Echolocation

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"An echolocating bat can pursue and capture a fleeing moth in complete darkness with a facility and success rate that would be the envy of any military aerospace engineer" - **Suga, 1990**

Echolocation - Echolocation, or biosonar, is an active process, used by the species that have it for sensing the environment when vision is ineffective, for example at night or in turbid water . It is the production of sound by animals and the subsequent determination of the position (and other features) of objects from information encoded in acoustic reflections.

Echolocation has evolved to its greatest sophistication in bats and toothed whales (dolphins and their relatives), though simple forms of echolocation are also used by cave *swiflets* and *oilbirds*, and by small *nocturnal mammals such as shrews and rats*

The main function of echolocation is orientation — calculating one's own position relative to the surroundings — although many bats and dolphins also use echolocation for detecting, localizing and even classifying prey

Mustached bat

Little brown bat

Horse shoe bat

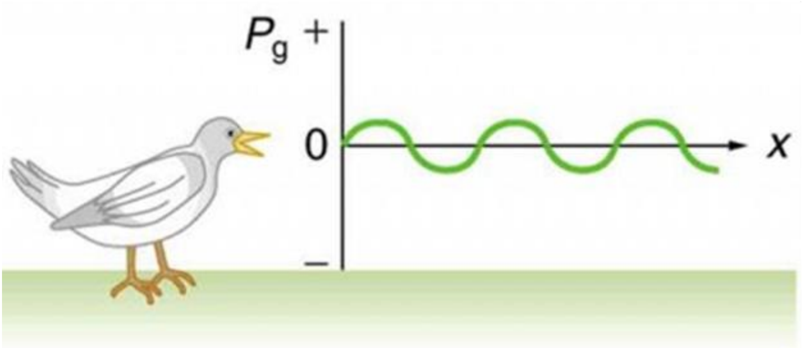
Although echolocation can give bats and dolphins sophisticated information about their surroundings, in certain situations it becomes of little use. For example, **mouse-eared bats use echolocation to detect airborne prey, but almost 'switch off' echolocation when detecting prey under leaf litter.** Echoes from leaves mask echoes from prey, and in these situations the bats must rely on rustling sounds made by the insects as they move through the leaf litter for successful prey detection.

Informations from the echo

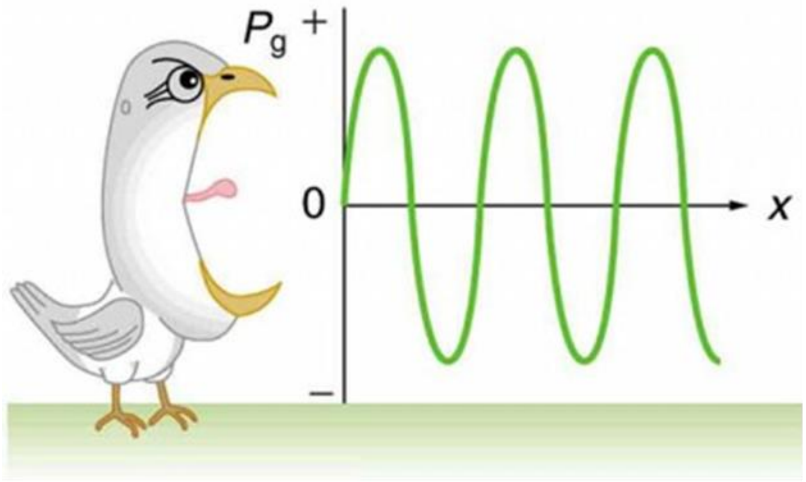
* Sound travels at 340 metres per second (approx.) in air

Properties of wave

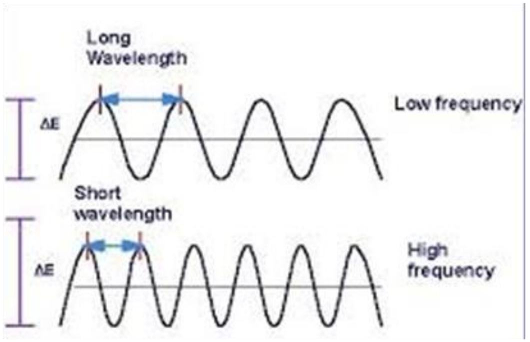
Frequency == Pitch
Amplitude == Loudness

