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REVIEW

Adaptive hearing in the vocal plainfin midshipman fish: getting in tune for the breeding season and implications for acoustic communication

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Abstract

The plainfin midshipman fish (*Porichthys notatus* Girard, 1854) is a vocal species of batrachoidid fish that generates acoustic signals for intraspecific communication during social and reproductive activity and has become a good model for investigating the neural and endocrine mechanisms of vocal-acoustic communication. Reproductively active female plainfin midshipman fish use their auditory sense to detect and locate "singing" males, which produce a multiharmonic advertisement call to attract females for spawning. The seasonal onset of male advertisement calling in the midshipman fish coincides with an increase in the range of frequency sensitivity of the female's inner ear saccule, the main organ of hearing, thus leading to enhanced encoding of the dominant frequency components of male advertisement calls. Non-reproductive females treated with either testosterone or 17β-estradiol exhibit a dramatic increase in the inner ear's frequency sensitivity that mimics the reproductive female's auditory phenotype and leads to an increased detection of the male's advertisement call. This novel form of auditory plasticity provides an adaptable mechanism that enhances coupling between sender and receiver in vocal communication. This review focuses on recent evidence for seasonal reproductive-state and steroid-dependent plasticity of auditory frequency sensitivity in the peripheral auditory system of the midshipman fish. The potential steroid-dependent mechanism(s) that lead to this novel form of auditory and behavioral plasticity are also discussed.

Key words: auditory plasticity, hair cells, saccule, sex steroids, tuning,

INTRODUCTION

Acoustic communication plays an important role in the social behavior of vocal teleost fishes in the Family Batrachoididae (order Batrachoidiformes) and is essential to their reproductive success. Vocal batrachoidid fish, which include the toadfishes and the midshipman fishes, have become good models for investigating the neural and endocrine mechanisms of vocal production and auditory reception shared by all vertebrates (Bass *et al.* 1999, Fay & Simmons 1999, Bass & McKibben 2003). Several recent studies have characterized the vocal-acoustic behaviors and have examined the neuro-

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ethology of acoustic communication in one species of midshipman fish, the plainfin midshipman (*Porichthys notatus* Girard, 1854) (e.g. Sisneros & Bass 2003; Sisneros *et al.* 2004a). Recent evidence suggests that this species of midshipman fish has undergone evolutionary adaptations for the seasonal enhancement of mate detection and localization during the breeding season. The purpose of the present paper is to review the recent evidence and to discuss the potential mechanism(s) that are responsible for this seasonal enhancement of acoustic communication that might be common to vertebrates.

This review primarily focuses on the auditory sensory-receiver system of the plainfin midshipman and the adaptive changes that occur in the response properties of the peripheral auditory system during the midshipman reproductive cycle. There are three main parts to this review. The first part briefly reviews the evidence for sound production and spawning behaviors in the plainfin midshipman fish. (For a more detailed review of the sonic motor behaviors and the associated neural mechanisms of the vocal motor system in the plainfin midshipman, see Bass and McKibben [2003] and Bass and Zakon [2005].) Next, evidence for seasonal plasticity of auditory frequency sensitivity in the peripheral auditory system of the midshipman will be reviewed and the steroid-dependent mechanisms that are responsible for such auditory plasticity will be discussed. The last portion of this review discusses current work and suggestions for future investigations.

VOCAL AND REPRODUCTIVE BEHAVIOR OF THE PLAINFIN MIDSHIPMAN FISH

Plainfin midshipman fish are known to have three adult reproductive morphs that include female and two male morphs: types I and II; each male type has a different reproductive and behavioral tactic (Bass 1996, Bass *et al.* 1999). Type I male midshipman fish build and defend nests positioned under rocky shelters in the intertidal zone during the late spring and summer breeding season. From these nest sites, type I males produce relatively long duration advertisement calls (>1 min with an upper range that can exceed 1 h [Bass, personal communication 2003] at night to attract females to their nests for spawning (Bass *et al.* 1999). The advertisement call or "hum" produced by type I males is a multiharmonic acoustic signal with a fundamental frequency that is established by the contraction rate of the sonic muscles attached to the swimbladder, which acts as a resonant structure in the midshipman fish to generate

