Hearing Research 252 (2009) 9–14

Contents lists available at ScienceDirect

Hearing Research

journal homepage: www.elsevier.com/locate/heares

Research Papers

Steroid-dependent auditory plasticity for the enhancement of acoustic communication: Recent insights from a vocal teleost fish

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ARTICLE INFO

Article history:
Received 20 September 2008
Received in revised form 2 December 2008
Accepted 29 December 2008
Available online 6 January 2009

Keywords:
Saccule
Sex steroids
Tuning
Hair cells
Inner ear

ABSTRACT

The vocal plainfin midshipman fish (*Porichthys notatus*) has become an excellent model for identifying neural mechanisms of auditory perception that may be shared by all vertebrates. Recent neuroethological studies of the midshipman fish have yielded strong evidence for the steroid-dependent modulation of hearing sensitivity that leads to enhanced coupling of sender and receiver in this vocal-acoustic communication system. Previous work shows that non-reproductive females treated with either testosterone or 17β-estradiol exhibit an increase in the degree of temporal encoding by the auditory saccular afferents to the dominant frequency content of male vocalizations produced during social-reproductive behaviors. The expanded frequency sensitivity of steroid treated females mimics the reproductive female's auditory phenotype and is proposed to improve the detection and localization of calling conspecific mates during the summer breeding season. This review focuses on the novel form of steroid-dependent auditory plasticity that is found in the adult midshipman fish and its association with the reproductive biology and behavior of this species. Evidence for midshipman reproductive-state and steroid-dependent auditory plasticity is reviewed and the potential mechanisms that lead to this novel form of adaptive plasticity are discussed.

1. Introduction

Steroid hormones have profound effects on the vertebrate CNS that can ultimately influence the expression of social behaviors in adults. Activating hormones modulate behavior by inducing a suite of morphological and physiological changes in the CNS that can shape the expression of adaptive behaviors necessary for reproduction and survival. Many vocal-acoustic behaviors which are expressed during courtship and reproduction and used for acoustic communication are good examples of adaptive social behaviors that are steroid sensitive. The vocal control network and auditory system of vertebrates are known to be greatly influenced by an animal's external (e.g. social environment and/or photoperiod) and internal (reproductive/endocrine) state. In the context of communication, the animal's internal endocrine state is often an important determinant of the type of communicative signal that is transmitted by a sender and how that signal is encoded and perceived by a conspecific receiver. It is in this context that I will review how steroid hormones modulate the production and perception of vocal-acoustic signals in an ancestral group of vertebrates from a single family of teleost fishes, the batrachoididae (the midshipman fishes and toadfishes). Recently, these batrachoidid fishes have revealed novel insights into steroid dependent mechanisms that enhance the production and perception of auditory signals used during social communication.

This review primarily focuses on the adaptive plasticity of the adult auditory system in the plainfin midshipman fish (*Porichthys notatus*) that occurs during its natural reproductive cycle and the associated activating effects of gonadal steroids on the response properties of the midshipman peripheral auditory system. There are two main parts to this review. The first part is primarily a review of the evidence for reproductive-state and steroid-dependent plasticity of auditory frequency sensitivity in the plainfin midshipman fish. The second part of this review addresses the potential steroid dependent mechanisms responsible for the plasticity in the midshipman auditory system and discusses current and future directions for work in this field.

2. The midshipman fish as a model system

During the past twelve years, a number of studies have characterized the neural and behavioral mechanisms of acoustic communication in the plainfin midshipman fish and have established the

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doi:10.1016/j.heares.2008.12.007