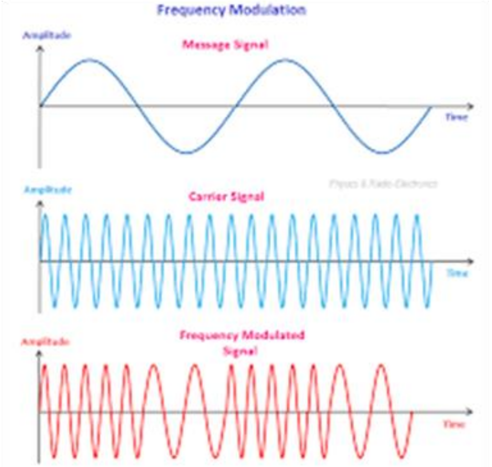


Low amplitude



High amplitude



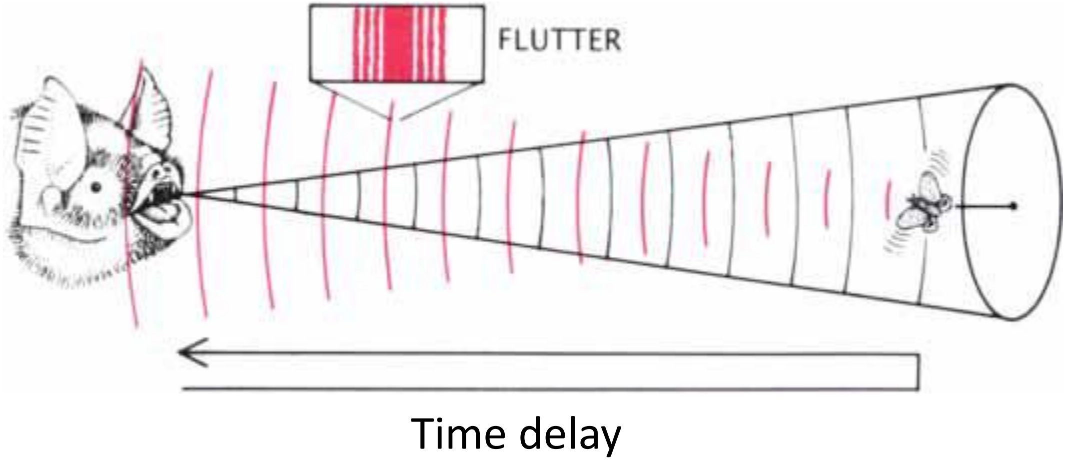


Relative velocity, Range and Flutter indication:

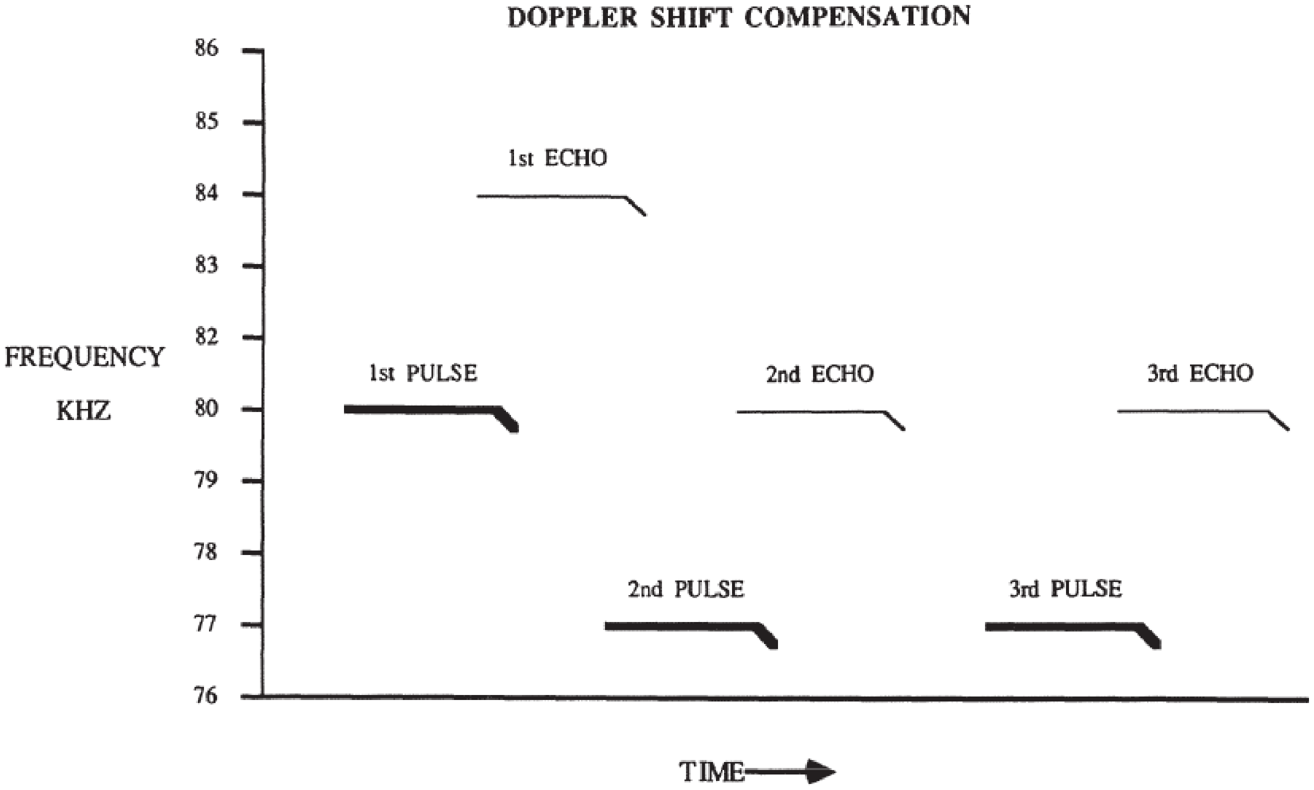
Doppler shifts-changes in the frequency of the echo relative to the original signal:

✓convey information not only about the relative velocity of a flying insect

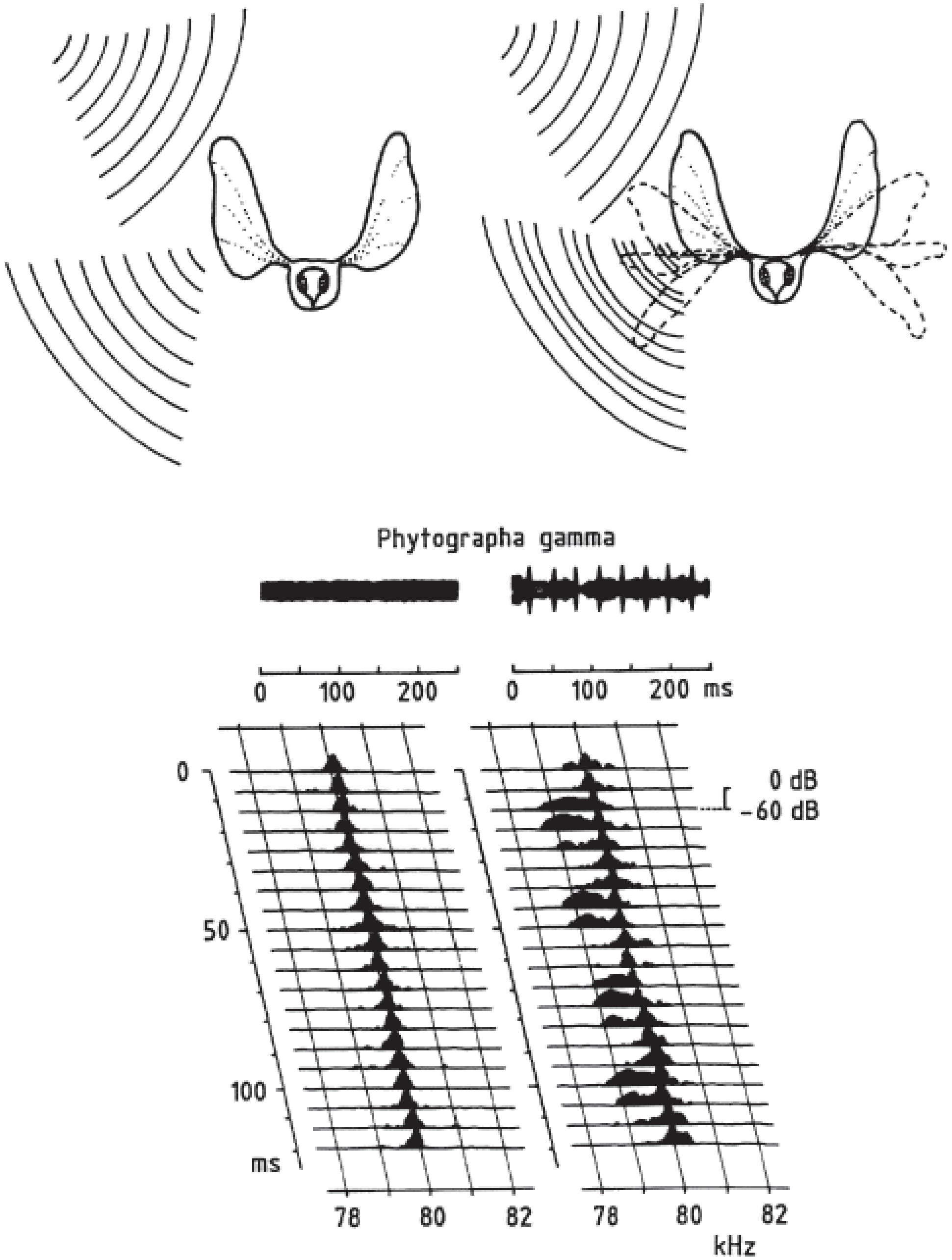
✓convey information about its wing beat.

