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The Paratympanic Organ: A Barometer and Altimeter in the Middle Ear of Birds?

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Abstract

A century has passed since the discovery of the paratympanic organ (PTO), a mechanoreceptive sense organ in the middle ear of birds and other tetrapods. This luminal organ contains a sensory epithelium with typical mechanosensory hair cells and may function as a barometer and altimeter. The organ is arguably the most neglected sense organ in living tetrapods. The PTO is believed to be homologous to a lateral line sense organ, the spiracular sense organ of non-teleostean fishes. Our review summarizes the current state of knowledge of the PTO and draws attention to the astounding lack of information about the unique and largely unexplored sensory modality of barometric perception.

Keywords

Paratympanic organ; mechanoreceptor; barometer; hair cell; middle ear; bird; lateral line; facial nerve; evolution; spiracular organ

History

The Italian anatomist Giovanni Vitali discovered the PTO in the middle ear of birds in 1911 (Vitali, '11). The organ was initially known as Vitali's organ or the "organ of flight" until named the PTO ("organo paratimpanico") by Ruffini ('20), a fitting name due to its location adjacent to the tympanic membrane. Vitali's discovery of the PTO was considered a major achievement, as evidenced by multiple nominations in 1934 for the Nobel Prize in Physiology or Medicine (see Nobel Prize Website). Following considerable excitement and enthusiasm about the PTO in the first half of the 20th century with about two dozen publications mostly on the development and anatomy of the organ, the PTO was largely forgotten and is now rarely mentioned in dictionaries or even in major textbooks of comparative anatomy. This neglect may be related in part to the fact that the distribution of the PTO is largely restricted to birds. Additional factors may be that nearly the entire body of literature on the PTO prior to 1978 was published in languages other than English (von Bartheld, '90), and the persistent failure of the PTO to neatly fit into any single established structural entity such as auditory system, vestibular system, lateral line system, or the facial nerve. Despite the fact that about 300 billion PTO pairs are currently operational worldwide

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(based on estimates of the world's bird population of 200-400 billion, Gaston and Blackburn, '97), no or very few resources mention or contain any information about this sense organ.

Structure

The PTO is located in the medial wall of the tympanic cavity, above the opening of the pharyngotympanic (Eustachian) tube, adjacent to the stapedial artery (a.k.a. external ophthalmic artery) and auricular vein, and dorsolateral to the columella in the avian middle ear (Fig. 1A). This tissue contains a rostrocaudally elongated vesicle; its lumen is filled with a mucous, gelatinous fluid, and its medial side contains a sensory (neuromast-like) epithelium covered by a gelatinous cupula (Fig. 1B). The sensory cells have been identified as type-II hair cells by electron microscopy (Fig. 1C), each with 40–100 stereocilia and one kinocilium that extend into the fluid-filled lumen (Jørgensen, '84; Giannessi and Pera, '86; Giannessi and Ruffoli, '96). The stereocilia and the kinocilium have a typical morphological orientation relative to the long axis of the PTO (Jørgensen, '84), suggesting measurement of fluid and cupula movement along this axis. Support cells may contribute to the fluid composition of the vesicle (Ruffoli et al., '98). The sensory hair cells receive both afferent and efferent innervation from myelinated and unmyelinated nerve fibers. Afferent innervation is mediated via neurons located in the facial ganglion that projects PTO fibers along the vestibular nerve to the cerebellum and vestibular nuclei in the brainstem (Federici, '27; von Bartheld, '90); efferent innervation arises from the facial motor nucleus, possibly from the same location of motoneurons as those that innervate the stapedius muscle (von Bartheld, '94). The number of hair cells in the PTO has been estimated at ~2,500 hair cells per avian PTO (Vitali, '41) – a number that is comparable with the number of hair cells in the spiracular sense organ of some cartilaginous fishes (Barry and Boord, '84; see below) and also in mammalian vestibular end organs (Desai et al., 2005). The size of the PTO varies between species. Falcons and the most aerial of birds, swifts (Collins, '85), were reported to have the most hypertrophied PTO (Vitali, '21; Simonetta, '59). Besides birds and juvenile alligators, only a vestigial PTO (with no clear evidence of hair cell innervation) was described in a few post-embryonic specimens of tetrapod species, including the ancient reptile *Sphenodon*, the monotreme *Echidna*, and one species of bat (Vitali, '24; Simonetta, '59; Neeser and von Bartheld, 2002).

