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**AUDIO-VESTIBULAR SYSTEM
AND FACIAL NERVE**

Audio-Vestibular System and Facial Nerve

Liber-Amicorum in Honour of L. B. W. Jongkees

Editor

W.J. OOSTERVELD, Amsterdam

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Preface

At the beginning of July 1975, a group of scientists and clinicians from all over the world assembled in Amsterdam for a special meeting. It was organized in honour of LEONARD B. W. JONGKEES, who celebrated his 5th lustrum of devoted work at the University of Amsterdam. The general subject of this Symposium was the tripod on which are based most of his important scientific and clinical activities: the facial nerve, the auditory and the vestibular system.

A system has been defined as an assembly of elements economically organized to perform of a given function or functions. In the case of the vestibular system the elements correspond, respectively, with the semi-circular canals, the otolith organs and the central processing, subserving spatial orientation. For this reason, morphological and physiological problems must include these three anatomical substrata and their functional interplay. The papers presented at the Symposium reflect this complex situation: morphology of the vestibular sensory organs, the interaction of the visual and vestibular system, the role of the cerebral cortex, central compensation of peripheral dysfunction and vestibular habituation were discussed, but a great number of questions had to be left open, or lead to new ones.

In the case of the auditory system the basic elements correspond, respectively, with the cochlea, the spiral ganglion, auditory nerve and again the central processing, subserving acoustic information. Most of the papers reflect this equally complex situation in the field of hearing research: the complicated interaction between physics, morphology, biochemistry, physiology, pathophysiology and psychology.

The third part of this Symposium was dedicated to the facial nerve: borderland between neuro-anatomy, neuro-physiology, neurology and otol-

ogy. Normal function of the seventh cranial nerve is the underlying neuro-physiological mechanism of mimic expression, one of the most important features of animal and human behaviour. Any disorder of the coordination of mimic function will result in disfigurement and may even cause a behavioural disturbance. Most of the papers are dealing with diagnostic and therapeutic procedures, subserving the restoration of facial nerve function.

The main goal of this meeting was to review concepts and theories, to exchange information and knowledge in an atmosphere of true friendship. Since this goal has been achieved we thought it would be worth-while to publish the scientific and clinical papers presented at this Symposium, in order to provide better information to a greater public, interested in these particular borderlands of otology, thus honouring our friend LEONARD B. W. JONGKEES, to whom we owe so much in the field of clinical and scientific otolaryngology.

C. R. PFALTZ, Basel

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Section 1

Hearing

The Genesis of the Auditory Action Potential

E. DE BOER

Physics Laboratory, E.N.T.-Clinic, Wilhelmina Gasthuis, Amsterdam

Introduction

The *action potential* of the auditory nerve can be recorded by an electrode placed in the vicinity of the cochlea. Measurement and interpretation of this potential in experimental animals have a long history [DAVIS, 1957]. Application of the same technique in human subjects (electrocochleography) is relatively new. For best results the recording electrode should be as close to the cochlea as possible. The transtympanic needle electrode, as used in a pioneering way by ARAN *et al.* [1971] and EGGERMONT *et al.* [1974], comes nearest to the ideal. Other authors advocate an electrode placement on, or on the rim of, the tympanic membrane [SALOMON and ELBERLING, 1971; COATS and DICKEY, 1970; CULLEN *et al.*, 1972]; in this case a definite loss of recording sensitivity must be incurred. Even with an electrode on the ear lobe [SOHMER and FEINMESSER, 1967] or on the vertex [DAVIS, 1974] usable recordings can be obtained.

Electrocochleography is especially useful for early assessment of hearing loss in babies; the recording gives a reliable index of cochlear functioning. A great problem is formed by the interpretation of pathological waveforms and abnormal properties of the cochlear action potential. In order to solve this problem, the genesis of the (normal) action potential should be understood as well as possible. The theoretical developments described in the present paper were produced with this aim in mind.

The auditory-nerve action potential is composed of contributions from activity in all the nerve fibers of which the nerve consists. Each nerve fiber, however, gives a contribution with a biphasic or triphasic waveform, so that the sum contribution will be zero when all the nerve fibers fire randomly.

