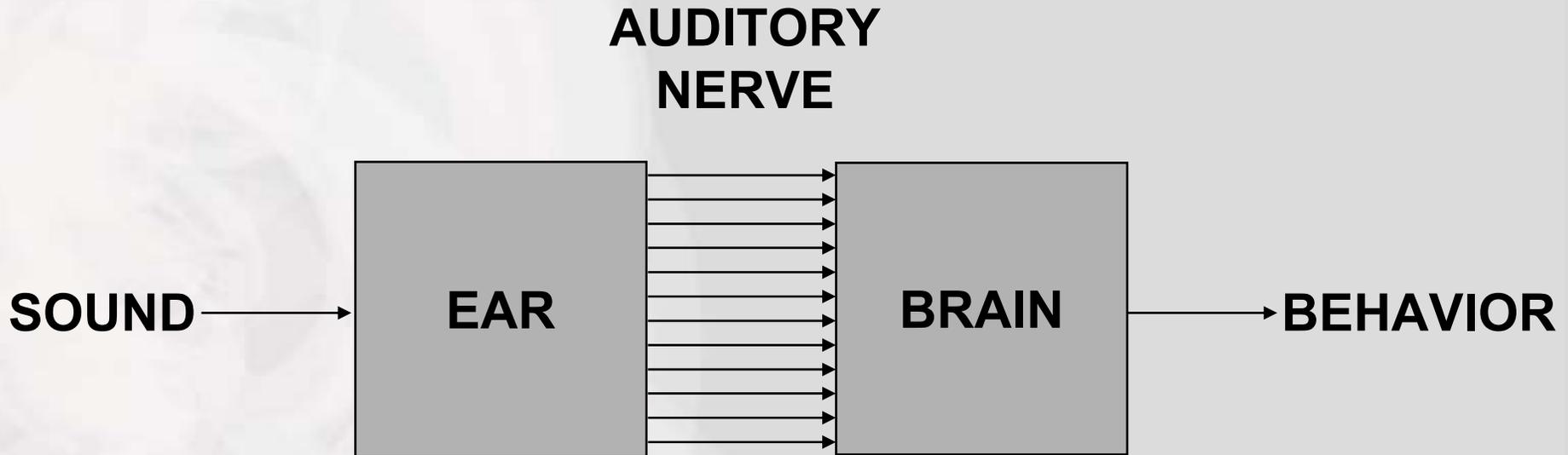


Stimulus Coding in the Auditory Nerve

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Point of View



- The auditory nerve conveys information about sound from the ear to the brain, which decodes this information to control behavior.
- Data on responses of the auditory nerve to sound are useful both to infer the processing performed by the ear, and to assess the brain's performance in various perceptual tasks against that of an ideal observer operating on auditory-nerve information.

Outline

- Anatomy and functional organization of the auditory nerve
- Frequency selectivity
- Phase locking
- Nonlinearities:
 - Compression
 - Adaptation
 - Suppression

Afferent innervation of the cochlea

Figure removed due to copyright reasons.
See: Berglund, A. M., and D. K. Ryugo. "Hair cell innervation by spiral ganglion neurons in the adult mouse." *J. Comp. Neurol.* 255 (1987): 560-570.

- The auditory nerve is formed by the axons of spiral ganglion cells, of which there are two types.
- Type I neurons have myelinated cell bodies and innervate inner hair cells.
- Type II neurons are unmyelinated and innervate outer hair cells.
- Type I neurons from the vast majority of the population (95% in cats).

Course of Type I and Type II fibers

- The auditory nerve is formed by the axons of spiral ganglion cells, of which there are two types.
- Type I neurons have myelinated cell bodies and innervate inner hair cells. In cats, each hair cell forms synaptic terminals with about 20 Type I fibers.
- Type II neurons are unmyelinated and innervate many outer hair cells longitudinally distributed along the cochlea.
- Both types of neurons project to the cochlear nucleus, albeit to different types of cells.
- Type I neurons from the vast majority of the AN population (95% in cats).
- All existing physiological data are from Type I neurons. Nothing is known about responses of Type II neurons to sound.

