charge amplifier (Brüel and Kjaer model 2692) and oscilloscope (model TDS-1002, Tektronix, Beaverton, OR, USA). The order of acoustic treatments was also randomized each night. Sound analysis was conducted using Raven Pro v1.4 (Ithaca, NY, USA). Hum-exposed males were subjected to a looped 30-minute playback of five field-recorded type I male advertisement calls (Fig. 1A). The audio files were equalized to the same maximum peak-to-peak sound level in MATLAB to account for any differences in amplitude between individual type I male callers. The average duration of hums (n = 5) contained in the looped playback was 7.8 (± 5.4 s.d.) min with a range of 2.2–13.6 min. Grunt-exposed type II males were subjected to a looped 30-minute playback of conspecific grunts (Fig. 1B). The average duration of n = 19 grunts sampled from the recording was 78.7 (± 9.3 s.d.) ms with a range of 67–97 ms. Control males were placed in the same arena for 30 min at the same time of night with only ambient noise (Fig. 1C). Animals were then isolated in a 5-gallon bucket for 120 min post-trial and anesthetized by immersion in seawater mixed with 0.025% benzocaine (Sigma-Aldrich, St. Louis, MO, USA), weighed, measured, and sacrificed via transcardial perfusion with ice-cold teleost Ringer's solution followed by ice-cold 4% paraformaldehyde (Sigma-Aldrich) in 0.1 M phosphate buffer (PB; pH 7.2). Testes were removed and weighed, and gonadosomatic index (GSI) was calculated as the ratio of testes mass to body mass minus testes mass × 100 (Table 2). Brains were dissected, post-fixed for one hour, and transferred to 0.1 M PB. Brains were stored in 0.1 M PB with 0.05% sodium azide until processed. After incubation in 0.1 M PB with 30% sucrose for 48 h, brains were sectioned on the coronal plane at 25 μm with a cryostat and collected in two series onto positively charged slides. One series from each animal was used for this study.

4.4. Immunohistochemistry

Fluorescence immunohistochemistry was slightly modified from a previous protocol (Petersen et al., 2013). Slides were warmed to room temperature prior to being washed 2 × 10 min in 0.1 M phosphate-buffered saline (PBS; pH 7.2), followed by a one-hour soak in blocking solution consisting of 10% normal donkey serum (DS, Jackson Immuno Research Labs, West Grove, PA, USA) + 0.3% Triton X-100 in PBS (PBS-DS-T). After blocking, tissue was incubated for 18 h at room temperature in PBS-DS-T containing mouse anti-TH (1:1000; cat no. MAB318, lot no. 246515; MilliporeSigma, Temecula, CA, USA) and rabbit anti-cFos (1:2000; cat no. sc-253, lot no. C2510; Santa Cruz Biotechnology, Dallas, TX, USA) primary antibodies. After incubation, slides were washed 5 × 10 min in PBS + 0.5% normal donkey serum (PBS-DS), followed by a two-hour incubation in PBS-DS-T combined with anti-mouse and anti-rabbit secondary antibodies conjugated to Alexa Fluor 488 and 568, respectively (1:200; Thermo Fisher Scientific, Waltham, MA, USA). Slides were then washed 3 × 10 min in PBS and coverslipped with ProlongGold containing DAPI nuclear stain (Thermo Fisher). Finally, slides were randomized and coded so that observers were blind to the experimental condition of each animal.

4.5. Image acquisition and anatomy

Images were acquired on an Olympus BX61 epifluorescence compound microscope using MetaMorph imaging and processing software (Molecular Devices, Sunnyvale, CA, USA). Each brain area was imaged with a 20X objective at a constant exposure time and light level. Each image was comprised of consecutively taken photomicrographs using Texas Red, GFP, and DAPI filter sets (Chroma, Bellow Falls, VT, USA) within a z-stack containing 6–9 levels, each with a step of 1 μm (Table S2). All nuclei were sampled unilaterally with the right side of the brain imaged (except TPp, which was sampled bilaterally) in the caudal-to-rostral direction. In the case of tissue loss or damage, the opposite side of the brain was used or the section was omitted, explaining any discrepancy between initial sample sizes and n for each analysis.