vocal plainfin midshipman fish as a model system for investigating the neural basis of auditory communication in all vertebrates (Bodnar and Bass, 1997; McKibben and Bass, 1998, 1999; Bass et al., 1999, 2005; Weeg et al., 2002; Bass and McKibben, 2003; Bass, 2006; Bass and Lu, 2007; Sisneros, 2007). One of the attractive features of the plainfin midshipman fish as a model for studying vertebrate vocal-acoustic communication is that this fish produces a rather simple repertoire of acoustic signals for intraspecific communication. The highly stereotyped vocal signals are produced by three different adult plainfin midshipman morphs that include females and two types of male morphs (type I and type II). Type I males are capable of generating the three known types of vocal communication signals for this species: the grunt, growl and hum (Bass et al., 1999; Bass and McKibben, 2003). Grunts are broadband acoustic signals that are short in duration (50–200 ms) and are used in agonistic contexts (Bass et al., 1999; Bass and McKibben, 2003). Reproductive type I males are known to produce trains of grunts composed of a rapid series of single grunts that are used to fend off potential nest intruders during the breeding season. Growls are another type of agonistic call that are multi-harmonic and relatively long in duration (>1 s) compared to grunts. Growls have an initial grunt-like component at the onset of the call that is then followed immediately by a multi-harmonic segment that has a fundamental frequency of 59–116 Hz that gradually changes throughout the duration of the call (Bass et al., 1999). The third type of vocalization known as the "hum" is a seasonal advertisement call only produced by reproductively active type I males during the breeding season to attract females for spawning. Hums are very long duration continuous advertisement calls (on the order of seconds to minutes and can be sustained as long as one hour in duration, pers. comm. A.H. Bass) that have fundamental frequencies that range from 90 to 100 Hz and typically contain several prominent harmonics that range up to 400 Hz. The fundamental frequency of the hum is highly stable and varies linearly with temperature (Bass and Baker, 1991; Brantley and Bass, 1994). Female and type II male midshipman do not produce hums or growls but are capable of producing single short duration grunts during agonistic encounters in non-spawning contexts.

Neurophysiological studies of the plainfin midshipman fish have shown that the midshipman peripheral and central auditory systems are well adapted to encode biological relevant signals similar to the natural vocal signals it produces during social and reproductive behaviors (Bodnar and Bass, 1997, 1999; Sisneros and Bass, 2003, 2005; Bass et al., 2005; Sisneros, 2007). The inner ear of the plainfin midshipman fish is composed of the three semicircular canals with their associated sensory regions (cristae ampullaris) and three otolithic end organs: the saccule, lagena and utricle. In contrast to its primarily vestibular function in tetrapods, the saccule is the main organ of hearing in the plainfin midshipman fish and is innervated by the eighth cranial nerve (Bass et al., 1994). However, saccular afferents of other vertebrates including amphibians and mammals are known to respond to acoustic stimuli (Lewis et al., 1982; McCue and Guinan, 1994).

In previous studies, the frequency response properties of midshipman saccular afferents have been quantitatively described using a variety of measures that include post-stimulus time histograms and iso-intensity response curves based on both average evoked spike rate and synchronization (phase-locking) based the vector strength of synchronization, which show the degree of phase-locking response to a stimulus waveform (McKibben and Bass, 1999, 2001a; Weeg et al., 2002; Sisneros and Bass, 2003, 2005). Midshipman saccular afferents from non-reproductive fish are broadly tuned with a peak-frequency response that is well suited to detect the low frequency components of midshipman vocalizations (McKibben and Bass, 1999; Sisneros and Bass, 2005). The auditory saccular afferents also show considerable variation in resting discharge activity, response time course, i/o intensity response curves and single tone suppression (McKibben and Bass, 1999; Sisneros and Bass, 2005). Iso-intensity response curves based on either average evoked spike rate or vector strength of synchronization (VS) show that best frequencies range from 60 to over 300 Hz with thresholds at 60 Hz ranging from 97 to 118 dB re 1 μPa (McKibben and Bass, 1999; Sisneros and Bass, 2003). In general, VS is thought to be a more accurate measure for the temporal encoding of frequency than average evoked spike rate, especially for frequencies <1 kHz in teleost fishes including the plainfin midshipman fish and the oyster toadfish, *Opsanus tau* (Fay, 1978, 1982; McKibben and Bass, 1999, 2001a).

More recently, the frequency response and auditory sensitivity of hair cells in the saccule of non-reproductive adult plainfin midshipman fish were determined using an evoked potential recording technique (Sisneros, 2007). Saccular potentials were recorded from populations of hair cells *in vivo* while sound was presented by an underwater speaker. Results indicated that midshipman saccular hair cells of non-reproductive adults had peak-frequency sensitivities that ranged from 75 (lowest frequency tested) to 145 Hz and were best suited to detect frequencies less than 105 Hz. Together, the studies of saccular potentials and afferents show that the frequency sensitivity of the peripheral auditory system in non-reproductive midshipman fish is well suited to encode the low frequency content of conspecific vocalizations.

