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Giovanni Vitali: Discoverer of the Paratympanic Organ

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Summary

One-hundred years ago, the Italian anatomist Giovanni Vitali reported the discovery of the paratympanic organ, a sense organ in the middle ear of birds, in two issues of the *Anatomischer Anzeiger* (1911, 1912). In this minireview, we summarize Vitali's biography, and examine the scientific impact of his discovery of this sense organ. We also compile – for the first time – the entire bibliography of published papers on the paratympanic organ. Vitali described the ontogenetic development of this sense organ, examined its distribution among species, recognized its evolutionary relationship with the spiracular sense organ of fishes, and he developed the theory that it functions as a detector of changes in air pressure. He was the first to postulate that the paratympanic and spiracular sense organs were homologous organs that originate from homologous placodes – currently a hotly debated topic. His morphological work indicating the sensory nature of the PTO was validated by subsequent ultrastructural studies. Vitali's discovery of the paratympanic organ prompted his nomination for the Nobel Prize in 1934. Nevertheless, the paratympanic organ and the presumed barometric sense of hundreds of billions of living birds have failed to receive the recognition they deserve. Conclusive evidence of the function of the paratympanic organ remains a formidable challenge in vertebrate sensory physiology.

Keywords

Paratympanic organ; Vitali's organ; Giovanni Vitali; Middle ear; Sense organ; Barometric sense; Epibranchial placode

1. Introduction

This minireview gives tribute to Professor Giovanni Vitali for his discovery of the paratympanic organ (PTO) that was first announced in a “preliminary note” in the *Anatomischer Anzeiger* in 1911, followed by a more detailed description in the same journal in 1912 (Vitali, 1911, 1912). We will first present a brief biography of Giovanni Vitali's academic career, followed by the scientific context in which he made his discovery: the ontogeny and fate of epibranchial placodes. We discuss Vitali's work on the ontogenetic origin of the PTO in light of recent molecular evidence for an independent PTO placode that is distinct from epibranchial as well as dorsolateral placodes (O'Neill et al., 2012). We also review and present examples (drawings) of Vitali's insightful work, and we discuss his investigations and speculation about the function of the new sense organ. We end with a summary of the impact of Vitali's discovery and a brief outlook into the future.

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2. Biography of Professor Giovanni Vitali (1876–1963)

Giovanni Vitali was born in 1876 in the town of Arezzo in Tuscany, Italy. He earned his degree in medicine at the University of Siena, one of the oldest Universities in Italy, with a brilliant thesis concerning the acute tuberculous meningitis (Vitali, 1908). Attracted by the insights that can be gained through morphological studies, he began to work as a Lecturer, and subsequently as an Assistant, in the Institute of Anatomy at the University of Siena. This is where he developed a passion for scientific research in general, and for attention to exquisite morphological details. In this Institute he discovered and published his pioneering work on the PTO (Vitali, 1911, 1912). In 1921, Vitali was called to assume the chair of Anatomy at the University of Cagliari, where he remained until 1926. Finally, he was appointed the chair of Anatomy at the University of Pisa, a position that he held for twenty-three years, until he retired in 1948. Vitali died in Pisa in 1963.

Vitali was a morphologist of great culture and a man who immersed himself deeply in the scientific discourse. Although the investigations of Vitali, valuable and accurate, have extended into other fields of histological research, his name remains most intimately linked to his main achievement, the discovery of the PTO, also known in the scientific community as “Vitali’s organ”. The discovery of the PTO, one of the most interesting scientific advances of the twentieth century in the field of vertebrate sensory biology, earned Vitali the nomination for the Nobel Prize in Physiology or Medicine in 1934. In fact, he was one of only 24 nominees (out of 74 that were considered) who received multiple nominations for the Nobel Prize in that year (Nomination Database, 1934). Vitali was not only an outstanding scientist, but also an excellent teacher, a cultivated man and a scientific humanist. The centennial anniversary of the PTO discovery is an opportunity to honor a talented scientist who made an impressive contribution to the advancement of science at his time. The photograph of Professor Vitali (Fig. 1) shows him at the age of sixty-three years.

