Auditory Periphery

external  middle  inner
Similarity of Frequency Tuning in Cochlea and Auditory Nerve

Comparison of frequency tuning at a basilar membrane site and in auditory nerve fibers innervating neighboring inner hair cells, recorded in the same cochleae in chinchillas.

- Only minor signal transformations intervene between cochlear vibration and AN excitation
- Cochlear frequency selectivity is fully expressed in the vibrations of the basilar membrane
- No need for a “second” filter

Tonotopic Projection from Cochlea to Brain

Precise mapping between auditory nerve fiber frequency tuning and cochlear place.

- Nearly logarithmic for CFs > 2 kHz.
1886 Rutherford
• Spike frequency codes tone frequency
• Refractory period limits firing rate

1949 Wever proposed volley principle
• nerve fibers work together
• 1970 Phase Locking

1961 Von Békésy
• Pressure vibrates Basilar membrane
• peak of vibration depends upon frequency
• maximal transduction occurs at peak
A NEW THEORY OF HEARING.

By Professor W. Rutherford, F.R.S.

In a lecture "On the Sense of Hearing," delivered to the members of the British Association for the Advancement of Science, in Birmingham, on 6th September last, Professor Rutherford, after referring to the well-known theory of Helmholtz, that the free termination of the nerve-fibres of the cochlea are set into sympathetic vibration by the sound-waves, proceeded to explain his new theory of hearing.

Some five years ago it struck the lecturer that the ease of the telephone might throw light on the difficulties regarding the sense of hearing. When sound-waves fall on the plate of one of the telephones it vibrates. The vibrations of the iron near the magnet affect the magnetism, and so induce in the wire currents of electricity whose frequency and amplitude correspond to those of the vibrations of the iron plate induced by the sound. The currents travel to the second telephone and induce oscillations of its magnetism, which in turn cause its iron plate to vibrate and produce sounds similar to those communicated to the first telephone. There is no analysis of the sound-waves. The transmitting telephone takes up simple or complex vibrations. The harmonies of an orchestra may fall upon it, and it does not fail to convert the complex sound-vibrations into electrical vibrations, and these again into the complex sound of the orchestra in the receiving telephone. The theory which the lecturer had arrived at, and which he published that night for the first time, might be termed the telephone theory of the sense of hearing—the theory that the cochlea does not act on the principle of sympathetic vibration, but that the hairs of all its auditory cells vibrate to every tone just as the drum of the ear does; that there is no analysis of complex vibrations in the cochlea or elsewhere in the peripheral mechanism of the ear; that the hair cells transform sound vibrations into nerve-vibrations similar in frequency and amplitude to the sound vibrations; that simple and complex vibrations of nerve energy arrive in the sensory cells of the brain, and there produce, not sound again of course, but the sensations of sound, the nature of which depends not upon the stimulation of different sensory cells, but on the frequency, amplitude, and form of the vibrations coming into the cells, probably through all the fibres of the auditory nerve. On such a theory the physical cause of harmony and discord is carried into the brain, and the mathematical principles of acoustics find an entrance into the obscure region of consciousness. Now, if nerve energy were only electricity, that theory would probably be accepted at once; but nerve motion is very sluggish when compared with electricity. The lecturer for five years had kept this theory back, because he felt that he had no evidence of the possibility of sending a rapid succession of vibrations along a nerve. It cost him a good deal of thought and experimental observation to find the evidence he required. If we give to a motor nerve of a frog or rabbit ten instantaneous shocks of induced electricity in a second, ten impulses will pass along the nerve to the muscle, and produce ten distinct contractions in the same period. If we send forty impulses along the nerve, we get not forty contractions of the muscle, but a single continuous contraction, because the several contractions are fused together. Now, if we listen to the muscle so stimulated, one hears a musical note having the pitch of forty vibrations per second. Each sound vibration results from the sudden shock of chemical discharge due to the arrival of each nerve impulse in the muscular substance. If we stimulate the nerve, say, 300 times per second, by causing a tuning fork to make and break the primary circuit of an induction machine, and so send 200 shocks per second into the nerve, the pitch of the note in the muscle exactly corresponds. It has the same pitch as the fork. The lecturer had experimented in this way, and eventually found that he could send as many as 392 impulses per second along the nerve, and get a note from the muscle of the pitch of 352 vibrations per second; that is to say, a note of the pitch of F on the lowest space of the treble clef. But when he tried by more rapid stimulation of the nerve to get a higher note from the muscle he failed. There was nothing but a noise heard. That a musical note is produced by a contracting muscle is known to every physiologist. One can hear it if he firmly clenches the jaws during the stillness of night, when other sounds are hushed. It is a low note, with a frequency of vibration less than 40 per second. There is therefore nothing new in the statement that a note may be heard in a muscle; the new point is that the pitch of the note may be increased by a more rapid stimulation of the nerve, and that as many as 392 impulses may be sent along a nerve and retain their individuality so sharply that they can produce a note in a muscle having a pitch-number of 352. That new fact, he thought, would give much support to a vibrational theory of nerve energy. Was he to conclude that, because he failed to get a higher note than one of 392 vibrations from the muscle, it was not possible to send more than 392 vibrations per second along a nerve? By no means. The fibres of a muscle are very different from those of a nerve, and also very different from nerve cells. The molecules in both of them can probably vibrate far more rapidly than 392 times per second. He had therefore directly proved that vibrations of the same frequency as all the lower tones of the scale, from the lower F of the treble clef downwards, can be transmitted by a nerve. He had, therefore, a very significant piece of evidence in support of his telephone theory of sound-sensation, and he could not but think that the evidence in favour of it would increase. For instance, there was in the vibration of the wing of an insect a proof that was enough at least to make his theory a feasible one. A bird's wing ordinarily vibrated so that one could hear it flap; in other words, we could hear each vibration distinctly. But in a bee's wing the vibration was so much more rapid that a musical note was produced. A honey-bee could make its wing vibrate at the rate of 460 vibrations per second, whereby producing the note A in the treble clef. That fact implied that there must pass through the motor nerve of the bee to produce these 460 nerve vibrations in a second. Therefore it was possible to get the notes of the scale from A to the treble clef downwards transmitted through nerve fibres. He could not say that more rapid vibrations could be transmitted; the proof there was still wanting. Should his theory of the sense of hearing find acceptance, it would lead to a reconstitution of theories regarding the other sense-organs.
ACTION CURRENTS IN THE AUDITORY NERVE IN RESPONSE TO ACOUSTICAL STIMULATION

