HOW DO TOOTHED WHALES (ODONTOCETI) PROTECT THEIR INNER EAR AGAINST PRESSURE WAVES?

by

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1. Introduction

Mammals possess an external ear with an external auditory passage (meatus acusticus externus), which ends at the ear-drum (membrana tympani). Behind the ear-drum the middle ear is situated. The middle ear contains the auditory ossicles which transmit sounds from the ear-drum to the ear-bones. The ear-bones (bulla tympanica and os perioticum) are tightly grown together with the skull-bones, and contain the semi-circular canals (labyrinth) and the inner ear (auris interna) with the cochlea. The cochlea of mammals has three auditory tubes: the scala vestibuli, scala tympani and scala media. The medial tube possesses nervous hair-cells which register the sound-waves.

The sound-waves run from the outer ear to the ear-drum, are transmitted by the auditory ossicles to the vestibular tube, run up to the tip of the cochlea (cupula cochleae), and return through the tympanic tube to the round window (fenestra rotunda). The round window is closed by a membrane.

During the period of adaptation to an aquatic life, the ear of odontocetes became more and more different from the auditory organs of terrestrial mammals.

Cetaceans have no outer ear and the external auditory passage is closed. The outer membrane of the ear-drum is funnel-shaped or very reduced. The internal part of the ear-drum, the radial fibres, still exists, but is transformed into a ligament. The ear-drum of odontocetes has no function in sound transmission. The manubrium of the malleus (MM: fig. 1) is connected to the bulla by ligaments. Sounds are received by the bulla and transmitted by the auditory ossicles to the inner ear. The three auditory ossicles (fig. 1, 3) are clearly present, but have changed in shape. The ear-capsule has lost its connection to the skull, and is only kept in position by filaments or tissue fibres. The bones of the ear-capsule are calcified and solid, and therefore very compact and heavy. Each ear-capsule consists of two large bones, the periotic bone and the tympanic bulla, which are connected but not fused. The periotic bone is like that of other mammals, and contains the inner ear with the cochlea and the semi-circular canals (LA: fig. 1).

The inner ear of all odontocetes has an additional tube, the ductus cochlearis (DC: fig. 4). The bulla (B: fig. 1), with its large cavum tympani, encloses the middle ear system and contains the auditory ossicles.

Odontocetes orientate themselves by echolocation. For this they generate sounds of up to 300 KHz, for which a high atmospheric pressure is required: 196 KHz correspond to approx. 6.5 atm, see Norris & Möhl (1983). These authors observed toothed whales during the capture of their prey and hypothesized that they paralyse the prey animals by means of sound waves. Such frequencies could, however, also affect the whales themselves, as such high-pressure waves might damage the sensory cells in the inner ear.

People protect their hearing organs against pressure waves (detonation) by closing the outer ear-passage with their fingers and by opening their mouth. How do toothed whales achieve this?

The external auditory passage of toothed whales is normally closed, but sound waves of high intensity penetrate the whole body. When the mouth is opened, sound waves would reach the inner ear via the air-sacs (pterygoid sinuses) in the head without major obstacles.

Through morphological examination of the auditory organs of some toothed whales, and with the help of an experiment, a possible explanation of how toothed whales may protect their auditory organs against pressure waves was discovered and further studied.

2. Morphological study

2.1. Material and methods

For a better understanding of the auditory organs of odontocetes, ear-capsules of nine species were examined. As the morphology of the auditory ossicles shows several interspecific differences, only three species, in which the incus has a similar structure, were used for this study: white-sided dolphin *Lagenorhynchus acutus* (Gray, 1828), white-beaked dolphin *L. albirostris* (Gray, 1846) and harbour porpoise *Phocoena phocoena* (L., 1758).

In order to study the middle ear and test the function of the auditory ossicles, the ear-capsules of three white-sided and two white-beaked dolphins were removed. The middle ear was opened by separating the ventral part of the bulla and the functions of the auditory ossicles and muscles were tested while still fresh. After this, the capsules were fixed in formalin and preserved in paraffin or resins.