3. The fate of epibranchial placodal thickenings

At the beginning of the twentieth century, embryologists were in agreement that the thickenings formed in the early stages of development on the dorsal edge of the first three branchial fissures (epibranchial placodes) went on to rapidly disappear, without giving rise to formation of specific structures (Froriep, 1885; Kastschenko, 1887). It was also asserted that the placode of the first fissure – even though destined to disappear similar to the other two placodes – persisted for a longer time. With brilliant insight, Vitali subjected to experimental examination the development of this placode in multiple vertebrate species. He observed that the placode, rather than disappearing, went through a series of transformations in birds, firstly into a diverticulum, and later into a vesicle that detached from the wall of the first branchial fissure. At the same time, the vesicle received nerve fibers from the neighboring ganglion of the facial nerve. This observation further stimulated Vitali’s interest. He noted that the vesicle, while maintaining its connection with the ganglion of the facial nerve, gradually migrated in the depths of the connective tissue, to establish its final position in the medial wall of the tympanic cavity, near the surface of the mucosa (Vitali, 1911, 1912, 1913/14, 1921). Based on Vitali’s observations and detailed descriptions, Ruffini coined in 1920 the term “organo paratimpanico” (paratympanic organ, PTO, Ruffini, 1920). Careful comparison of different stages of development as well as experimental studies led Vitali to conclude that the PTO – and also the spiracular sense organ (SSO in fishes, see below) – developed from the same dorsal region of the first branchial cleft, apparently the first epibranchial placode (Vitali, 1925, Fig. 2).

This conclusion appeared to be supported by the work of subsequent embryologists (Yntema, 1944; D’Amico-Martel and Noden, 1983, Satoh and Fekete, 2005; Ladher et al.,

2010), but it also created a major dilemma in vertebrate developmental and evolutionary biology. While there is general agreement among investigators that the amniote PTO and non-teleostean SSO appear to be homologous based on position, structure and development, an epibranchial placodal origin contradicts the “general rule” that these ventrolateral placodes do not generate mechanoreceptors (hair cells), and that their neurons should have central projections to epibranchial sensory domains in the brain rather than dorsolateral ones (Baker et al., 2008). However, if the placodal origin of the PTO and SSO is considered to be dorsolateral, as commonly assumed for the SSO (reviewed by Baker et al., 2008), then proponents of the homology between the two organs would be forced to accept that amniotes possess a lateral line remnant. Recent work by O’Neill (2010) provides a novel and elegant solution to this nearly century-old problem, by showing that the PTO placode, although adjacent to the epibranchial placode, is molecularly and spatially distinct, apparently representing a previously unrecognized placodal module in vertebrates. Thus, Vitali’s work provided crucial seminal information about the astounding potential of ectodermal placodes in the vertebrate phylum.

4. The distribution of the PTO among species and its evolution

After completion of his embryological studies, Vitali turned his attention to adult birds. He recognized the PTO in numerous species of birds, with the exception of two owls, the owllet (*Athene noctua*) and the barn owl (*Strix flammea*) (Vitali, 1923). The most elaborate structure of the PTO was found in two skillful flyers, the kestrel (*Tinnunculus tinnunculus*), and the swift (*Cipselus apus*) (Vitali, 1914). Vitali hypothesized that the degree of development and hypertrophy of the PTO and variations of its structural organization may relate to the diverse habitats and behaviors of birds. Vitali also attempted to identify the PTO in other classes of vertebrates. The PTO was not found in any of the examined species of amphibians and reptiles (Vitali, 1921, 1924). With regard to mammals, Vitali described a vesicle, derived from the epithelium of the first brachial fissure, in some species of bats during the early stages of embryological development, which rapidly regressed. He did find a PTO-like vesicle in the middle ear of an adult bat (*Vesperugo pipistrellus*). However, the vesicle was not clearly equipped with a sensory epithelium and was largely lacking innervation (Vitali, 1920, 1924). Recently, Scott (2003) re-examined the middle ears of this and five other bat species and failed to observe a PTO (Scott, 2003). Thus, the PTO appears to be of variable occurrence in the bat *Pipistrellus pipistrellus*, and to date, the evidence for a PTO in bats is inconclusive.