3. Adaptive hearing in the midshipman fish

Plainfin midshipman fish migrate seasonally from deep offshore along the Pacific coast of the western United States into the shallow sub-tidal and intertidal zones where they court and spawn in the late-spring and summer (Miller and Lea, 1972; Bass, 1996). During this seasonal reproductive period, "singing" type I males produce their advertisement call or hum at night to attract reproductive females into their nests positioned under rocky shelters. Behavioral studies from the lab of Andrew Bass at Cornell University on the midshipman spawning behavior and the sound playback responses to natural and synthetic hums show that reproductive females that are "gravid" (containing ripe eggs) exhibit strong phonotactic responses to the hum, whereas females that are "spent" (containing little or no eggs) no longer respond to the hum (Brantley and Bass, 1994; McKibben and Bass, 1998, 2001b). Based on these behavioral observations, we tested the hypothesis that seasonal variation in female reproductive-state (gravid vs. spent) influenced the neurophysiological response properties of the midshipman auditory system (Sisneros and Bass, 2003). Our results showed that the saccular afferents of females exhibited a higher phase-locking accuracy to a broad range of frequencies (120–400 Hz) and had higher best frequencies during the summer breeding season when females were gravid than during the non-breeding winter season when females were non-gravid (Fig. 1) (Sisneros and Bass, 2003).

Comparisons of the hearing frequency sensitivity between gravid and non-gravid females revealed that summer reproductive females were better suited than winter non-gravid females to detect the higher harmonic components of the type I male's advertisement call, especially those harmonics that ranged from 180 to 420 Hz, where significant portion of the energy in the call is contained. We proposed that the functional significance for this seasonal plasticity of hearing sensitivity in the female plainfin midshipman fish was for the increased detection and localization of mates. The summer enhancement of phase-locking accuracy by the saccular afferents improves the detection of the dominant frequencies in the hum and thus should increase the probability of detecting and locating a mate, especially in shallow water and sometime noisy environments like those where plainfin midshipman fish court and breed.