After this introductory study, the much smaller ear-capsules of a harbour porpoise were studied. By the same procedure the middle ear was opened, and photographs were taken. A deep-frozen ear-capsule of another harbour porpoise was cut into 5 mm thick sections, fixed and impregnated with resins.

2.2. Results

The malleus (M: fig. 1, 3) is rotated caudo-ventrally. The caput mallei has an oval-roundish shape and is not connected to the bulla (B: fig. 1, 3). The longish, narrow process of the malleus (manubrium mallei, MM) ends ventrally in a notch of the bulla wall. Only the tip of the manubrium is tightly connected to the bulla by small ligaments. The caput mallei has a connection with the bulla and the periotic bone, in the form of longish filaments (T: fig. 1, 3). These tympanic filaments, also called musculus tensor tympani (Reysenbach de Haan, 1957), are the transformed radial fibres of the ear-drum and thus represent the internal end of the external auditory passage (EA: fig. 1). A muscle (musculus mallei, MU) extends from the caudal side

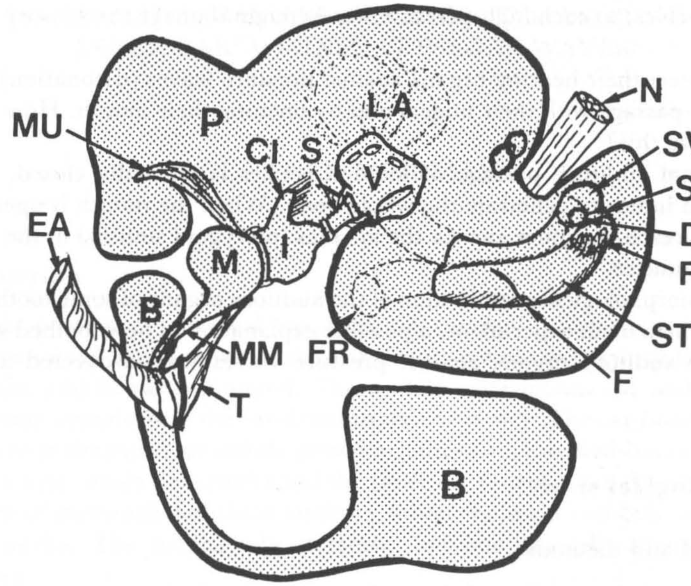

Fig. 1. Schematic cross-section of the ear-capsule of a harbour porpoise *Phocoena phocoena*.

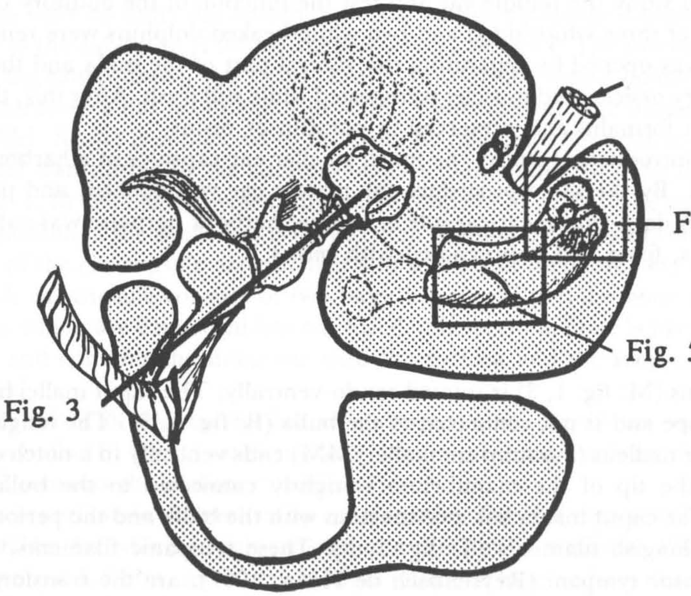

Fig. 2. The positions of the photographs.

