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Research Note

Visually mediated inhibition of lateral line primary afferent activity by the octavolateralis efferent system during predation in the free-swimming toadfish, *Opsanus tau*

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Summary. The activity of single lateral line afferent neurons was chronically recorded in free-swimming toadfish. CNS efferent neurons, known to be inhibitory upon peripheral lateral line mechanoreceptors, were activated by stroboscopic and natural visual stimuli. Discharges from irregular-type afferents caused by water movement relative to lateral line neuromasts decreased following stroboscopic stimulation of unrestrained and behaving fish. Visual presentation of natural prey also decreased mechanically evoked afferent firing rates. We show that visual stimuli can activate the efferent system and function in the peripheral processing of mechanical stimuli to the lateral line in biologically relevant contexts.

Key words: Efferent – Lateral line – Lateralis – Octavolateralis – Prey detection – Toadfish – Vestibular

Introduction

Efferent neurons in the teleost brainstem project to all peripheral sensory organs of the eighth and lateral line nerves (Bell 1981; Highstein and Baker 1986; Meredith and Roberts 1987) where they make axo-somatic contact on the base of mechanosensory hair cells or axo-axonic contact directly upon primary afferent neurons (Flock 1965; Nakajima and Wang 1974; Hama 1978; Sans and Highstein 1984). In the fish lateral line, hair cells are grouped in neuromasts located on the skin surface (superficial neuromasts) or within subdermal canals (canal neuromasts), respond to local water movements relative to the body surface, and serve biological functions for schooling behavior, localization of underwater objects, and prey detection (reviewed by Coombs et al. 1989). In the dogfish and burbot, electrical stimulation of lateral line *efferents* inhibits spontaneous and mechanically evoked lateral line *afferent* discharges and is hypothesized to prevent transmitter depletion from sensory hair cells of lateral line organs during locomotion or vigorous movements (Russell and Roberts 1972; Flock and Russell 1973; 1976).

Acute experiments on numerous fish species demonstrate that octavolateralis efferents can be activated via polysynaptic pathways by visual stimuli (Klinke and Schmidt 1970; Spath and Schweickert 1975; Hartmann and Klinke 1980). In the toadfish, efferent action on peripheral sensory afferents can be evoked by behavioral stimuli (including visual) and is abolished when the efferent vestibular nerve is severed (Highstein and Baker 1985). Behavioral and electrical activation of the efferent system have similar actions upon vestibular afferents (Boyle and Highstein 1990).

Despite the well-documented actions of octavolateralis efferents upon peripheral sensory organs, no previous study has identified natural stimuli in a biologically relevant context which activate the efferent system. Further, lateral line efferent effects upon sensory transduction in an alert unrestrained animal have not been previously demonstrated. To address these questions we used the oyster toadfish *(Opsanus tau)*, a common sedentary inhabitant of the northwest Atlantic coastline. During daylight hours this species sits at rest on the bottom and uses a visually-mediated ambush predator

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strategy to feed upon small fishes (Phillips and Swears 1979). We developed a recording technique that permits behavioral activation of the efferent system by visual stimuli from natural prey while recording its effect upon sensory transduction in single lateral line primary afferents.

Methods

Long-term extracellular records (up to two weeks) were obtained from 15 primary afferents in eight toadfish with an electrolytically sharpened and insulated tungsten wire (0.005 in. diam.) electrode mounted in a micromanipulator. The manipulator consisted of a nylon sleeve (3 mm diam. × 11 mm L) threaded at one end that held a stainless steel screw attached by a ball-and-socket joint to a sliding nylon slug. Unit signals were carried from the electrode to a small external preamplifier (300–10kHz bandpass) by a fine insulated silver wire that passed within the wall of the micromanipulator sleeve.

Adult toadfish (20–25 cm total length) were collected near Woods Hole, Mass. USA, lightly anesthetized with methansulfonate, and immobilized with pancuronium bromide. Fish were clamped in a shallow tank filled with seawater to the top of the gills and perfused through the mouth with running seawater. A small craniotomy (4–5 mm diam.) was made dorsal to the root of the anterior lateral line nerve and a reference electrode wire set 1–2 mm away from the recording site. The micromanipulator was then positioned dorsal to the anterior lateral line nerve, fixed to the skull with dental acrylic, and the incision sutured in layers. The preamplifier was sutured on the dorsal midline caudal to the manipulator and passed unit analog signals by 0.5 mm diam. insulated wire to standard amplification, display, and audio monitor equipment. After electrode implantation, fish were removed from the surgical tank and placed in a shallow experimental tank (50 cm L × 40 cm W × 15 cm D) supplied with circulating sea water. Fish showed no adverse affects from the surgery, exhibited normal swimming, feeding, and aggressive behavior within a few hours following release, and had long term survival (months).

