PITCH DISCRIMINATION IN THE HIGHER LEVEL OF THE BRAIN

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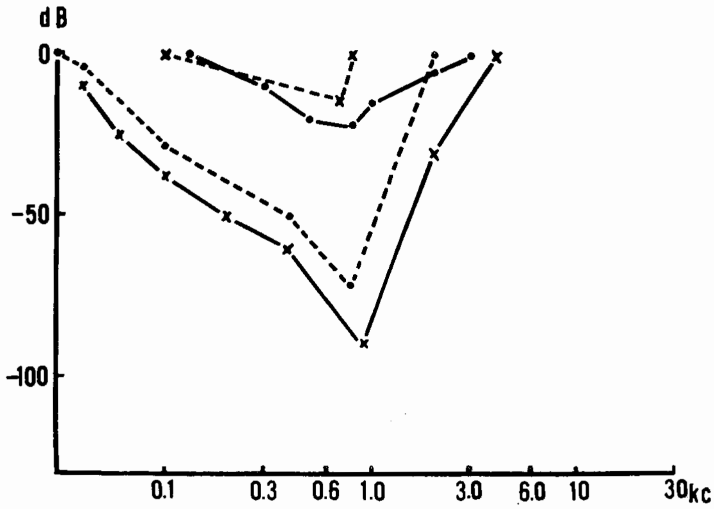
Since the publication of Galambos and Davis' work, electrophysiological data have been accumulated which show that the analysis of sound is performed in a special way in the cochlea. The examination of discharge patterns and the response areas of single primary auditory neurons in the cochlear nerve bundle reveals that they are sending enough informatoion about intensity of sound, but not about the frequency of analysed sound. This fact recalls to us Rutherford's telephone theory which had once been supplanted by Helmholtz's place theory of the cochlear function. The telephone theory tells us that the frequency analysis of sound is not performed in the cochlea at all, but it is done in the auditory cortex. This hypothesis seems in a sense to be valid for us, because the primary auditory neurons send only very poor information about the frequency of sound in spite of the fact that cats and monkeys and, especially, human beings are remarkably capable of discriminating the freqency of sound. In order to explore this problem, the present author tried to record the responses of neurons with capillary microelectrodes filled with 3M-KCl solution from several relay nuclei along the auditory tracts in the brains of cats and monkeys.

Cochlear nerve

Each primary auditory neuron has a response area which covers a very wide frequency range of sounds. The shape of the response area of the neuron in reference to the intensity and frequency of sound is thought to be delineated, primarily by a vibration mode of the basilar membrane which was revealed by von Békésy (1943) and secondarily by an innervation mode of the primary auditory neurons in the hair cells which was revealed by Lorente de Nó (1933) and others. Very many neurons have response areas of the well-known triangular shape. These areas have a peak value called the characteristic frequency of the neuron and do not extend much beyond this characteristic frequency, being sharply cut off at the higher frequency side (the asymmetrical type). This asymmetrical type is mainly represented by neurons which have a characteristic frequency higher than 1-3 kcps. There are also neurons showing response areas which extend further, even to higher frequencies than the characteristic one (the symmetrical type) (Fig. 1. A). An attempt was made in our laboratory to divide the response areas in monkeys into two types, the symmetrical and the asymmetrical one, because an elaborate study of the cochlear nerve of the monkey revealed that the nerve consists purely of primary neurons. But it was difficult to draw a line between those two groups, because there were many intermediate types. The author then treated the thresholds of neurons statistically. As seen in Fig. 1 B, in the case of neurons, the characteristic frequencies of which were taken in the range of 600 and 1,000 cps, the histogram in relation to their threshold shows two peaks; that is, the neurons are separated into two groups, the theoretical curve of the normal distribution being drawn in full lines. The

A



B

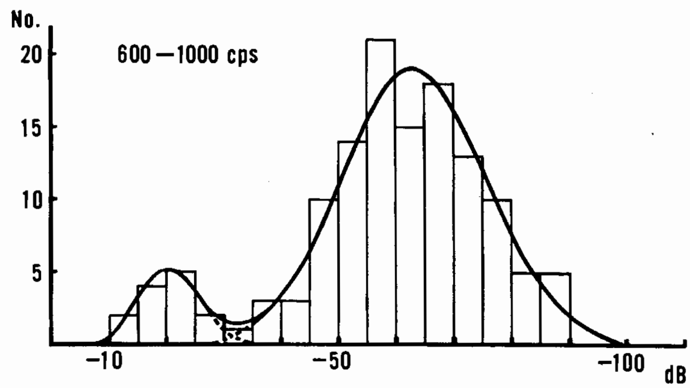


Fig. 1. A. Response areas of 4 primary auditory neurons of monkey.
Abscissa. frequency of sound. Ordinate: intensity of sound.
Range of characteristic frequency is between 600 and 1,000 cps.