Catecholaminergic nuclei of interest included Vp, VM-VL, TPp, and LC (Table 1). Sampling of TH-ir neurons was done as previously described (Forlano et al., 2015a, 2017; Ghahramani et al., 2015; Petersen et al., 2013). Activation of these nuclei was measured by the occurrence of a cFos-ir nucleus within a TH-ir neuron, referred to herein as colocalization (Bharati and Goodson, 2006; Kelly and Goodson, 2015; Petersen et al., 2013). Individual TH-ir neurons were counted only if the perimeter of the cell was clearly outlined with a labeled neurite in addition to having a nucleus that showed colocalization with DAPI. The sum of TH-ir neurons containing cFos-ir was divided by the total number of TH-ir neurons × 100 for a percentage of TH + cFos-ir colocalization. There were no differences in numbers of sections sampled for any TH-ir nuclei (one-way ANOVA, p ≥ 0.0769 in all cases) (Table S2).

SBN and auditory nuclei analyzed for the presence of cFos-ir in non-catecholaminergic neurons included the Vv, Vs, AT, CPc, and PAG (Table 1). Sampling of these nuclei was carried out as previously described (Forlano et al., 2015a, 2017; Ghahramani et al., 2015; Petersen et al., 2013). Quantification of DAPI-labeled cell nuclei containing cFos-ir signal was carried out through user interaction with a custom-written macro in ImageJ (NIH, USA) (Forlano et al., 2017). The average number of cFos-ir cells per section (total number of cFos-ir cells divided by total number of sections sampled) was then calculated per brain region in each animal. There were no differences in numbers of sections sampled for any SBN nuclei (one-way ANOVA, p ≥ 0.1 in all cases) (Table S2).

4.6. Statistics

Statistical analyses were performed at the α = 0.05 significance level using GraphPad Prism version 7 (La Jolla, CA, USA). Data for %TH + cFos-ir (Vp, VM-VL, TPp, LC) and cFos-ir/section (Vv, Vs, AT, CPc, PAG) were analyzed with the three acoustic treatments (Hum, Grunt, and Ambient Noise) as independent groups of comparison. Shapiro-Wilk and Brown-Forsyth tests were used to assess normality and equality of group variances. While the data were homoscedastic, several nuclei (Vp, VM-VL, TPp, AT, CPc) showed significant departure from normality. Therefore, Kruskal-Wallis tests were used to rank group medians since the data violate assumptions of parametric ANOVA. Data for fish in each treatment group were then pooled and three separate Spearman correlation matrices were computed between all nuclei of interest to investigate functional relationships between cFos colocalization within TH-ir nuclei and cFos response within SBN nodes as a function of acoustic condition. To control for multiple comparisons within the same dataset, p-values were adjusted using the Benjamini-Hochberg correction (Benjamini and Hochberg, 1995) with a false discovery rate of 0.25 (Butler and Maruska, 2016). A subset of significant correlations did not remain so after correction and are appropriately indicated as such (Tables 3–5). Networks formed among TH-ir nuclei and SBN nodes were characterized with UCINET version 6.531 (Borgatti et al., 2002) using density as a measure of cohesion and eigenvalues as a measure of centrality (Makagon et al., 2012). Density measures the degree to which all nodes of a network interact with all other nodes. Eigenvalue centrality takes into account not only how well a node is connected (degree centrality), but also how well connected each of its connected nodes are. This measure of centrality emphasizes that, all else being equal, an individual node is more likely to play a key role in information processing when its immediate connections are well connected themselves (Makagon et al., 2012). The Quadratic Assignment Procedure (QAP) was used with 5000 permutations to test for shifts in functional connectivity among network nodes between treatments. The null hypothesis under QAP entails no association between the two matrices being compared, hence an insignificant p-value indicates that they are different (Roleira et al., 2017; So et al., 2015; Teles et al., 2015). Finally, network density was compared between treatments using a *t*-test bootstrapped to 5000 subsamples. Networks were visualized with Gephi 0.9.3 (Bastian et al., 2009). Statistics are reported as mean ± standard deviation (s.d.) unless otherwise indicated. All p-values reported are two-tailed.

Competing interests

The authors wish to declare no conflicts of interest.

Author's contributions

Z.N.G., J.A.S., and P.M.F. conceived of the study and designed the experiments; Z.N.G., M.T., J.A.S., and P.M.F. performed field work and ran experiments; Z.N.G., M.T., and J.V. collected the data; Z.N.G. carried out the statistical analyses; Z.N.G. and P.M.F. drafted the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.brainres.2018.09.014.

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