Mechanical aspects of hearing
van Dijk, J.S.C.

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1. The peripheral auditory system

Abstract. This chapter gives a brief survey of the peripheral auditory system. An important part of this system is the cochlea, the receptor organ of hearing. Inside this organ sound is translated into a neural message.

1.1 Introduction

After sound has been produced and before it is perceived, the sound signal undergoes several metamorphoses. During its travel from the external ear to the interpreting centre in the temporal lobe of the cerebrum, subsequent parts of the auditory pathway put their mark upon the shape of the signal.

In the peripheral auditory system, or more specifically in the cochlea (Fig. 1.1), a rather special transformation takes place. The classical idea is that the auditory pathway, as far as the cochlea is concerned, resembles a transmission line. Vibration energy is transmitted along this line. The effective length of the line is frequency dependent. For a single frequency, resonance determines the length of the line. Thus, for different frequencies it holds that the respective places of resonance are distributed over the whole length of the cochlea. Most natural vibrations comprise a broad spectrum of frequencies. Therefore, acoustic events are transformed into vibration patterns in which the distribution of resonances in the length direction of the cochlea, and related phenomena, occupy a special place.

After the cochlea, the auditory pathway consists of numerous, probably interacting parallel channels in the shape of bundles of nerve fibres. The collection of these bundles forms the auditory nerve. The entryways of this natural neural network are the nerve endings at the bases of the hair cells in the organ of Corti (Fig. 1.2). This organ is found at the basilar membrane and runs over the whole length of the cochlea. In consequence of this, the entries of the network possess a considerable spatial extent. Here we meet a characteristic function of the cochlea; namely vibration patterns of the composed transmission line are mapped on the entries of the network. The language for this network consists of series of nerve impulses. Therefore, a continuous vibration pattern is translated into a time varying discrete code and is transported in this shape to the higher centres of the nervous system.

For the time being it is believed that the main properties of the vibration pattern are closely related to the resulting image in the primary part of the auditory nerve (Allen and Neely, 1992). The development of techniques of measurement both at a physiological and especially at a mechanical level (Sellick et al., 1982; Sellick et al., 1983; Ruggero et al., 1990) strongly contributed to these views. It seems as if the gap between the vibration image and its neural counterpart can be bridged at the level of the cochlea (Narayan et al., 1998). Here, the recent observations on the contractions of the outer hair cells as a result of mechanical or electrical stimuli (see for instance Brundin and Russell, 1993; Dallos et al., 1993; Nuttall and Dolan, 1993) could help to explain this. However, at this moment it is not yet quite clear how the hair cell contractions act upon the vibration pattern. About twenty years ago the main differences between the well-defined neural image and the mechanical patterns in the cochlea were almost completely ascribed to a possible interaction of neighbouring fibres in the cochlear nerve.
Figure 1.1. Structure of the peripheral auditory system. The first part of the system is the external ear, the auricle and the external auditory canal. The canal leads inward to the eardrum. This membrane separates the external ear from the second part, the middle ear. A small cavity in the petrous part of the temporal bone houses the ossicular chain. The chain consists of three small bones: the malleus, the incus and the stapes. The footplate of the stapes fits into the oval window. This window is the entrance to the labyrinth. The outer bony wall is called the osseous labyrinth. The osseous labyrinth encloses the membranous labyrinth. The cochlea is coiled like a snail-shell. Its osseous part is divided into two scalae, the scala vestibuli and the scala tympani. The scala vestibuli runs from the oval window to the apex; the scala tympani from the round window, a small membrane just below the oval window, to the apex. Both scalae converge at the apex in a small opening, the helicotrema. The membranous labyrinth of the cochlea consists of the cochlear duct or scala media. In this duct the organ of Corti is found. This organ contains rows of hair cells. Nerve endings of the auditory nerve make synaptic contact with the bases of the hair cells. (Reproduced, with permission, from Beck, 1971.)
In spite of the recent results this opinion again made their entrance in literature (Irano and Patterson, 1997).

The cause for this is presumably the absence of 'simple' models for the mechanical action of the cochlea that are both reliable from a theoretical point of view and in which the influence of the outer hair cell activity has been incorporated. In this work we give a contribution to the development of such models. The results lead to a system of filters that is applicable to study properties of sophisticated signals at the level of the cochlea.

1.2 Anatomical features of the inner ear

The structure of the (human) hearing organ is shown in Fig. 1.1. The auricle and the external auditory canal form the external ear. At the end of the auditory canal the eardrum separates the external ear from the second part, the middle ear. The middle ear is a small cavity in the petrous part of the temporal bone. This cavity houses the ossicular chain that consists of three small bones: the malleus, the incus and the stapes. The stapes has the shape of a stirrup. Its footplate fits into the oval window, a small membrane that separates the middle ear and the inner ear cavity. Sound pressure variations at the end of the auditory canal cause vibrations of the eardrum. These vibrations are transmitted by the ossicular chain to the inner ear. The inner ear or labyrinth is an cavity embedded in the petrous part of the temporal bone. The osseous labyrinth encloses the membranous one. The fluid perilymph fills the osseous labyrinth. The membranous labyrinth contains the fluid endolymph. Both fluids are watery. The cochlea is the snail-like part of the labyrinth. Its osseous part consists of two scalae, the scala vestibuli and the scala tympani. The scala vestibuli runs from the oval window to the apex of the cochlea. The scala tympani runs from the round window, a small membrane just below the oval window, to the apex. Both scalae converge at the apex in a small opening, the helicotrema.
Figure 1.3. The arrangement of hair cells and nerve fibres in the organ of Corti. oH: outer hair cells; iH: inner hair cells. HA: habenular openings. Through little holes in the spiral lamina, the habenular openings, nerve fibres penetrate the organ of Corti and terminate in endings at the hair cells. The majority of the nerve fibres is afferent and runs straightforwardly to the inner hair cells (Spoendlin, 1970). The afferent fibres conduct information to the higher nerve centres. Efferent fibres conduct information in the opposite direction. (Reproduced, with permission, from Spoendlin, 1970.)

