In all the theories discussed above the basilar membrane plays a primary rôle in the explanation of the hearing function. Various anatomical objections, such as the variable structure in man (Wever) and in different animals (Shambaugh, Hardesty) may, however, be raised against the basilar membrane holding such a predominant place in most theories of hearing. Moreover, if we accept that sound-waves enter the inner ear by way of the fenestra ovalis, the tectorial membrane lies nearest to the incoming wave-movement and it seems logical to assume that this membrane is first and more easily activated by this movement than the basilar membrane, which is covered by a thick layer of cells. The primacy of the movements of the tectorial membrane as the stimulating factor for the hair-cells was already put forward by Kishi and Shambaugh, both writers ascribing a resonant function to this structure. On account of its anatomical structure, however, Hardesty thought it very improbable that the tectorial membrane was capable of acting as such a sympathetic resonator.

The view that the tectorial membrane may form the principal vibrating element has recently again been advanced by Mygind. Proceeding from the assumption that the cuticular membranes covering the cupula, the otoliths, as well as the organ of Corti operate as pressure-transformers, a theory is developed which accounts for a localized pitch-perception in the cochlea.

The primacy of the movements of the basilar membrane as the sole source of hair-cell stimulation is also questioned by Larsell and co-workers. It was shown that in the developing cochlea of the pouched opossum young the tectorial and the basilar membrane are well differentiated long before cochlear function appears. This applies also to the hair-cells and the nerve-fibres. Not until the pillars of Corti and the remainder of the supporting apparatus which undergo a slower differentiation, have reached adult state was this function established. The supporting apparatus may thus be regarded as a resiliant apparatus between the two membranes, acting as a cushioning and tension mechanism. In such a conception pressure in the perilymph of the scala vestibuli, transmitted through Reissner's membrane and the endolymph, and localized according to the pressure-gradients, as was suggested by Reboul, would impinge on the tectorial membrane and, through it, on the hair-cells. This conception does not deny movements of the basilar membrane in response to vibrations of the perilymph, but it does not assign to the basilar membrane alone the stimulating function.

Whereas the function of the middle-ear system relative to its structure is now fairly well recognized, the functional mechanism of the inner-ear system has not yet been fully elucidated.

If the hair-cells of the organ of Corti are to be considered as the receptive elements for the physical energy of the sound-impulse, any theory of hearing must now provide for a localized stimulation mechanism of these sensory cells. Ever since Helmholtz the basilar membrane has played a dominating rôle in the explanation of such a localized receptivity.

In these theories concerning the movements of the basilar membrane the intricate structure of the organ of Corti has usually been disregarded. But since this structure is capable of receiving the very minute mechanical stimuli occurring at threshold intensity of the audiofrequencies, the prime importance of the basilar membrane in this refined mechanism is open to considerable question. Not until methods are found, which allow of an experimental approach to this delicate structure, can the ultimate function of its different parts be evaluated and the real basis be found for a theoretical approach to the problem of the mechanism of the cochlear system.

SAMENVATTING.

Het is mogelijk het gehele gehoorproces schematisch in drie phasen te verdelen. Door het geluidsgeleidingssysteem wordt de geluidsprikkel naar het eigenlijke zintuigorgaan, het orgaan van Corti, gevoerd (phase I). Hier wordt de physische energie in zenuwenergie omgevormd (phase II), waarna tenslotte het zenuwgeleidingssysteem de impuls overbrengt naar de acoustische centra in de grote hersenen (phase III).

Na een korte beschrijving van de anatomische structuur

van het binnenoor en een historisch overzicht over de ontwikkeling van de gehoortheorieën tot het midden der 19de eeuw, wordt in dit proefschrift hoofdzakelijk de eerste phase van het proces, die der geluidsgeleiding, beschreven. Hierbij is onderscheid gemaakt tussen:

a. theorieën en experimenten betreffende de *geluidsgeleiding* en
b. theorieën en experimenten aangaande de *geluidsanalyse* in het oor.

Bij de bespreking van de eerste groep werd uitgegaan van de theorie van Weber-Helmholtz, waarbij de verschillende hypothesen, waarop deze theorie is gegrondvest, in het licht der experimentele gegevens nader worden bezien (Hoofdstuk IV). Het uitgangspunt voor de tweede groep vormde de klassieke resonantietheorie van Helmholtz, die tracht de geluidsanalyse, als een der fundamentele eigenschappen van het gehoororgaan, te verklaren door resonantie van verschillende segmenten van de basilairmembraan. De diverse argumenten voor en tegen deze opvatting worden in Hoofdstuk V nader besproken, waarbij mag worden geconcludeerd, dat een geluidsanalyse door resonantie in de oorspronkelijke zin van Helmholtz, als zeer onwaarschijnlijk mag worden beschouwd, doch dat de gelocaliseerde toonperceptie, zoals door Helmholtz aangegeven, door een groot aantal experimenten overtuigend is bewezen.

De hydrodynamische theorieën, die de geluidsanalyse in het algemeen trachten te verklaren zónder gebruikmaking van het principe der physische resonantie, gaan uit van de gedachte, dat als gevolg van een beweging van de stapes zich een lopende golf langs de basilairmembraan voortplant. Een plaatselijk optredend drukmaximum, bepaald door de verschillende physische factoren van de cochlea, zou dan als prikkel voor het orgaan van Corti fungeren. De modelexperimenten van von Békésy, waarbij inderdaad deze lopende golf kon worden aangetoond, alsmede de verschillende physisch-mathematische berekeningen over de voortplanting van een golf in een ten dele elastische buis worden in Hoofdstuk VI besproken.

Tenslotte is getracht, uitgaande van de gedachte dat het geluidsgeleidingssysteem een mechanisch systeem is, dat in staat is gedwongen trillingen uit te voeren, in Hoofdstuk VII de verschillende physische eigenschappen van dit systeem na te gaan, waarbij de eigenschappen van geluidsontvangers in het algemeen als uitgangspunt werden genomen.

SUMMARY.

The entire process of hearing may be divided into three stages. The sound-conducting system transfers the sound-stimulus to the sensory organ proper, the organ of Corti (stage I). Here the physical energy is transformed into nervous energy (stage II), and the acoustic pathways finally conduct the impulse to the acoustic centres in the brain.

After a short description of the anatomical structure of the inner ear and a historical survey of the development of the theories of hearing up to the middle of the 19th century, this thesis deals essentially with the first stage of the hearing process. A distinction has been made between:

a. theories and experiments concerning *sound-conduction* and
b. theories and experiments concerning *sound-analysis* in the ear.

In the discussion of the first group an attempt was made to proceed from the theory of Weber-Helmholtz, in which the various hypotheses on which this theory is founded are studied in the light of experimental data (Chapter IV). The starting-point for the second group was the classic resonance-theory of Helmholtz, which tries to explain sound-analysis, as one of the basic principles of the hearing organ, by means of resonance of various segments of the basilar membrane. The arguments for and against this conception are discussed in Chapter V, and it may be concluded, that sound-analysis by resonance in the original sense of Helmholtz is highly improbable, but that a localized frequency-reception, as indicated by Helmholtz, has been confirmed by a great number of experiments.

The hydrodynamic theories, which attempt to explain sound-analysis without making use of the principle of physical resonance, proceed from the idea that consequent to a movement of the stapes a travelling wave travels up the vestibular scale, along the basilar membrane. A local pressure-