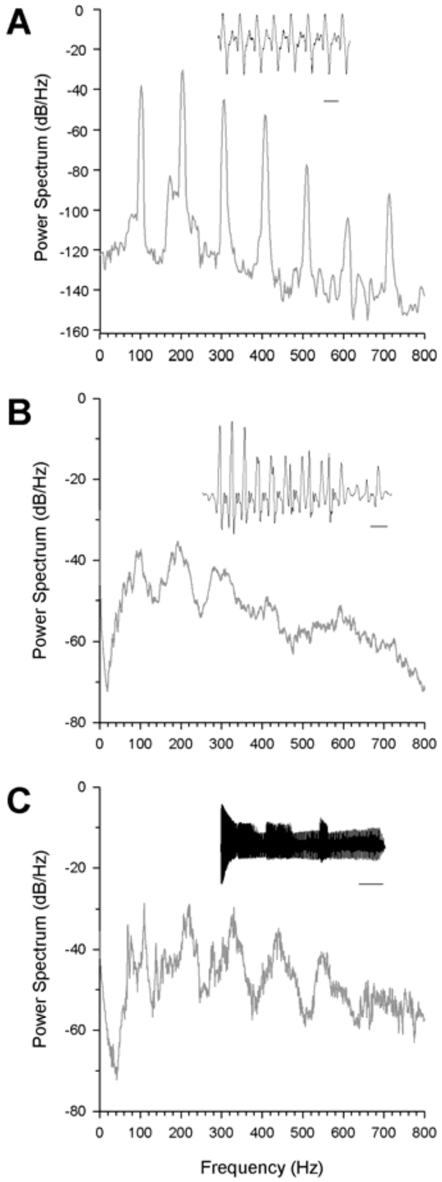

Figure 1 Acoustic signals of the Plainfin midshipman fish, *Porichthys notatus*, recorded from type I male midshipman fish. (A) Representative example of an advertisement call or "hum" (inset) and the associated power spectrum (grey trace). Bar, 10 ms. (B) Representative example of a single grunt (inset) and its power spectrum (grey trace). Bar, 10 ms. (C) Representative example of a growl (inset) and its power spectrum (grey trace). Bar, 500 ms. Modified from Sisneros and Bass (2005).

the acoustic signals. The fundamental frequency (F_0) of the hums can range from 90 to 100 Hz at a temperature of 15–16° C, although the F_0 does vary linearly with temperature (Brantley & Bass 1994, McKibben & Bass 1998). The F_0 and the several prominent harmonics that extend up to 800 Hz (Fig. 1A: power spectrum of hum, grunt and growl) are highly stable across the entire duration of the advertisement call. Typically, the hum's harmonics that range up to 400 Hz contain as much or more spectral energy than the F_0 and have been hypothesized to be important for the detection and sound source localization of the advertisement signal during the reproductive season (Sisneros & Bass 2003, Sisneros *et al.* 2004a). Reproductive females full of mature eggs use their auditory system to detect and locate the source of the multiharmonic hums produced by "singing" type I males during the breeding season. After a gravid female has spawned with a nesting type I male and has deposited all her eggs, she will then leave the seasonal intertidal breeding grounds and return to offshore sites in deeper water. Type I males remain with the fertilized eggs in the nest and will then continue to court and spawn with other females over the course of the breeding season from late spring (April–May) to summer (July–August) until their nests are filled with multiple clutches of eggs and embryos (DeMartini 1988, Brantley & Bass 1994, Bass 1996). In this teleost species, type I males provide all the parental care, which often consists of fanning and brushing the fertilized eggs to keep them clean and free of detritus and bacteria. During the nesting period, type I males vigorously defend and guard their nests from potential egg predators until the developing embryos have absorbed all of their yolk and detach from the nest and become free swimming after approximately 30–40 days post fertilization (Brantley & Bass 1994). In contrast to type I or "nesting" males, type II males, also known as "sneakers," use an alternative reproductive tactic that does not require them to build nests nor acoustically court females. Instead, type II males satellite and/or "sneak" spawn to steal fertilizations from type I males that are actively courting females (Brantley & Bass 1994).