Fig. 1. B. Histogram of thresholds of primary neurons of monkey.
Abscissa: threshold of neuron at its characteristic frequency.
Ordinate: number of occurence.
Range of characteristic frequency is between 600 and 1,000 c.
Two solid curves show calculated curves of normal distribution.

group of neurons with low thresholds seems to correspond to the external spiral fibers, whereas those with high thresholds correspond to the internal radial fibers. The change in the number of impulse discharges in response to the change of the sound intensity was different between the two groups; namely, small in the former group while large in the latter (Fig. 1. C). According to Békésy's recent discovery on skin sensation (1959) when two skin regions with different thresholds are simultaneously stimulated with vibration, sensation moves from the region with low threshold to that with high threshold in accordance with the increasing intensity of stimuli. From such results the author is of the same opinion as Békésy that the neuron innervating the internal hair cells which are provided with a high threshold for delivered vibratory stimulus may, eventually, send the discriminatory information on pitch sensation while the neurons connecting many external hair cells are concerned with loudness sensation of sound, although both pitch and loudness sensation are not strictly independent of each other.

Change of responses found at relay nuclei.

The one-to-one relation between the impulse discharge and the sound wave could be found only when the frequency of sound was below ca. 800 cps. Therefore the volley theory of hearing is certainly not valid for pitch discrimination of high frequency sound. In cats it was not easy to record the responses from the primary neurons, but the recording of the neuronal responses could be done extracellularly from the secondary, tertiary and other neurons in the cochlear nerve bundle, the dorsal and ventral cochlear nuclei, the trapezoid body, the inferior colliculus, the medial geniculate body and the auditory cortex, respectively. In those cases successive changes in the latency of response, in the discharge pattern and particularly in the response

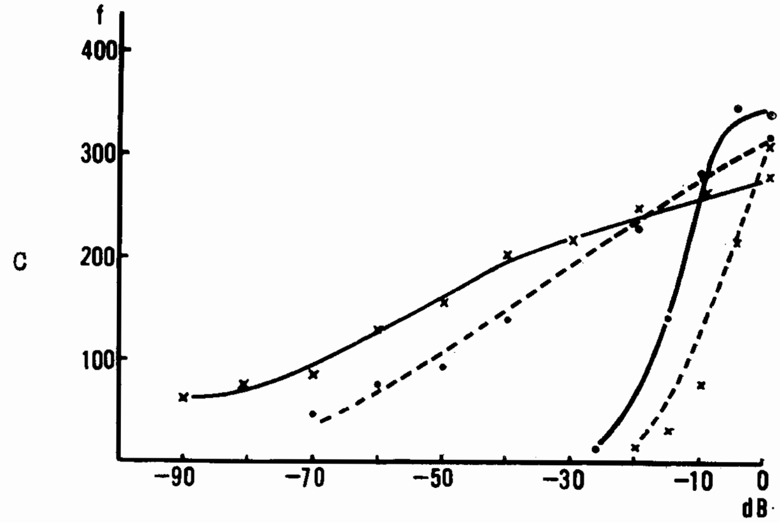


Fig. 1. C. Rate of increase in impulse frequency of 4 neurons in A.
Abscissa: intensity of sound. Ordinate: impulse frequency.

