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HOW DO ODONTOCETES PERCEIVE THEIR OWN SOUNDS?

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INTRODUCTION Nobody can confirm whether a dead person has been able to hear. One can only assume that he/she was able to hear if auditory organs were present. Very much the same holds true for dead cetaceans. I have to rely upon similar indications when trying to demonstrate with which sense organs odontocetes are able to perceive and use the sounds they emit.

Basing himself on studies of the middle ear, Lange (1922) concluded that cetaceans must be deaf. Yamada (1953) assumed a reduced hearing capacity, and supposed that odontocetes could register certain frequencies by means of their free-swinging bullae. In the light of the morphology of the inner ear, Reysenbach de Haan (1957), Fraser & Purves (1960), Dudok van Heel (1962, 1966), Purves (1966), and Fleischer (1982) all assume that odontocetes can indeed hear.

THE STUDY The free-swinging bullae of odontocetes are very massive, their specific weight being twice that of the other skull bones. This feature led Yamada (1953) to his theory that the heavy bullae would function like seismographs, and that differences in oscillation between the lighter and heavier bones would be registered through the sense of touch. Yamada's theory, however, was ignored since he could not find the required receptive organs.

In the harbour porpoise *Phocoena phocoena*, I have now discovered sense organs between the occipital bone and the bulla, which would enable odontocetes to perceive just such oscillations (Behrmann, 1987; see Fig. 2).

The organ in question is situated in a groove of the occipital, which has always been regarded as an air-sac (peribullary sac: Purves, 1966). This groove contains bell-shaped vacuoles with an opening pressed against the bulla. The vacuoles are filled with fluid and contain sense cells, viz. corpuscles of Vater-Pacini, which are connected with the occipital by nerves (Fig. 3). The fluid in the vacuoles is thus influenced by oscillations of the bulla, the sense cells by those of the occipital. The oscillations of the heavier bullae differ from those of the lighter skull bones, and the differences are registered by the sense cells. Since this organ is situated far backwards, one may assume that it perceives only such frequencies as are able to penetrate deep into the head, i.e. frequencies below 900 Hz.

High frequencies do not penetrate very deep into the body and are mainly used for locating food. If the prey consists of soft-bodied animals, the echoes would no doubt be weak. Therefore, for any organ to register such frequencies, it would have to be at the front of the head.

The rostrum of the odontocete skull in its central part has a long, cartilaginous structure: the rostral cartilage (cartilago rostralis: Figs. 4-8). Purves & Pilleri (1983) suppose that this might serve for echolocation. Laterally and ventrally, the rostral cartilage is surrounded over its entire length by an organ which possibly could perceive quite weak sound waves (Fig. 5).

This rostral organ consists of long vessels filled with liquid, the walls of which are covered with ciliate cells (Fig. 8). These are stereocilians, and are surrounded by the fluid just like those in the equilibrium organ in mammals. Throughout this rostral organ there is a network of nerves leading to the nervus trigeminus below the base of the skull (Fig. 7). By means of this sense organ, odontocetes might perceive very weak oscillations. Since the entire organ, moreover, is situated in a long cavity formed by the rostral bone, it could be directed with great precision. This structure shows a striking similarity to a directional microphone. Through this organ odontocetes might be able to register all frequencies that are above their hearing capacity, and which would only give a very weak echo.

DISCUSSION and THEORY Odontocetes orientate themselves by means of echoes of the sounds they emit. Since the animals modify their frequencies according to circumstances, recordings of these show a wide range of variation. Frequencies of up to 300 kHz have been registered to date (Evans, 1973).

Odontocetes have a reduced cochlea and strongly modified earbones. On account of these attributes, some authors have expressed doubt as to whether those animals have any ability to hear and utilize their sounds.

In the head of the harbour porpoise, however, sense organs have now been discovered that might be able to register certain frequencies. According to their morphology and location, these organs would either be sensitive to very low, or to very high frequencies. Since the rudimentary cochlea is still completely functional, one may assume that intermediate frequencies are perceived by the sense of hearing.