All adult morphs (males and females) are capable of producing short duration (approximately 50–200 ms), broad-band signals known as "grunts" (Fig. 1B) during agonistic encounters (Ibara *et al.* 1983, Brantley & Bass 1994). However, only type I males are able to produce "trains" of grunts, which consist of a rapid succession of single grunts at a repetition rate that ranges from 97 to 110 Hz (Brantley & Bass 1994, Bass *et al.* 1999). Grunt trains are often used by type I males to fend off potential nest intruders.

A third type of midshipman vocalization that is only produced by reproductive type I males is the "growl." Like the hum, growls (Fig. 1C) are multiharmonic and relatively long in duration (>1 s). However, growls have an initial grunt-like signal that is followed immediately by a multi-harmonic component with a F_0 of 59–116 Hz that gradually changes through the duration of this agonistic call. Growls are typically heard at the beginning of the breeding season when type I males are establishing their nest sites and are highly aggressive and territorial.

MIDSHIPMAN PERIPHERAL AUDITORY SYSTEM

The inner ear of the plainfin midshipman fish and other fishes, both teleosts and elasmobranchs, includes three semicircular canals with their associated sensory regions (cristae ampullaris) and three otolithic end organs: the saccule, the lagena and the utricle (Fig. 2). In contrast to primarily its vestibular function in tetrapods, the saccule is the main end organ used for hearing in the midshipman, and most teleost fish, and is innervated by the

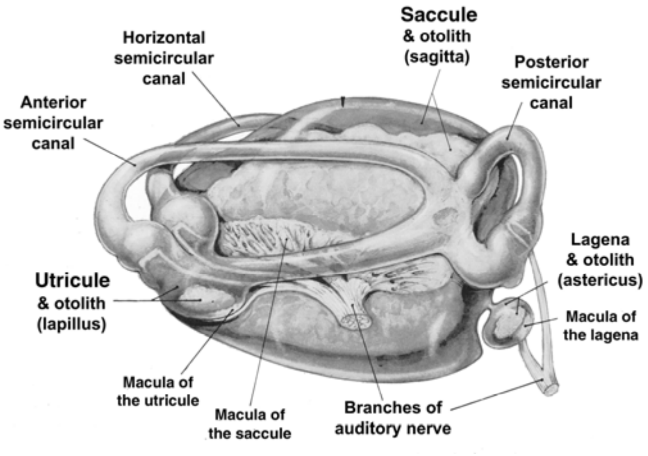

Figure 2 The inner ear of the plainfin midshipman fish, Porichthys notatus, which shows the three semicircular canals and the three end organs, including the saccule, the lagena and the utricle, with their associated maculae. Modified from Cohen and Winn (1967).cluding the saccule, the lagena and the utricle, with their associated maculae. Modified from Cohen and Winn (1967).