BY ERNEST GLEN WEVER AND CHARLES W. BRAY

PSYCHOLOGICAL LABORATORY, PRINCETON UNIVERSITY

Read before the Academy April 28, 1930

This experiment was planned in the effort to discover an answer to certain fundamental questions of auditory theory through a determination of the relationship obtaining between the character of the response of the auditory nerve and the frequency and intensity of sound affecting the ear. The cat was selected as the experimental animal, and the investigation consisted of placing electrodes on the exposed auditory nerve, and detecting the action currents in the nerve resulting from stimulation of the ear by sound.

Procedure.—The procedure was as follows: After decerebration under deep ether anesthesia by the trephine method, the skull was opened sufficiently to gain access to the right auditory nerve. An electrode, which usually took the form of a small wire hook, was then placed around the nerve, while a second electrode was placed elsewhere on the body, usually on the severed tissue of the cerebrum.

The currents picked up by these electrodes were conducted through 60 feet of shielded cable to a vacuum tube amplifier located in a sound-proof room and, after amplification, were led to a telephone receiver. The ear of the animal was then stimulated, and the resulting nerve impulses detected as sound by an observer listening at the receiver in the sound-proof room.

Results.—The results so far obtained in this investigation bear upon the question of the relation between the qualitative aspect of the stimulus and the nature of the nerve response. It was found that sound stimuli applied to the ear of the animal set up in the auditory nerve action currents of frequencies corresponding to those of the sound waves. These action currents, after amplification, were audible in the receiver as sounds which, so far as the observer could determine, were identical with the original stimulus.

Speech was transmitted with great fidelity. Simple commands, counting, and the like were easily received. Indeed, under good conditions the system was employed as a means of communication between operating and sound-proof rooms.

