The peripheral nerve ends in the tongue of the harbour porpoise
Phocoena phocoena (Linne, 1758)

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Introduction

Tongues (Lingua) of dead harbour porpoises are much smaller than those of comparable terrestrial mammals (Boenninghaus, 1903). With the exception of a small area at the tip of the tongue, the entire margin (Margo linguæ) is covered with papillae (Papillae fungiformis). A longitudinal section through the tongue shows differences when compared with the tongues of terrestrial mammals, their inner parts consist of muscles. The inner parts of harbour porpoise tongue and of their papillae consist of cavernous tissue (Corpus cavernosus) and muscles are very poorly developed. The corpus cavernosus is an extension of the venous vessel system and enable it to carry larger quantities of blood (Boenninghaus, 1903). The corpus cavernosus is covered by the integument (Integumentum commune). The boundary lines between different skin parts, the subcuticle (Tela subcutaneae), corium (Corium) and the cuticle (Epidermis), are clearly recognized. The cuticle is covered by a squamous muscosa. This means that the integument of the tongue of the harbour porpoise is of the same structure as the integument of other terrestrial mammals. Some toothed whales possess taste buds, but mainly of a residual nature (Stadtmüller, 1938). The anatomy of odontocete brains shows that they are able to taste. It is also confirmed that toothed whales can use the tip and the margin of their tongues as organs of touch (Caldwell & Caldwell, 1972).

If the harbour porpoise is able to taste and to touch, its tongue must have nervous receptors. As the integument of the harbour porpoise tongue is similar to the one of other mammals, it was important to find out whether its nerves are comparable to the nerves of the tongues of terrestrial mammals, and how sensitive they are.

Material and Methods

Two harbour porpoise tongues were sectioned to prepare macroscopical and histological sections. A special histological colouring with lithium carbonate, combined with different colour filters permitted the determination of nerves and the nervous end-corpuscles.

The photographs of the histological sections were taken with phasecontrast objectives. Magnifications indicated in the text refer only to optical and not to photographic magnifications.

Results

In the integument of the tongue (Figure 12) and of the papillae (Figure 11) are many nerves and nervous end-corpuscles. However, the numbers of the nerve ends decrease caudally, and millimeters behind the tips and the bases of the papillae, nerves became very poor. It is remarkable that in the skin of the tips of the tongue (Apex linguæ) and of the papillae, there exist numerous concentrations of nerve-ends (Figure 18).

The uncovered free ends of the nerves ramify out of covered nerve fibres (Axon) (Figure 13, Figure 14A). Many thick fascicles of nerves covered with perineurium are present in the cuticles and in the subcuticle. These nerves fascicles combine sensitive, motor and vegetative nerve fibres (Leonhardt, 1985) (Figure 13 NB). In the epidermis different shapes of

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Figure 1. Longitudinal section through an oval nerve end-corpuscle. Inside, the nervous dendrites ramify like a chandelier (Figure 15 OE).
Figure 2. Golgi-Mazoni corpuscle covered by a voluminous stratum of connective tissue. Inside, the nerves ramify irregularly (Figure 16 GM).

Figure 3. Meißner tactile corpuscle in a cyst by collagenous fibrils (Figure 17 KF).

Figure 4. Tuberous organ with six swellings situated in the subcutica (Figure 5, Figure 13 TU).

Figure 5. Transverse section through the tuberous organ (Figure 4).

Figure 6. Multi-tuberous organ situated near the epidermis. The swellings are differently formed (Figure 13 VTU).

Figure 7. Cyst with ampoulate nervous end-corpuscles (Figure 18 BE). In many cysts the corpuscles are shrunk (Figure 8).
nervous end-corpuscles are found (Figures 1–8). There exist three kinds of mechano-receptors (Hirsch et al., 1973; Welsch & Storch, 1973; Leonhardt, 1985) all over the skin of the tongue (Figures 1–3). Another three kinds of nervous end-corpuscles were detected only in the tip of the tongue (Figures 4–8).

Discussion
Observation by the author at whale stations showed that tongues of living harbour porpoises are larger than of dead ones. This leads back to the corpus cavernosus. If the blood-pressure is reduced or the animal dies, the corpus cavernosus is compressed by muscles and empties and the tongue gets smaller.