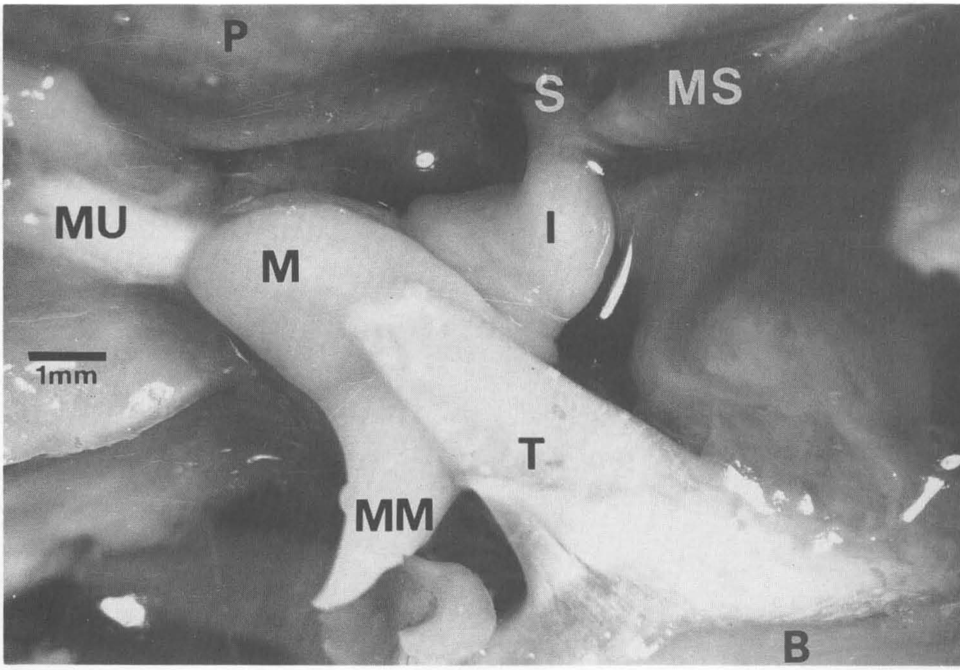

Fig. 3. Horizontal section through the ear-capsule of the harbour porpoise after removing the ventral part of the bulla. The malleus is detached from the bulla, and therefore the auditory ossicles are somewhat displaced.
Legend to the figures: B = Bulla tympanica; CI = Crus incudis; DC = Ductus cochlearis; EA = Meatus acusticus externus; F = Flabellum scalae tympani; FR = Fenestra rotunda; I = Incus; LA = Labyrinth; M = Malleus; MM = Manubrium mallei; MS = Musculus stapidis; MU = Musculus mallei; N = Nervus statoacusticus; P = Os perioticum; S = Stapes; SM = Scala media; ST = Scala tympani; SV = Scala vestibuli; T = Tensor; V = Vestibulum.

of the caput mallei to the periotic bone (P: fig. 1, 3), where it is fixed. This muscle is innervated by the trigeminal nerve (Reysenbach de Haan, 1957). The malleus and incus (I: fig. 1, 3) are flexibly connected by an oval articulation and small ligaments.

In shape the incus is very different from that of other mammals. It is roundish-triangular and has a short, massive process (crus incudis, CI: fig. 1). This finger-like process is situated in a notch of the periotic bone, to which it is movably connected by ligaments. The stapes (S: fig. 1, 3) is flexibly connected to the incus by a small articulation and ligaments. The stapes of toothed whales is massive and has a thick base (basis stapidis), by which it is inserted in the oval window (fenestra ovalis or f. vestibuli) like a plug. From the stapes, ligaments extend to the edge of the oval window. From the neck of the stapes a large muscle (musculus stapidis, MS: fig. 3) extends to the rostral part of the periotic bone. This muscle is innervated by a branch of the facial nerve (Reysenbach de Haan, 1957).