A simple tone sounded into the cat's ear gave rise to that tone in the receiver. The observer was able to detect no difference in pitch between this tone and the original stimulus. The range of frequencies to which response can be obtained has not as yet been thoroughly investigated, but the response has been observed to tones as low as 125 and as high as 4100 ~/sec. There was manifested a high degree of tonal discrimination: e.g., if two tones of adjacent frequencies, such as 3200 and 3300 ~, were given in succession, the observer could report accurately which was the higher.

These facts show, then, that in the nerve as a whole the frequency of response is correlated with the frequency of stimulation.

There was evidence also of a correspondence between the intensity of response in the nerve as a whole and the intensity of stimulation.

The above results are not what have been expected on the basis of recent work on other sensory nerves. The nerve responses recorded by Adrian and others on stimulation of the end-organs of pressure, pain, vision, and muscle-sensitivity, have in every case shown frequency of nerve impulse to be correlated with intensity of stimulation. Here, on the contrary, we have found frequency of impulse correlated with frequency of stimulation.

Because of the divergence of our findings from what is beginning to be accepted as a general law of sensation, and the obvious suspicion aroused by what appears to be a direct correlation of stimulus and end-effect, it is necessary to produce evidence eliminating every possibility of artifact, and to supply checks beyond what have ordinarily been considered necessary in experiments of this nature in order to establish the results as in reality due to action currents in the nerve set up in the response of the ear to sound.
Simultaneous recording of the aural microphonic and a single auditory nerve fiber response
Phase-Locking

- Responses to low-frequencies tend to occur at a common phase within the stimulus cycle.
- Phase locking is evident as a single mode within a period histogram, and by modes at multiples of the stimulus period in interspike interval histograms.

Cochlea
Russell & Sellick

Auditory Nerve
Rose et al, 1967
Vector Strength

*Synchronization index for circular distributions*

Neural sensitivity to the modulation frequency is evident as synchronization to the modulation period ($T$).

**Mean Phase**

$$\bar{\theta} = \arctan \left( \frac{\sum_i \sin \theta_i}{\sum_i \cos \theta_i} \right) \quad \text{where} \quad \theta_i = 2\pi \frac{\text{mod}(t_i, T)}{T}$$

Each spike time $t_i$ is treated as a vector of unit length and phase $\theta_i$ measured as spike time modulo the stimulus period.

**Vector Strength**

$$r = \frac{1}{N} \sqrt{\left( \sum_i \cos \theta_i \right)^2 + \left( \sum_i \sin \theta_i \right)^2}$$

$N$ spikes are combined by vector addition; the resultant vector is normalized to $N$.

*1st Fourier coefficient of period histogram
spectral magnitude of the response at $\omega_m$ normalized by mean spike-rate

significance determined by the Rayleigh statistic:*

$$2r^2 N$$
Some Effects of Stimulus Intensity on Response of Auditory Nerve Fibers in the Squirrel Monkey

JERZY E. ROSE, JOSEPH E. HIND, DAVID J. ANDERSON, AND JOHN F. BRUGGE

Period histograms for AN fiber response at CF to various SPLs. Response histograms are fitted with stimulus waveforms, illustrating phase-locking.
Rose et al. used complex stimuli to show how the waveform of the stimulus is reflected in the time structure of the response. They presented two low-frequency tones, then adjusted their SPLs.
Volley Principle (Wever)

Frequency represented in the population synchrony
Temporal coding in Auditory nerve

- Distributions of population intervals created by summing intervals from all auditory nerve fibers.
- AN response intervals are most commonly related to pitches heard at fundamentals of harmonic complexes.

Cariani & Delgutte (1996ab)

Dial-anesthetized cats.
100 presentations/fiber, 60 dB SPL
Pitch of Tones Probably Coded by Timing & Place Mechanisms

Timing theories:
- sufficient for musical pitch, which deteriorates at high frequencies
- best explain our ability to distinguish frequencies of brief tones

Place theories:
- best explain diplacusis (same tone giving different pitches in the two ears)

Intensity also has an effect:
- high frequency pure tones sound flat when played loud.
Auditory Nerve Classification

**Type I ~95%**
- Large myelinated axons
- Synapse on IHCs (20:1)

**Type II ~5%**
- Smaller unmyelinated axons
- Synapse on OHCs (1:many)
Auditory Nerve: Frequency selectivity

Type I: 95%
Type II: 5%

Relative Sound Level (dB) vs. Frequency (kHz)

