

as the pulse during which re-excitation of the same section of fiber is impossible. Thus the theoretical maximum pulsing rate of a fiber is about 1000 pulses per second. However, this theoretical rate is seldom approached. For present purposes, all pulses in a particular type of nerve can be regarded as having the same magnitude and shape regardless of the nature, frequency and intensity of the stimulus. How then are the nerve fibers able to transport to the brain information which can define the intensity and frequency of signals?

Working with cats, whose auditory system is much like that of humans, GALAMBOS and DAVIS [25] conducted tests which support previous beliefs that intensity is signaled by the total pulsing rate of groups of nerve fibers. In these tests, measurements were made of the pulsing rate of individual nerve fibers of the auditory nerve of a number of animals in response to acoustic stimulation of their ears, using single frequency tones. By varying the intensity of the stimulating tone, while employing the frequency most effective for each particular fiber, it was found that the pulsing rates of the individual fibers could be changed from an occasional pulse up to maximum rates generally of the order of several hundred per second. Furthermore, something like 90% of the total change in the pulsing rate of an individual fiber occurred with an intensity change of the order of only 30 db. Thus the range of intensities which can be reported to the brain by a single nerve fiber is only one-quarter of the full range to which the auditory system is responsive.

The manner in which this limitation of individual fibers is overcome can be inferred from Fig. 6 which shows the pulsing rates of one particular fiber. With a sufficiently low signal level, the fiber responded to only one particular frequency (7000 cycles), plus and minus a few cycles. At high signal levels the fiber was responsive to a wide range of frequencies but the degree of responsiveness, i.e., the pulsing rate, varied with frequency. From this it can be concluded that with any signal, such as a 7000 cycle tone, one effect of raising intensity is to excite more fibers, from a few at very low levels to many at high levels. This, of course, is consistent with the previously discussed vibratory movements of the basilar membrane, sharply localized at low intensities and of extensive span at high intensities. The other effect is to increase the pulsing rates of any fiber after it has once become susceptible to the influence of the signal. These two effects together enable the pulsing rate of a group of fibers to increase long after many of them have reached their maximum rates.

Other fibers were also tested. In general, at a sufficiently low intensity each fiber, like the fiber of Fig. 6, was also responsive to only one particular tone although, as would be expected from the mechanical properties of the cochlea, the frequency of the tone varied from fiber to fiber. Since the neural system from hair cells to the auditory receptive centers is a projection system, the above discussion suggests that the excitation of these centers by single frequency tones

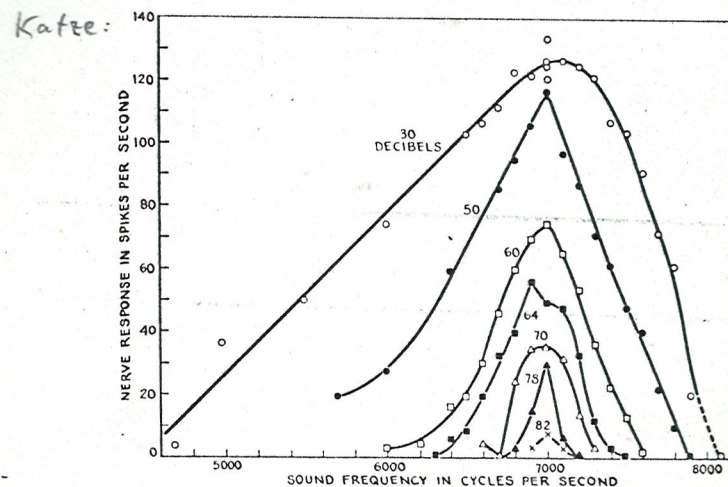


Fig. 6. Iso-intensity contours for a single nerve fiber, one which responds best to a frequency of 7000 cycles. Each contour shows how this nerve responds when the frequency of a fixed level of acoustic stimulus is varied. The number on each contour represents the level of the stimulus in db below a level arbitrarily designated as 0 db (GALAMBOS and DAVIS [25]). *an Katzen*

of low intensity would also be sharply localized and occur in different positions as frequency is varied. Similarly, as intensity is increased, the excitation would be expected to increase and also spread over wider portions of the receptive areas to form a spatial pattern, a pattern whose position of maximum excitation should vary with frequency and whose form, magnitude and extent should vary with signal intensity. Excitation patterns, of this general nature have been observed in the receptive centers of animals [27]. Available information suggests that the total excitation is related to the intensity of the external signal and the magnitude of sensation to the total excitation.

One might infer from the above discussion that the distinctive character of an auditory sensation is related to the particular place in the receptive center which is stimulated, i.e., the location of the in-