

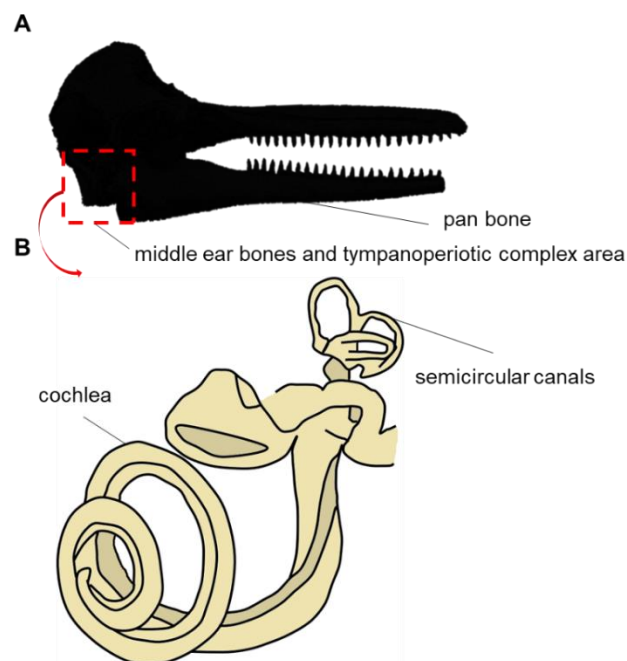
## Introduction to hearing in marine animals

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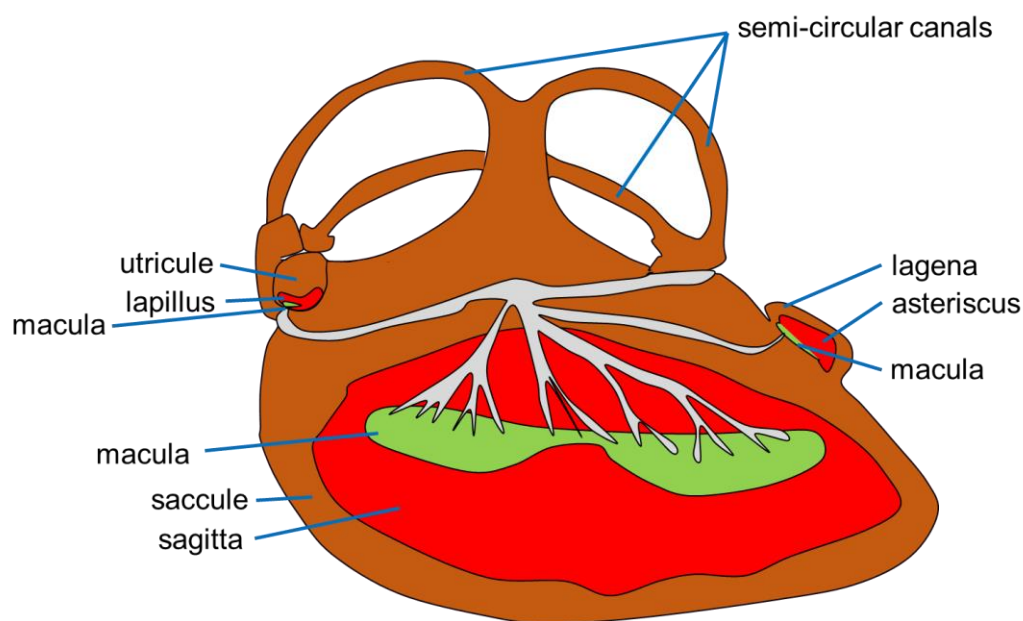
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In terrestrial mammals, the ear is divided into three parts: the **outer ear** (consisting of the pinna and external auditory meatus), the **middle ear** (including the tympanic membrane and ossicles), and the **inner ear** (comprising three semicircular canals, the vestibule, and the cochlea). The vestibule contains two cavities known as the **saccul**e and **utricule**. Otoconia, small calcium carbonate concretions, are associated with the **macula** (the area containing hair cells) of the saccula and utricule, and they play a role in detecting linear accelerations. In contrast, the additional hair cells found in the three **ampullae** (enlargements of each semicircular canal) are involved in detecting rotation and angular acceleration. Cetaceans have the same divisions as terrestrial mammals with some modifications, such as the absence of a pinna and a very narrow external auditory meatus. The external auditory meatus may still serve as the primary pathway for sound transmission [1,2], or it may be non-functional [3]. In that case, sounds would enter through the **mandible** and be conducted via a fat-filled canal [3]. Cetaceans have reduced semicircular canals (less pronounced in mysticetes than in odontocetes) compared to the cochlea [4] (Fig. 1).



**Fig. 1** Schematic representation of (A) a lateral view of the neurocranium of a dolphin with (B) a close-up of the inner ear. The figure has been redrawn and adapted from [4,5].