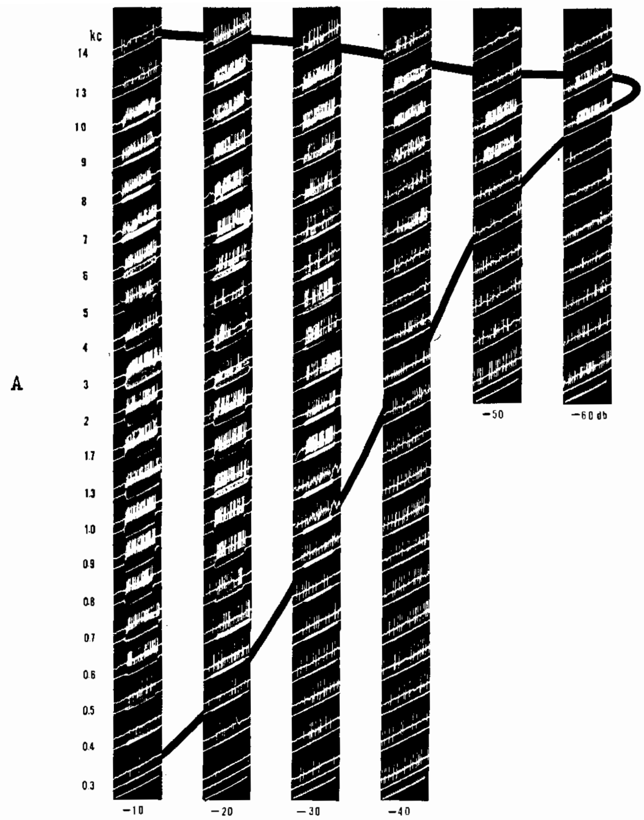


Fig. 2. A. Response area of a neuron obtained from the cochlear nerve of a cat.

area of the neuron were found at each level in the ascending auditory pathway. In the trapezoid body, it was found that the neurons show narrower response areas than those in the cochlear nerve; that is, each of the neurons is getting the specificity for sound frequency (Fig. 2. A and B). Such a tendency becomes sharper while the impulses are going up to the higher level in in the brain, and the narrowest response areas were finally found at the neurons in the geniculate body. (Fig. 2. B). In the extreme case, a certain neuron responded to a 6 kcps sound with a low threshold of-80dB, but never to sounds of 5 and 7 kcps. Microelectrodes inserted deeply into the auditory cortex picked up a similar response pattern to that of the geniculate body. Contrary to our expectation, the neurons in the surface layer of the auditory cortex have very wide response areas like those of the primary auditory ones. These results show us that the frequency analysis of sound is accomplished at the level of the geniculate body, not at the auditory cortex, and are in agreement with Neff and other's work which described no change in pitch and intensity discrimination after the complete bilateral destruction of the auditory cortex A I and A II. It was concluded that the neurons in the ascending reticular system of the midbrain were not responsible for pitch discrimination, because they were not limited to specific sound frequencies and their response areas were generally very broad. The connection between the ordinary auditory pathway and the upper reticular system is so far not clarified.

Inhibition.

At the dorsal cochlear nucleus, spontaneous discharges are often inhibited by a tone burst stimulus. When the neuron shows quite a few spontaneous discharges, such an inhibition occurs and is more clearly shown by delivery of a continuous pure tone in the background. Sometimes the response of frequent discharges to a tone burst changes to a perfect inhibition of impulses when background discharges are produced by a continuous pure tone. The intensity and frequency of the tone burst were changed and the response area was measured before and during the delivery of a continuous pure tone. It was found that the inhibition described takes place at both sides of the characteristic frequency (Fig. 3) and, consequently, the response area becomes narrow. Therefore it is quite certain that the inhibition plays an important role in pitch discrimination. It is well known that the efferent fibers, so-called ,,olivo-cochlear bundle" by Rasmussen, come to the cochlea. However, the inhibition described above may not be evoked by these efferent fibers, because the primary auditory neurons have so far not shown any convincing sign of such an inhibition according to the present experimental technique. The inhibition described above seems to result from the interaction of afferent fibers.

B

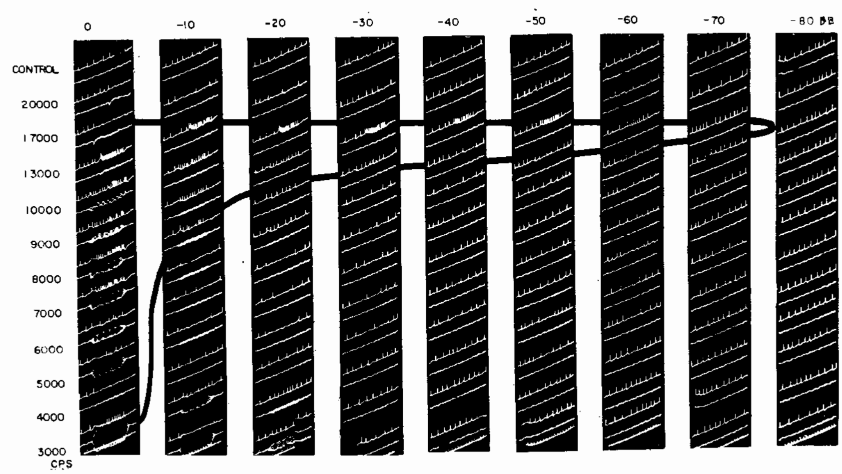


Fig. 2. B. Response area of a neuron obtained from the medial geniculate body of a cat. Frequency and intensity of sound is shown outside the figure.