Number of spikes vs. Time (ms)

Tone burst
Some Effects of Stimulus Intensity on Response of Auditory Nerve Fibers in the Squirrel Monkey

JERZY E. ROSE, JOSEPH E. HIND, DAVID J. ANDERSON, AND JOHN F. BRUGGE

Consistent with the concept of “spread of excitation” in auditory masking
Spontaneous Activity and Threshold

Bimodal distribution of spontaneous discharge rates

Thus, the auditory nerve is organized simultaneously by:

- cochlear place (frequency)
- threshold & spontaneous rate

<table>
<thead>
<tr>
<th>% of population</th>
<th>high-SR</th>
<th>low-SR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Synaptic terminals on IHCs</td>
<td>~60%</td>
<td>~40%</td>
</tr>
<tr>
<td>Synapse site on IHCs</td>
<td>large</td>
<td>small</td>
</tr>
<tr>
<td></td>
<td>pillar side</td>
<td>modiolar side</td>
</tr>
</tbody>
</table>
Brainstem Modulation of Cochlear Function

_Efferent projections to the cochlea from two groups of superior olivary cells_

LOC projects bilaterally to
Type I terminals under IHCs

MOC projects bilaterally to
base of OHCs
Olivocochlear Pathway Modulates Dynamic Range

Tone Level (dB SPL) vs. Discharge Rate (spikes/s)

- Left graph: Tone burst
- Right graph: Tone burst and Masking noise

With stimulation of OC neurons
Morphology and function

- CN has 3 major subdivisions: AVCN, PVCN and DCN
- Each subdivision contains distinct cell types differing in morphology, cytochemistry, patterns of inputs and outputs, and responses to sound
Superior Olivary Complex

MSO  LSO
MNTB
Binaural Cues for Sound Localization

**Interaural Time Difference (ITD):**

Time-of-arrival between the two ears indicates source location primarily for low-frequency sounds.

For sinusoids, this can be expressed as a phase difference. As the maximum delay approaches a lag of 180°, the phase difference becomes ambiguous. This occurs for $f > 1.5 \text{ kHz}$.

Max natural ITD in human: $\sim 680\mu\text{s}$
($c \approx 340 \text{ m/s}; \text{max. path difference } \approx 0.23 \text{ m}$)
Binaural Cues for Sound Localization

**Interaural Level Difference (ILD):**

Sound pressure level differences between the two ears indicate source location primarily for high-frequency sounds. The head starts to create an acoustic shadow at frequencies above about 500 Hz. The effect is most apparent above 2 kHz.
Low-frequency hearing limits in mammals

Heffner & Heffner (2001)

Low-frequency hearing limits fall into two distinct groups.
Sound localization limits in mammals
Heffner & Heffner (2001)

Figure 19.4  Relationship between maximum interaural distance and the highest frequency at which the use of the binaural phase-difference cue has been observed. Although the binaural phase-difference cue is physically available at higher frequencies for animals with smaller heads, the limits shown here represent an animal’s behavioral upper limit, not physical availability. C, domestic cat; Ch, chinchilla; Cw, cow; E, Egyptian fruit bat; H, horse; J, Jamaican fruit bat; K, kangaroo rat; M, man; Mk, Japanese macaque; P, domestic pig; Pt, pig-tailed macaque; W, least weasel. (Modified from R. S. Heffner, et al., 2001c).