The orientation system of odontocetes (Fig. 9) is based on emitting (A) and receiving (B) sounds, commonly called echolocation. The sounds are produced by the Eustachian tubes (A1), acoustic membranes (A2) and air-tubes (A3). They are received by the rostral (B1) and caudal (B2) sense organs as well as the auditory organ (B3). Sounds are generated by waves (frequencies), the nature of which is expressed by the number of oscillations per second (Hz or kHz). These oscillations can be made visible by means of an oscillograph. Such graphs are called sonagrams and show which frequencies are emitted within a certain period of time. Three characteristic sonagrams from the harbour porpoise, are figured here:

1. (C) For short-distance orientation, a harbour porpoise uses very high frequencies, of up to 300 kHz. These have a short range but can be concentrated in powerful bundles. They are emitted at very short intervals of only a few thousandths of seconds, and hence are called clicks.

2. (D) Busnel *et al.* (1966) recorded a harbour porpoise during courtship. The animal communicated using whistles and squeaks, sounds that can be produced by the air-tubes. Given the structure of the cochlea, such tones would be within the hearing range of odontocetes, i.e. between 800 and 100,000 Hz.

3. (E) For long-distance orientation, low tones are produced by the sound membranes, since frequencies of up to 300 Hz range very far in seawater. Given their short cochlea, the animals are unable to hear such sounds. The echoes of these penetrate deep into the body, causing oscillations of the bony structures. These oscillations are transmitted to the caudal sense organs, where they are perceived through the sense of touch.

Since high frequencies have such a short range, their echoes may be quite weak, particularly when reflected by soft-bodied prey. Thus it would be useful if these weak echoes, inaudible to odontocetes and unable to penetrate far into the body, could be received by the rostral sense organ. In this way, harbour porpoises would be able to perceive and utilize all sounds they emit, inaudible tones being registered through the senses of touch. It might, however, prove difficult to determine the range over which the various sense organs could operate.

Since other odontocetes (with the exception of sperm whale *Physeter macrocephalus* and bottlenose whale *Hyperoodon ampullatus*) are similar to the harbour porpoise morphologically, one may assume that their system of orientation is essentially similar.

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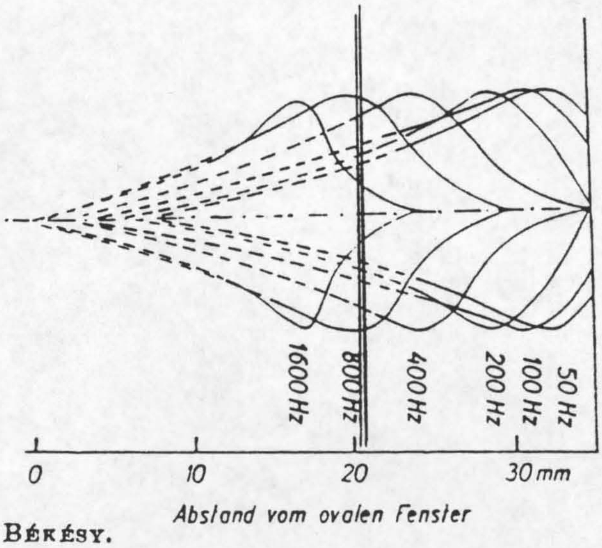

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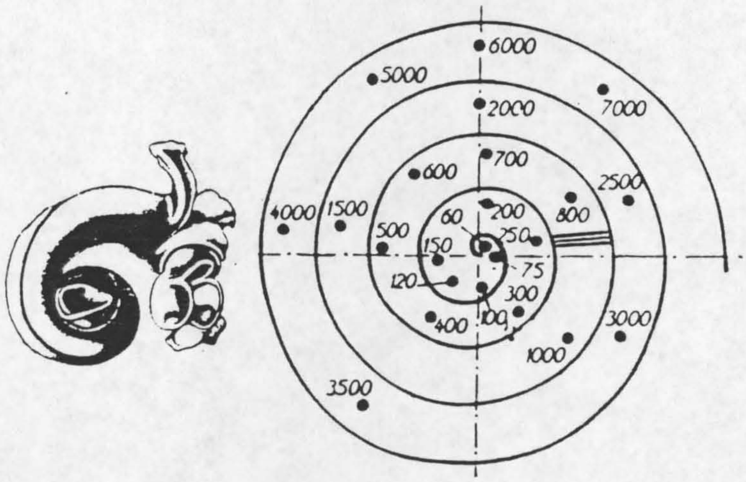

