THE CODING OF SOUND IN THE AUDITORY SYSTEM

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When listening to speech or music we are aware that the sound is composed of many different frequencies which are constantly changing and also varying in intensity. This constantly modulating sound is encoded into electrical discharges by the cochlea. The coded information then passes as a series of electrical discharges along the auditory pathways and is processed and refined in the auditory centres. Finally, all the data is decoded, possibly in the auditory cortex, to produce the sensation we perceive as musical notes or someone speaking.

The auditory system is composed of a number of nuclei and pathways. There are more nuclei or cellular stations required to code sound than are necessary for coding in other sensory systems. The complexity of the pathways and the possible sites for interaction of sound from both ears can be seen by referring to Figure 1.

In Figure 1 it can be seen that second order neurones leave the dorsal and ventral cochlear nucleus and pass to the ipsilateral and contralateral superior olivary nuclei. This cellular station is the first where auditory information from both ears can interact. It is now thought that the medial superior olivary nucleus is particularly important in integrating differences in intensity and the time of arrival of two sounds at each ear (Hall, 1965). These are of course important in localizing the direction from which a sound comes. From the superior olive, information then passes along the lateral lemniscus to the inferior colliculus and here again in the inferior colliculus, data from both ears can interact. Consequently, this cellular station may also be involved in sound localization (Rose et al., 1966). From the inferior colliculus, third


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A diagram of the auditory pathways (Jungert).

en = cochlear nucleus; son = superior olivary nucleus;
sc = inferior colliculus; mgb = medial geniculate body;
ac = auditory cortex
and fourth order neurones pass to the medial geniculate body of the same side, and finally the pathways project to the auditory cortex.

This description of the auditory pathways only gives a rough outline of the areas of the brain that are stimulated by sound. The effects of acoustic stimulation are really much more widespread, and slow waves may be recorded in such diverse areas as the visual cortex and cerebellum. The reason for this widespread activity is not clear, but it is probably important in coding.

We have made certain advances in understanding coding, but many interesting everyday problems require solution. One of the most difficult things to understand is how the brain can perceive the very small changes in frequency that are an integral part of speech and other naturally occurring sounds. For example, it is remarkable how a mother can distinguish the cry of her newly-born baby from all the other cries in the nursery. The differences could not be detected by the spectral analysis of their frequencies with the equipment at present available. Another important problem in coding is how the brain can suppress unwanted auditory information. We are all aware of the experience of not hearing the clock until it stops. Another intriguing problem is the way in which intensity is coded. Normally the ear can perceive a sound pressure range of 120 db. This means that at the maximum pressure the amplitude of vibration of the basilar membrane is a million times greater than the amplitude at threshold. Not only can the ear perceive such an enormous range of pressures, but at threshold it has been calculated that it should detect the vibration of the basilar membrane that is a tenth the size of a hydrogen atom!

The complexity of these problems naturally makes investigation more difficult. For many years research has been limited to a study of slow waves. It is only during the last 20 years that we have been able to study coding in an individual cell, a study made possible by the introduction of the microelectrode. The microelectrode has a tip diameter small enough to place close to a single cell and record the electrical events taking place in it. Furthermore, for many years, research workers have investigated the auditory system using clicks and pure tones. These are unnatural stimuli and further advances in understanding coding will only come when natural stimuli can be presented to the brain and the responses studied (Bishop, 1967). For example, Galambos was examining an area of the auditory cortex of a cat, and could not produce a response with any stimulus, but he found a mouse squeaking caused the cells under investigation to fire vigorously.

![Figure 2](image-url)

**FIGURE 2**

A diagram of the travelling wave along the basilar membrane (von Békésy).

The two main aspects of sound are frequency and intensity, and as they are so important, their coding will be discussed in more detail. The coding of frequency begins in the cochlea. Acoustic energy is converted into electrical energy by a transducer mechanism situated in the organ of Corti. This electrical energy is probably the cochlear microphonic and is responsible for initiating a discharge in the auditory nerve. Furthermore, it has been shown by von Békésy (1960) that sound produces a travelling wave which passes along...
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The basilar membrane. The place where this wave reaches its maximum amplitude varies with frequency, and the corresponding portion of the organ of Corti also fires more rapidly when it is stimulated by this same frequency. For each frequency the area of stimulation is however a broad one, so that it is difficult to see how small differences in frequency can be detected unless we postulate some form of lateral inhibition in the cochlea. Reference to Figure 2 shows that a certain tone stimulates a wide area of the basilar membrane. If, however, we record the responses of a single auditory nerve fibre, we find that it responds to a certain frequency much more selectively than would be expected from the shape of the basilar membrane response.

Distinguishing small changes in frequency response. However, the tendency for tuning curves to become narrower is only slight, and at all levels of the brain there are neurones having the same characteristic frequency but some with broad tuning curves and others with narrow ones.