Figure removed due to copyright reasons.
See: Berglund, A. M., and D. K. Ryugo. "Hair cell innervation by spiral ganglion neurons in the adult mouse." *J. Comp. Neurol.* 255 (1987): 560-570.

Auditory-Nerve Anatomy

Figure removed due to copyright reasons.
See: Kiang, N. Y. S. "Peripheral neural processing of auditory information." In *Handbook of Physiology-The nervous system III*. 1984, pp. 639-674.

- Cross sections of the auditory nerve (AN) show an homogeneous bundle of fibers, most of which are myelinated.
- There are about 50,000 AN fibers in cats, 30,000 in humans.

All-or-none action potentials in nerve fibers

- In the classic experiments of Hodgkin and Huxley, a stimulating electrode was inserted into a giant squid axon, and recording electrodes were used to measure the membrane voltage at several points along the axon.
- Left: Hyperpolarizing (outward) currents and small depolarizing (inward) currents produce small changes in membrane potentials which quickly attenuate along the axon.
- Right: Depolarizing currents exceeding a threshold produce a large, “all-or-none” action potential which travels along the axon without attenuation.

Figure removed due to copyright reasons.

Ionic basis of the action potential

Figures removed due to copyright reasons.

The action potential is due to the coordinated action of Na^+ and K^+ channels in the nerve membrane. Depolarization causes Na^+ channels to open and current to flow into the cell, leading to further depolarization (positive feedback). Na^+ channels rapidly deactivate, no longer passing current. In addition, K^+ channels open, leading to outward currents that repolarize the membrane voltage.

The depolarization caused by an action potential spreads to neighboring locations along the axon, leading Na^+ channels to open and the action potential to propagate. In contrast, locations that just fired an action potential do not respond to further depolarization so long that the Na^+ channels remain deactivated (refractory period).

Response to Pure Tones

- Each vertical bar represents one spike (action potential) recorded from an AN fiber in response to a pure tone swept in frequency at different intensities.
- Spike discharges occur in all conditions: There is spontaneous activity.
- For low intensities, discharge rate increases above spontaneous only for a narrow range of frequencies. As intensity increases, so does the range of frequencies to which the fiber responds.
- The outline of the response area is the pure tone *tuning curve* or *frequency threshold curve*. The frequency for which threshold is minimum is the *characteristic frequency (CF)*.

Figure removed due to copyright reasons.
See: Evans, E. "The cochlear nerve and cochlear nucleus." In *Handbook of Sensory Physiology*. Edited by D. N. W. Keidel. Heidelberg: Springer, 1975, pp. 1-109.

Cochlear Frequency Map

Figure removed due to copyright reasons.
See: Liberman, M. C., and M. E. Oliver.
“Morphometry of intracellularly labeled
neurons of the auditory nerve: Correlations
with functional properties.” *J. Comp. Neurol.*
223 (1984): 163-176.

Figure removed due to copyright reasons.
See: Liberman, M. C. “The cochlear
frequency map for the cat: Labeling auditory-
nerve fibers of known characteristic
frequency.” *J. Acoust. Soc. Am.* 72, no. 5
(1982): 1441-1449.

- Physiologically-identified AN fibers were labeled with horseradish peroxidase (HRP) to identify their point of innervation along the cochlea.
- There is a precise mapping between the CF of an AN fiber and the cochlear place it innervates.
- The *cochlear frequency map* is nearly logarithmic for CFs > 2 kHz, and flattens out at low CFs. This relationship fits well with estimates of frequency selectivity based on psychophysical masking data.

Spontaneous Activity and Threshold

Figure removed due to copyright reasons.
See: Liberman, M. C. "The cochlear frequency map for the cat: Labeling auditory-nerve fibers of known characteristic frequency." *J. Acoust. Soc. Am.* 72, no. 5 (1982): 1441-1449.