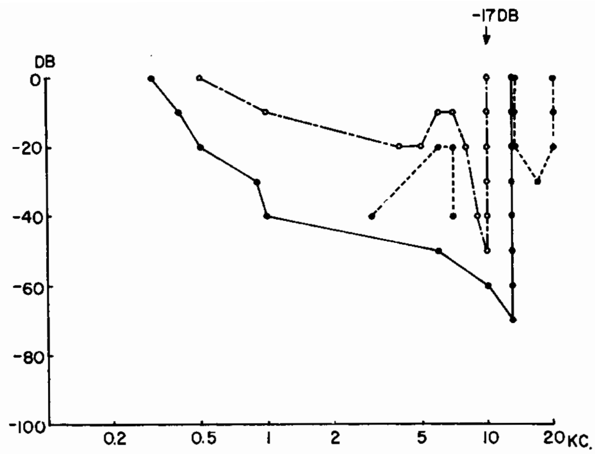


Fig. 3. Response area of a neuron obtained with single tone bursts (solid line) and with single tone bursts and a background sound together (dotted line). Areas represented with broken lines are the inhibitory areas.

Auditory cortex.

Tunturi described the beautiful tonotopic localization on the auditory cortex A I in dogs. Though our studies with microelectrodes in cats do not show such clearly defined tonotopic localization, the auditory cortical neurons may be statistically arranged in such a manner that the neurons with high charecteristic frequency are located anteriorly, while those with low ones are posteriorly in A 1. Sometimes the neurons with different characteristic frequencies were found by a single insertion, but they were at different depths from the cortical surface. As shown by Woolsey, the cortical organization of neurons is very complex and several projection areas from the cochlear are recognized on the cortical surface. The response pattern of the cortical neuron is mostly of the phasic „on" or „off", or „on-off" type and the response area is very wide as described above, although a few neurons have narrow areas and high thresholds. Therefore the cortical neuron seems to play a sound-integrating role. The sounds have already been analysed by the neural network in the lower levels from the cochlear nucleus to the geniculate body; that is, the cortex is the place for perception of timbre of complex sound.

In order to know electrophysiologically the role of the cortical auditory neurons, two sound stimulations were used. The most interesting finding was that some cortical neurons respond with synchronous discharges to a beat sound which is produced by certain different frequencies of two sounds. The response area measured with a tone burst changes irregularly in accordance with delivery of a continuous pure tone together with the tone burst. These facts show that the auditory cortex is really the place of perception of the compound sound. The phasic response pattern of the cortical auditory neurons seems to be adequate to following the rapid change of sound. By the use of the intracellular recording of the membrane potential we often observed the hyperpolarization in the response of the cortical neuron after impulse discharges. (Fig. 4). If the neural mechanism of narrowing the response area is called the funneling mechanism for pitch discrimination, that of the phasic response pattern may also be called the funneling mechanism for detection of the change of sound. The former is spatial and the latter is temporal. The change in the number of impulses in the response of a neuron correlated with the change in the sound intensity is less when the neuron is located at higher levels in the auditory tract. Finally, the cortical neuron discharges only a few impulses at the „on" or/and „off" set of the sound stimulation. Therefore the number of impulses in the response of the latter neuron can scarcely be changed by the change in the intensity of sound. When the cortical neurons acquire integrative ability, they lose the ability for pitch discrimination. The pitch discrimination may thus be done not at the cortex, but somewhere at a lower level.

DISCRIMINATION D'HAUTEUR DE SON AU NIVEAU SUPERIEUR DU NEVRAXE

Comme l'étude de mécanique de limaçon avait démontré que l'analyse de son est exécuté d'une façon spécifique, nous avons étudié le mécanisme neural de la voie auditive chez le chat et le singe, en enregistrant la réponse

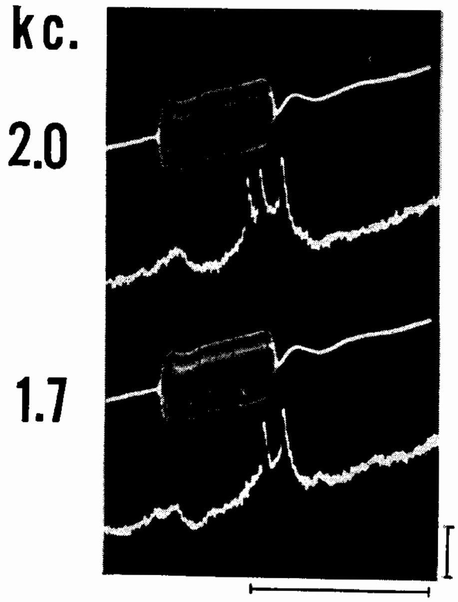


Fig. 4. Responses recorded intracellularly of a cortical neuron of a cat in response to a tone burst of 2 kcps and 1.7 kcps. The upper beam shows a sound wave and the lower figure is a neuronal response. Calibration is 10 mV. and 100 msec.

