THE EXCITATORY PROCESS IN THE COCHLEA*

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Introduction.—The nature of the excitatory process by which sensory cells initiate nerve impulses in afferent nerve fibers is very obscure. In the case of the ear, the most widely accepted theory has been that an electrical potential known as the "cochlear microphonic" is generated by the hair cells in the organ of Corti and serves as a direct electrical stimulus to the peripheral terminations of the fibers of the auditory nerve.

The cochlear microphonic, it will be recalled, seems to be simultaneous with the mechanical movements of the cochlear partition and it follows the wave form of the sound very closely, at least at moderate intensities of stimulation. It shows no refractory period or all-or-none characteristics like the action potentials of nerve.1 Action potentials of the auditory nerve, probably generated in the cell bodies in the spiral ganglion, not in the fine non-myelinated terminal twigs, can also be recorded from electrodes placed in or near the cochlea.

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Sound waves at 2000 to 6000 cycles per second are very efficient as auditory stimuli. This high efficiency led Wever to postulate an intermediate excitatory effect or process which had the property of summatiing the excitatory effects of two or more sound waves. We now present experimental evidence for the existence of such a process of summation. We also have found a third electrical potential in the cochlea in addition to the cochlear microphonic and nerve action potentials. The new potential exhibits summation and seems to represent the local excitatory process that initiates auditory nerve impulses.

Methods.—All experiments were performed on guinea pigs anesthetized with dial in urethane. Electrodes consisting of No. 38 enamel-insulated silver wire were introduced into the cochlea through small holes drilled into scala tympani, scala vestibuli and/or scala media of the basal turn.

Electrodes in first turn of guinea pig's cochlea

![Electrodes in first turn of guinea pig's cochlea](image)

In some experiments electrodes were placed in other turns as well.) The position in turn 1 is at the site of maximal stimulation by tones of 8000 c. p. s. The electrical circuit was completed by a reference electrode attached to the wound in the neck. The cochlea of the guinea pig protrudes into an air-filled bulla, and thus the electrical circuit from the reference electrode enters the cochlea chiefly by way of the internal auditory meatus. The reference electrode is thus roughly equivalent to one placed on the auditory nerve.

Electrical responses were recorded simultaneously from several combinations of electrodes by means of a three-channel cathode-ray oscilloscope assembly (Grass). Two of the channels could be connected in parallel so as to either add or subtract the signal in one to (or from) the signal in the other. In this way the action potential of the auditory nerve, which appears as a negative electrical change at all of the cochlear electrodes,
could be completely canceled by subtracting the scala tympani signal from the scala vestibuli signal, after appropriate adjustment of amplification. The cochlear microphonic, on the other hand, appears in opposite phase in scala tympani from what it is in scala vestibuli and scala media (see Fig. 1). It can be canceled by adding the signals from scala vestibuli (or media) and scala tympani. By this method action potentials of moderate voltage can be viewed, and their latency measured, in spite of the simultaneous presence of a large cochlear microphonic which otherwise usually obscures them almost completely.

The acoustic stimuli employed included clicks and pure tones, but were chiefly brief tone-pips. Our usual "tone-pip" consisted of sound waves at a basic frequency of 8000 c. p. s. This signal begins gradually and reaches maximum amplitude during the fourth or fifth wave and immediately diminishes again (see Fig. 3). The "2000 c. p. s. tone-pip" has a basic frequency of 2000 c. p. s. The maximum in this case is reached during the third sound wave. The pips were presented at pulsing frequencies from 1 to 60 per second. The tone-pips have several advantages: (1) nearly all of the acoustic energy is concentrated in a band less than an octave wide, so that they presumably activate a relatively restricted region of the cochlear partition, yet (2) the relatively rapid onset may allow identification of the particular sound wave that initiates a nerve impulse and (3) at frequencies of 1000 c. p. s. and higher only one impulse is set up in each fiber because of the rapid increment and decrement of sound waves and the refractory period of the nerve fibers.

Evidence for Summation.—For frequencies of 2000 c. p. s. and less, each volley of nerve impulses revealed by the action potential can be clearly associated with one sound wave or another. We find that only the portion
of the wave corresponding to acoustic rarefaction at the ear drum causes auditory stimulation. If one (negative) wave in a tone-pip has set up an action potential, the next wave, if stronger, may activate other neurons of higher threshold even though the neurons stimulated by the first wave are still refractory. Thus the composite action potential may show two peaks separated by one wave-length of the basic frequency of the tone-pip (see Fig. 2). Reversal of the polarity of the tone-pip, i.e., starting with a negative instead of a positive sound wave, will change the latency of the first effective sound wave because the first adequate negative sound wave now comes either a half wave earlier or a half wave later than it did previously. (The first effective wave may be either stronger or weaker than the first effective wave with the original polarity. The two peaks of action potentials will in general, therefore, be different in amplitude as well as showing a difference in latency. Both of these effects are illustrated in figure 2.) The basic frequency employed in figure 2 was 2000 c. p. s. and it is clear that at this frequency the auditory nerve is responding to individual sound waves in the tone-pip.