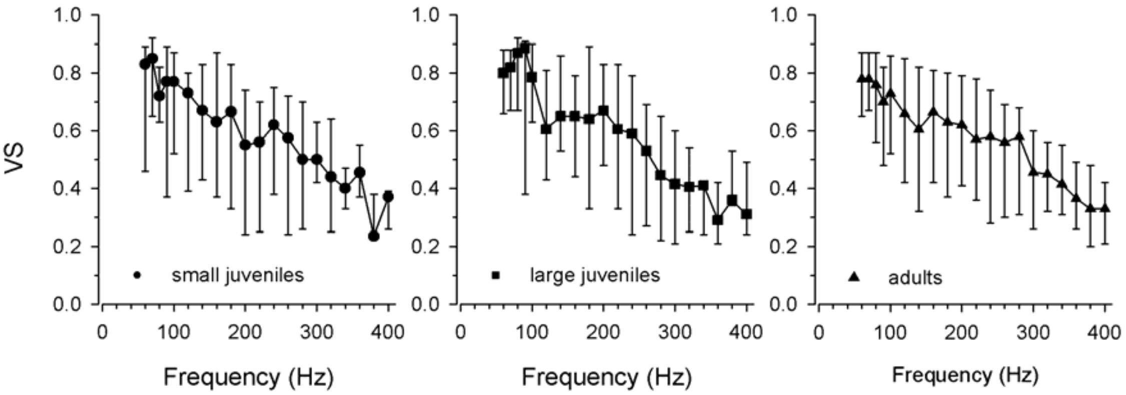

Figure 3 Iso-intensity response curves for auditory saccular afferent neurons from juvenile and adult midshipman fish to 130 dB (re 1 μPa) iso-intensity tones. Iso-intensity curves based on vector strength of synchronization (VS) show VS values for each frequency tested in terms of median (black filled symbols) with 25th percentile (bottom bar) and 75th percentile (top bar) values for small juveniles (*n* = 12 animals, 27 auditory saccular afferent records), large juveniles (*n* = 14, 35) and nonreproductive adults (*n* = 28, 101). Modified from Sisneros and Bass (2005).

eighth cranial nerve. Although the saccule serves primarily an auditory function in teleost fishes, saccular afferents are known to respond to acoustic stimuli in amphibians (Lewis *et al.* 1982) and in mammals (McCue & Guinan 1994).

The frequency response properties of midshipman saccular afferents have been quantitatively described using spike rates, poststimulus time histograms, iso-intensity response curves and synchronization (phase-locking) measures based the vector strength of synchronization, which show the degree of phase-locking response to a stimulus waveform (McKibben & Bass 1999, 2001b; Sisneros & Bass 2003, 2005). In comparison to terrestrial vertebrates, midshipman saccular afferents are broadly tuned with a peak frequency response best suited to detect the low frequency components of midshipman vocalizations (McKibben & Bass 1999; Sisneros & Bass 2005). Midshipman auditory saccular afferents show considerable variation in resting discharge activity, rate-intensity curves, response time and suppression by single tones (McKibben & Bass 1999; Sisneros & Bass 2005). Iso-intensity response curves based on either evoked spike rates or vector strength of synchronization as a metric show that best excitatory frequencies range from 60 to over 300 Hz, with thresholds at 60 Hz from 97 to 118 dB re 1μPa (McKibben & Bass 1999; Sisneros & Bass 2003). In general, the vector strength of synchronization rather than the spike rate is a more accurate measure of frequency encoding among teleost fishes, including midshipman (Fay 1978, 1982; McKibben & Bass 1999, 2001b). Comparisons of saccular afferent data from adult and juvenile midshipman show that resting discharge activity and auditory threshold sensitivity at best excitatory frequency increase with age/size, but iso-intensity profiles reveal that temporal encoding of frequency does not change during ontogeny (Fig 3; Sisneros & Bass 2005). Furthermore, recent results indicate that the saccular afferents of juveniles, like those of non-reproductive adults, are best suited to temporally encode the low frequency components of midshipman vocalizations (Sisneros & Bass 2005).

SEASONAL PLASTICITY OF AUDITORY FREQUENCY SENSITIVITY IN THE MIDSHIPMAN FISH

The midshipman auditory system provides an excellent model for investigating seasonal changes in auditory reception and neural processing of vocal-acoustic signals, in part, because vocal signals are essential to the reproductive success of this species. During late spring to mid summer, midshipman fish migrate from deep offshore sites to court and spawn in the shallow subtidal and intertidal zones along eastern Pacific coast of the western