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Fig. 1. Distance of the various frequencies from the fenestra ovalis (in Hz)

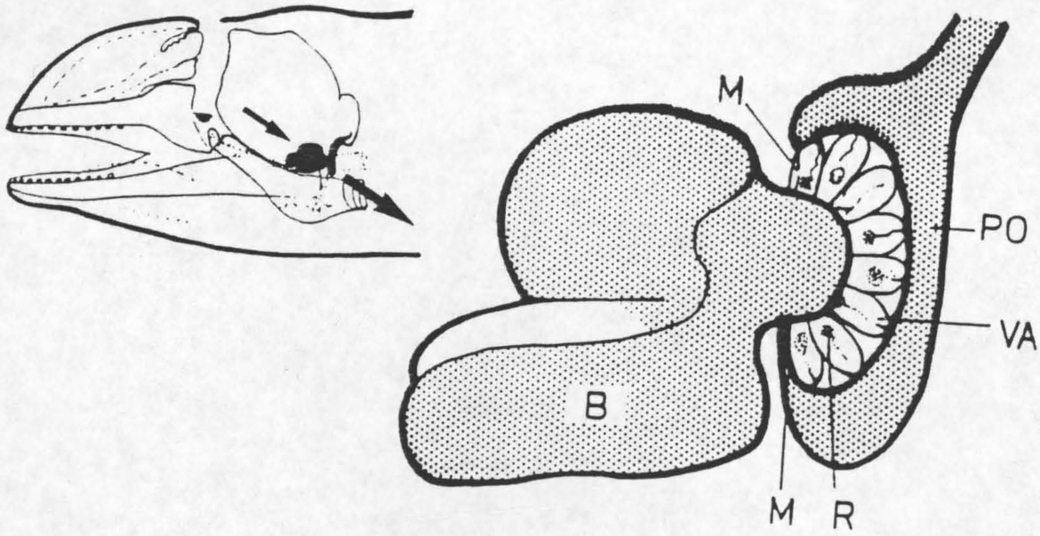

Fig. 2. Schematic longitudinal section through the bulla (B), caudal sense organ and vacuoles (V), occipital bone (PO), membrane (M), and nervous receptors (R) of a harbour porpoise.

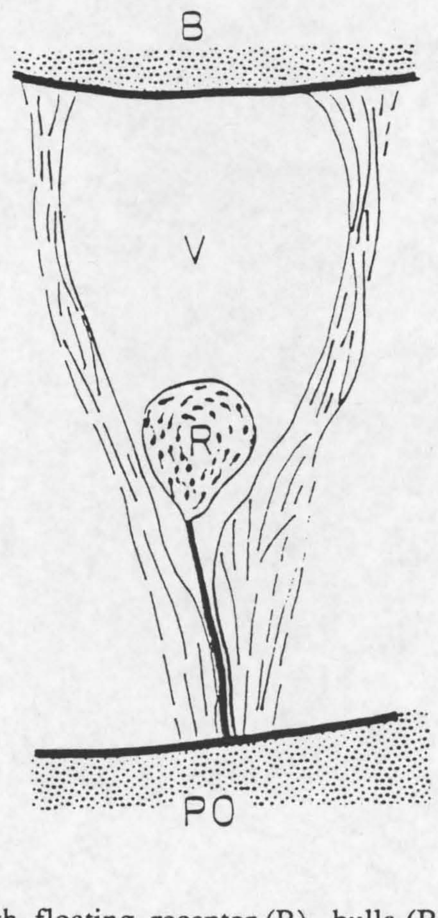

Fig. 3. Vacuole (V) with floating receptor (R), bulla (B), and occipital bone (PO).