Table 19.1  Sound localization acuity and use of binaural cues in mammals

<table>
<thead>
<tr>
<th>Species</th>
<th>Midline Acuity</th>
<th>Binaural Phase Cue</th>
<th>Binaural Intensity Cue</th>
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<tbody>
<tr>
<td>Indian elephant</td>
<td>1.2</td>
<td>yes</td>
<td>yes*</td>
</tr>
<tr>
<td>Human</td>
<td>1.3</td>
<td>yes</td>
<td>yes</td>
</tr>
<tr>
<td>Harbor seal</td>
<td>3.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Domestic pig</td>
<td>4.5</td>
<td>yes</td>
<td>no</td>
</tr>
<tr>
<td>Virginia opossum</td>
<td>4.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Domestic cat</td>
<td>5.2</td>
<td>yes</td>
<td>yes</td>
</tr>
<tr>
<td>Squirrel monkey</td>
<td>5.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Japanese macaque</td>
<td>6.8</td>
<td>yes</td>
<td>yes</td>
</tr>
<tr>
<td>Dog</td>
<td>8.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sea lion</td>
<td>8.8 **</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jamaican fruit bat</td>
<td>9.9</td>
<td>yes</td>
<td>yes</td>
</tr>
<tr>
<td>Greater spear-nosed bat</td>
<td>10</td>
<td>no</td>
<td>yes</td>
</tr>
<tr>
<td>Egyptian fruit bat</td>
<td>11.6</td>
<td>yes</td>
<td>yes</td>
</tr>
<tr>
<td>Ferret</td>
<td>11.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Least Weasel</td>
<td>12</td>
<td>yes</td>
<td>yes</td>
</tr>
<tr>
<td>Norway rat</td>
<td>12.2</td>
<td>no***</td>
<td>yes</td>
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<tr>
<td>Fox squirrel</td>
<td>14</td>
<td>yes</td>
<td>yes</td>
</tr>
<tr>
<td>Big brown bat</td>
<td>14</td>
<td>yes</td>
<td>yes</td>
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<tr>
<td>African pigmy hedgehog</td>
<td>14.3</td>
<td>no</td>
<td>yes</td>
</tr>
<tr>
<td>Short-tailed fruit bat</td>
<td>14.5</td>
<td>no</td>
<td>yes</td>
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<tr>
<td>Chinchilla</td>
<td>17.5</td>
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<td>yes</td>
</tr>
<tr>
<td>Domestic goat</td>
<td>18</td>
<td>yes</td>
<td>yes*</td>
</tr>
<tr>
<td>Hamster</td>
<td>18.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spiny mouse</td>
<td>18.9</td>
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<td>yes</td>
</tr>
<tr>
<td>Desert hedgehog</td>
<td>19</td>
<td>no</td>
<td>yes</td>
</tr>
<tr>
<td>Wood rat</td>
<td>19</td>
<td></td>
<td></td>
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<tr>
<td>Grasshopper mouse</td>
<td>19.3</td>
<td>no</td>
<td>yes</td>
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<tr>
<td>Domestic rabbit</td>
<td>22.3</td>
<td></td>
<td></td>
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<tr>
<td>Horse</td>
<td>25</td>
<td>yes</td>
<td>no</td>
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<tr>
<td>Cottontail rabbit</td>
<td>27</td>
<td></td>
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<tr>
<td>Gerbil</td>
<td>27</td>
<td>yes</td>
<td>yes</td>
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<tr>
<td>Merriam’s kangaroo rat</td>
<td>27 **</td>
<td>yes</td>
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<tr>
<td>Groundhog</td>
<td>27.8</td>
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<td>yes</td>
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<tr>
<td>Domestic Cattle</td>
<td>30</td>
<td>yes</td>
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<td>Black-tailed Prairie dog</td>
<td>32.8</td>
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<td>yes</td>
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<tr>
<td>Eastern chipmunk</td>
<td>33</td>
<td>yes</td>
<td>yes</td>
</tr>
<tr>
<td>House mouse</td>
<td>33</td>
<td>yes</td>
<td>yes</td>
</tr>
</tbody>
</table>

Dashes indicate no data.
*Unable to use binaural intensity cue in the upper octaves of its hearing range.
**Localization tested with clicks. For all other animals, the stimulus was broadband noise.
***Wesolek, C.M. (2004). The inability of the laboratory rat (Rattus norvegicus) to use the binaural phase cue to localize sound.
Medial Superior Olive (MSO)

**Initial locus for processing interaural time difference (ITD)**

- receives phase-locked excitatory input bilaterally
- contains an array of cells forming a delay line
Medial Superior Olive processes ITD

MSO neuron response

Ipsilateral sound source

Contralateral sound source

Ipsilateral lead

Contralateral lead

Interaural Time Difference (ITD)
A sound on the left side of the head reaches the left ear first, evoking activity in left cochlear nucleus, which sends activity to the superior olivary complex.

Meanwhile, activity from the left side has traveled further.