The reports by Vitali concerning the presence of the PTO in birds were validated in the 1920s by multiple authors (Benjamins, 1925; Oldenstam, 1925; Federici, 1927). After these studies, the interest of researchers in the PTO declined for a long period of time until the 1950s. Simonetta extended Vitali’s survey in many birds and other vertebrate species, confirming his results concerning the regression of the PTO in owls (Simonetta, 1953, 1959). In addition, he noted the absence of the PTO in a species of parakeet that had been suspected by Oldenstam (1925) and this was later confirmed (Neeser and von Bartheld, 2002). Overall, the above-mentioned studies indicate that the presence, or absence, of the PTO in different bird species and its structural variations need to be further explored.

Tracing studies with a fluorescent probe provided evidence that afferent nerve fibers from the PTO enter the brainstem with the facial nerve, but then project to vestibular nuclei in the brainstem (von Bartheld, 1990). These results are consistent with those of Vitali, who observed a similar site of termination of damaged fibers in the brainstem after lesion of the PTO (Vitali, 1921). Recently, a PTO with hair cells was described in juvenile alligators (Neeser and von Bartheld, 2002). This suggests the possibility that the PTO was present in ancestral progenitors of reptiles and birds (von Bartheld and Giannessi, 2011). Vitali and

Ranzi were the first to express the belief that the PTO is homologous with the spiracular organ, a sense organ near the spiracle in non-teleost fishes (Vitali, 1925; Ranzi, 1926). Most investigators share this hypothesis (Barry and Boord, 1984; Baker et al., 2008; von Bartheld and Giannessi, 2011).

5. The morphology of the PTO and verification of its sensory nature

The drawing shown in Fig. 3 was handcrafted by Vitali on the basis of the observations he carried out with the optical microscope (Vitali, 1912). The original drawing is currently housed in the Institute of Human Anatomy, University of Pisa. The picture shows the PTO shortly after it detaches from the epithelium of the first branchial fissure. Despite the limitations imposed by the tissue processing and imaging techniques of his epoch, Vitali described with remarkable precision the morphology of the PTO and its relationship with adjacent structures. He observed that the PTO resembles a spindle-shaped vesicle, characterized by a sensory epithelium along the medial wall. The drawing shown in Fig. 4, also handcrafted by Vitali, shows the morphology of this epithelium. Vitali described in the epithelium two types of cells: supporting cells and sensory cells. The sensory cells, located in the distal part of the epithelium, showed an apical protrusion, which was named “sensory hair” (Vitali, 1912). With this term, Vitali wished to emphasize the importance of this structure for the excitation of the sensory cells. Since the 1980s, several ultrastructural, histochemical and developmental studies were performed on the PTO. The ultrastructural studies confirmed that the description of the sensory epithelium and cell types made by Vitali was correct. In fact, the epithelium is characterized by supporting cells and hair cells; the latter are similar to type II hair cells present in the acoustic-lateralis system (Petrash et al., 1983; Giannessi and Pera, 1984; Jørgensen, 1984; Giannessi and Pera, 1986, 1987; Giannessi, 1989, 1990; Giannessi and Ruffoli, 1996a, 1996b).

6. Investigations and speculation about the function of the PTO

With great intuition, and despite the lack of knowledge of the hair cells and their mechanism of function, Vitali hypothesized that changes in atmospheric pressure could cause movements of the fluid contained in the PTO, leading to stimulation of the sensory cells (Vitali, 1921). Furthermore, Vitali observed that the PTO was placed obliquely, with the anterior end closer to the surface of the mucosa compared to the posterior one. The anterior end was regarded as the specific site of stimulation of the organ. Vitali formulated the hypothesis that changes in air pressure, recorded by the PTO during flight, could affect the muscles of the wings so as to stabilize the movements of the animal (Vitali, 1921). Moreover, he supposed that those changes were transmitted to the tympanic cavity, and then to the PTO, through the Eustachian tube. A subsequent study indicated that a ligament of the transmission apparatus of the middle ear (the superior drum-tubal ligament), which terminates on the medial wall of the tympanic cavity at the anterior end of the PTO, may transmit changes of air pressure to the PTO from the tympanic membrane, causing displacement of the fluid between the two ends of the PTO (von Bartheld, 1994). The polarization of the hair cells along the longitudinal axis of the PTO is consistent with this operating mechanism. Nevertheless, the functions of the PTO still need to be clearly defined.