électrique à l'aide de microélectrodes extrèmement fines. L'enregistrement de champ de réponse et de seuil au niveau de neurons primaires auditifs nous montrait qu'il existe deux types de champ de réponse, l'un symétrique et l'autre asymétrique, ce qui serait dû à la différence de leurs modes de connexion avec les cellules auditives. Cependant, la classification nette entre ces deux types est difficile en raison de beaucoup de types intermédiaires. Par ailleurs, nous avons remarqué deux sommets dans l'histogramme relatif au seuil de neurons correspondant aux fréquences les plus sensitives. Ce fait devrait être dû à la différence de fonctionnement entre cellules auditives interne et externe. En ce qui concerne l'allure de surcroît de discharges correspondant au changement d'intensité sonore, nous avons aussi trouvé la différence entre ces deux types. Elle est petite pour les neurons dont le seuil est bas tandis que large pour ceux qui sont de seuil haut. Ces résultats suggèrent que les neurons innervant les cellules auditives internes, qui sont de seuil haut pour le son délivré, donnent des renseignements sur la sensation d'hauteur pendant que ceux qui sont de seuil bas et se combinent avec beaucoup de cellules auditives externes, s'occupent de la sensation de force de son.

Les enregistrements de réponse aux divers niveaux de la voie auditive chez le chat révèlent que les changements successifs de latence, de „patern" de réponse, de champ de réponse etc, peuvent être observés suivant que les réponses courent le long de trajet: noyaux ventral et dorsal du nerf cochléaire, corps trapézoïde, tubercule quadrijumeau postérieur, corps genouillé interne et aire auditive. Le rétrécissement de champ de réponse à chaque niveau se traduit par la spécificité pour fréquence de sons et le champ de réponse le plus rétréci est obtenu au niveau du corps genouillé interne. A l'encontre de nos prévisions, les neurons situés au niveau de la couche superficielle de l'aire auditive ont le champ de réponse très étendu, comme ceux de stations primaires auditives. Ces résultats nous montrent que l'analyse de fréquence de sons est accomplie au niveau du corps genouillé interne, non pas au niveau du cortex.

Nous avons remarqué que les neurons appartenant au système réticulé ascendant du mésencéphale ne sont pas résponsable pour la discrimination d'hauteur de son, parce qu'ils ne sont pas limités à la fréquence sonore spécifique et leurs champs de réponse sont en général très étendus. Au niveau inférieur du névraxe y compris noyaux cochléaires ventral et dorsal, des discharges spontanées et excitées sont souvent inhibées l'un et l'autre par d'autres stimulations sonores. La comparaison du champ de réponse d'un neuron soumis à son continu à l'arrière-plan avec celui obtenu sans aucun bruit nous permet de trouver qu'il est remarquablement plus étroit dans le premier cas que dans le second et que l'inhibition a lieu des deux côtés de la fréquence caractéristique au neuron. Il est donc évident que l'inhibition joue un rôle important dans la discrimination d'hauteur de son. Il parait que l'inhibition de cette nature soit consécutive à l'inhibition synaptique par action réciproque de fibres afférentes, non pas à celle par fibres efférentes que certains auteurs discutent recémment.

La majorité des neurons de l'aire auditive a un champ de réponse étendu et ils montrent des réponses phasiques „ouvert", „fermé" ou „ouvert-fermé".

Il nous semble que ces neurons jouent un rôle dans l'intégration sonore; les sons ont été déjà analysés par le réseau neural au niveau inférieur depuis noyaux cochléaires jusqu'à corps genouillé interne. Les enrégistrements intracellulaires de potentiel de membrane neuronique nous permettent d'observer souvent des hyperpolarisations après les réponses. Ce mécanisme neural est vraiment adéquat à suivre le changement rapide de son. Il se peut que „spatial and temporal funneling mechanism" joue le rôle le plus important pour la discrimination d'hauteur de son au point de vue de mécanisme neural.

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