Figure removed due to copyright reasons.
See: Liberman, M. C., and M. J. Mulroy. "Acute and chronic effects of acoustic trauma: Cochlear pathology and auditory nerve pathophysiology." In *New Perspectives on Noise-induced Hearing Loss*. Edited by R. P. Hamernik, D. Henderson, and R. Salvi. New York: Raven, 1982, pp. 105-135.

- The distribution of spontaneous discharge rates (SR) is bimodal, separating AN fibers into two groups. The high-SR group ($SR > 18$ spikes/s) forms 60% of the fiber population. The remaining fibers are further subdivided into a low-SR group ($SR < 0.5$ sp/s, ~15%) and a medium-SR group ($0.5 < SR < 18$ sp/s, ~25%).
- High-SR fibers form a large synaptic terminal on the "pillar" side of inner hair cells, while low- and medium-SR fibers form smaller terminals on the "modiolar" side (not shown).
- Spontaneous discharge rate is inversely related to threshold at the CF, high-SR fibers being the most sensitive.
- The auditory nerve can be thought of as a two-dimensional array of fibers organized by CF (cochlear place) and sensitivity or threshold (spontaneous rate).

Frequency Tuning: Basilar membrane vs. ANF

- Iso-rate tuning curves of AN fibers and basilar membrane motion were measured in the same chinchilla (basal cochlear region) for pure-tone stimuli.
- AN fiber tuning curves are very similar to (but not identical to) basilar-membrane iso-velocity curves.

Figure removed due to copyright reasons. See: Narayan, S. S., A. N. Temchin, A. Recio, and M. A. Ruggero. "Frequency tuning of basilar membrane and auditory nerve fibers in the same cochleae." *Science* 282 (1998): 1882-1883.

Phase Locking

- In response to low-frequency (< 5 kHz) pure tones, spike discharges tend to occur at a particular phase within the stimulus cycle. However, spikes do not always occur on every cycle, i.e. there can be 2, 3, or more cycles between consecutive spikes.
- Phase locking can be quantified using period histograms, which display the distribution of spikes within a stimulus cycle. With perfect phase locking, the period histogram would be an impulse. Period histograms of AN fibers for low-frequency pure tones are nearly sinusoidal at near-threshold level, and become more peaky at moderate and high levels.
- Alternatively, phase locking can be visualized from *interspike interval histograms*, where it shows up as modes at integer multiples of the stimulus period, i.e. at $1/f$, $2/f$, $3/f$, etc for a pure tone of frequency f . This analysis is appealing from the viewpoint of central auditory processing because, unlike period histograms, it does not require an absolute time reference locked to each stimulus cycle.

Figure removed due to copyright reasons.
See: Javel, E., J. A. McGee, W. Horst, and G. R. Farley. *Temporal mechanisms in auditory stimulus coding*. Edited by G. M. Edelman, W. E. 1988.

The volley principle (Wever)

Figure removed due to copyright reasons.
See: Geisler, C. D. *From Sound to Synapse*.
New York: Oxford University Press, 1998.

Even though spike discharges of a single ANF do not occur on every cycle of a pure-tone stimulus, the frequency can still be accurately coded in the synchronized firings of a population of fibers (e.g. those that innervate the same hair cell). This is known as the *volley principle*.

Phase Locking: Frequency Dependence

Figures removed due to copyright reasons.
See: Johnson, D. H. "The relationship between spike rate and synchrony in responses of auditory-nerve fibers to single tones." *J. Acoust. Soc. Am.* 68, no. 4 (1980): 1115-1122.

- For very low-frequency pure tones, period histograms can show severe deviations from a sinusoidal waveform, with sometimes two peaks per cycle ("peak splitting"). Period histograms for higher frequency tones show less distortion.
- The *synchronization index* (a.k.a *vector strength*) is a measure of the degree of phase locking varying from 0 for a flat period histogram (no phase locking) to 1 for a pulsatile histogram (perfect phase locking).
- Synchronization index falls rapidly with frequency for pure tones above 1 kHz. Above 5-6 kHz, the synchronization index reaches the noise floor of the measurements. There is no absolute upper frequency limit to phase locking.