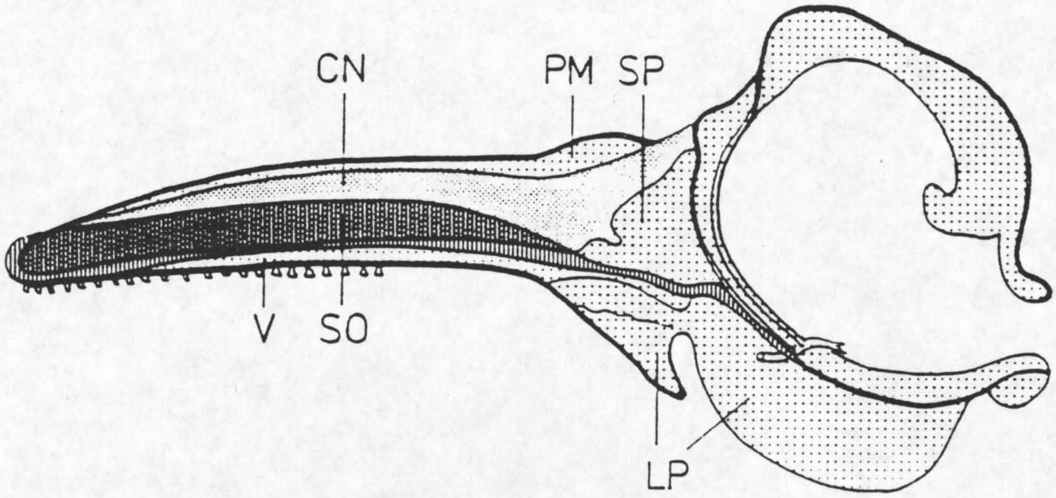

Fig. 4. Longitudinal section through the skull of a harbour porpoise: cartilago rostralis (CN), praemaxillare (PM), sphenoidale (SP), vomer (V), rostral sense organ (SO), and lamina pterygoidea (LP).

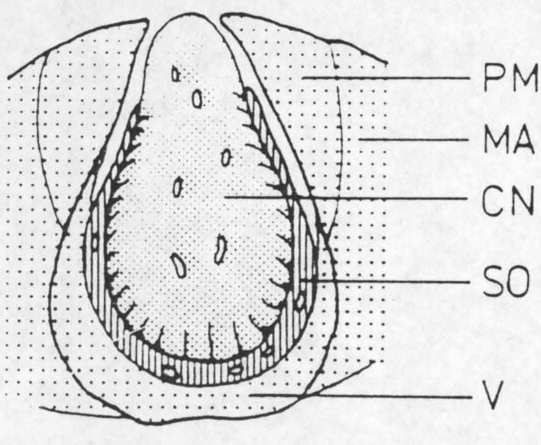

Fig. 5. Transverse section through the rostral sense organ (SO), praemaxillare (PM), maxillare (MA), cartilago rostralis (CN), and vomer (V).