Fish do not possess an outer ear, middle ear, or cochlea. Instead, they have an inner ear composed of three semicircular canals and three fluid-filled otolithic organs: the saccule, utricle, and **lagena**. These otolithic organs contain otoliths, equivalent of the otoconias found in mammals, named **sagitta**, **lapillus**, and **asteriscus** (Fig. 2). In fish, the perception of linear and angular accelerations is similar to that observed in mammals. However, the otolith organs in fish also play a role in sound perception [6]. This is possible because fish have a density similar to that of the surrounding water, allowing them to move with the oscillatory motion of a sound wave. In contrast, the otoliths are much denser than water, creating relative motion between the otolith and the macula [7,8]. This pathway is referred to as “**the direct path**” [9]. Additionally, many fish species possess auxiliary structures such as modified swim bladder, other air chambers, or modified vertebrae known as **Weberian ossicles**, which are involved in sound reception [10,11]. When present, Weberian ossicles connect the anterior part of the swim bladder to the inner ear, functioning similarly to the ossicles in mammals [12–14]. This pathway is called “**the Weberian path**” [15].

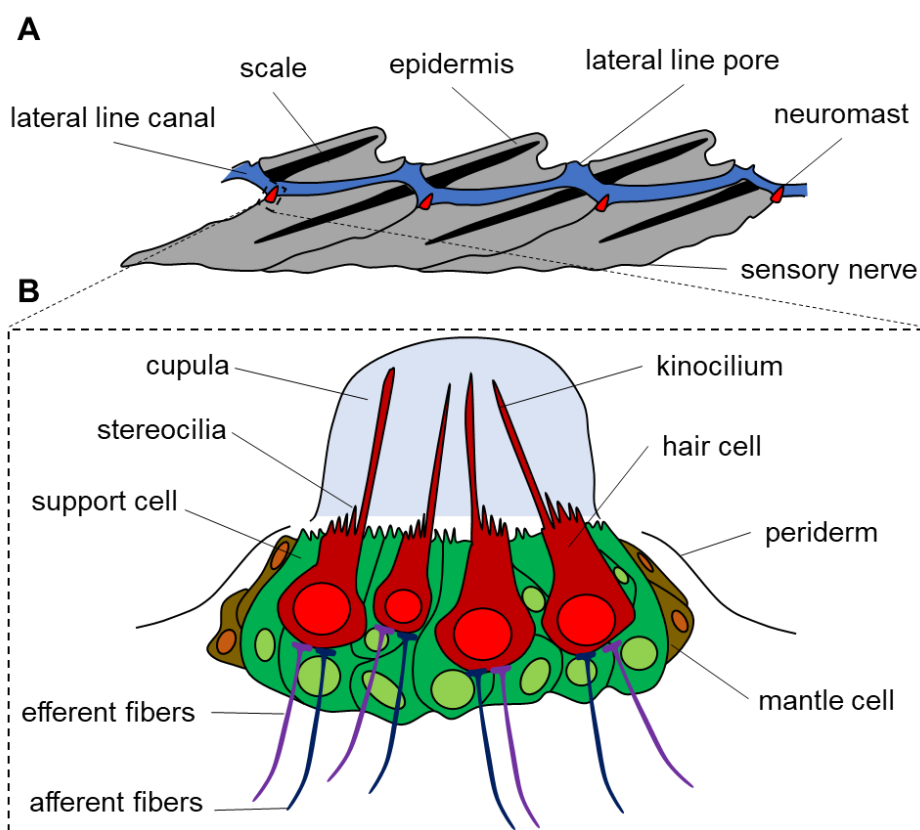


**Fig. 2 Schematic representation of the inner ear of a fish, highlighting the maculae in green and the otoliths in red. Adapted and redrawn from [16].**

Species without a swim bladder are most likely to respond to hydrodynamic water motion in the acoustic near field and to acoustic particle motion in the acoustic far field, rather than sound pressure [17]. Fish with a swim bladder that utilize only the direct path of sound perception are referred to as “**hearing generalists**”, while those using both paths are known as “**hearing specialists**”. However, hearing generalists also appear to respond to sound pressure, at least within a portion of their hearing range [18], suggesting a potential switch

between detecting pressure and particle motion [19]. Fish are capable of **discriminating source location** [20,21] but the underlying mechanisms are not yet fully understood [22]. It remains unclear whether they rely on far-field hearing or utilize near-field mechanisms, potentially involving the lateral line system [23].

