

VARIATION IN CEPHALIC NEUROMASTS SURFACE AND CAVE-DWELLING FISHES OF THE FAMILY AMBLYOPSIDAE (TELEOSTEI: PERCOPSIFORMES)

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Abstract

Cave adaptation has led to unique sensory specializations to compensate for the lack of visual cues in aphotic subterranean habitats. As the role of vision is reduced or disappears, other sensory modalities become hypertrophied, allowing cave-adapted organisms to successfully detect and interact with their surrounding environment. The array of aquatic subterranean habitats, from fast-flowing streams and waterfalls, to quiet phreatic pools, presents a diverse palette to examine what possible sensory solutions have evolved against a backdrop of complete darkness. Mechanosensation is enhanced in many subterranean animals to such an extent that a longer appendage is recognized as a prominent troglomorphic adaptation in many metazoans. Fishes, however, not only interact with the environment using their fins, but also with specialized sensory organs to detect hydrodynamic events. We hypothesize that subterranean adaptation drives the hypertrophy of the mechanosensory lateral line, but that other environmental forces dictate the specific neuromast phenotype. To this end, we studied differences in the cephalic lateral line of the fishes in the North American family Amblyopsidae, which includes surface, cave-facultative, and cave-obligate species. None of the taxa we examined possessed canal neuromasts on the head. Primarily surface-dwelling species, *Chologaster cornuta* and *Forbesichthys agassizii*, possessed receded neuromasts throughout most of the head, with a few on papillae located in front of the nostrils and on ventral grooves on each side of the mouth. The cavefishes *Amyblopsis spelaea* and *Typhlichthys subterraneus* possessed papillate superficial neuromasts all over the head. We speculate that the change from the surface to the cave environment has led to papillate neuromasts in this group, which are likely shaped to detect the hydrodynamic characteristics of the boundary layer created by the swimming fish. Moving sensory organs from the surface of the body out into the boundary layer could increase sensitivity to high frequency stimuli created by prey, predators, and conspecifics.

Introduction

Water currents are a pervasive feature of all aquatic environments and provide obvious cues influencing fish behaviors. Fishes themselves can also create water displacement and pressure fluctuations (Kalmijn, 1989). Hydrodynamic stimuli provide important physical and biological information about the surrounding environment, and fishes have evolved a unique mechanosensory organ to detect hydrodynamic stimuli: the mechanosensory lateral line system (Bleckmann, 1994). The lateral line system is present in all fishes but varies in morphology and distribution.

The functional unit of the lateral line is the neuromast, which can be free standing on the skin (i.e., surface or superficial neuromasts) or in canals that are open to the environments via pores (i.e., canal neuromasts). The distribution of neuromasts across the body and head determines the ability of a fish to detect moving, as well as stationary, stimuli. Each object, be it a rock or a conspecific, creates a unique hydrodynamic signature. The information gained from these hydrodynamic images influences many aspects of fish behavior. For example, fish use their lateral line to examine novel objects (Teyke, 1990; de Perera, 2004), to detect prey (Hoekstra and Janssen, 1985; Janssen, 1999; Yoshizawa et al., 2010), to monitor the movement of conspecifics (Partridge et al., 1980; Faucher et al., 2010) and predators (McHenry et al., 2009), and to maintain position in flowing water (Sutterlin and Waddy, 1975; Montgomery et al., 1997). Superficial and canal neuromasts differ in function and performance but are overlapping in hydrodynamic selectivity. Physiological studies have shown that canal neuromasts respond to water movements that are produced by moving objects, such as prey, that is maximized in the direction of the canal axis (Denton and Gray, 1989; Montgomery et al., 1994). Canal neuromasts typically occur in a distinct line at the base of a canal that runs and extends over the head and flanks. In contrast, superficial neuromasts are located on the surface of the skin and preferentially respond to the velocity of water flow that is not orthogonal to their orientation axis (van Netten and Kroese, 1989; Coombs and Montgomery, 1994; Montgomery et al., 1994) and appear to be best suited to encode flow velocity (Baker and Montgomery, 1999; Van Trump and McHenry, 2013).

The principle sensory cell of the neuromast is the hair cell (Carton and Montgomery, 2004). These hair cells have a bundle of stereovilli that grow longer from one side of the apical surface to the other. A single true kinocilium occurs in the center on of the stereovilli bundle. The stereovilli of superficial hair cells are embedded in a gelatinous matrix called

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