Hence, in order to elicit a clear auditory-nerve action potential, the nerve fibers should be caused to fire synchronously. This can be achieved, for instance, by using *clicks* as acoustical stimuli.

One problem with click stimuli is that the various regions of the cochlea all contribute equally to the response, so that in a pathological ear the distribution of hearing loss over the range of frequencies cannot be measured. To remedy this shortcoming, *tone bursts* should be used as stimuli. Continuous tones hardly give an action potential (because of a lack of synchrony between firings), so that the action potential is mainly caused by switching-on of the tone. A compromise is in order between an abrupt onset of the tone – causing a click-like excitation throughout the entire cochlea – and a gradual onset of the tone which produces a very weak action potential.

EGGERMONT *et al.* [1974], who are the pioneers of electrocochleography in the Netherlands, use carefully tailored tone bursts as acoustical stimuli. They proved that with their technique it is possible to estimate hearing loss at distinct frequencies with good accuracy [EGGERMONT *et al.*, 1975]. With this method, electrocochleography has become a powerful tool for objective audiometry. In Amsterdam we have closely followed this approach in the execution of clinical electrocochleographies. In animal experiments, exactly the same technique of stimulation and recording was followed. In the present paper we will give an outline of the experimental and theoretical background of our work on the genesis of the action potential. The full description of the action potential theory is published elsewhere [DE BOER, 1975].

Cochlear Excitation

Every fiber of the auditory nerve represents a frequency region which is specific for that fiber. This region is centered around the 'characteristic frequency' (CF) of that fiber. The frequency specificity is expressed by the famous 'place theory of hearing'. The principle of frequency specificity implies that a fiber will react maximally to a stimulus component of a particular frequency, namely the CF. The principle implies also that the fiber will be less sensitive to other components. It is as if every acoustical stimulus were filtered before it acts to excite a nerve fiber. In other words, a specific filter can be thought to be associated with every nerve fiber (different filters with different fibers, of course). A most important question, then, is whether the filter for one fiber is the same for every type of stimulus.

An answer to this question can only be obtained when the characteristics

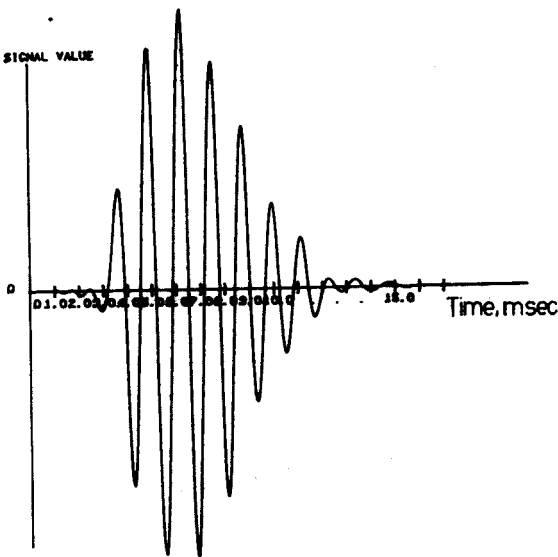


Fig. 1. Typical revcor function (smoothed) for an auditory nerve fiber.

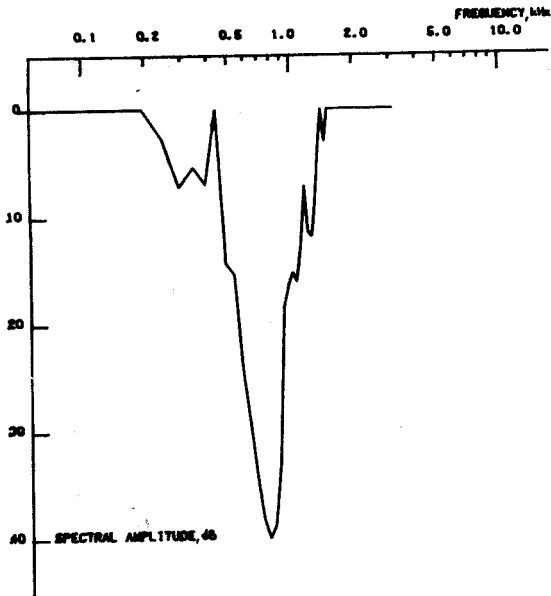


Fig. 2. Spectrum associated with function of figure 1.