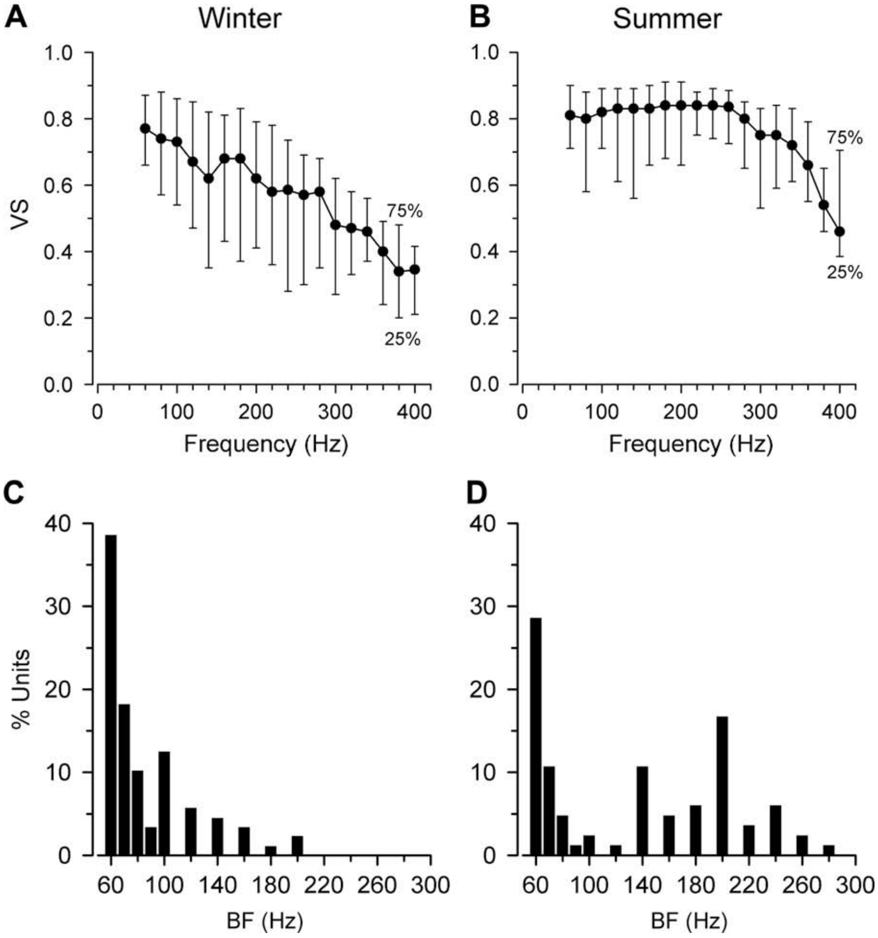

Fig. 1. Iso-intensity response curves and best frequency histograms of auditory saccular afferent neurons recorded from a wild population of female midshipman fish. Adult females were collected during the non-reproductive winter (left column) and reproductive summer (right column) seasons. (A and B) Response curves of saccular afferents to 130 dB (re 1 μPa) iso-intensity tones based on vector strength of synchronization (VS) that show the VS values for each frequency tested in terms of median (black circles), 25th percentile (bottom bar), and 75th percentile (top bar). (C and D) Distribution of best frequencies (BF) for saccular afferents of winter non-reproductive (C) and summer reproductive (D) females based on VS to iso-intensity tones of 130 dB (re 1 μPa). Median BF was higher for summer females (95 Hz) than winter females (80 Hz). Adapted from Sisneros and Bass (2003).

The hum's harmonics likely afford greater signal detection of the mate call by the receiver because the higher frequency harmonics of the hum will propagate further than the hum's fundamental frequency in shallow water due to the inverse relationship between water depth and the cutoff frequency of sound transmission (in other words, as water depth decreases, the cutoff frequency increases) (Fine and Lenhardt, 1983; Roger and Cox, 1988; Bass and Clark, 2003). In very shallow water (<5 m), substrate composition (e.g. the rocky substrate like that of the nesting material found in intertidal zone) is also likely to influence the cutoff frequency of sound transmission (or the frequency below which sound transmission is negligible) and affect long range acoustic signals with energy below 500 Hz (Roger and Cox, 1988; Bass and Clark, 2003). The higher harmonics of the midshipman's hum may also affect the encoding of the hum's fundamental frequency and be important for mate localization when near the sound source. Previous work by McKibben and Bass (2001a) shows that the encoding of the hum-like fundamental frequency by saccular afferents is enhanced when harmonics are added to tonal stimuli. Thus, the seasonal plasticity of female auditory frequency sensitivity may represent an adaptation of the midshipman's auditory system to improve detection of the multi-harmonic hums and enhance the acquisition of auditory information for species recognition, mate identification, and localization during the breeding season.

4. Steroid-dependent modulation of the auditory sense

In wild populations of plainfin midshipman fish, gonadal steroid levels are known to seasonally fluctuate with the animal's annual reproductive cycle, which corresponds to seasonal changes in their reproductive biology and behavior (Brantley et al., 1993; Knapp et al., 1999; Sisneros et al., 2004a). In midshipman females, seasonal variation of steroid hormone levels occurs during four time periods that include the non-reproductive, pre-nesting, nesting and post-nesting periods (Fig. 2) (For a more detailed description of seasonal steroid level changes in type I males, see Sisneros et al., 2004a). The non-reproductive period occurs during the winter months of December–February when females have low plasma levels of testosterone (T) and 17β-estradiol (E_2) and a corresponding low gonadal somatic index (GSI) with ovaries containing only small (<1 mm diameter) undeveloped ooyctes. The pre-nesting period occurs during the spring from March to April when females undergo a seasonal recrudescence of the ovaries and exhibit a brief annual peak of T and E_2 levels during April, about one month prior to when females are first found in the nests of type I males during the breeding season. The nesting period occurs during late-spring and summer from May to August when gravid females with well developed eggs (~5 mm diameter) have with low levels of T and E_2 but a high GSI. The post-nesting period occurs during the fall months from