Phase Locking: Relation to IHC Receptor Potentials

- Phase locking in AN fibers ultimately derives from the polarization of the hair cell bundle and the resulting half-wave rectification seen in hair-cell receptor potentials.
- The fall-off of synchronization index with frequency in AN fibers resembles the decrease in the AC component of the IHC receptor potential relative to its DC component. This lowpass filtering action is due to the hair-cell membrane capacitance. However, on closer examination, this decay is too slow to fully account for the rapid fall-off of synchrony in AN fibers, so that additional stages of lowpass filtering (presumably occurring at the hair-cell synapse) must also play a role.

Figure removed due to copyright reasons.
See: Hudspeth, A. J., and D. P. Corey. "Sensitivity, polarity, and conductance change in the response of vertebrate hair cells to controlled mechanical stimuli." *Proc. Natl. Acad. Sci. USA* 74 (1977): 2407-2411.

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Frequency Selectivity for Broadband Noise

Figure removed due to copyright reasons.
See: Pickles, J.O. *An introduction to the physiology of hearing*. 2nd ed. Academic: London, 1988.

Figure removed due to copyright reasons.
See: Evans, E. F. "Frequency selectivity at high signal levels of single units in cochlear nerve and cochlear nucleus." In *Psychophysics and Physiology of Hearing*. Edited by E. F. Evans, and J. P. Wilson. London: Academic, 1977, pp. 185-192.

- A general method for system identification is to measure the system response to a white noise input. For a linear system, the crosscorrelation between input and output is proportional to the system's impulse response.
- When the output consists of temporally punctate spikes, the crosscorrelation is the average stimulus waveform preceding each spike, reversed in time. This is known as the *reverse correlation* or "revcor" function.
- Revcor functions of low-CF AN fibers resemble the impulse response of a bandpass filter centered at the CF. Fourier transforms of revcor functions roughly match the tip of tuning curves over a wide range of noise levels.
- The revcor technique shows that AN fibers selectively respond to frequency components of the noise stimulus that are near their CF. This technique only works for low-CF (< 3 kHz) fibers, which phase lock to the noise stimulus.

Compression in ANFs and basilar membrane

- Discharge rate vs. level functions of ANFs for tones at CF can either show a hard saturation or a soft, “sloping” saturation. Low-threshold fibers tend to have a hard saturation, high-threshold fibers a sloping saturation.
- These observations can be accounted for by a model comprising two cascaded nonlinearities: A peripheral soft compression (power-law type), and a central, hard sigmoid nonlinearity whose operating point correlates with fiber threshold. The peripheral nonlinearity is consistent with the compression seen in basilar membrane motion, while the central nonlinearity presumably arises at the hair-cell auditory-nerve synapse.
- The model predicts that the knee in the rate-level function should occur at the same SPL for all fibers innervating the same place, broadly consistent with observations.

Figure removed due to copyright reasons.
See: Sachs, M. B., R. L. Winslow, and B. H. A. Sokolowski. “A computational model for rate-level functions from cat auditory-nerve fibers.” *Hearing Res.* 41 (1989): 61-70.

Effect of compression on place coding of complex sounds

- Responses to the synthetic vowel [ε] were recorded from ~300 AN fibers in the same cat. Average discharge rate was plotted against fiber CF to visualize the pattern of neural activity along cochlear place.
- For low sound levels, the first two formant frequencies are clearly marked in the rate-place profile. However, for conversational speech levels, most high-SR fibers saturate and information about formant frequencies is only available in the rate-place profile for low-SR fibers.