By analyzing the consequences of the ablation of the PTO in pigeons, Vitali arrived at the conclusion that the PTO is indispensable for bird flight (Vitali, 1921). In fact, the operated animals showed a reduced tone and progressive atrophy of the wing muscles, with impairment of flight performance. Benjamins challenged the experiment when he found no alterations of flight in his operated animals (Benjamins, 1926). He also noted that penguins, despite their inability to fly, were equipped with a PTO, and he claimed that PTOs could

register water pressure, and in flying birds air pressure, but were not essential for the bird's flight (Benjamins, 1939). In a sharp response, Vitali (1941) pointed out that the region of the medial wall of the tympanic cavity selected by Benjamins for the PTO ablation was inadequate (Benjamins, 1926). To clarify this issue, Giannessi and his colleagues repeated the ablation experiment in pigeons, providing histological evidence for the absence of the organ in the operated animals, but the integrity of the adjacent structures (Giannessi et al., 1996). No impairment of flight was found, and the animals showed normal homing behavior. Recently, we reviewed the literature and evidence that suggests that the PTO may function as a barometer and/or altimeter in the middle ear of birds (von Bartheld and Giannessi, 2011). Indeed, birds are sensitive to small changes in atmospheric pressure of 10–20 mm H₂O (Griffin, 1969; Kreithen and Keeton, 1974). The PTO may sense the tension of the tympanic membrane, and thereby register differences in air pressure. Clarification of the functional role of the PTO, which is used daily by an enormous number of living animals (200–300 billion of birds), represents currently one of the major unsolved mysteries and challenges in sensory physiology of vertebrates.

7. Outlook

The first decade of PTO research was accomplished exclusively by Vitali himself (Table 1). Vitali carried out research studies on the PTO's ontogeny, distribution among species, phylogeny, and function. Initial dissemination of knowledge about the PTO may have been slowed by exclusive publication in Italian, Dutch, French and German languages (Benjamins, 1925; Table 1). Even when publication in English became dominant in the 1980s, recognition of the PTO remained sparse. This is evident by its omission in encyclopedias (e.g., Wikipedia, Encyclopedia Britannica and Encyclopedia of Neuroscience) as well as major textbooks of vertebrate neurobiology such as Ariens Kappers et al. (1936), Jacobson (1991), Nieuwenhuys et al. (1998), and Kaas (2007), although the PTO is mentioned in other textbooks (Romanoff, 1960; Kuhlenbeck, 1973–1978; Butler and Hodos, 2005). The history of the discovery of the PTO is a unique example that shows how a single researcher can pioneer an entirely novel direction of research when creativity is combined with great persistence and a comprehensive view of the scientific question. The legacy of Vitali's work is that it will continue to impact and shape fundamental aspects of the vertebrate Bauplan and its ontogeny, refine knowledge about the modular nature and astonishing potential of placodes, enrich our understanding of middle ear mechanics, evolution of sensory systems, and hopefully, some day, the mechanisms of a barometric and altimetric sense.

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Fig. 1. Photograph of Professor Giovanni Vitali at the age of 63 years. Source: University of Pisa, Department of Morphology and Applied Biology, Archives of the Library.

Fig. 2.

A schematic of a theoretical ancestral embryo shows the location of the otic vesicle (ov) and dorsolateral placodes (black, hatched), and the epibranchial placodes (grey) of the three most rostral clefts. Note the intermediate, ambiguous position of the paratympanic/spiracular (PTO/SSO) placode (large black arrow). Schematic is based on data presented and discussed in Baker et al., 2008.

Fig. 3.

Vitali's drawing of the paratympanic organ (o) and its relationship with adjacent structures of the middle and inner ear. Transverse section through an embryo of an Italian sparrow of 8.5 mm body length. This figure was published in *Anat. Anz.*, 1912. Other abbreviations: ce, external acoustic meatus; ct, tympanic cavity; gg, geniculate ganglion; oi, inner ear; q, quadratum bone.