Behind the oval window lies the vestibulum (V: fig. 1) with its openings to the semicircular canals and the passage to the vestibular tube of the cochlea (scala vestibuli, SV: fig. 1, 4, 5).

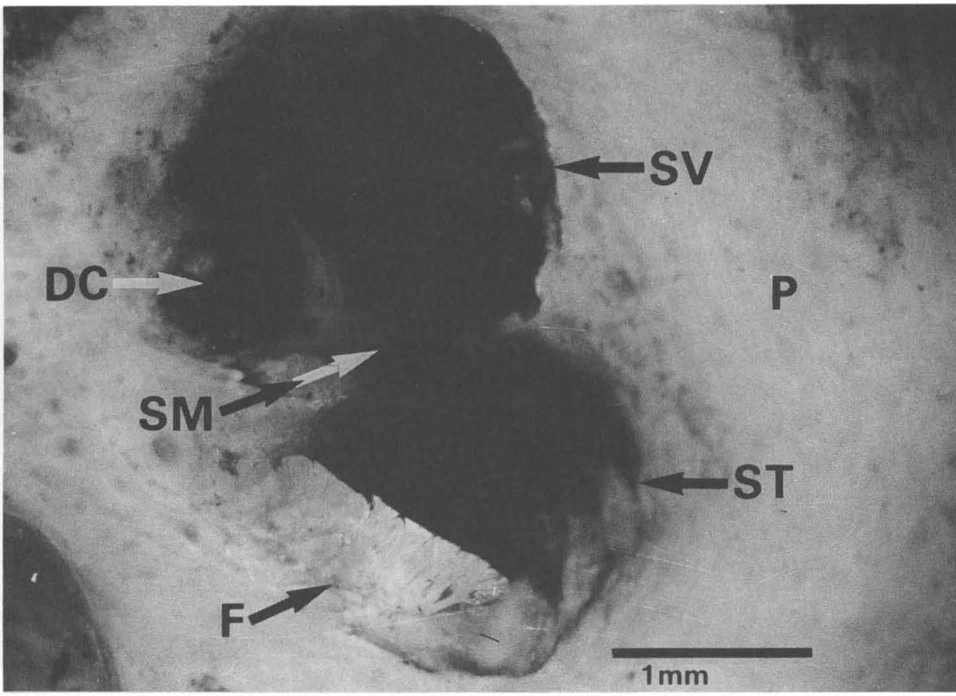

Fig. 4. Cross-section through the cochlea. In the tympanic tube the "fan" is clearly visible.

The second tube (scala tympani, ST) leads from the tip of the cochlea to the round window (fenestra rotunda, FR), which is closed by a membrane. In the tympanic tube of the harbour porpoise, two diagonally placed, fan-like bony structures ("flabellum scalae tympani", F: fig. 4, 5) were discovered. Such bones appear to be undescribed. They consist of small bone segments connected by cartilages, which distally ramify like fingers. They are linked by filaments to the base of the tympanic tube. Similar structures were not found in the specimens of *Lagenorhynchus*, possibly because the material was of insufficient quality.

The medial tube (scala media, SM: fig. 4) is situated between the vestibular and the tympanic tube, and contains the actual auditory organs. Medially in the cochlea there is a fourth tube (ductus cochlearis, DC: fig. 4), which is very large in all odontocetes (de Burlet, 1934) and has a calcified wall. This tube is filled with loose connective tissue penetrated by perineural tissue.