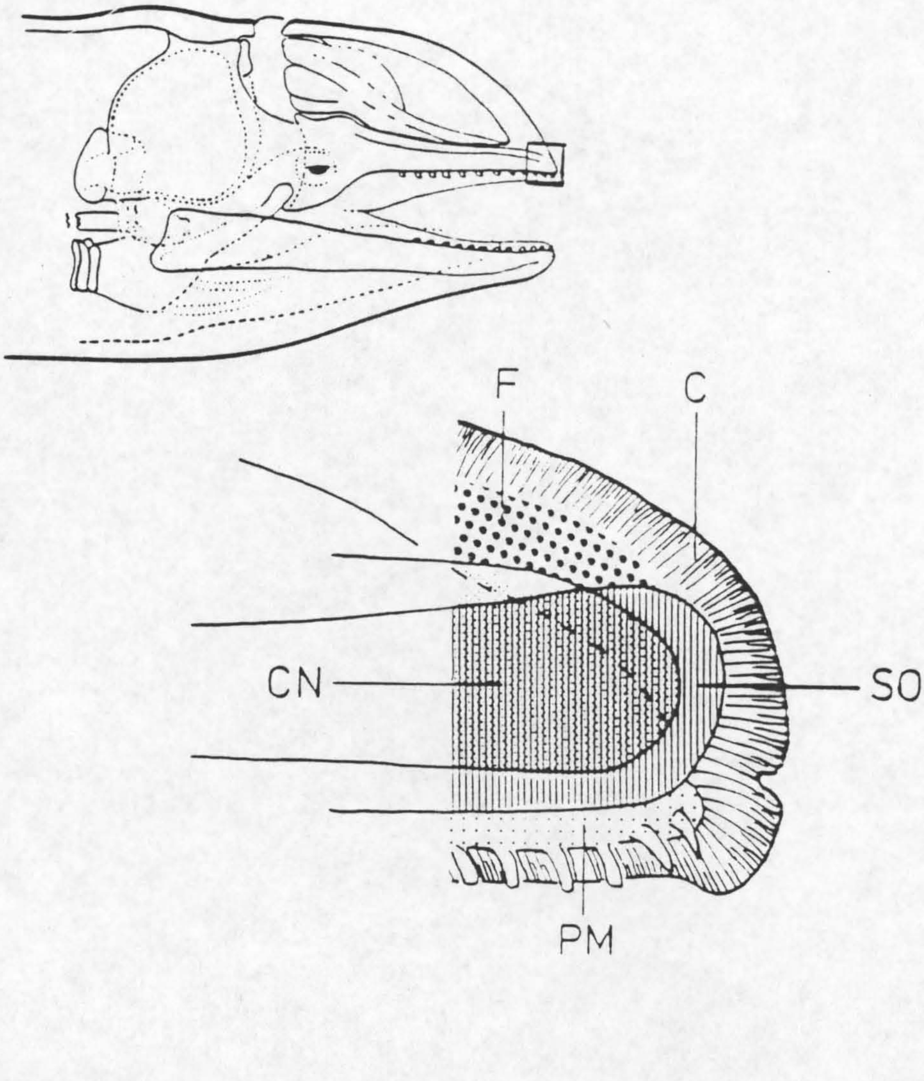

Fig. 6. Longitudinal section through the tip of the rostrum: cartilago rostralis (CN), blubber (F), cutis (C), tip of the rostral sense organ (SO), and praemaxillare (PM)