Function

The function of the PTO has not been conclusively demonstrated. Initial lesion experiments by Vitali ('21) suggested a profound influence on muscle tone and flight of pigeons, but such effects could not be replicated and appear to have been caused by damage to the adjacent stapedial blood vessels with compromised vestibular function (Benjamins, '26; Giannessi et al., '96). Ranzi and Vitali noted that a PTO and its homolog in fishes, the spiracular sense organ (SSO, see below), appeared to be associated with vertical movement in space (Ranzi, '26; Vitali, '41). Subsequently, however, the SSO in elasmobranchs turned out to be a joint proprioceptor that responds to flexion of the hyomandibula at its cranial joint, a movement that occurs during intense respiration or during jaw protrusion while feeding (Barry et al., '88a, b). The PTO is connected via elastic ligaments to both the tympanic membrane as well as the columella, the homolog of the hyomandibula, in the avian middle ear (von Bartheld, '94) (Fig. 2A). Pressure onto the tympanic membrane significantly deforms the fluid-filled luminal space of the PTO, resulting in movement of the fluid within the vesicle (von Bartheld, '94) (Fig. 2B). Fluid displacement within an enclosed luminal space is the same mechanism that has been demonstrated to stimulate the hair cells and the nerve innervating the elasmobranch SSO (Barry et al., '88a, b). A similar vesicle deformation is likely the natural stimulus for the mechanosensory hair cells that may allow

animals with a PTO to sense tympanic membrane position or tension, and thereby to register absolute and/or relative differences in air pressure (Jørgensen, '84; von Bartheld, '94). Indeed, birds are extremely sensitive to small changes in atmospheric pressure of 10–20 mm H₂O, equivalent to an altitude differential of about 10–20 meters (Kreithen and Keeton, '74). The PTO is considered the most likely sense organ to transmit the modality of barometric pressure to the brain of birds (von Bartheld, '94) and possibly bats (Paige, '95). This is consistent with the notion that birds can use the PTO as both a barometer (awareness of low pressure associated with impending storms), as well as an altimeter. Birds can fly level within ± 20 meters for distances of 2–3 km at altitudes of 700–1,100 meters, even at night (Griffin, '69), which is highly suggestive for guidance by some sort of altimeter. Bilateral lesions of pigeons' PTOs and subsequent behavioral experiments ruled out an alternative or additional function for the PTO in navigation and homing (Benjamins, '26; Giannessi et al., '96). Some mammals lacking a PTO appear to have a more limited ability to detect air pressure changes, presumably via hair cells of the inner ear (Funakubo et al., 2010).