Just as there is a tendency for neurones to respond selectively to certain characteristic frequencies, there is also a tendency for certain areas of the auditory pathways to respond selectively to frequencies. Neurones in most auditory nuclei are arranged in an orderly fashion according to the frequencies to which they respond, so that a frequency scale is preserved. This grouping of neurones is referred to as tonotopic localization, and is illustrated in Figure 4 taken from the work of Tsuchitani and Boudreau (1966).

From the above descriptions it can be seen that the coding of frequency depends on the manner in which neurones are connected to one another. Information about frequencies may also be conveyed by the pattern of nerve discharge.

Normally there is spontaneous activity in a nerve and this becomes added to the auditory response. For this reason it is necessary to repeat the stimulus a number of times in order to sort out evoked responses from spontaneous activity. A common way of analysing the pattern of nerve discharge is to measure the time of occurrence of each spike or nerve discharge.

The type of response that can be expected from an auditory nerve fibre is shown in Figure 3, which indicates the frequency response pattern or tuning curve of four neurones in the cochlear nucleus, which are similar to those in the auditory nerve. Each tuning curve is obtained by stimulating the neurone with a number of tones, and measuring the intensity of the threshold response for each frequency. This also enables one to determine for each unit, the frequency to which it is most susceptible, i.e. its characteristic frequency.

A number of workers have shown that there is a tendency for the tuning curves of neurones to become narrower or more selective as we pass higher in the auditory system. At first sight this may explain how the brain can distinguish small changes in frequency response.
after the auditory stimulus. The summed responses of the time delays of spike discharges can be plotted as a post-stimulus histogram.

The construction of a post-stimulus histogram is illustrated by the diagram in Figure 5. The vertical strokes indicate nerve discharges the interval of time after acoustic stimulation at which nerve discharges occur. From this histogram it can be seen that there has been a burst of cell firing a few milliseconds after the onset of a tone and this has been repeated a number of times, thus accounting for the peaks.

and the arrows marked S are the points of acoustic stimulation. The type of coding describe measures the time from Stimulus S to nerve discharge 1, 2, 3, etc., over a number of stimuli. The frequency with which these time intervals occur over a number of stimuli is then plotted as a post-stimulus histogram, as shown in Figure 6, taken from Aitkin et al. (1960). Here, the ordinate refers to the probability of a cell firing and the abscissa to the post-stimulus histogram can indicate a variety of response patterns by different cells which are responding to an auditory stimulus; the response pattern for a single cell, however, remains fairly constant, but this is only a summed response and does not indicate the firing pattern from moment to moment. It would be very helpful to know the latter in order to understand the coding of a frequency that is constantly changing or modulating.
as in speech and other naturally occurring sounds.

Inten-sity is the other important modality of sound, and its effects will be considered first at the level of the cochlea and auditory nerve. As the loudness of a sound is increased, the cochlear microphonic follows intensity change in a linear manner up to a certain level. The auditory nerve is like other nerves in the body and can only fire in an all-or-nothing fashion. For this reason it must respond to intensity changes in a different way from that of the cochlear microphonic. It has been shown by Kiang (1965) and by Reddick et al. (1962) that the auditory nerve fibre encodes intensity by firing at a faster rate, and that more fibres are made to discharge as the intensity of the sound increases. Many workers have shown that this mechanism of coding intensity, where the nerve fires more rapidly, operates at all levels of the auditory system.

This interpretation of the coding of intensity is not the complete explanation, because the difference between the minimum and maximum rate of firing only corresponds to a change of 20 decibels, which is much less than our normal range of 120 decibels. The answer may lie in two further explanations. Firstly, as a sound becomes louder more fibres are stimulated, and this may enable summation to occur at higher auditory centres. Secondly, it has quite often been noticed that neighbouring cells with the same characteristic frequency may have quite different thresholds. This could mean that the cell with the higher threshold is connected to the higher auditory centres in such a way that when it is stimulated the brain interprets this as being due to a louder sound.

These are some of the ways in which intensity is encoded. It is still far from clear how it is decoded into the familiar sensations that we hear. Ablation studies on conditioned cats show at what levels the interpretation of intensity takes place. It has been demonstrated by Raab and Ales (1946) that the cat can still discriminate intensity changes although...
certain areas of both auditory cortices and inferior colliculi have been removed. Therefore part of the interpretation of intensity change must occur at a lower level, probably in the medial superior olivary nucleus. This nucleus has been found to be of great importance in localizing the direction from which a sound comes. It is thus appropriate that it should be concerned with the coding of intensity changes.

The coding of frequency and intensity have now been discussed, but only the aspects that are better known have been mentioned. There are many other facets that are more imperfectly understood, for example the coding of the duration and order of presentation of tones.

Further advances in understanding the coding of sound could lead to advances in the clinical field. It will probably lead to improved objective tests of hearing and enable us to make a better diagnosis of the different types of nerve deafness. Finally it may allow us to treat surgically certain types of nerve deafness.

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References