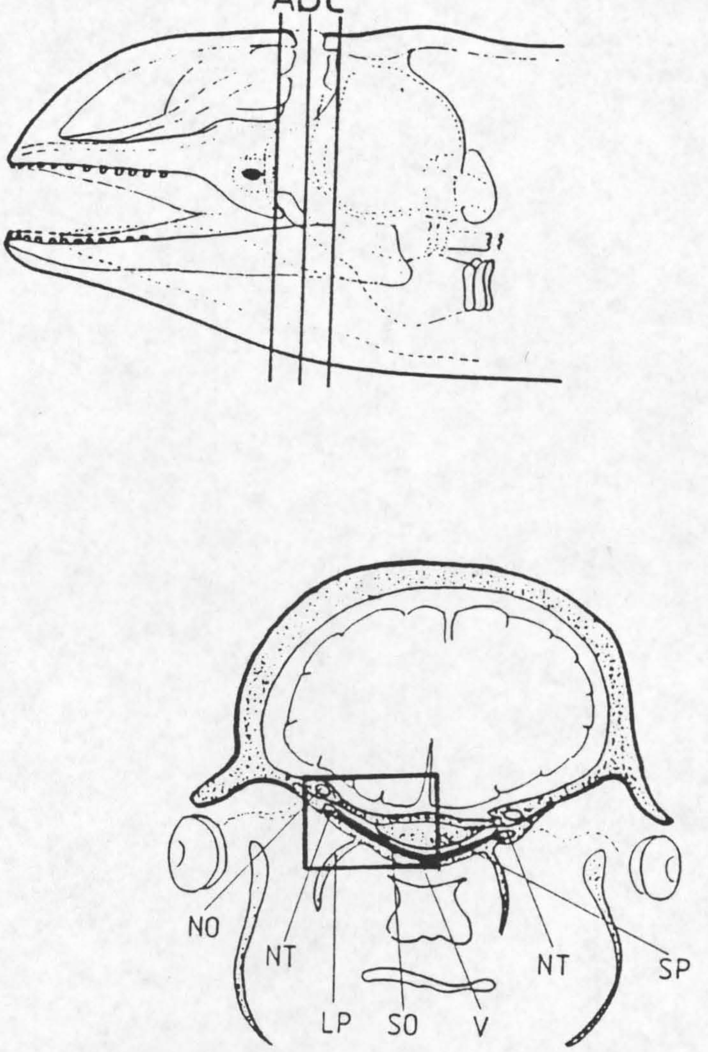

Fig. 7. Transverse section through the rostral sense organ (SO), nervus opticus (NO), nervus trigeminus (NT), lamina medialis proc. ptertygoidei (LP), vomer (V), and os sphenoidale (SP).

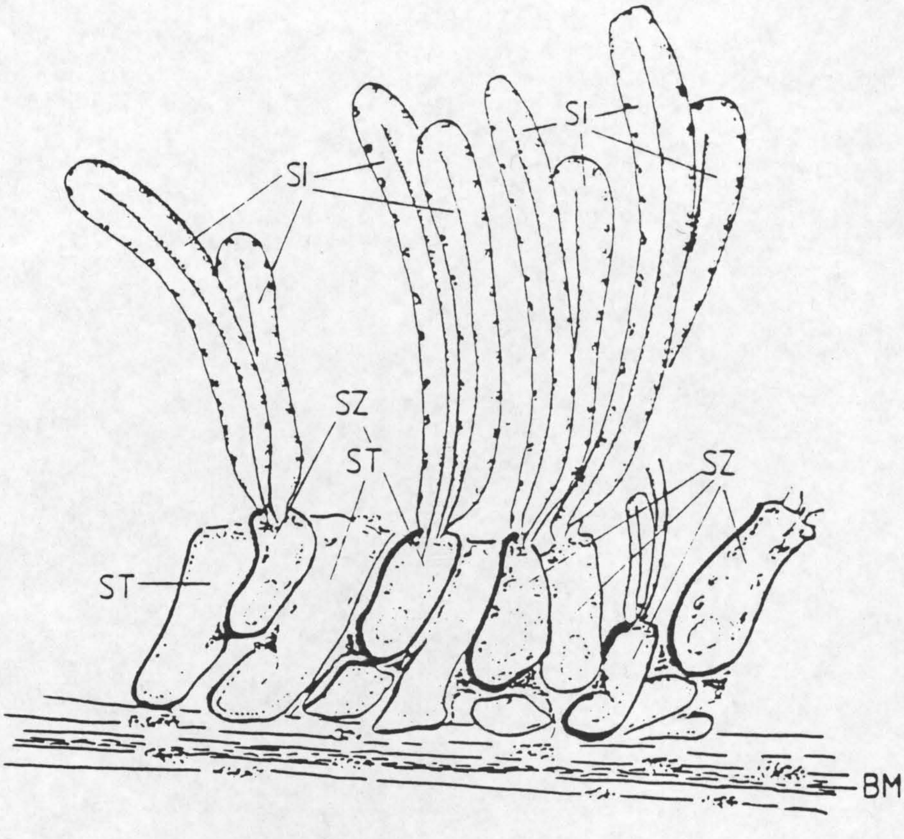

Fig. 8. Sense cells in the rostral sense organ (SZ), with stereocilians (SI) and the membrane (BM).