The anatomy of the brain in toothed whales indicates that they are able to taste (Caldwell & Caldwell, 1972). This is demonstrated by the large number of functional taste buds on the stems of the papillae. Because the mucosa of dead animals is

Figure 8. Shrunken ampoules.

Figure 9. Taste buds situated in the mucosa of the stems of papillae (Figure 19 GS).

Figure 10. A muscus alveola gland, situated in the subcutica of the papillae.

Figure 11. Longitudinal section through a papilla, magnification 10 ×. In the centre the cavernous corpus (K). The dark peripheral integument presents concentrations of nerve-ends.

Figure 12. Longitudinal section through the tip of the tongue, magnification 25 ×. Every dark point is an accumulation of a large number of peripheral nerve-ends.
Figure 13. Transverse section through the tip of the tongue, magnification 100×. Nerve fascicules (NB), tuberous organ (TU), multi-tuberous organ (VTU).

Figure 14. Clusters of peripheral nerves in the tip of the tongue, magnification 250×. Covered peripheral nerve (A), uncovered nerve (NE), blood corpuscle (B)Ø 8μ for comparison.

Figure 15. Horizontal section through the integument, magnification 250×. Serous mucus gland (SD), oval corpuscle (OE), Meißner-tactile corpuscle (ME).

Figure 16. Transverse section of a Golgi-Mazoni corpuscle (GM), magnification 250×. The lamellas of the conjunctiva are clearly seen.

Figure 17. Meißner tactile corpuscle (ME), magnification 250×. Upper part: a transverse section with the incoming nerve (A). Lower part: A horizontal section of the Meißner tactile corpuscle with collagenous fibrils.
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quickly eroded, in former times it was believed that the sense organs for taste exist only rudimentarily (Stadtmüller, 1938). It is therefore possible that in well preserved tongues of toothed whales taste buds could be discovered in other parts of the tongue.

‘Conversely, behavioural observations lead to the conclusion that the sense of touch is one of the most important sense in dolphins’ (Caldwell & Caldwell, 1972). Because the skin of whales is very thick, it is supposed that touch-regions may be situated in areas where the skin is very thin, e.g. at the tip of the rostrum or the tongue. The great number of free nerve-ends and the accumulation of nervous end-corpuscles confirms this.

Through the many free nerve-ends toothed whales can register pain, heat and cold (Leonhardt, 1985); with the mechanoreceptors situated in the whole skin of the tongue, they can register touch (Welsch & Storch, 1973; Hirsch et al., 1973; Leonhardt, 1985). The function of the nerve-corpuscles in the tip of the tongue (Figure 4–8) are unknown. Comparable corpuscles are described in connection with lateral electoreceptive organs of mormyrid fishes (Boek, 1934; Szabo & Yvette, 1974). Further studies are required.

Much of the small ampulate nervous end-corpuscles (Figure 7) are shrunk (Figure 8). This may result from stress before death. In situations of stress, adrenaline pours out and the nervous receptors are paralysed for some time (Albert et al., 1986).

The tongue of the harbour porpoise is a highly sensitive organ and may even be more sensitive than the tongues of terrestrial mammals. This may be the reason why harbour porpoises avoid estuaries and coastal waters, which in past times were their preferred milieu.

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**Figure 18.** Cyst with three ampoulate nervous end-corpuscle (BE), magnification 250 x. From the axon (A) neurites (NE) ramify to the nervous end-corpuscles. Below: an uncovered neurite (NE).

**Figure 19.** Mucosa of the stem of the papilla, magnification 250 x. Longitudinal section through a taste bud (GS) and a taste pore (GP).

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**Key**

A Axon
B Blood-corpuscle
BE Ampoularly organ
EK Nervous end-corpuscle
GP Taste organ
K Corpus cavernosus
KF Collagenous fibres
ME Meißner-touch-corpuscle
MN Myelinated neuron
NB Nerve bundles
NE Neuron
NS Nerve fibre
OE Oval corpuscle
SD Mucous gland
SH Mucosa
S Schwann cell
SS Myelin sheath
TU Tuberous organ
VTU Multi-tuberous organ
References