With a basic frequency of 8000 c. p. s., however, the behavior of the nerve is fundamentally different. There is no visible change in latency when the polarity of the tone-pip is reversed (see Fig. 3). We have sought for a change of latency with great care on the face of the oscilloscope and have assured ourselves that if there is a change of latency it is certainly less than 30 microseconds. The change which should occur if the nerve were responding to individual sound waves is 62 microseconds. We conclude that at this frequency the nerve does not respond to individual sound waves but that a stimulating effect is carried over, even from the earliest subliminal waves. The stimulating effects are integrated by some process that we call "summation" so that the nerve responds to the tone-pip as a whole instead of to the individual waves. Summation seems to dominate the picture at 8000 c. p. s. (At 4000 c. p. s. a small change of latency with reversal of polarity can still be demonstrated, however.)
A second line of evidence for summation at high frequencies is found in
the change of latency with the intensity of a tone-pip. At low frequencies
the latency diminishes in stepwise fashion as the intensity of the stimulus
is increased. Each step means that an earlier sound wave, originally
too weak to stimulate, has now become strong enough to set up nerve
impulses. At 2000 c. p. s. the number of steps that can be observed corre-
sponds to the number of sound waves (counting only the negative peaks)
from the beginning of the tone-pip to the largest negative peak. At 8000

RESPONSES TO TONE-PIPS: BASAL TURN OF GUINEA PIG'S COCHLEA

A 2000 CPS

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ACTION POTENTIALS

B 8000 CPS

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SUMMATING POTENTIAL

FIGURE 4

tone-pip (gains adjusted to give minimum residue) reveals
two volleys of action potentials (I) separated by one wave-
length of the stimulating frequency. They are preceded by
small waves of summating potential and cochlear microphonic
in uncertain proportion. The late waves (II) include the
second neural response (from the cochlear nucleus in the me-
dulla).

B. Responses from scala vestibuli and from scala media
(slightly retouched). No cancellation. In this experiment
the cochlear microphonic disappeared almost completely when
an electrode was inserted into scala media. Small action
potentials are visible and the 8000 c. p. s. ripple is partly
cochlear microphonic but the main deflections are summating
potential. An upward deflection means cochlea more positive
to reference electrode.

c. p. s., however, the shortening of latency as intensity increases seems to
be continuous. More important, the total shortening as the stimulus
is increased from threshold to a rather high level may be greater by at
least two wave-lengths than the time from the beginning of the pip to the
largest wave. It seems, therefore, that at threshold the process of stimula-
tion must have been completed by a wave later than, and therefore smaller
than, the maximum wave at the center of the tone-pip. We believe that
this is good supporting evidence for the existence of summation, although
the argument makes the tacit but unproved assumptions that the conduction time for the nerve impulse and also the time required for the excitatory process to set off a nerve impulse are the same whether the stimulus be weak or strong.

The Summating Potential.—About a year ago we described what we called "rectification" of the cochlear microphonic. Under several adverse circumstances, such as anoxia, the electrocoagulation of part of the cochlea, or the insertion of several electrodes deeply into the cochlea, the cochlear microphonic may apparently shrink to a few per cent of its original amplitude. The remaining response is "rectified," meaning that only one-half of each wave (the half in which scala vestibuli becomes electrically negative) still remains. This description is adequate for frequencies below 2000 c. p. s. We have recently observed that at higher frequencies there is also a shift of the base line in the direction of negativity in the scala vestibuli. The negative deflection appears to be produced by fusion of successive electrical pulses that recur with the frequency of sound waves. With an 8000 c. p. s. tone-pip the pattern resembles the negative half of the envelope of the pip, with an 8000 c. p. s. ripple also clearly visible (see Fig. 4). These "rectified" potentials are actually quite independent of the cochlear microphonic. They represent a third electrical potential of the cochlea which shows the property of summation at frequencies above 2000 c. p. s. This third potential decays rapidly enough, however, so that there is usually no effective carry-over (summation) below 2000 c. p. s. The maximum voltage of the third potential has not yet been measured because of serious technical limitations but it is well over 50 microvolts (scala media vs. reference electrode).