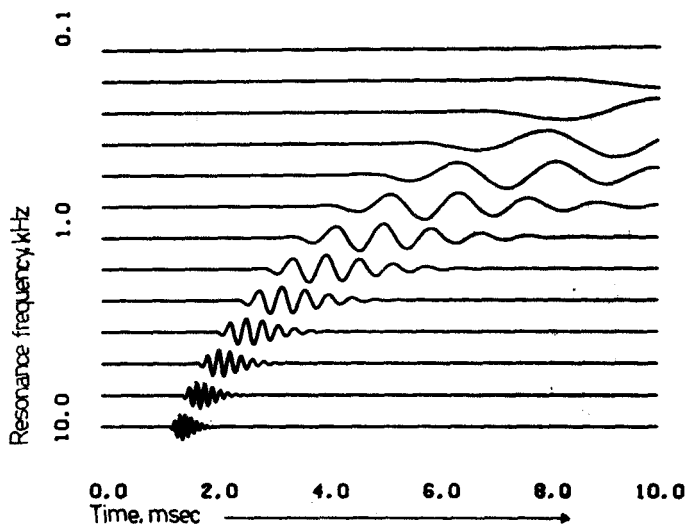


Fig. 3. Normalized revcor functions of 13 hypothetical nerve fibers.

of the pertinent filter are determined experimentally. This can be done by a method known as the 'technique of reverse correlation' [DE BOER, 1973]. It requires stimulation of the ear of the experimental animal with white noise and recording of the series of 'spikes' from one fiber of the auditory nerve. The result of the procedure comes in the form of a function, the *revcor function* (abbreviation for reverse-correlation function), which function can be interpreted as the impulse response of the best-fitting filter for the fiber. An impulse response of a linear filter is the response of that filter to an impulse, in acoustic terms to a click. A linear filter is specified completely by way of its impulse response.

Let us consider a filter constructed in such a way that the experimental revcor function of a nerve fiber is the impulse response of that filter. The ear of the animal and the filter can then be subjected to the same stimulus signal. The output of the filter will be the filtered stimulus and the output of the physiological preparation will be a series of 'spikes' from the (same) nerve fiber for which the revcor function was determined previously. Comparison of the two responses shows that the filtered stimulus is a good

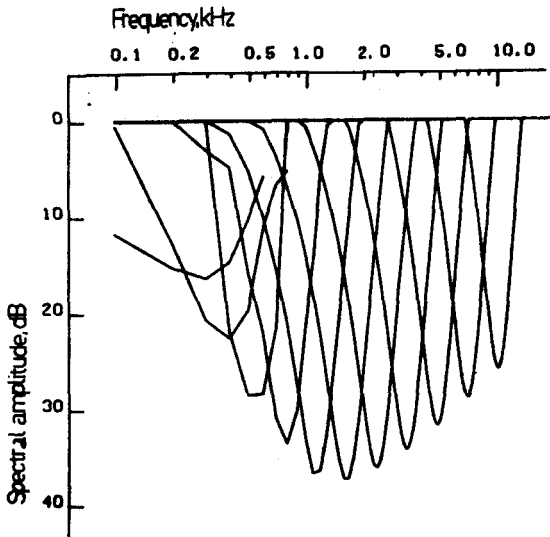


Fig. 4. Spectra associated with 11 of the functions of figure 3.

predictor for the probability of spikes, and this applies with good approximation to all stimuli [DE JONGH, 1972]. Hence the question posed above can be answered affirmatively: one filter can describe the responses of one fiber for all stimuli. In summary, we can visualize the main part of the cochlear encoding process by way of a set of filters, each one representing the stimulus-response relationship for one nerve fiber.