A broad band vibration applied to the base of the tank was used in some experiments to mechanically activate neuromasts and raise the discharge rates of primary afferents. A video camera mounted directly above the tank monitored for any movement by the fish during experiments that could influence lateral line afferent discharge patterns. Unit and stimulus events were recorded on the audio tracks (20–20kHz frequency response) of the video recorder. A small fiber optic light was used to illuminate the margin of one operculum to aid in video monitoring of respiratory activity in the dark.

Two experimental paradigms were used to activate the efferent system by visual stimuli in toadfish implanted with chronic electrodes that recorded from lateral line primary afferents. In the first, stroboscopic flash trains (60–100 flashes per s) were delivered from above the tank to dark adapted fish. In the second, the efferent system was activated with visual stimuli from natural prey. A small killifish *(Fundulus heteroclitus)*, a natural prey for the toadfish (Chrobot 1959), was enclosed in a clear plastic chamber (15 cm W × 6 cm H × 4 cm D) in order to mask all chemical, mechanical, and tactile cues, and then concealed behind an opaque partition positioned in front of the resting toadfish. Afferent neuron activity was recorded for a 2-minute prestimulus period as toadfish sat motionless in front of the partition that was subsequently raised to present the prey and then lowered to conceal it again. Because swimming motion may produce destructive interactions with mechanical stimuli to lateral line neuromasts and can obscure efferent effects upon afferent activity (Russell and Roberts 1974), only data from experiments in which the toadfish did not move following visual stimulation (as viewed on video records) were used in the analyses.

Results

Primary afferents of the toadfish lateral line can be classified by their spontaneous interspike intervals into four classes: irregular, regular, burster, and silent (Tricas and Highstein, unpublished data). The topographic location of individual superficial neuromasts or the canal segment that enclosed canal neuromasts associated with each lateral line afferent neuron could be located by lightly probing the head with a fine jet of water or a 1-mm diameter bead attached to a fine wire. Resting discharges of most recorded lateral line afferents were modulated by respiratory motions of the operculum; this modulation could be extinguished by restraining opercular motion with a probe. We used the low frequency mechanical stimulus, i.e. opercular motion, to verify that visual stimuli could activate the lateral line efferent system in the toadfish sufficiently to affect lateral line peripheral receptors. Following stroboscopic stimulation, discharges of irregular-type fibers that were phase locked to water motion across the operculi during the respiratory cycle consistently demonstrated a decrease in gain to mechanically evoked stimulation. This inhibitory effect was clearly independent of the amplitude of respiratory ventilations (Fig. 1). By recording from afferent neurons that innervated single neuromasts located on the operculum, we were able to quantify a proportional measure of water flow parallel to the skin surface which activated the neuromast. Since the rhythmic opercular movements (and thus the water flow across the neuromast) were quantitatively similar before, during, and following

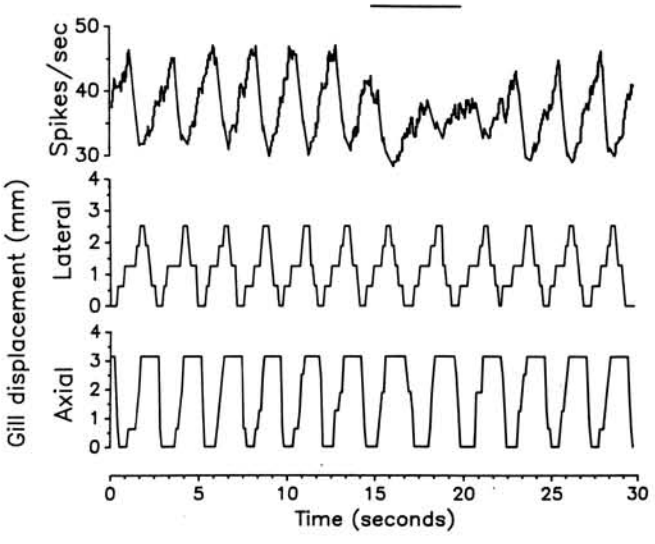

Fig. 1. Stroboscopic activation of efferents inhibits lateral line afferent activity evoked by movements of the operculum during respiration in the unrestrained toadfish. Upper trace shows mean firing rate of an irregular afferent neuron that innervated a neuromast on the operculum. Horizontal bar indicates period of stroboscopic stimulation (100 flashes/s for 5 s). Freeze frame analyses of the video tape show that both lateral (center) and axial (lower trace) opercular displacements remain constant during the photostimulation period, thus decreased firing of the afferent was not due to changes in the mechanical stimulus generated by opercular movement