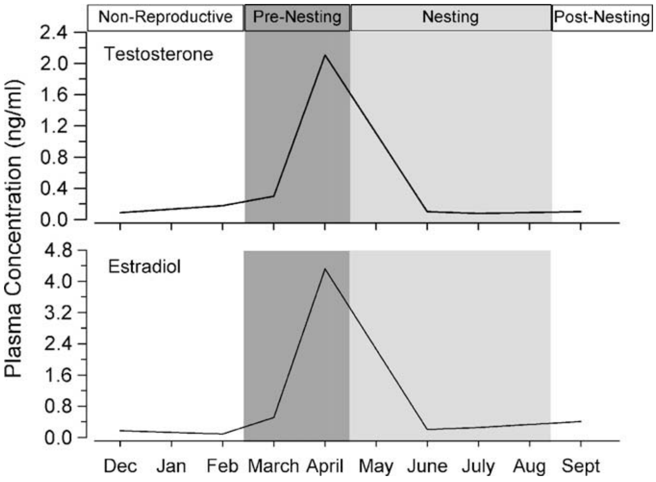

Fig. 2. Summary diagram of steroid hormone levels for wild-caught female plainfin midshipman fish collected during the non-reproductive, pre-nesting, nesting and post-nesting periods from Monterey Bay and Tomales Bay, CA. Median steroid concentrations (ng/ml) are plotted. Adapted from Sisneros et al. (2004a).

September to October and is marked by decreased plasma levels of E_2 and T and low GSI.

Based on the observation that females exhibit a spring pre-nesting peak of E_2 and T levels approximately one month before the summer spawning season (Fig. 2), we tested the hypothesis that T and E_2 can induce increases in the phase-locking accuracy and best frequency of saccular afferents in non-reproductive female midshipman fish. We subsequently discovered that ovariectomized winter non-reproductive females implanted with either T or E_2 capsules that elevated the steroid levels to that of pre-nesting levels resulted in an increase in phase-locking accuracy of the saccular afferents at higher frequencies within the midshipman's hearing range (Sisneros et al., 2004b). The steroid-induced changes in auditory frequency sensitivity were especially apparent at the higher frequencies that corresponded to the second (~200 Hz) and third (~300 Hz) harmonics of the hum, which are the dominant harmonic components of the call and often contains either as much or more energy as the hum's fundamental frequency (~100 Hz). Thus, winter non-reproductive midshipman females treated with either T or E_2 exhibited an enhancement in the temporal encoding of the dominant frequency components of male hum that mimicked the summer reproductive female's auditory phenotype (Fig. 3). Furthermore, midshipman-specific estrogen receptor alpha (ERα) receptor (Fig. 4) was identified in the saccular epithelium of the inner ear by reverse transcription polymerase chain reaction and the use of midshipman-specific primers from an ERα clone (Sisneros et al., 2004b). This first demonstration of steroid-dependent plasticity at the level of the primary auditory filter in the female midshipman fish represents an adaptable mechanism that acts to enhance the coupling of sender and receiver in this vocal communication system and may ultimately increase the probability of the detection, recognition and localization of conspecific mates during the breeding season.