The membranous labyrinth of the cochlea is often called the cochlear duct or the scala media. In this scala the organ of Corti is found. The organ of Corti is the receptor organ of hearing because it contains receptor cells. Fig. 1.2 shows a cross section of the cochlea.

The separation between the scala vestibuli and the cochlear duct is Reissner's membrane. The basilar membrane separates the cochlear duct from the scala tympani. This membrane and a bony shelf, the osseous spiral lamina, form the upper side of the scala tympani. The organ of Corti rests on the basilar membrane. This organ contains hair cells. Hairs on the cells bridge over a slit between the tectorial membrane and the upper side of Corti's organ. In consequence of their place within this organ, hair cells are divided in two groups: the inner and outer hair cells. The inner hair cells form a single row and are mechano-receptors. The outer hair cells are arranged in three parallel rows (Fig. 1.3). In a healthy cochlea these cells have an important mechanical influence on the motion of the basilar membrane. Therefore we will call these cells mechano-motors.

When a sound wave is transmitted through the external and middle ear, the last ossicle of the middle ear ossicular chain, the stapes (Fig. 1.1), is forced to perform an oscillating motion. In consequence of this, both fluid and membranous structures in the cochlea are forced to follow this motion. At the same time, fluid and membranes exert an impeding action. After some time there will be a state of dynamic equilibrium. If this state is caused by a simple harmonic sound stimulus, the motion of the basilar membrane is a peculiar one. The motion is undulating and behaves as a travelling wave. During its travel along the membrane the deflection of the wave becomes maximal in a limited region of the membrane. When the frequency of the stimulus increases the place of this region at the membrane shifts towards the stapes. In conformity with classical hearing theory (see for instance Yost and Nielsen, 1983),
we shall assume that the motion of the basilar membrane is the root of the forced motion of the organ of Corti. Then, shearing forces between the upper side of Corti’s organ and the tectorial membrane deform hairs of a hair cell. These deformations are the putative stimulus of a cell. A stimulated receptor cell produces chemical substances at the basis of the cell body. Usually, the ‘messenger’ substances are called transmitters. The transmitters diffuse over the thin slit between the hair cell and a nerve ending and evoke a potential in the corresponding fibre. The potential is conducted to a cell of the spiral ganglion (Fig. 1.2). This ganglion consists of the cell bodies of the first nerves of the bundle of cochlear nerves. In consequence of this stimulus the nerve can generate spikes.

Spoendlin (1970) showed that the majority of the auditory nerve fibres are in contact with the inner hair cells only. It appeared that the shape of most inner hair cell fibres is radial and their function is afferent. Moreover, each inner hair cell is in contact with a small bundle of about twenty fibres. Thus the code of an acoustic message is generated at this level.

According to Zwislocki and Sokolich (1973) the spike density in afferent fibres is maximal when the velocity of the basilar membrane reaches its maximum and moves from the scala vestibuli to the scala tympani. A motion in the opposite direction tends to suppress the generation of spikes. This property can be used to find a simplified impression of the image of cochlear vibration patterns in terms of spike densities (Bregman, 1990; Van Dijk, 1991). Here, the question concerning the accuracy of this kind of image building remains a point of discussion. According to our opinion this question is not unimportant but of limited significance especially from a perceptual point of view, for making decisions on spike density patterns is rather a statistical process with an inherent uncertainty than a process in which the accuracy of a number is of great importance. The numbers, which lay the foundation of the image, must reflect the essential physical properties of a vibration pattern so that at a statistical level decisions can be made with a suitable measure of confidence.

In the last two decades there has been a growing interest in the behaviour of the outer hair cells. There are two reason for this. The first one is already mentioned in the preceeding section. The motility of the outer hair cells can have an influence on the vibration pattern of the basilar membrane. This influence could enhance the relation between a cochlear vibration pattern and its image in the auditory nerve. The second one is that Kemp (1978) demonstrated that the ear can also produce sounds. These oto-acoustic emissions can be both evoked and spontaneous. After him several investigators carefully described the main properties of different kinds of emissions. For an overview we refer to Zurek (1985) and Probst (1990). Here again it is the almost unanimous opinion of investigators in this field that the motile properties of the outer hair cells are responsible for these observations.

In summary, the motion of the stapes, which is the end of the external-middle ear transmission line, is mapped on the entryways of a neural network. The entries are the radial nerve endings at the inner hair cells. In this mapping process the motion of the basilar membrane, which partly follows from outer hair cell motility, is of primary importance.

In the next chapter we will study consequences of a striking property of the basilar membrane, namely the membrane as a typical example of a non-isotropic mechanical medium. We will apply ‘state of the art’ methods from classical mechanics. It will appear that complicated models of the recent past possess a high amount of redundancy.