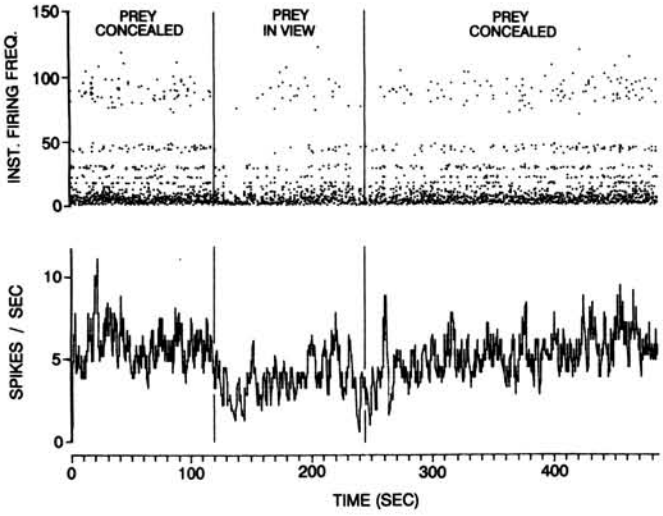

Fig. 2. Inhibition of mechanically evoked lateral line afferent activity in the behaving toadfish following visual presentation of a natural prey fish. Upper trace (instantaneous firing frequency) and lower trace (mean firing frequency) show activity of neuron during prestimulus (prey concealed), stimulus (prey in view), and post-stimulus (prey concealed) periods of the experiment. Irregular-type afferent innervated superficial neuromast on the operculum. Mild vibration applied to the tank base biased the low spontaneous activity upward. Firing decreased to lowest rates within 20 s after prey came into view, and returned to prestimulus rates approximately 60 s following removal of prey from view. Fish did not approach or strike at prey during the experiment

stroboscopic stimulation, the pronounced decrease in neural gain could not be a result of changes in respiratory activity, but must be due to a CNS efferent effect. When the average afferent discharge rate was increased by introducing a broadband background vibration, both the low frequency respiratory-related modulation and the extrinsic evoked activity were inhibited following stroboscopic stimulation. No pronounced inhibition was detected in burst-type afferents under these test conditions in the same experimental animals that showed strong inhibition in irregular units.

In the experiments where prey killifish were presented visually, chronically implanted toadfish became highly aroused (dorsal fins raised), sometimes reduced or momentarily ceased gilling while they watched the killifish swim, and often made strikes at the prey. When toadfish became aroused but did not move to approach or strike at prey, evoked afferent activity from applied background noise decreased with a latency of 10–20 s and this decrease often persisted for the full presentation period (Fig. 2). Recovery of lateral line afferent discharge rates to prestimulation levels took over one minute after the prey was removed from the view of highly aroused toadfish.

Discussion

The experimental results demonstrate that the octavolateralis efferent system in the toadfish can be activated by visual stimuli in a natural predatory context. The inhibition of irregular-type lateral line afferents but apparent lack of effect upon burst-type neurons suggests that efferent action differs among afferent fiber classes. This may be due to differential peripheral ultrastructural features such as terminal morphology and/or segregated innervation of hair cells by primary afferents, or selective innervation patterns by efferents (Flock 1965; Wegner 1982; Highstein and Baker 1986; Meredith and Roberts 1987; Sento and Furukawa 1987).

These experiments bear upon the hypothesis that efferent activation serves primarily to prevent depletion of transmitter from hair cells of the lateral line during locomotion or rapid movements (Russell and Roberts 1972; Flock and Russell 1973). It is significant that neither locomotion, rapid movement, nor any motor activity invariably followed efferent action in the unrestrained behaving fish. Further, afferent discharges due to water movement past the skin were robust when toadfish approached or struck at their prey. Thus, although the original hypothesis remains viable, it does not account for the incomplete inhibition during subsequent locomotion or selective consequences of efferent action on afferent activity. Alternatively, the decreased gain to low frequency mechanical stimuli from gilling and reduction of background noise levels in irregular-type afferents could function to enhance detection and characterization within the stimulus frequency and amplitude domains of biologically relevant mechanical stimuli such as that produced by prey near the head and snout. Additionally, because burster afferents were apparently unaffected by visual activation of the octavolateralis efferent system in these experiments, the relative input of this class of neurons might increase during periods of inhibition of irregular-type fibers. Experiments to determine efferent action upon the response dynamics of different lateral line afferent classes and whether differential central projections exist for each cell type will bear upon our hypothesis that efferents function to filter or tune mechanical stimuli at the periphery of this sensory system when activated in biologically relevant contexts.

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