Evidence that the summating potential differs from both the cochlear microphonic and the action potential is as follows:

1. The summating potential (SP) is unidirectional (like the action potential) for any particular pair of electrodes. The cochlear microphonic (CM), on the other hand, is a change of electrical potential both above and below the original resting level.

2. SP shows summation. It outlasts the mechanical movement (unlike CM) and it shows no all-or-none behavior or refractory period (unlike action potentials (AP)).

3. SP and CM are differently oriented anatomically. The most favorable combination of electrodes for recording SP is scala media vs reference electrode. The most favorable combination for CM is scala vestibuli vs. scala tympani. Figure 1 shows how these axes are approximately at right angles to one another.

4. The anatomical location of SP is apparently in the organ of Corti (like CM) and not in the spiral ganglion (unlike AP). AP appears equally and in the same direction at electrodes in scala vestibuli, media or tympani
(vs. reference electrode). SP appears strongly in scala media (vs. reference) but may be completely absent in scala tympani (unlike CM and AP), or, if the electrode is placed as far as possible away from the basilar membrane, its sign may actually be reversed. The possibility of placing an electrode on the positive side of the isopotential line in scala tympani shows that the origin of the potential difference must be well out in the cochlear canal and not within the modiolus.

5. The SP lags in time (or phase) behind CM. If CM from scala tympani is used to cancel CM from scala vestibuli, some SP as well as AP therefore remains (see Fig. 4 A). The lag seems to be of the order of 100 microseconds.

6. The SP may remain in the face of adverse conditions, such as anoxia or operative trauma, after the cochlear microphonic has virtually or completely disappeared. Action potentials have been observed under such conditions of operative trauma. This point is of special importance as it shows that *neither the summating potential nor the action potentials are in any way dependent on the cochlear microphonic*. The cochlear microphonic may be a good indicator of the time and a fair indicator of the intensity of mechanical movement of the organ of Corti, but it is not part of the chain of events that generates the nerve impulse.

7. At high intensities of stimulation, although still within limits perfectly tolerable to the human ear, the SP continues to increase with the intensity of the 8000 c. p. s. tone-pips, although the increase (like that of CM) becomes non-linear. While SP is still increasing CM reaches its maximum and may even begin to shrink again. It is worth noting that the behavior of SP is more in line with the behavior of AP, which is still increasing at this intensity, not to mention the sense of loudness to the human ear which is also still increasing.

8. Electrical polarization between scala vestibuli and scala tympani increases or decreases SP according to its direction. When the SP is increased the AP increases also. When SP is diminished AP diminishes or vanishes. The same intensity of electrical polarization causes a small, but only very small, change in the cochlear microphonic. If the cochlear microphonic is already absent it may be restored (or an equivalent microphonic may be introduced) by electrical polarization. The polarity of the microphonic relative to the sound wave will in this case depend on the direction of the polarizing current. We have not been able to reverse SP by polarization.

9. On the death of the animal AP disappears first; SP continues for a time after death; CM may continue longer, although at the low post-mortem level that is already so familiar. Sometimes SP outlasts CM.

*Interpretation of the Summating Potential.*—We believe that the summating potential arises in the terminal twigs of the auditory nerve fibers
which are arranged like baskets around the hairless ends of the hair cells. We believe also that the summing potential is a local excitatory process analogous to the end-plate potential at the neuro-myal junction and to the post-synaptic potentials of spinal neurons. 8 How the mechanical movement sets up the local excitatory process (the summing potential) is unknown.

The latency of the action potential relative to the mechanical movement we interpret as due mostly to conduction time from the nerve endings to the cell bodies. The shortest latency that we have measured for the foot of the action potential from the beginning of the cochlear microphonic following a strong, sharp click (rarefaction) is 550 microseconds.

General Significance.—We have described a summing potential which seems to represent the excitatory process initiated by the sensory cells of the cochlea in their afferent nerve fibers. Similar electrical potentials, probably representing the same type of excitatory process, have been recorded from muscle spindles 9 and from Pacinian corpuscles, 10 and by analogy we may expect to find them also in the related sense organs for touch, pressure, vibration, muscle sense, orientation to gravity and acceleration. The summing potential in the ear and perhaps elsewhere should be a useful tool for determining the mode of action of drugs, fatigue, etc., on the sense organ and for investigation of the process whereby mechanical force initiates the excitatory process.

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† Former Fellow of the W. K. Kellogg Foundation.
‡ Read under the titles: "Audition—A Physiological Survey" and "Summation in the Auditory Sensory Process." Some material has been added in preparing the paper for the press.

2 Davis, H., unpublished, but reported at the meeting of the National Academy of Sciences, April 24, 1949.