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Adaptive auditory plasticity for social communication in the plainfin midshipman fish (*Porichthys notatus*)

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Acoustic communication plays an important role in the social behaviours of vocal teleost fishes in the family Batrachoididae (midshipman and toad fishes). The midshipman and toadfishes have become good models for investigating the neural and endocrine mechanisms of auditory perception and vocal production shared by all vertebrates (Bass and Lu 2006), in part, because the reproductive success of these batrachoidid fishes is highly dependent on acoustic communication. Recent neuroethological studies of acoustic communication in the plainfin midshipman fish (*Porichthys notatus*) have provided strong evidence for the related reproductive-state and steroid-dependent modulation of hearing sensitivity in this species that leads to enhanced coupling of sender and receiver in this communication system (Sisneros and Bass 2003; Sisneros et al. 2004a).

The plainfin midshipman fish is a vocal marine teleost fish found along the west coast of the USA. During the late spring and summer, midshipman fish migrate from deep water into the rocky intertidal zone to court and spawn. Midshipman fish are known to have three adult reproductive morphs that include female and two male morphs known as type I and II. Type I or 'singing' males acoustically court females with their seasonal advertisement calls or 'hums', which is a multiharmonic acoustic signal with a fundamental frequency (F_0) that ranges from 90 to 100 Hz (Brantley and Bass 1994). The dominant harmonics of the hum range up to 400 Hz and can contain as much or more spectral energy than the F_0. These harmonics have been hypothesized to be important for the detection and localization of the advertisement signal during the reproductive season (Sisneros and Bass 2003). Type II males or 'sneaker' males use an alternative reproductive tactic that does not require them to build nests or acoustically court females. Instead type II males satellite and/or 'sneak' spawn in the nests of type I males to steal fertilizations from 'singing' males when they are actively courting females. Females rely heavily on their auditory sense to detect and locate advertising males that produce the multiharmonic hums during the breeding season and will often exhibit robust phonotaxis to a synthesized hum (and even to a low frequency tone near the F_0 of the male's advertisement call).

Previous work showed that the frequency sensitivity of the auditory afferents that innervated the saccule, the main organ of hearing in the midshipman, changed seasonally with reproductive state such that reproductive females were better suited than non-reproductive females to encode the dominant harmonics of the male's advertisement call (Sisneros and Bass 2003). An investigation of the seasonal periodicity of reproduction

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and steroid hormone levels in *P. notatus* revealed that females exhibited peaks in circulating plasma levels of testosterone and estradiol approximately one month before the spawning season (Sisneros et al. 2004b). Experimental implants of testosterone and separately with estradiol in ovariecotomized females confirmed a steroid-dependent effect and induced the reproductive auditory phenotype in females and enhanced frequency sensitivity to the dominant higher harmonic components in the male's advertisement call (Sisneros et al. 2004a). In addition, midshipman-specific oestrogen alpha receptor was identified in the saccular epithelium by reverse transcription polymerase chain reaction and the use of midshipman-specific primers from an oestrogen alpha receptor clone. More recently, midshipman-specific androgen receptor was also been identified in the saccule (Forlano et al. 2010).

More recently, Sisneros (2009) examined the evoked response properties of midshipman saccular hair cells from non-reproductive and reproductive females to test the hypothesis that seasonal reproductive-dependent changes in saccular afferent tuning is paralleled by similar changes in saccular sensitivity at the level of the hair cell. Saccular potentials of non-reproductive and reproductive females were compared to determine whether reproductive state affects the frequency response and threshold of the saccule to behaviourally relevant single tone stimuli. Results indicated that the saccular hair cells from reproductive females had thresholds that were approximately 8 to 13 dB lower than non-reproductive females across a broad range of frequencies (75–385 Hz) that included the dominant higher harmonic components and the F_0 of the male's mate call.

In sum, the results from previous and recent work suggest that the related reproductive-state and steroid-dependent plasticity of auditory sensitivity in the midshipman fish may occur at the level of the saccular hair cell. This novel form of reproductive-state and steroid-dependent auditory plasticity may represent an adaptive mechanism that increases the probability of the detection, recognition, and localization of conspecific mates during the breeding season and could potentially enhance the acquisition of auditory information needed for mate choice decisions during courtship and reproduction. Similar mechanisms of auditory plasticity may also be operative in other vertebrate groups were studies have suggested either seasonal or steroid-related changes in the hearing of birds (Lucas et al. 2002), amphibians (Goense and Feng 2005, Gordon and Gerhardt 2009) and humans (Hultcrantz et al. 2006).

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