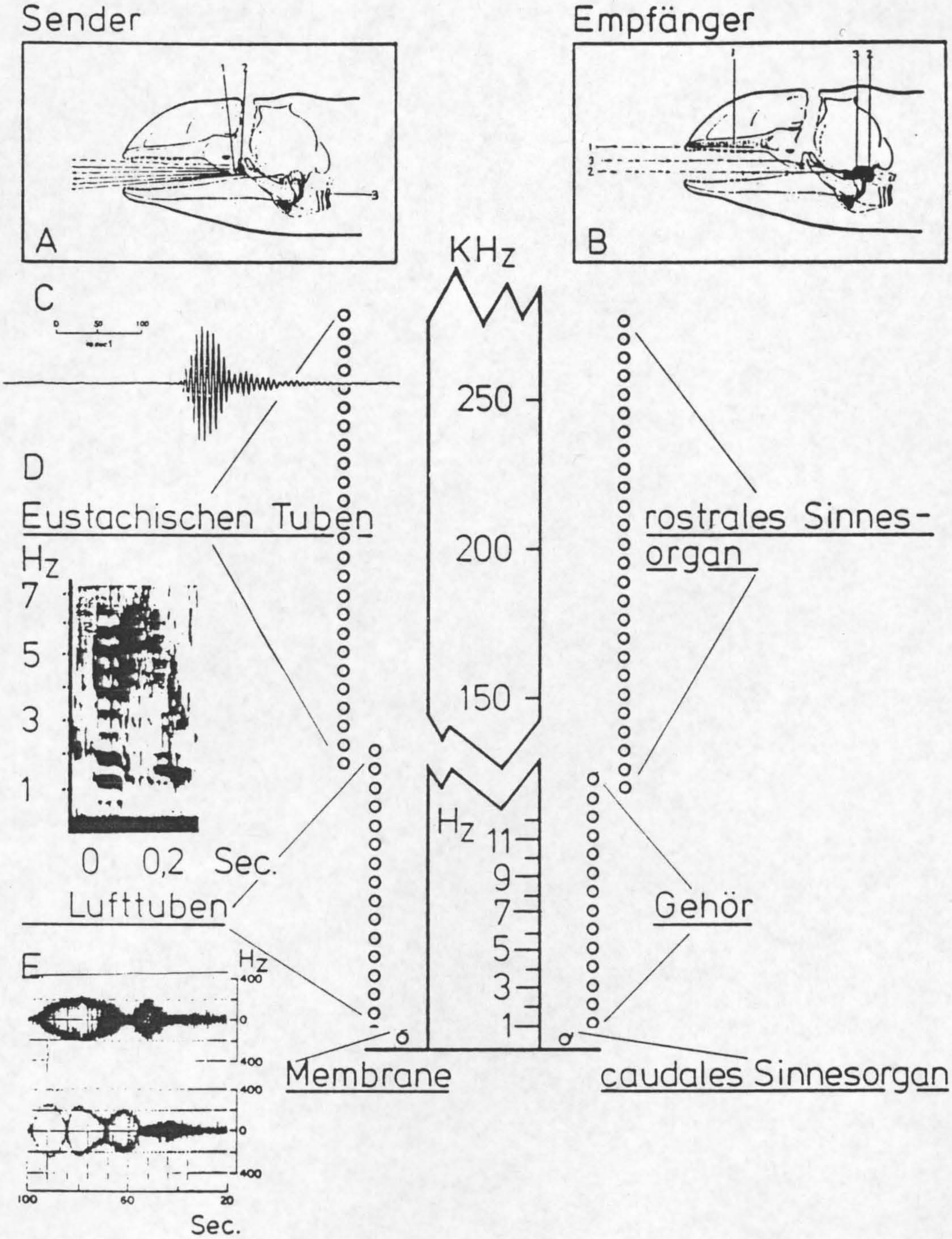

Fig. 9. The orientation system of odontocetes: the probable frequencies produced by air-tubes and membranes, and the probable frequencies perceived by the sense organs and the ear.