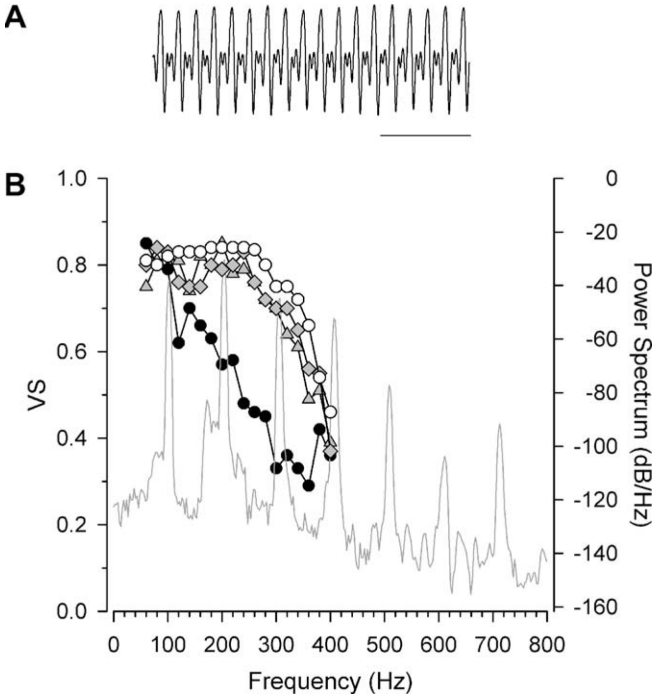

Fig. 3. Match between the degree of frequency encoding of the auditory saccular afferents and the vocal characteristics of the advertisement call in the plainfin midshipman fish. (A) Representative example of the type I male midshipman advertisement call or "hum" recorded at 16 °C. Bar, 10 ms. (B) Combined plot of the phase-locking precision of saccular afferents as a function of the vector strength of synchronization (VS, left *y*-axis) and the power (amplitude) spectrum of the hum (right *y*-axis, in relative dB values) from a nesting type I male midshipman. Plotted are the median VS values of the saccular afferents emphasizing the overlap in frequency sensitivity between testosterone-treated (gray triangles) and 17β-estradiol-treated (gray diamonds) non-reproductive females and wild-caught reproductive females (white circles). Steroid-treated and wild-caught reproductive females show robust encoding of the fundamental frequency (~100 Hz) and the second (~200 Hz) and third (~300 Hz) harmonics of the hum. In contrast, winter non-reproductive females (black circles) show comparable encoding only for frequency close to the fundamental frequency at approximately 100 Hz. Adapted from Sisneros et al. (2004b).

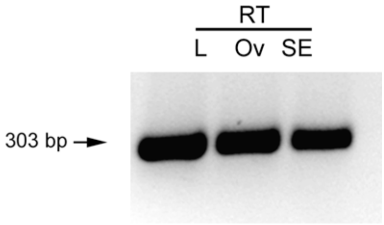

Fig. 4. Estrogen receptor alpha (ERα) in the saccule of the midshipman inner ear. Identification of ERα expression in the saccular epithelium (SE) by reverse transcription polymerase chain reaction (RT-PCR) using midshipman-specific primers from an ERα clone. A predicted 303-base pair (bp) product is observed in the SE and also in positive control tissues of liver (L) and ovary (Ov). Note: the SE tissue samples also contained auditory eighth nerve branches with ganglion cells that were proximal to the SE hair cell layer and were pooled from four ovariectomized female plainfin midshipman fish that were implanted with E_2 and allowed to survive 4–6 weeks. Adapted from Sisneros et al. (2004b).

5. Potential mechanisms for steroid-dependent plasticity of auditory sensitivity

The mechanism(s) responsible for the steroid-dependent auditory plasticity found in the midshipman are still unknown and remained to be determined. One of the first steps in elucidating such mechanisms is to determine the site of action for steroid hormones in the midshipman auditory system. Recent studies of the midshipman inner ear saccule show that midshipman-specific ERα is expressed in peripheral auditory sites that include the saccular epithelium and in the saccular nerve branches that are proximal to the saccular epithelium (Sisneros et al., 2004a; Forlano et al., 2005). Results from these studies suggest that there maybe a direct steroid effect on the midshipman inner ear. Thus, a prime candidate site for the site of action for this novel form of steroid-dependent auditory plasticity is at the level of the auditory hair cell.

Activating steroid hormones and their direct effects on sensory receptors have been proposed for similar steroid-related changes in the frequency sensitivity of electroreceptors in weakly electric fishes (Zakon, 1987; Zakon et al., 1991). The electric sense of weakly electric and elasmobranch fishes is known to be modulated by the reproductive-state of the animal and its natural circulating levels of gonadal steroids (Meyer and Zakon, 1982; Bass and Hopkins, 1984; Sisneros and Tricas, 2000). In weakly electric fish, experimental implants of dihydrotestosterone lower the frequency sensitivity of tuberous electroreceptors and the discharge frequency of the tail's electric organ in tandem so that the electrosensory and electromotor systems remain matched or "coupled" for social communication and electrolocation (Meyer and Zakon, 1982; Bass and Hopkins, 1984; Keller et al., 1986). Steroid-induced changes in the electromotor system are mediated by hormone receptors within the electrocytes that affect the biophysical properties of Na+ and K+ currents (i.e. inactivation rate of Na+ channels and activation rate of K+ channels) of the electric organ and are thought to be genomicaly regulated by the differential expression of Kv1 and two different Na+ channel genes with its associated β subunits (Bass et al., 1986; Dunlap et al., 1997; Dunlap and Zakon, 1998; Few and Zakon, 2001; Bass and Zakon, 2005). Consequently, it is the steroid-induced changes in the electrocytes of the electromotor system that establishes the sexually dimorphic electrocommunication signals that produced by weakly electric fishes (Zakon, 1987, 1996, 1998; Bass and Zakon, 2005).