Figure removed due to copyright reasons.
See: Sachs, M. B., and E. D. Young.
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Adaptation

- After the onset of a tone-burst stimulus, discharge rate of AN fibers quickly reaches a maximum, followed by a gradual decay called *adaptation*. Adaptation occurs on different time scales ranging from a few msec to several seconds.
- Because there is no visible adaptation in hair-cell receptor potentials *for tone-burst stimuli*, adaptation is thought to arise at the hair-cell auditory-nerve synapse. Recordings of postsynaptic potentials from the goldfish auditory nerve show a form of adaptation consistent with a depletion of neurotransmitter on the presynaptic side.
- Functionally, adaptation enhances the neural representation of rapid intensity transients, which are perceptually important in speech and music.

Figure removed due to copyright reasons.
See: Kiang, N. Y. S. "Peripheral neural processing of auditory information." In *Handbook of Physiology-The Nervous System III*. 1984, pp. 639-674.

Adaptation enhances onset transients in speech

- Speech shows an alternation between intense vowels containing predominantly low-frequency energy, and weaker consonants often containing mostly high-frequencies. This alternation occurs at the average syllabic rate of 3-4 Hz.
- The response of the auditory nerve to an utterance is shown above the spectrogram. Each trace shows the average response of several AN fibers with similar CFs.
- High-CF fibers show a pronounced peak in discharge rate followed by adaptation at the onset of high-frequency consonants (white arrows). Low-CF fibers show a similar rate peak at onset of vocalic segments (black arrows). Thus, adaptation enhances the representation of rapid onset transients in speech.

Figure removed due to copyright reasons. See: Delgutte, B. "Auditory neural processing of speech." In *The Handbook of Phonetic Sciences*. Edited by W. J. Hardcastle, J. Laver. Oxford: Blackwell, 1997, pp 507-538.

“Two-Tone” Suppression

Figure removed due to copyright reasons.
See: Kiang, N. Y. S., T. Watanabe, E. C. Thomas, and L. F. Clark. *Discharge Patterns of Single Fibers in the Cat's Auditory Nerve*. Cambridge, MA: The MIT Press, 1965.

Figure removed due to copyright reasons.
See: Sachs, M. B., and N. Y. S. Kiang. “Two-tone inhibition in auditory-nerve fibers.” *J. Acoust. Soc. Am.* 43 (1968): 1120-1128.

- A pure tone can suppress the average discharge rate in response to another, excitatory tone at the CF. Although suppression also occurs for other complex stimuli, it is best characterized for tone pairs and is called “two-tone” suppression.
- Two-tone rate suppression occurs when the suppressor tone lies in either of two suppression areas flanking the CF. Both suppression areas span the pure-tone tuning curve, i.e. a tone which, by itself, would excite a fiber can suppress the response to a CF tone.

Two-Tone Suppression: Level and Frequency Dependence

- To a first approximation, the effect of a fixed suppressor is to shift the rate-level function for a CF tone towards higher intensities. The amount of horizontal shift (in decibels) is taken as a measure of suppression.

Figure removed due to copyright reasons.

See: Javel, E., J. A. McGee, W. Horst, and G. R. Farley. "Temporal mechanisms in auditory stimulus coding." In *Auditory Function: Neurological Bases of Hearing*. Edited by G. M. Edelman, W. E. Gall, and W. M. Cowan. Wiley: New York, 1988, pp. 515-558.

Figure removed due to copyright reasons.

See: Delgutte, B. "Two-tone suppression in auditory-nerve fibers: Dependence on suppressor frequency and level." *Hearing Research* 49 (1990): 225-246.

- Suppression (in dB) increases with the intensity of the suppressor tone. The rate of growth of suppression depends strongly on suppressor frequency. For suppressors whose frequency is higher than the CF, suppression grows by less than a dB if suppressor level is increased by 1dB. In contrast, for suppressors much lower in frequency than the CF, the rate of growth of suppression can exceed 2 dB/dB.

- This rapid growth of low-side suppression is likely responsible for "upward spread of masking", the rapid growth of psychophysical masking when the masker frequency is well below the signal frequency.