Evolution and relationship with the spiracular sense organ

Comparative anatomical and ontogenetic studies have shown that the PTO is structurally similar and developmentally related to a lateral line component in ancient bony and cartilaginous fishes, the mechanoreceptive spiracular sense organ (SSO) (Vitali '25, '41; Ranzi, '26; Simonetta, '53; Barry and Boord, '84; Barry et al., '88a, b; Barry and Bennett, '89; von Bartheld and Rubel, '92; Baker et al., 2008) (Fig. 3A, B). The SSO is a specialized sense organ associated with the first visceral pouch that is present in elasmobranchs (sharks, rays and skates), the lungfishes, sturgeons and paddlefishes, holosteans (gars and *Amia*), and possibly chimaeras (Wright, 1885; Norris and Hughes, '20; Barry and Bennett, '89). The SSO was apparently lost in all teleost fishes, and in bichirs (Gardiner, '84), and it is not known whether an SSO is present in the coelacanth, *Latimeria* (Northcutt and Bemis, '93) (Fig. 4B). The structure and function of the SSO was most thoroughly investigated in sharks and rays. In these fishes, the SSO contains hair cells whose cilia are deflected by displacement of the cupula when movement of the hyomandibula causes deformation of the SSO (Barry et al., '88b). The hair cells are innervated by a branch of the anterior lateral line nerve which projects to the mechanoreceptive lateral line nucleus, the vestibulocerebellum, octaval nuclei and the reticular formation (Barry and Boord, '84). The ontogenetic development, morphology, structural relationship with the first gill cleft and hyomandibula/columella, mode of innervation, and central nerve projections all support the conclusion that the PTO and SSO are homologous structures, albeit the functions of the PTO and SSO apparently differ. When the earliest tetrapods transitioned from water to land, they likely possessed a spiracle with an SSO, but no tympanic membrane and a rather massive hyomandibula (Clack, '90, '94). Nevertheless, transformation of the middle ear with a shortening of the hyomandibula may have begun with adaptations of the spiracular breathing apparatus and possibly anchoring of a spiracle valve to the hyomandibula (Brazeau and Ahlberg, 2006). With ensuing middle ear evolution, the hyomandibula connected with an emerging tympanic membrane, allowing for a change of function of the associated sense organ from a primary function (in proprioception) to a secondary function in, presumably, detection of barometric pressure. The "ancient" sense organ, the SSO, likely was originally associated with both breathing and feeding functions (jaw protrusion with hyomandibular movement) (Barry et al., '88b; Clack, '90, '94; Brazeau and Ahlberg, 2006), but as new skull components arose, a shortened hyomandibula (stapes/columella) and its associated sense organ became available for a new use, while remaining in contact with the bony surrounds of the inner ear (Fig. 3A,B) (Manley, 2010). Therefore it is possible that a lateral line derivative persists in some amniote vertebrates (Baker and Bronner-Fraser, 2001; Baker et al., 2008).

Distribution of the PTO among species

Among the about 100 tetrapod species that have been examined, a presumably functional (innervated) PTO was found in post-embryonic animals only in birds, juvenile alligators (Neeser and von Bartheld, 2002), and one species of bat (Vitali, '24); a PTO was absent in all amphibians, turtles, squamata (lizards and snakes), and marsupials that have been examined (Simonetta, '59) (Fig. 4A). A vestigial PTO (=thickened epithelium without evidence of innervation) persists in a few non-avian vertebrate species, including *Sphenodon* (the sole survivor of an ancient reptilian lineage), the monotreme echidna, and embryonic dolphins (Simonetta, '53, '59; Werner, '63; Neeser and von Bartheld, 2002) (Fig. 4A). Therefore, the PTO is most parsimoniously interpreted as an ancestral amniote feature that was lost in turtles, squamates, and most mammals. Nearly all of the about forty bird species that have been examined possess a PTO (Vitali, '14; Oldenstam, '25; Simonetta, '53, '59; Jørgensen, '84; Neeser and von Bartheld, 2002). The loss of PTOs in posthatch owls (Vitali, '23), night hawks (Simonetta, '59), and parakeets (Neeser and von Bartheld, 2002) appears to be secondary, presumably due to the emergence of pronounced cranial kinesis incompatible with PTO function (Neeser and von Bartheld, 2002). Such specializations for food capture are believed to have significantly affected middle ear evolution (Manley, 2010). The distribution of PTOs among bird species indicates that a PTO is valuable not only for birds that can fly, but also for flightless birds who may be excellent swimmers and divers such as penguins (Benjamins, '26; Vitali, '41). One may speculate that a PTO in water could register water pressure, relevant for penguins or alligators. The ability to predict impending (winter) storms would be more relevant for small birds (or bats), and less so, due to life style and habitat, for owls and parakeets – some of the few groups of birds lacking a PTO (Neeser and von Bartheld, 2002).