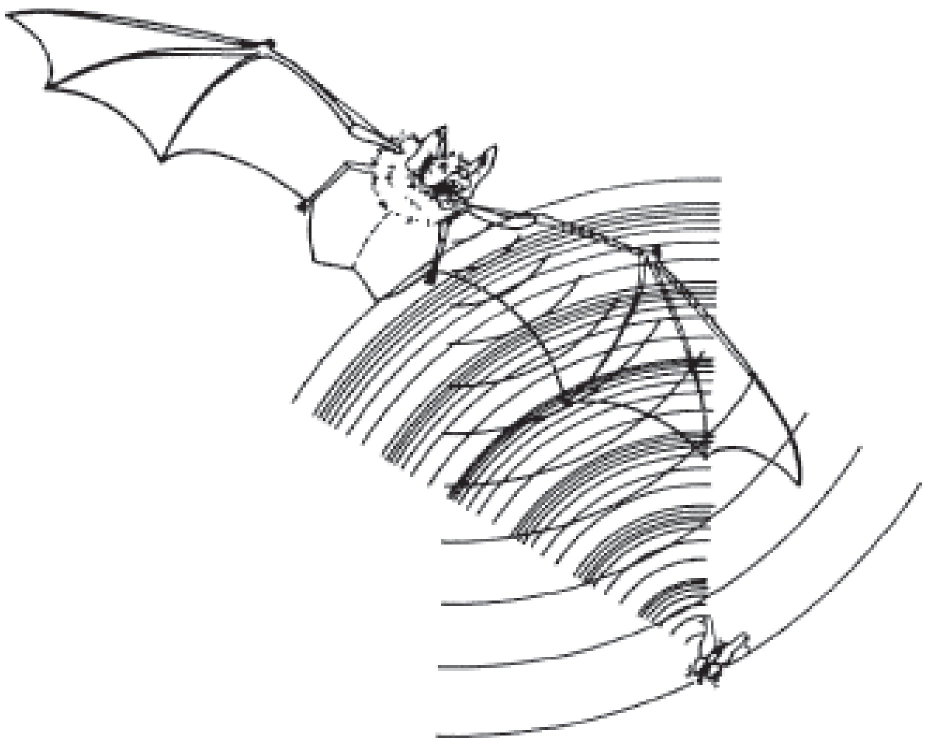


Doppler shift and flutter



Doppler effect: the change in the observed frequency of a wave when the source of the wave is moving with respect to the observer