3. Experimental study

3.1. Material and methods

The movements of the muscles and the function of the auditory ossicles were tested in unfixed material of the white-sided dolphins, white-beaked dolphins and harbour

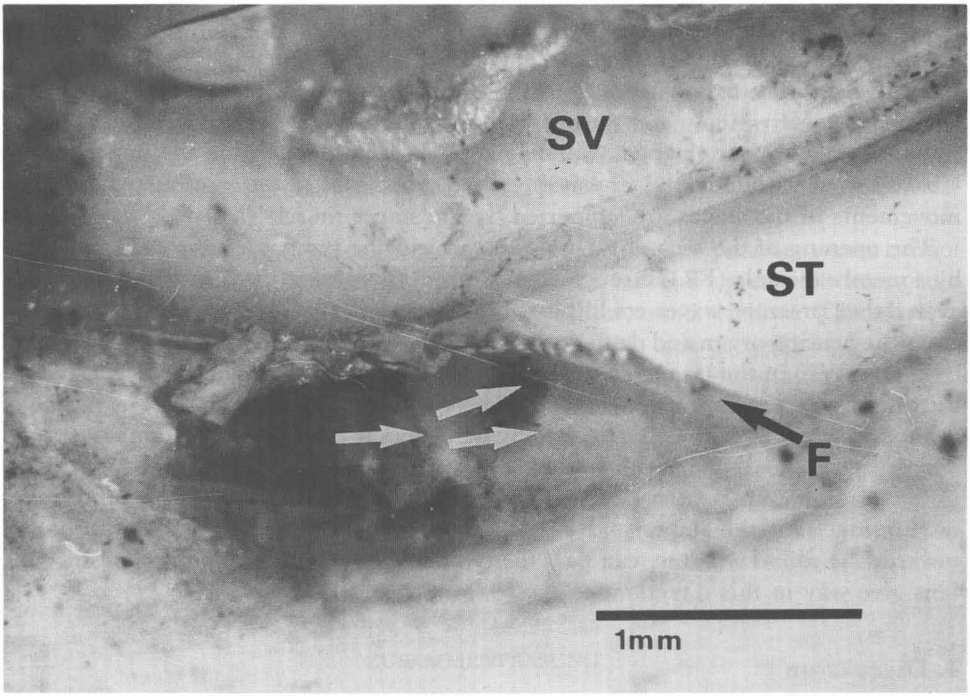

Fig. 5. Longitudinal section through the cochlea with a cross-section of the second fan. Fluid (white arrows) enters by the round window, and is held up by the fan.

porpoises, under magnifications of up to 10 × and by using surgical instruments. The function of the fan-like structures was examined in the ears of the harbour porpoises.

In addition, the ear-capsule of the second harbour porpoise was frozen and cross-sectioned. The cut surface was cleaned and immediately closed by a glass plate. After the ice had melted, the function of the ''fan'' was tested by touching the membrane of the round window. After this the tympanic tube was filled with staining fluid through the membrane of the round window (fenestra rotunda, FR: fig. 1). By these experiments the function of the fan was demonstrated (F: fig. 5).

3.2. Results

In all examined toothed whales the auditory ossicles are movable. In the manubrium (MM) the malleus has an elastic connection to the bulla. The tensor filaments (T) act like a rubber band. When the malleus muscle (MU) is contracted, the caput mallei moves in the direction of the traction and the malleus is lifted a little. The incus (I) follows the movement of the malleus and the connected stapes is slightly pulled back from the oval window. The displacement of the stapes is less than 0.3 mm. In this position the stapes can vibrate, so that the oscillations of the auditory ossicles are transferred to the cochlea.

When the malleus muscle (MU) relaxes, the tensor filaments (T), the ligaments of the incus process (CI), and the ligaments of the stapes, all acting like rubber bands, draw the auditory ossicles back into their basic position. The stapes (S) is pressed against the oval window and the vestibulum is hermetically closed. The base of the stapes fits exactly into the oval window like a plug. In this position the stapes cannot vibrate, so that sounds and pressure waves cannot pass to the vestibular tube. The movements of the stapes are supported by the stapes muscle (MS).