Very soon the sound reaches the right ear, evoking activity in right cochlear nucleus.

Impulses from the 2 sides simultaneously reach neuron 3, which sums the coincident input and generates an action potential.
Delay line - Jeffress (1948)

the delay-sensitive cells:
- cross-correlate their inputs
- act as coincidence detectors

A PLACE THEORY OF SOUND LOCALIZATION
LLOYD A. JEFFRESS
William G. Kerckhoff Laboratories of the Biological Sciences, California Institute of Technology
Received September 16, 1947

THE MECHANISM FOR THE REPRESENTATION OF A TIME DIFFERENCE AS PLACE

The proposed mechanism for representing a time difference as a difference in place depends upon two well established physiological functions: the slow rate of conduction of small nerve fibers, and the phenomenon of spatial summation. A schematic diagram of the mechanism is given in figure 1. The question of its possible location in the auditory tract will be considered in a later section.
Lateral Superior Olive processes ILD
LSO neurons are “EI”

ipsi-excited, contra-inhibited

Response to fixed ipsi stimulus inhibited by sufficiently loud contra stimulus.

Latencies of ipsi-Ex & contra-Inhib typically match, despite inhibition’s added distance & intervening synapse.
End bulb of Held: *Medial Nucleus of Trapezoid Body*

Large axons synapse on principal cells of the contralateral MNTB at the calyx of Held, a glutamatergic synaptic terminal.

MNTB cells are glycinergic and provide contralateral inhibition to LSO, which also receives excitatory input from AVCN.
Cellular specializations for precise auditory timing

**AVCN bushy cells**
- inputs via end bulbs of Held ensure secure synaptic transmission
- low-threshold $K^+$ conductance rapidly resets membrane voltage after each spike or EPSP

**EPSCs** are much shorter in VCN bushy cells than in hippocampal neurons
Cellular specializations for precise auditory timing

**MNTB**

- *input via calyx Held.*
- *low-threshold $K^+$ conductance rapidly resets the membrane voltage after each spike or EPSP.*
• can detect a 1-msec ITD and catch mice in complete darkness.

• highly asymmetric external ears create an ILD cue for vertical localization.

• localization along the horizontal plane largely based on ITD
The barn owl's asymmetric external ears mean that ILD provides a cue for elevation, whereas ITD is a better cue for azimuth.
Spaced-tuned neurons in barn-owl midbrain

- Neurons in the barn owl’s external nucleus of the inferior colliculus (ICx) are tuned to a specific azimuth and elevation. Unlike neurons in the central nucleus (ICc), they have broad frequency tuning.
- Azimuth tuning of ICx neurons depends primarily on ITD, whereas elevation tuning depends primarily on ILD (not shown).

Knudsen and Konishi (1978)
Midbrain map of auditory space

- The barn owl’s ICx (the region which contains space-tuned neurons) forms a neural map of acoustic space.
- Contralateral space is represented caudally within ICx; medial azimuths are represented rostrally (C). Low elevations are represented ventrally, and high elevations dorsally.
- There are also maps of auditory space in both mammalian and avian superior colliculi. On the other hand, no convincing space map has been found in the mammalian IC.
Barn Owls are Specialized for Phase-Locking at High Frequencies

- Barn owl auditory-nerve fibers show a much higher upper frequency limit for phase-locking than any other species

*Köppl (1997)*
Two separate auditory pathways in the barn owl

- The barn owl’s auditory system processes ITD and ILD in separate parallel pathways — via n. angularis & n. magnocellularis.

- Both pathways and different frequency bands converge in the auditory midbrain, merging selectivities to particular combinations of ITD and ILD.