The shape of a revcor function is shown in a stylized form by figure 1. The waveform has an initial delay which is partly the result of wave traveling time in the cochlea. This delay will, of course, be larger for those nerve fibers that are located farther away from the cochlear windows, i.e. that have a lower CF. Figure 2 shows the spectrum associated with the revcor function; this is drawn in such a way that it resembles a 'tuning curve'. This spectrum quantitatively indicates in which proportions stimulus components of different frequencies contribute to excitation of the nerve fiber. The most sensitive point is the resonance frequency of the filter, i.e., the CF of the fiber. It has been found that the shape of the revcor function is almost independent of the intensity for which it is determined.

General Theory

We want to set up a general theory describing the stimulus-response relations for the entire set of nerve fibers in the auditory nerve. For this purpose we first construct a set of hypothetical filters that describe the signal transformations for a limited set of hypothetical idealized nerve fibers. From numerous experiments on single-fiber responses in cats the conclusion is drawn that the waveform of a revcor function can be simplified to a standard waveform dependent upon only one parameter: the resonance frequency. Figure 3 shows the waveforms of a number of these *standard functions*, the resonance frequencies are distributed over the audible range of frequencies just as for real nerve fibers. Note how the latency (initial delay) of response depends in a characteristic way upon the resonance frequency. Figure 4 shows a number of the corresponding spectra, drawn in the same way as figure 2. The relative bandwidth of these functions decreases slightly with increasing resonance frequency.

With this set of hypothetical impulse responses it is possible to construct a set of hypothetical filters that describes the first stages of the encoding process for the entire cochlea. In particular, this model serves to describe how any particular acoustical stimulus causes nervous excitation and how this excitation is distributed over the set of nerve fibers. Excitation is meant here in the physical sense, i.e. in terms of the filtered stimulus. Between this excitation and the actual initiation of nerve impulses in a nerve fiber there are many physiological processes. We will concentrate here, however, on the physical parameters of the 'excitatory signals', i.e. the output signals of the filters. To simplify matters, we will not describe the waveforms of these excitatory signals in detail but will content ourselves with their *amplitudes* and the way these amplitudes depend on time. The amplitudes will be expressed in decibels, of course.

Let us now consider stimulation of the cochlea with a tone burst typical for electrocochleography: for instance, a tone burst of 1 kHz frequency, with a duration of 3 msec and a rise time of 0.7 msec. Figure 5 shows the excitation resulting from the set of hypothetical filters as a function of time and resonance frequency. The horizontal cross-sections correspond to level differences of 20 dB. For the case of stimulation with a tone just above threshold we must imagine this entire figure to be shifted down, so that only the central part of it corresponds to nerve fibers that are capable of being excited. The number of activated fibers is small and, consequently, the resulting whole-nerve action potential (in the sequel to be referred to as: AP) is small. The