Ontogenetic development

Early embryologists suggested that the epibranchial placodes were vestiges of ancestral sense organs ("Kiemenspaltenorgane" = "gill cleft organs", Froriep, 1885; Vitali, '14; Oldenstam, '25; Baker et al., 2008). Such organs were believed to be transient structures during development. However, in some vertebrates, they persist beyond embryonic stages and form a functional sense organ. This discovery was Vitali's main achievement. Experimental embryological studies confirmed that the geniculate placode of birds gives rise to the PTO (Vitali, '14, '21; Yntema, '44; D'Amico-Martel and Noden, '83; Baker et al., 2008). Furthermore, clonal relationships between some PTO hair cells and geniculate neurons have been demonstrated (Satoh and Fekete, 2005). This suggests that the ability to form mechanoreceptors (sensory hair cells) is actually more widespread in terrestrial vertebrates, and that the geniculate placode is using a latent sensory potential to generate hair cells and a PTO (Ladher et al., 2010). Alternatively, however, the PTO may be derived from a "hidden" lateral line placode that is closely associated with the first epibranchial placode (Baker and Bronner-Fraser, 2001; Baker et al., 2008). It has been noted that hair cells in the PTO express the neurotransmitter gamma-aminobutyric acid (GABA) much earlier than any of the other mechanoreceptors in the inner ear (von Bartheld, '90), possibly indicating precocious development of the PTO in both early embryonic development and evolution.

Future/Outlook

The ontogenetic and phylogenetic origin of the PTO/SSO is puzzling. Did this organ evolve from a lateral line system, or is it an entity that coexisted early in evolution and was parallel to the lateral line and inner ear? Can all epibranchial placodes give rise to mechanoreceptors? Was, and if so, why was this capacity lost in some and not other

lineages? An important task for the future is to definitively prove or disprove that the PTO conveys barometric and altimetric information to the brain. The fluid displacement theory remains to be confirmed and the precise biomechanics of this sensory system need to be elucidated. Does the PTO function as a sensory relay in conjunction with the stapedial muscle to control the tension and position of the tympanic membrane? Do some reptile, monotreme and bat species indeed contain a functional PTO? While most mammals lack a PTO, a crude barometric perception can be achieved even in humans, and apparently without a PTO (Funakubo et al., 2010). It would be of considerable interest to identify where the barometric information in the brain of birds is processed, and which mechanisms may make this system remarkably precise and sensitive. This would help to better understand a unique and abundant, yet largely unexplored sensory modality: barometric/altimetric perception.

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Fig. 1.

A–C. The structure of the paratympanic organ (PTO). A. Location of the PTO in the middle ear of late-stage embryonic chicken. C, columella; M, middle ear cavity; E, external meatus. B. The cross section through the PTO shows immuno-(GABA)-labeled hair cells in the sensory epithelium with an overlying cupula (von Bartheld, '90). C. Electron-microscopic image of a hair cell in the PTO. All tissue sections are from chicken.

Fig 2.

A–B. Putative function of the paratympanic organ (PTO). A. Schematic drawing of elastic ligaments (Platner's ligament, PL) and the columella (C) in the chicken's middle ear and their relation to the PTO. StA, stapedial artery; TM, tympanic membrane. B. Similar to lumen changes observed in the spiracular sense organ with movement of the hyomandibula (Barry et al., '88b), differential pressure exerted onto the tympanic membrane caused lumen changes of the PTO (von Bartheld, '94). These data are consistent with a barometric function of the PTO.

Fig 3.

A–B. Comparison of spatial relationships with adjacent structures for the paratympanic organ (PTO, A) in birds and the lateral line-derived spiracular sense organ (SSO, B) in sharks. Note remarkable similarities in the association with the hyomandibula and its homolog, the columella, as well with its ligaments. Other abbreviations: c, columella; hy, hyomandibula; li, ligaments. The SSO schematic is based on the work of Barry et al. ('88a).

Fig 4.

A–B. Phylogeny showing relationships between major groups of extant tetrapods (A) and fishes (B). A. The presence of a paratympanic organ (PTO) among adult species of major tetrapod lineages is indicated (“P”), and a vestigial PTO (“P?”) according to the work of Vitali (‘14, ‘24), Simonetta (‘53, ‘59), and Neeser and von Bartheld (2002). Note that many more species have a transient PTO during embryonic development (not shown). B. The presence of a spiracular sense organ (SSO) among adult species of major fish species is indicated (“S”), or coded as “S?” when this organ is questionable or its status is unknown. The distribution of an SSO is listed according to the work of Norris and Hughes (‘20), Ranzi (‘26), Simonetta (‘53), Gardiner (‘84), Barry and Bennett (‘89), and Northcutt and Bemis (‘93). In these cladograms, the width of clades on the tree is approximately proportional to the species diversity (number of species within the clade).