USA (Miller & Lea 1972; Bass 1996). "Singing" type I males acoustically court females with their seasonal advertisement calls or hums that they produce while in their nests. Studies of the midshipman's nocturnal spawning behavior as well as underwater acoustic playback experiments with natural and synthetic advertisement calls by the lab of A. Bass at Cornell University show that reproductive gravid females respond to the type I male's hums by exhibiting strong phonotactic responses to the sound source, whereas spent females no longer show such phototactic responses to the hum (Brantley & Bass 1994; McKibben & Bass 1998, 2001). Because nocturnally active females rely on their auditory sense to detect and locate humming males during the breeding season, we tested the hypothesis that seasonal variation in reproductive state (gravid *vs* non-gravid state) can influence the neurophysiological response properties of the midshipman auditory system (Sisneros & Bass 2003). Our results showed that the auditory saccular afferents of female midshipman had higher best excitatory frequencies (Fig. 4) and exhibited a higher phase-locking accuracy to a broad range of frequencies (120–400 Hz) during the summer breeding season when females were gravid than during the non-breeding winter season when females were non-gravid (Sisneros & Bass 2003). Therefore, summer gravid females are better suited than winter non-gravid females to detect the higher harmonic components of the type I male's hum, which has a significant portion of its spectral energy in the harmonics between 180 and 420 Hz, with the second and third harmonics typically containing as much or more spectral energy than the fundamental frequency (Fig 1A). The summer enhancement of the phase-locking accuracy by the saccular afferents to the dominant frequencies of the hum should improve the probability of conspecific mate detection and localization, especially in shallow water environments like those where midshipman fish court and breed. The hum's harmonics likely increase signal detection of the advertisement call by the receiver because the higher harmonics of the hum will propagate over a greater distance than the F_0 in shallow water because of the inverse relationship between water depth and the cutoff frequency of sound transmission (Fine & Lenhardt 1983; Bass & Clark 2003). Although auditory saccular afferents of the midshipman are known to be adapted to encode the F_0 of the hum (McKibben & Bass 1999; Sisneros & Bass 2003), the encoding of the hum-like F_0s by saccular afferents is known to be enhanced with harmonics are added to tonal stimuli (McKibben & Bass 2001). In sum, the summer enhancement of the frequency response properties of the saccular afferents may represent an adaptive plasticity of the female midshipman's auditory system to improve detection of the multi-harmonic hums and enhance the acquisition of auditory information for mate identification, recognition and localization during the breeding season.

STEROID-DEPENDENT MODULATION OF THE AUDITORY SENSE

Wild populations of plainfin midshipman fish are known to exhibit an annual reproductive cycle containing

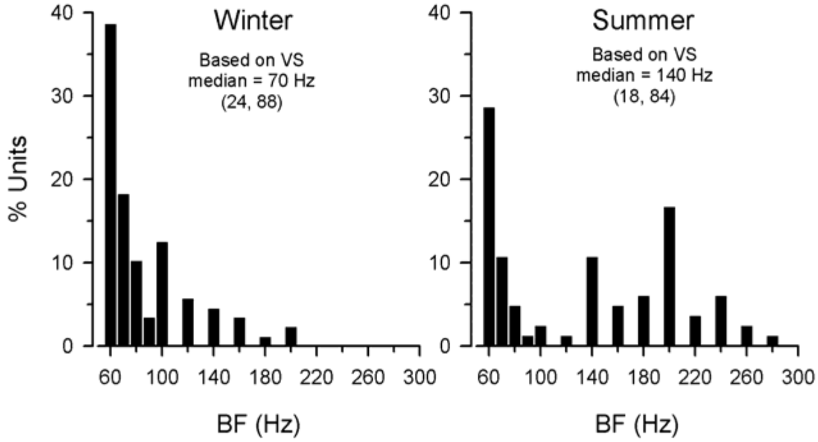

Figure 4 Best frequency histograms of auditory saccular afferents recorded from wild caught female midshipman fish collected during the nonreproductive winter (left column) and reproductive summer (right column) seasons. Distribution of best frequencies (BF) for auditory saccular afferents of winter and summer females based on the vector strength of synchronization (VS) to iso-intensity tones of 130 dB (re 1 μPa). Note that the median BF for summer females is twofold that for winter females. The numbers of animals and auditory saccular afferents sampled are indicated in parentheses. Modified from Sisneros and Bass (2003).