As proposed for electroreceptors (Zakon, 1987; Zakon et al., 1991), steroid hormones may exert similar effects on the frequency sensitivity of auditory hair cells in the midshipman fish by genomically up regulating the differential expression of multiple ion-channel genes (e.g. calcium-dependent BK and Kv channel genes) and/or related subunits that influence the biophysical properties of hair cells, which in turn can affect the electrical resonance of saccular hair cells. Hair cell electrical resonance is caused by the interaction between inward calcium and outward Ca+-dependent K+ currents that produce an electrical oscillation of the receptor potential along the hair cell receptor epithelium (Lewis and Hudspeth, 1983; Roberts et al., 1988). In general, the electrical resonance that arise from the ion-channel current kinetics of the basolateral membrane of auditory hair cells is considered to be the major contributing factor that establishes the low frequency tuning (<1 kHz) of hair cells in non-mammalian auditory systems (Fettiplace and Fuch, 1999) including the oyster toadfish, *Opsanus tau* (Steinacker and Romero, 1991, 1992), a close relative of the plainfin midshipman fish. Alternatively, steroid hormones could induce changes in auditory hair cell morphology (i.e. changes in hair cell membrane resistance and capacitance) that in turn change the high-pass frequency tuning characteristics of the saccular afferents. This alternative explanation of induced changes in hair cell morphology, may in part, account for the minimum T or E_2 implant duration of 23 days needed before changes in saccular afferent tuning are observed in female midshipman fish (Sisneros et al., 2004b).

Alternative candidate sites for the steroid-dependent effects on the frequency response properties of the midshipman auditory system include the saccular afferents and hindbrain efferent nuclei. The gonadal steroids T and E_2 may have direct effects on the auditory saccular afferents that are post-synaptic to the hair cells in the saccular epithelium. Recent work by Forlano et al. (2005) provides evidence for the expression of ERα mRNA just outside the saccular hair cell layer and aromatase-ir ganglion cells in the branches of the VIIIth auditory nerve that are adjacent to the hair cell layer in the saccule. In addition, saccular efferents which project from hindbrain efferent nuclei and directly innervate the midshipman inner ear (Bass et al., 1994) may offer other steroid sensitive sites that may potentially affect peripheral auditory processing. Saccular efferents provide inhibitory input from the CNS to saccular afferents and hair cells in the auditory periphery that can modulate the gain or sensitivity of the inner ear saccule (Furukawa and Matsura, 1978; Lin and Faber, 1988). Xiao and Suga (2002) have shown in the mustache bat that mammalian auditory neurons in the cortex can modulate the frequency sensitivity of cochlear hair cells out in the auditory periphery. Thus, future studies that examine potential steroid sensitive sites in both the peripheral and central auditory system will be instrumental in determining the neural substrates and mechanism(s) responsible for the steroid-dependent neurophysiological changes observed in the midshipman auditory system.

6. Concluding remarks

As reviewed here, previous studies of the vocal-acoustic behavior, neurophysiology, and endocrinology of the plainfin midshipman fish have established this ancestral vertebrate as an excellent model for identifying neural mechanisms of auditory perception that may be shared by all vertebrates. This well established vocal-acoustic midshipman model has yielded strong evidence for the steroid-dependent modulation of frequency sensitivity in the vertebrate peripheral auditory system. Similar mechanisms of auditory plasticity may also be operative in other vertebrate hearing models where studies have suggested seasonal and/or steroid-related changes in hearing sensitivity, which includes recent studies of birds, amphibians and humans (Lucas et al., 2002, 2007; Goense and Feng, 2005; Guimaraes et al., 2006, but also see other papers in this special issue on Sex Hormones and Hearing). The novel form of auditory plasticity observed in the plainfin midshipman fish and its yet unknown mechanism will no doubt provide the basis for exciting future discoveries that may reveal novel mechanisms of auditory plasticity common to all vertebrates, including humans.

Acknowledgments

Research support for work reported here was provided by the National Institutes of Health (1F32DC00445) and a Royal Research Fund grant from the University of Washington.

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