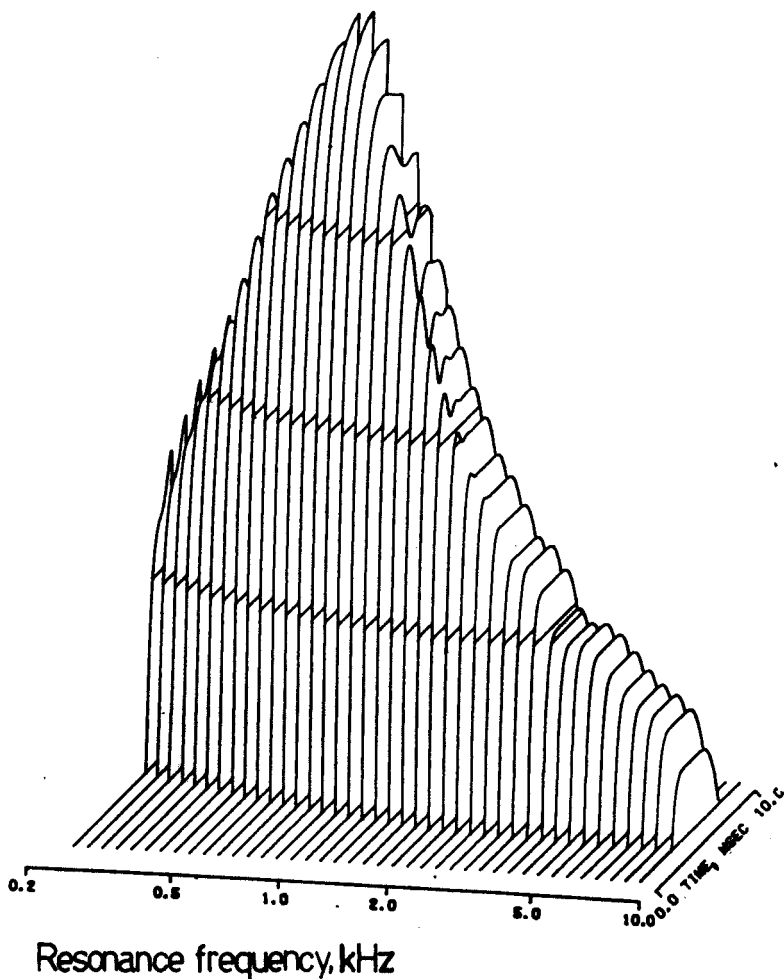


Fig. 5. Excitation in the cochlea: the physical intensity for a 1 kHz tone burst as a function of time and resonance frequency, computed for a set of 40 hypothetical nerve fibers.

latency of the AP will correspond with the latency of the response of those filters that have a resonance frequency in the 1-kHz region. The latter latency is determined by the fundamental latency of the 1-kHz nerve fibers (figure 3) and the rise time of the stimulus.

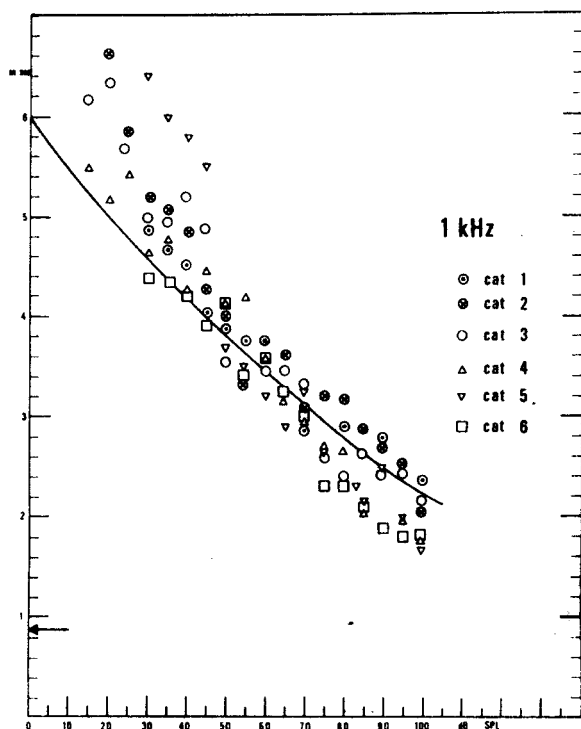


Fig. 6. Comparison of theoretical and experimental latencies of the AP. Stimulus frequency is 1 kHz.

When stimulus intensity is increased, e.g. by 20 dB, the figure shows quantitatively how many hypothetical nerve fibers will be excited. It shows also how the excitation proceeds as a function of time. For further increases of stimulus intensity, the 'central' nerve fibers will soon get saturated. Hence the amplitude of the AP will be slightly less than proportional to the number of activated nerve fibers. The variations in the AP for increments in stimulus intensity are mainly due to the activity of nerve fibers that are located on the boundaries of the excitation pattern of figure 5. Amongst these fibers, those that are located near the cochlear windows – in figure 5 the units at the right side – are the most important ones. There are two reasons for this dominance: these fibers have the shortest latencies and thus contribute to the earliest excursions of the AP waveform, and, furthermore, they produce a large potential on the AP-recording electrode, relative to other fibers [EGGERMONT *et al.*, 1975; DE BOER, 1975].