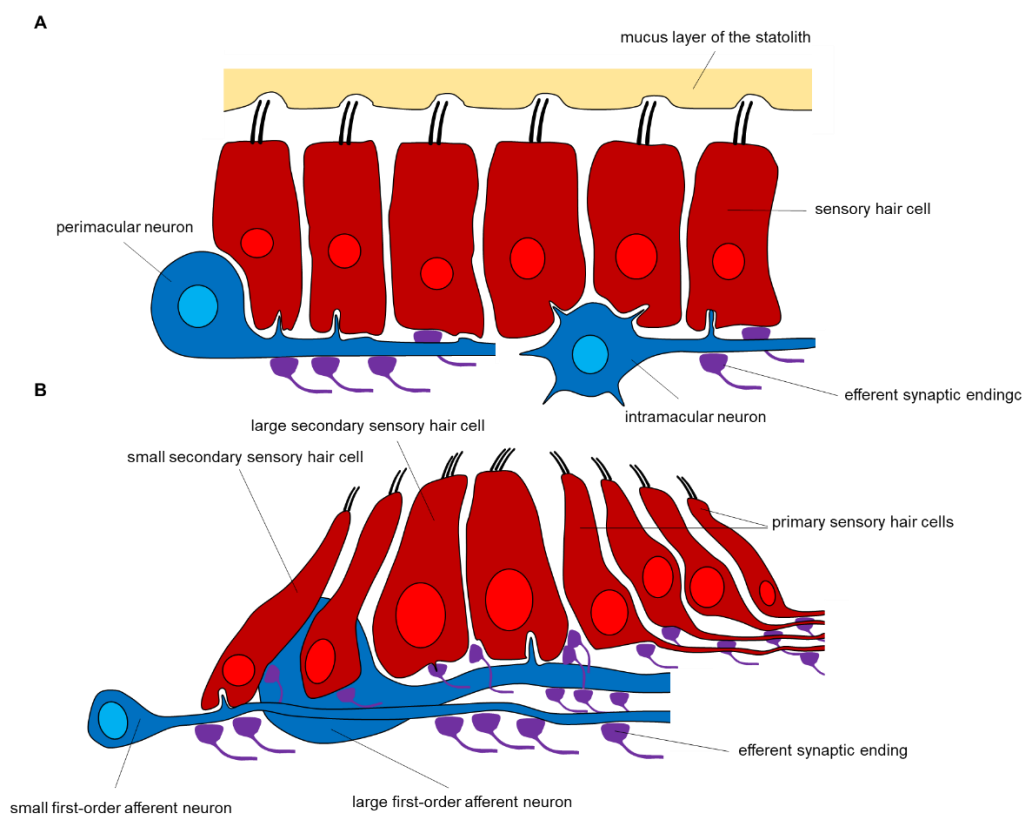
In addition to connections between the swim bladder and the inner ear, certain fish taxa have connection between the swim bladder and the **lateral line system** [24]. In such cases, the lateral line system may be sensitive to sound pressure [23]. Even in the absence of this connection, the lateral line system still plays a role. It has long been thought to be involved in low-frequency hearing [19,25]. More recently, it has been discovered that the lateral line system has fundamentally different biomechanisms compared to the ears [23]. The **neuromast** receptors of the lateral line are activated by near-field hydrodynamic motion within one or two body lengths, (Fig. 3). However, the lateral line system cannot respond in the far field because there is no longer any significant relative motion between the body and the surrounding medium [23].



**Fig. 3 (A) Schematization of the neuromasts' positions in the lateral line system, redrawn from [26]. (B) Schematization of a single neuromast, redrawn from [27].**

In invertebrates, several taxa possess sound receptors called **statocysts** [28,29], which provide them with vibrational and directional sensitivity [30–32]. These statocysts display

remarkable diversity. For instance, cephalopods have two types of receptors: macula-statolith receptors for sensing gravity and linear accelerations, and crista-cupula receptors for detecting angular accelerations [33]. In cephalopods, it has been suggested that particle motion affects their entire body, stimulating the statolith organs through whole-body displacements [32,34]. Recently, this hypothesis has been confirmed using laser Doppler techniques [35]. In crustaceans, statocysts are located in the basal segment of the first antenna [36] and function as equilibrium organs [37]. In crustaceans, the combination of hair cells and **statolith** (dense agglomerate of grains of sand found in the statocyst) is believed to function analogously to the otolith structures in vertebrates [36–39]. Additionally, **chordotonal organs** (stretch receptors), which are receptors cells embedded in muscle or connective tissue, are found at the joints of flexible body appendages and may be involve in the detection of joint position, movement, acceleration, tension [40,41], and low frequency vibrations [37]. Lastly, crustaceans possess **sensory hair** on the external surface of various appendages (e.g., legs and antennae), some of which have been shown to function similarly to the lateral line system [42].



**Fig. 4 Schematization of the cellular organization (A) a macula-statolith and (B) a crista-cupula receptor in *Octopus vulgaris*. In this species, a statocyst consists of nine crista-cupula receptors associated with one macula-statolith receptor. Redrawn from [33] based on [43,44].**

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