four time periods that corresponds to seasonal fluctuations in their reproductive biology and behavior (Sisneros *et al.* 2004b). These four seasonal time periods include the non-reproductive, pre-nesting, nesting and post-nesting periods. During the non-reproductive period, which occurs during the winter months from December to February, female midshipman have a low gonadal somatic index (GSI) with ovaries containing only small (<1 mm diameter) undeveloped ooyctes and low plasma levels of testosterone (T) and estradiol (E_2), whereas type I males have a similar low GSI with no sperm in their testes and low plasma levels of T and 11-ketotestosterone (11-KT). During the pre-nesting period, which occurs during the spring from March through April, both females and type I males undergo a seasonal recrudescence of the ovaries and testes, respectively, with females exhibiting a brief peak of plasma levels of T and E2 during April approximately 1 month prior to the summer breeding season, while type I males continue to show a gradual increase in plasma levels of T and 11-KT during gonadal recrudescence. During the nesting period, which occurs during late spring and summer from May to August, gravid females with well developed eggs (approximately 5 mm diameter) have high GSI, with low levels of T and E_2, whereas type I males exhibit an intermediate GSI with levels of T and 11-KT that peak at the beginning of the summer nesting season. The post-nesting period, which occurs during the fall months from September and October, is marked by a decrease in GSI and in plasma levels of E_2, T and 11-KT in both females and type I males, respectively.

The spring pre-nesting peak of circulating blood plasma levels of T and E_2 exhibited by female midshipman approximately 1 month before the beginning of the summer spawning season (Fig. 5) led to the hypothesis that T and E_2 can induce the seasonal enhancement of phase-locking accuracy and increase the best excitatory frequency of saccular afferents in a nonreproductive

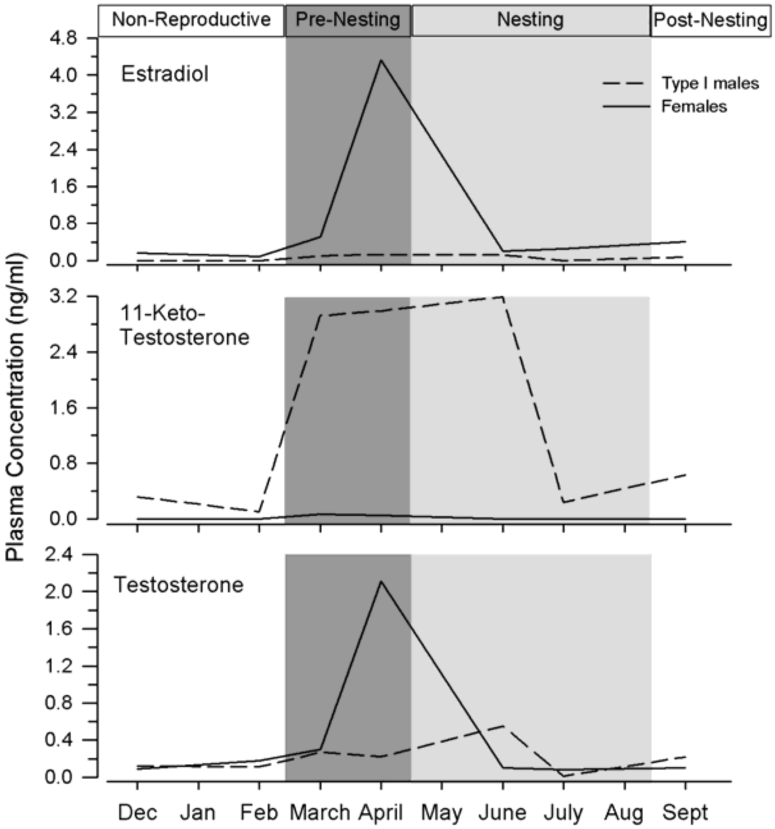

Figure 5 Plasma sex steroid levels for wild caught type I male and female midshipman fish collected from Monterey Bay and Tomales Bay, California during the nonreproductive, pre-nesting, nesting and post-nesting periods. Median steroid concentrations are plotted for both females and type I males. Note that a single peak of estradiol and testosterone in females prior to spawning reflects a single spawning event, while the maintenance of elevated levels of 11-keto-testosterone in males into the spawning (nesting) period reflects their continued courtship and spawning activity throughout the summer. Modified from Sisneros *et al.* (2004b).