The opening of the second tube of the cochlea, the tympanic tube (ST), is closed by a membrane only (FR), through which sound waves leave the hearing organ. However, other pressure waves could pass this membrane from the other end, and thus enter the hearing organ and damage the auditory nerve-cells. This would be prevented by the fans (F) in the tympanic tube. The fans act like "breakwaters" and so reduce the intensity of pressure waves that could enter the cochlea through the membrane of the round window. The fans are fixed by ligaments to the base of the tympanic tube. The fans are "floating" in the fluid of the tympanic tube; they follow the movements of the fluid and return every time to their diagonal position. Thus, the sound waves originating from the stapes and passing through the cochlea from the vestibulum towards the round window, can pass the tympanic tube without hindrance, since the fans give way in this direction.

4. Discussion

The auditory organs and the function of the inner ear of odontocetes are similar to those of other mammals. But the function of the fourth tube in the cochlea of odontocetes, the ductus cochlearis, is still unknown. The transfer of sound waves in odontocetes is different from that in other mammals. An outer ear is absent and the outer ear-passage and the ear-drum of whales would seem functionless. Sounds are received by air-sacs and transmitted via bulla and auditory ossicles to the inner ear. The stapes, however, has a second function, which is connected with the protection of the inner ear. Its base can hermetically close the oval window, thus enabling odontocetes to protect their cochlea against high-pressure waves. The ligaments of incus and stapes act like rubber bands, drawing the stapes tightly into the oval window. Only by the innervated muscles of the malleus can the stapes be pulled out of the oval window, as was discovered by Fleischer (1978). This author points out that, in the combination of ligaments, muscles, stapes and periotic bone, toothed whales possess a "safety-valve" as the ligaments of the stapes act like a spring, pressing the stapes into the oval window.

The shape of the auditory ossicles differs between species and not all toothed whales have a process on the incus. Differences also exist in the arrangement of the muscles. "In the literature there has been some controversy as to whether these muscles (i. e. m. mallei, m. stapidis) exist or not" (Reysenbach de Haan, 1957: 42). There are also disputes on the function of the additional muscles (Purves & Pilleri, 1983). With the exception of the fans in the cochlea, the three examined odontocetes have a very similar ear anatomy. The situation found in the three species does, of course, not necessarily apply to all odontocetes. However, the species examined have the same filaments and ligaments, the function of which apparently is to close the oval window.

Even after death, these ligaments, like rubber bands, keep the stapes tightly pressed against the oval window.

When the stapes is brought into hearing position, i.e. is pulled slightly away from the oval window, sound waves pass through the vestibular tube to the tip of the cochlea and return via the tympanic tube to the round window. The latter is closed by a membrane through which the sound waves leave the hearing organ, as is the normal situation in mammals.

As long as the oval window is closed by the stapes, sound and pressure waves cannot penetrate into the fluid of the cochlea. In odontocetes, however, pressure waves could also pass to the cochlea through the membrane of the round window. Therefore, it would be important that the cochlea is protected at this side as well. Some kind of "breaks" would be needed here, to prevent such waves from entering from this end. The fans discovered in the tympanic tube of the harbour porpoise appear suited to stopping such waves and thus protecting the auditory organs against possible damage from this side. The presence of fans in the tympanic tube could only be demonstrated in the habour porpoise. Lack of suitable material has prevented a satisfactory examination of other species. However, it is assumed that all odontocetes protect their ear in a similar way.

ZUSAMMENFASSUNG

Wie schützen Zahnwale (Odontoceti) ihr inneres Ohr vor Druckwellen?

Zahnwale orientieren sich durch Echolokation, wobei sie Frequenzen bis zu 300 KHz erzeugen. Norris & Möhl (1983) vermuten, daß hohe Schallwellen auch zur Debilisierung von Nahrungstieren verwendet werden. Solche Schallwellen müßten aber dann auch das innere Ohr der Zahnwale selbst beschädigen. Über morphologische Untersuchungen wurde nun erkundet, wie das innere Ohr vor Druckwellen geschützt werden kann.