Suppression is caused by decrease in gain of cochlear amplifier

- Suppression occurs when the OHC stereocilia bend into their saturation range, resulting in a decrease in gain of the cochlear amplifier
- Cochlear amplification of a test tone occurs primarily in a small BM region slightly basal to the test tone place.
- High side suppression has a low threshold because the suppressor's traveling wave maximum is located in the BM region where maximal amplification of test tone occurs. Suppression grows only slowly because the suppressor response has a compressive growth.
- Low side suppression has a high threshold because it requires the tail of BM traveling wave for the suppressor to reach saturation threshold. Growth is rapid because the suppressor affects a broad region of cochlear amplification and the suppressor response grows linearly, much faster than compressive growth of test tone.

Figure removed due to copyright reasons.
See: Geisler, C. D. *From sound to synapse*. New York: Oxford University Press, 1998.

Summary: Cochlear origin of auditory-nerve response properties

Cochlear Processing Stage	AN Response Properties
Cochlear mechanics	Frequency tuning, suppression, soft compression
Hair cell transduction	Phase locking and its frequency limit, half-wave rectification
Synaptic transmission	Spontaneous activity, hard compression, adaptation
Spike initiation	Refractory period

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Extra slides

Frequency Tuning

Figure removed due to copyright reasons.

See: Kiang, N. Y. S. "Peripheral neural processing of auditory information."

Handbook of Physiology-The nervous system III. 1984. 639-674.

Figure removed due to copyright reasons.

See: Liberman, M. C. "Auditory-nerve responses from cats raised in a low-noise chamber." *J. Acoust. Soc. Am.*, 63 (1978): 442-455.

- Frequency tuning curves are approximately V-shaped for low-CF (< 2 kHz) fibers. High-CF fibers (> 2 kHz) have both a sharp "tip" near the CF and a broad "tail" extending far to the low frequency side.
- Low-SR fibers are more sharply tuned than high-SR fibers, even though the same inner hair cell is innervated by fibers from all 3 groups. This is consistent with the compressive nonlinearity in basilar-membrane motion.

Feedback: Effect of Olivocochlear Stimulation

- A classic method for studying effects of olivocochlear efferents is to electrically stimulate the floor of the 4th ventricle at the point where axons from contralaterally-projecting MOC neurons cross the midline (previous page). These form about 2/3 of all MOC neurons.
- To a first approximation, electrical stimulation of MOC neurons causes a shift in the rate-level function for a CF tone towards high intensities. This shift can reach 15-20 dB for high rates of stimulation.
- MOC-induced shifts are smaller for tones well below the CF than for CF tones (not shown).
- Largest efferent-induced shifts are observed for fibers with CFs in the 5-10 kHz region. This corresponds to the cochlear region where the density of efferent innervation of outer hair cells is highest.
- Olivocochlear efferents can also be stimulated by presenting loud sounds to the contralateral ear. The effects are similar, but smaller, in part because only a relatively small fraction of the MOC neurons participate in this reflex.

Figure removed due to copyright reasons.
See: Wiederhold, M. L., and N. Y. S. Kiang. "Effects of electric stimulation of the crossed olivocochlear bundle on single auditory-nerve fibers in the cat." *J. Acoust. Soc. Am.* 48 (1970): 950-965.

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Temporal representation of complex sounds

- All fibers that respond to a low-frequency pure tone phase lock to the same tone frequency. In contrast, for spectrally complex stimuli such as speech and most musical sounds, AN fibers with different CFs phase lock to different frequency components of the stimulus (the ones closest to their CF). Thus, the distribution of phase locking across CFs provides a code for the stimulus spectrum.
- In response to a steady-state vowel ([ae] in the figure), most fibers phase lock to one of the first two formant frequencies. Thus, formant frequencies, which are key for vowel perception, are prominently represented in the temporal discharge patterns of auditory-nerve fibers.