individual. We subsequently discovered that ovariectomized winter females experimentally implanted with either T or E_2 capsules to simulate the spring pre-nesting steroid levels resulted in an increase in the phase-locking precision of the saccular afferents at higher frequencies that corresponded to the dominant higher harmonic components of the male's advertisement call (Sisneros *et al.* 2004a). These steroid-induced changes in frequency sensitivity were especially apparent at frequencies that corresponded to the second (approximately 200 Hz) and third (approximately 300 Hz) harmonics of the hum, which often contains either as much or more energy as the F_0 (approximately 100 Hz). Therefore, winter non-reproductive midshipman females treated with either T or E_2 exhibited an improvement in the precision of temporal encoding by the inner ear saccule to the dominant frequency components of male advertisement calls that mimicked the summer reproductive female's auditory phenotype (Fig. 6). This steroid-dependent plasticity of peripheral auditory frequency sensitivity in female midshipman fish may represent an adaptable mechanism that acts to increase the probability of detection, recognition and localization of mates during the breeding season by enhancing the frequency coupling between sender and receiver in this vocal communication system.

The mechanism(s) by which T and E_2 modulate peripheral frequency sensitivity in the midshipman is unknown and remains to be demonstrated. Similar adaptive shifts in peripheral frequency sensitivity are known to occur in the electroreceptor systems of weakly electric fish and elasmobranchs. The adaptive plasticity observed in the electric sense of weakly electric fishes and elasmobranch fishes is also modulated by circulating levels of gonadal steroids and the reproductive state of the animal. Previous work indicates that gonadal steroids can influence the tuning of tuberous electroreceptors in weakly electric fish (Meyer & Zakon 1982; Bass & Hopkins 1984) and the ampullary electroreceptors in elasmobranch fish (Sisneros & Tricas 2000). Experimental implants of T and dihydrotestosterone (DHT) are known to lower in tandem both the peak frequency sensitivity of tuberous electroreceptors and the discharge frequency of the electric organ in weakly electric fish so that the electrosensory and electromotor systems remain matched or "frequency coupled" for electrolocation and social communication (Meyer & Zakon 1982; Bass & Hopkins 1984; Keller *et al.* 1986). Previous studies indicate that the steroid-induced changes in the electromotor system are mediated by steroid receptors within the electrocytes of the electric organ (Bass *et al.* 1986; Dunlap *et al.* 1997; Dunlap & Zakon 1998, Few and Zakon 2001). These steroid-dependent changes are thought to result in the differential genomic expression of multiple ion channel types (e.g. Na^+ and/or K^+) that regulate the current kinetics of the electrocytes and es-

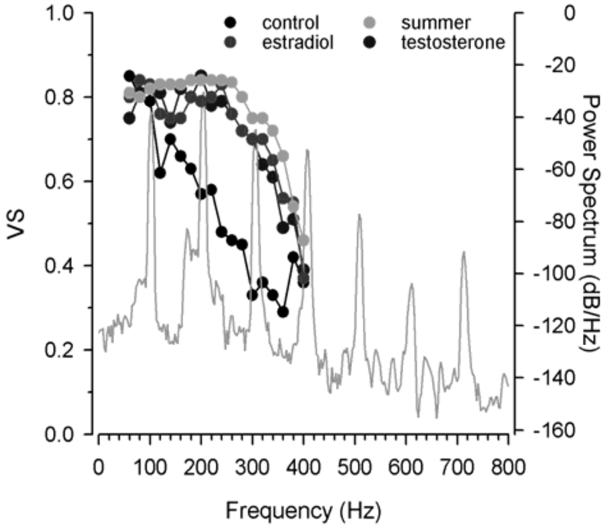

Figure 6 Adaptive plasticity of the peripheral auditory system in the midshipman fish that enhances coupling between sender and receiver for acoustic communication. Note the match between the vocal characteristics and the degree of frequency encoding of auditory saccular afferent neurons. Comparison of the power (amplitude) spectrum (right y-axis, in relative dB values) of the type I male advertisement call or "hum" recorded at 16°C and the phase-locking precision of saccular afferents as a function of vector strength of synchronization (VS, left Y axis). Frequency is plotted along the x-axis for both sets of measures. Median VS values of saccular afferents are plotted, emphasizing the overlap in frequency sensitivity between testosterone-treated (blue circles) and 17β-estradiol-treated (red circles) nonreproductive females and reproductive females (green circles). The saccular afferents of nonreproductive females (black circles) show robust encoding only for frequencies close to the fundamental frequency of the male's hum, whereas testosterone-treated, estradiol-treated, and reproductive females show robust encoding of the fundamental frequency and the second and third harmonics. Modified from Sisneros *et al.* (2004a).