- This map projects to the optic tectum (OT) to form a bimodal map of space.
Summary of specializations for sound localization in the barn owl

Barn owls show sound-localization specializations that distinguish them from mammals and other birds:

• Asymmetric arrangement of the external ears allows ILD to code elevation
• Neural phase locking at high frequencies
• Separate pathways for ITD and ILD processing
• Spaced-tuned neurons with broad frequency selectivity
• Neural map of auditory space in the IC
ITD processing may be different in birds and mammals

- Birds and mammals independently evolved the ability to hear airborne sounds.
- The Jeffress model is consistent with data from studies in birds, but less consistent for mammals.
**Localization ability is frequency-dependent**

![Diagram](image1.png)

**Localization depends on ITD at low freq, and ILD at high freq**

![Diagram](image2.png)

**Many more Front-Back localization errors occur at low freq**

![Diagram](image3.png)

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**Stevens & Newman (1936)**

**Fig. 2. Dependence of Localization on Frequency**

The ordinate represents the average of the errors in degrees made by both Os. The crosses are for the shorter series of judgments made in 1933. The circles represent the results obtained in 1934. The triangles represent the results obtained with unfiltered tones. Note the critical region at about 3000 cycles.

**Fig. 3. Absence of Phase-Effect at High Frequencies and of Intensity-Effect at Low Frequencies**

The solid curve represents theoretically the maximum angle by which a tone can be displaced by 180° change in phase. The circles on the dotted curve are the observed maxima of displacement (Halverson). The dot-dash curve represents the observed difference in intensity at the two ears of tones originating at the side of the observer (Sivian and White).

**Fig. 4. Percentage Reversals of the Front-Back Quadrants**

The crosses are for the data obtained in 1933, the circles for 1934. The critical region is at about 3000 cycles; cf. Fig. 2.
ITD processing based on the Jeffress model

- ITD curves are narrower for higher frequencies (green)
- curves coincide at one “characteristic delay”
- for pure excitation, characteristic delay is at a common peak
Evidence for delay lines in mammals

meandering route of a AVCN spherical bushy cell projection to ipsilateral MSO

Course of an intracellularly-filled spherical bushy cell axon and its primary collaterals in the ipsilateral brainstem, illustrating the "round-about" route taken. Collaterals are not drawn to their termination sites for the sake of simplicity.

Implication: the path meanders to create the necessary time delay for coincidence at MSO with activity from the more distant contralateral AVCN.

Evidence for delay lines in mammals

projection to contralateral MSO looks like a delay line for cells # 1, 2, 3. Cells 4-9 show different organization.

projection to ipsilateral MSO is inconsistent with the Jeffress Model in all cases (cells 10-16)

One interpretation:
the contralateral path creates the delay line, and the indirect path creates the time delay necessary for coincidence at MSO.

Another interpretation:
the best evidence for delay lines in mammals is unconvincing.

Smith, Joris & Yin (1993)
Phase-locked inhibition influences ITD tuning

MSO receives bilateral excitation and inhibition
Inhibitory inputs to MSO are refined during development

• MSO principal neurons are bipolar, with both dendrites largely covered by excitatory synaptic terminals from AVCN. Inputs from the two AVCNs are segregated, each one ending on one of the two dendrites of MSO cells.

• Inhibitory inputs are intermingled with the excitatory inputs early in life, but during development inhibitory inputs are pruned until they are almost all on the soma.
Role of inhibition in MSO

effect of blocking inhibition:
slope shifts outside the physiological range

Possible mechanism:
well-timed, phase-locked inhibition
Another candidate mechanism for neural delay

Cochlear place (frequency) not identical from two ears

differences in cochlear wave propagation could provide delays if coincidence detectors receive input arising from different loci in the left and right cochlea

similar to Bonham and Lewis (1999)
Neural delay

internal delays grow with decreasing CF

Candidate mechanisms

Axonal delays invoked by the Jeffress model

Excitatory inputs from the right ear are preceded by inhibitory inputs from the same side.

Inputs derive from slightly different loci along the BM. This cochlear disparity creates delays due to the traveling wave’s slow motion from base to apex.
Divergent Brainstem Pathways Converge at the Auditory Midbrain

- Parallel processing pathways diverge from CN and converge at IC.
- Some projections are direct from CN to IC; others synapse in SOC and/or LL.
- IC responses are more complex than those of its inputs.
Inferior Colliculus

*tonotopic organization*

Low freq  
High freq
Structure of Inferior Colliculus

- External Nucleus
- Dorsal Cortex
- Central Nucleus
Laminar Structure of Central Nucleus

- Lateral lemniscus fibers
  - Interleave cell layers
- Disc-shaped cells
  - Arranged in laminae
- Stellate cells cut across laminae
Inferior Colliculus Projects to Medial Geniculate