Figure removed due to copyright reasons.
See: Delgutte, B. "Auditory neural processing of speech." In *The Handbook of Phonetic Sciences*. Edited by W. J. Hardcastle, and J. Laver. Oxford: Blackwell, 1997, pp. 507-538.

Adaptation: Post-stimulatory effects

Right:

- Effects of adaptation continue after an adapting stimulus is turned off: Both spontaneous activity and responses to subsequent stimuli are depressed. This poststimulatory depression can last for over 100 msec and increases with the intensity of the adapting stimulus.

Figure removed due to copyright reasons.
See: Delgutte, B., and N. Y. S. Kiang.
“Speech coding in the auditory nerve: IV.
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See: Delgutte, B. “Representation of speech-
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auditory-nerve fibers.” *J. Acoust. Soc. Am.* 68
(1980): 843-857.

Left:

- To demonstrate effects of adaptation on speech coding, a set of synthetic speech stimuli was created. These stimuli share a common part which sounds like [da]. They differ in the preceding context so as to sound like [ada], [na], and [sha].
- Responses of AN fibers to these stimuli show adaptation during the variable context, and differ in the response to the common [da] as well. The greater the response to the variable context, the smaller the response to the common [da].
- These poststimulatory effects of adaptation tend to enhance spectral contrast between successive segments in neural responses.

Suppression and Masking

- Masking in AN fibers can result from several physiological mechanisms.
- When the signal and the masker are close in frequency, masking occurs because the signal level has to be increased in order to exceed the masker response. This is *line-busy masking*.
- When the masker precedes the signal in time, the poststimulatory depression of neural activity resulting from adaptation can lead to a *adaptive masking*.
- If a nonexcitatory masker is located in a fiber's suppression area, *suppressive masking* results.
- In many situations of practical importance, such as a transient signal in a continuous masker, all three forms of masking can co-occur.

Figure removed due to copyright reasons.
See: Delgutte, B. "Physiological models for basic auditory percepts." In *Auditory Computation*. Edited by H. Hawkins, T. McMullen, A. N. Popper, and R. R. Fay. New York: Springer Verlag, 1996, pp. 157-220.

Feedback: Olivocochlear Pathways

- In addition to its afferent innervation by Type I and Type II fibers, the cochlea receives efferent projections from two groups of cells located in the superior olive in the brainstem.
- One group of cells whose somata are located near the medial superior olive (MSO) projects bilaterally to the base of outer hair cells. This is the *medial olivocochlear* (MOC) pathway.
- Another group of cells whose somata are located near or in the lateral superior olive projects bilaterally to afferent (Type I) terminals under inner hair cells. This is the *lateral olivocochlear* (LOC) pathway.
- Attempts to selectively stimulate the LOC system have been largely unsuccessful. Most known efferent effects can be accounted for by the MOC system alone.

Figure removed due to copyright reasons.

See: Guinan, J. J. J. "Physiology of olivocochlear efferents." In *The Cochlea*.

Edited by P. Dallos, A. N. Popper, and R. R. Fay. New York: Springer, 1996, pp. 435-502.

Feedback: Effect in Background Noise

- Background noise and olivocochlear efferents combine to create complex effects. We have seen that olivocochlear stimulation horizontally shifts the rate-level function for tone-burst stimuli in quiet. On the other hand, continuous background noise vertically compresses the rate-level function by both raising the background rate (line-busy masking) and lowering the maximum rate (adaptive masking). When olivocochlear efferents are stimulated in the presence of continuous noise, the response to the noise background can be suppressed, resulting in a *decompression* of the rate-level function for transient stimuli.
- These results suggest that olivocochlear efferents may aid detection of transient signals in continuous backgrounds.

Figure removed due to copyright reasons.

See: Guinan, J. J. J. "Physiology of olivocochlear efferents." In *The Cochlea*. Edited by P. Dallos, A. N. Popper, and R. R. Fay. New York: Springer, 1996, pp. 435-502.