tablish the sexually dimorphic electrocommunication signals produced by weakly electric fishes (Zakon 1987, 1996, 1998; Bass & Zakon 2005). As proposed for electroreceptors (Zakon 1987; Zakon *et al.* 1991), gonadal steroids may exert similar effects on the frequency selectivity of saccular hair cells by genomically upregulating the differential transcription of ion channels that affect hair cell current kinetics and the resultant electrical resonance that arises from the basolateral membrane of auditory hair cells. The electrical resonance of auditory hair cells is caused by the interaction between inward calcium and outward calcium-dependent potassium currents that produce an electrical oscillation of the receptor potential along the hair cell receptor epithelium (Lewis & Hudspeth 1983; Robert *et al.* 1988) and is considered to be the major contributing factor to hair cell frequency sensitivity or "selectivity" in non-mammalian vertebrates, including the toadfish (Steinacker & Romero 1991, 1992; Fettiplace and Fuch 1999).

FUTURE WORK

Two recent studies show that midshipman-specific estrogen receptor alpha has been identified in the midshipman peripheral auditory system in sites that include the saccular epithelium (Sisneros *et al.* 2004a) and in the auditory saccular nerve branches adjacent to the hair cell layer in the saccule (Forlano *et al.* 2005). These studies now provide support for a direct steroid effect on the inner ear. Therefore, a prime candidate site where this novel form of steroid-dependent auditory plasticity might occur is at the level of the saccular hair cell. Future studies that examine the expression of androgen receptors in the midshipman inner ear and characterize the frequency response and electrical resonance of receptor potentials from localized populations of saccular hair cells (Sisneros 2007) as well as from individual saccular hair cells in both non-reproductive and reproductive midshipman females will be instrumental in determining the possible mechanism(s) responsible for the steroid-dependent neurophysiological changes observed in the midshipman auditory periphery.

In addition to the saccular hair cells, another possible candidate site for the steroid-dependent changes in auditory frequency sensitivity that warrants future investigation includes the hindbrain efferent nucleus that directly innervates the midshipman inner ear (Bass *et al.* 1994). Saccular efferents provide inhibitory input from the central nervous system to hair cells and saccular afferents in the auditory periphery that can modulate their gain or auditory sensitivity (Furukawa & Matsura 1978; Lin & Faber 1988). Previous work has shown that auditory neurons in the mammalian cortex can modulate the frequency sensitivity of cochlear hair cells in the mustache bat (Xiao & Suga 2002). Therefore, future studies should examine both possible seasonal reproductive-state dependent and steroid-dependent effects of efferent modulation on the frequency sensitivity of the midshipman peripheral auditory system.

Currently, it is not known whether type I or type II midshipman males also exhibit reproductive state and/or steroid-dependent auditory plasticity. There is no a priori reason to expect that auditory plasticity be limited to females since the seasonal enhancement of conspecific detection and localization would also be adaptive for males during male–male competition for the establishment of nest sites and in the case of type II males for the selection of cuckoldry sites for satellite or sneak spawning. Therefore, future studies need to determine whether reproductive state and/or steroid-dependent auditory plasticity also occurs in males. In addition, similar mechanisms of auditory plasticity might also be operative in other vertebrate groups: studies have suggested either seasonal or steroid-related changes in audition, including recent studies of birds (Lucas *et al.* 2002, 2007), amphibians (Goense & Feng 2005) and humans (Guimaraes *et al.* 2006).

Studies of the vocal-acoustic behavior, neurophysiology and behavioral neuroendocrinology of the midshipman fish reviewed here have established that the midshipman fish as an excellent model for identifying the reproductive-state and steroid-dependent neural mechanisms responsible for auditory plasticity. This novel form of steroid-dependent auditory plasticity observed in the midshipman provides an adaptable mechanism that enhances the coupling between sender and receiver in vocal communication. Future neurophysiological and neuroendocrine studies of the midshipman auditory system might reveal novel mechanisms responsible for steroid-dependent auditory plasticity that might be common to all vertebrates, including humans.

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