Durch gummibandartige Filamente und Ligamente, die an den Gehörknöchelchen ansetzen, wird der Steigbügel in das ovale Fenster gedrückt, welches er dann stopfenartig verschließt. Weil der Steigbügel in dieser Stellung nicht mehr schwingen kann, können auch keine Schallwellen mehr auf die Scala vestibuli übertragen werden. Um hören zu können, muß aber der Steigbügel schwingen. Dies ermöglicht ein kleiner Muskel, der am Hammerkopf ansetzt. Wird dieser Muskel angespannt, wird der Steigbügel aus dem ovalen Fenster gezogen, so daß er schwingen kann. Entspannt sich der Muskel, kehrt der Steigbügel in seine Ausgangslage zurück.

Um aber hören zu können, müssen die Schallwellen die Gehörschnecke durchlaufen. Dies ist nur möglich, wenn die zweite Öffnung der Gehörschnecke, das runde Fenster, nicht hermetisch verschlossen ist. Es ist deshalb nur von einer dünnen, schwingenden Membran verschlossen. Durch diese könnten aber auch Druckwellen in das innere Ohr gelangen. In der zweiten Windung der Gehörschnecke, der Scala tympani, des Schweinswals *Phocoena phocoena* (L., 1758) wurden nun fächerförmige Knochengebilde gefunden, die auf Grund ihrer Morphologie und ihrer Lage Wellenbrecher sein könnten. Damit wäre das innere Ohr des Schweinswals auch von dieser Seite her vor Beschädigungen durch Druckwellen geschützt. Wie die anderen Zahnwale ihre tympanische Tube gegen eindringenden Druckwellen schützen, ist zur Zeit noch nicht bekannt, vermutlich aber auf ähnliche Weise.

SAMENVATTING

Hoe beschermen tandwalvissen (Odontoceti) hun gehoororgaan tegen drukgolven?

Tandwalvissen oriënteren zich met behulp van echolocatie; daarbij brengen ze geluidssignalen voort tot 300 KHz. Norris & Möhl (1983) vermoeden dat hoge geluidsgolven ook gebruikt kunnen worden om prooidieren uit te schakelen. Zulke golven zouden echter ook het gehoororgaan van de tandwalvissen zelf kunnen beschadigen. Door studie van de bouw van het gehoororgaan van enkele Odontoceti is onderzocht hoe het binnenoor tegen deze drukgolven beschermd zou kunnen zijn.

Door elastische ligamenten die aangehecht zijn aan de gehoorbeentjes, wordt de stapes (stijgbeugel) in het middenoor tegen het foramen ovale gedrukt; dit wordt daardoor hermetisch afgesloten. Daar de stapes in deze positie onbeweeglijk is, worden er geen geluidsgolven naar de scala vestibuli in het binnenoor geleid. Een dier kan echter pas horen, als de stapes kan vibreren. Dit wordt mogelijk gemaakt door een kleine spier, aangehecht aan de malleus (hamer). Als deze spier wordt gespannen, wordt de stapes uit het foramen ovale getrokken, zodat hij kan vibreren. Ontspant deze spier zich, dan keert de stapes in zijn uitgangspositie terug.

Een dier kan pas horen, als de geluidsgolven het labyrint (slakkenhuis) doorlopen. Dit is mogelijk doordat de tweede opening van het labyrint, het foramen rotundum, niet hermetisch afgesloten is: de afsluiting bestaat uit een dunne, beweeglijke membraan. Door deze membraan zouden echter ook drukgolven het labyrint kunnen binnendringen. In de tweede winding van het labyrint, de scala tympani, van de bruinvis *Phocoena phocoena* (L., 1758) werden tijdens deze studie waaiervormige, benige structuren aangetroffen. Gezien hun bouw en ligging, zouden deze als ''golfbrekers'' kunnen fungeren. Daarmee zou het binnenoor van de bruinvis ook vanaf deze kant beschermd zijn tegen drukgolven.

Het is nog niet duidelijk hoe andere tandwalvissen hun gehoororganen tegen drukgolven beschermen, vermoedelijk echter op vergelijkbare wijze.

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