Fig. 4. Vitali's drawing of the sensory epithelium of a paratympanic organ in a pigeon. The sensory cells (dark cells) are characterized by an apical protrusion (sensory hair). Clear cells: supporting cells. This figure was published in *Int. Mschr. Anat. Physiol.*, 1913/1914.

Table 1**Bibliography of the Paratympanic Organ, 1911–2011.**

Year	Authors	Journal	Language	Topic(s)
1911	Vitali	Anat Anz	Italian	Anatomy, Ontogeny
1912	Vitali	Anat Anz	Italian	Anatomy, Ontogeny
1913/14	Vitali	Int Mschr Anat Physiol	Italian	Review: Ontogeny, Comparative
1915a	Vitali	Atti R Acad Fisiocritici Siena	Italian	Ablation
1915b	Vitali	Arch. It. Biol.	French	Ablation
1920	Vitali	Atti R Acad Fisiocritici Siena	Italian	Comparative
1920	Ruffini	Boll Sci Med Soc Med-Chir Bologna/Archo Ital Otol Rhinol Lar	Italian Italian	Review Review
1921	Vitali	Riv Biol	Italian	Review, Ablation
1923	Vitali	Richerche Morfol	Italian	Comparative, Ontogeny
1924	Vitali	Richerche Morfol	Italian	Comparative
1925	Vitali	Monitore Zool Ital	Italian	Comparative
1925	Benjamins	Anat Anz	German	Ontogeny
1925	Oldenstam	Dissertation Groningen	Dutch	Ontogeny
1926	Benjamins	Arch Neerl Physiol	French	Ablation
1927	Vitali	Arch Fis	Italian	Function
1927	Federici	Anat Anz	German	Ontogeny, Innervation
1939	Benjamins	Acta Otolaryngol	French	Comparative, Function
1941	Vitali	Anat Anz	Italian	Comparative, Function
1944	Yntema	J Comp Neurol	English	Ontogeny
1953	Simonetta	Arch Ital Anat Embriol	Italian	Review: Comparative
1959	Simonetta	Atti Soc Tosc Scienze Naturali B	Italian	Review: Comparative
1963	Werner	Z Anat Entwicklungsgesch	German	Comparative
1978	Jaskoll & Maderson	Anat Rec	English	Ontogeny
1983	D'Amico-Martel & Noden	Am J Anat	English	Ontogeny
1983	Petrash et al.	Anat Anz	German	Ultrastructure
1984	Giannessi & Pera	Boll Soc Ital Biol Sper	Italian	Ultrastructure
1984	Jørgensen	Acta Zool	English	Ultrastructure
1986	Gianessi & Pera	J Anat	English	Ultrastructure
1987	Giannessi & Pera	Boll Soc Ital Biol Sper	Italian	Innervation, Ultrastructure
1989	Giannessi	Anat Embryol	English	Ultrastructure
1990	Giannessi	Boll Soc Ital Biol Sper	Italian	Ultrastructure
1990	von Bartheld	Brain Behav Evol	English	Ontogeny, Innervation, GABA
1992	von Bartheld and Rubel	Evolut Biol Hearing	English	Comparative
1994	von Bartheld	Brain Behav Evol	English	Function, Innervation
1996	Giannessi and Ruffoli	Anat Embryol	English	Ultrastructure
1996	Giannessi and Ruffoli	Ann Anat	English	Ultrastructure
1996	Giannessi et al.	J Exp Biol	English	Ablation, Function
1998	Ruffoli et al.	J Morphol	English	Ultrastructure
1999	Molea et al.	J Comp Neurol	English	Tubulin

Year	Authors	Journal	Language	Topic(s)
2002	Neeser & von Bartheld	Brain Behav Evol	English	Comparative
2003	Scott	Trans Missouri Acad Sci	English	Comparative
2005	Satoh & Fekete	Development	English	Ontogeny: Placode
2010	Ladher et al.	Development	English	Ontogeny: Placode
2010	O'Neill	RIKEN FY2009 Researchers	English	Ontogeny: Placode
2011	von Bartheld & Giannessi	J Exp Zool B Mol Dev Evol	English	Review