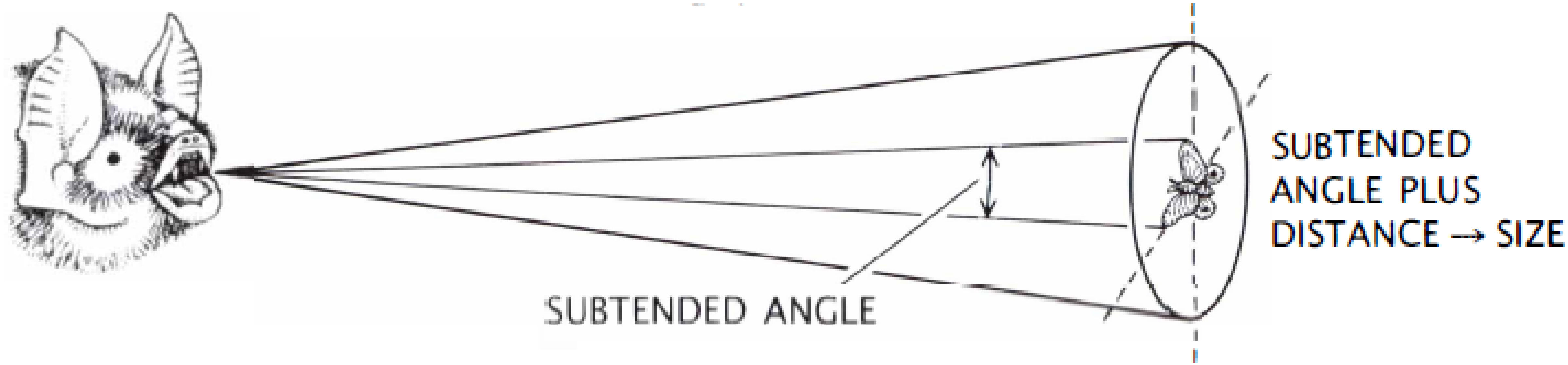




- Drawing of the emitted pulse of a mustache bat and the frequency modulations in the echo due to the wing movements of a nearby moth
- The emitted constant frequency component is depicted as a series of regularly spaced waves
- ***The echo reflected from the beating wings of the moth is shown as a series of irregularly spaced waves that are repeated periodically (i.e., the frequency modulations)***

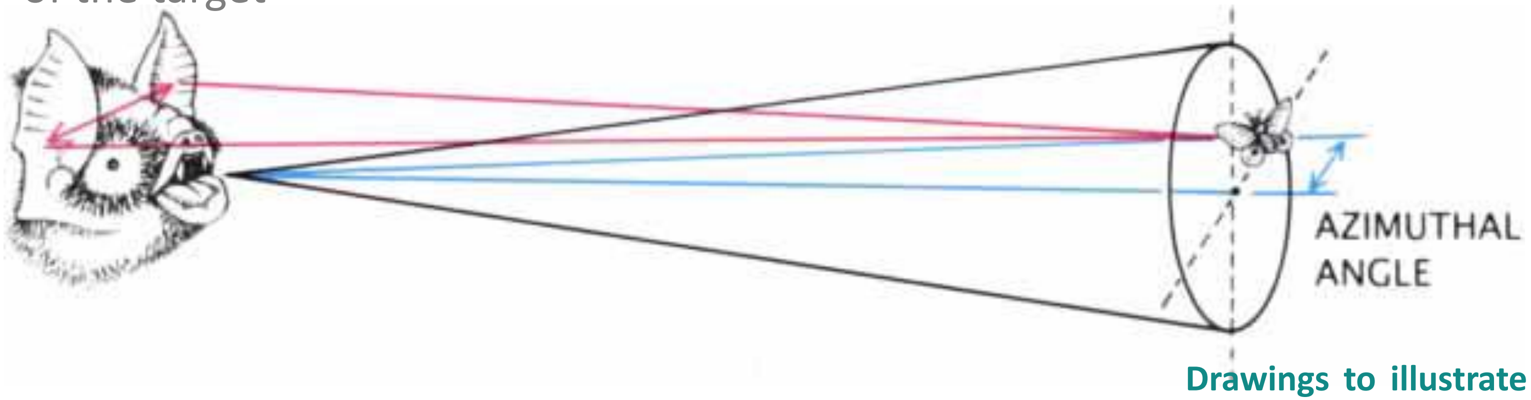
Size indication:

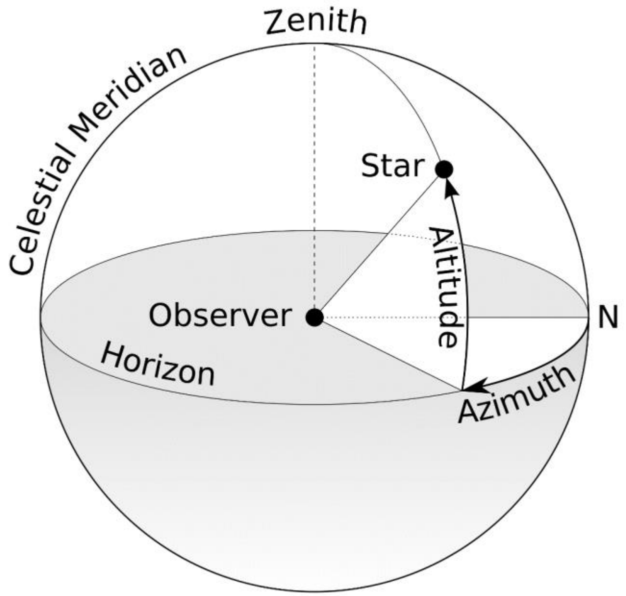
- ✓The amplitude of the echo, combined with the delay, indicates the size of the target
- ✓The amplitudes of the component frequencies correspond to the size of various features of the target.

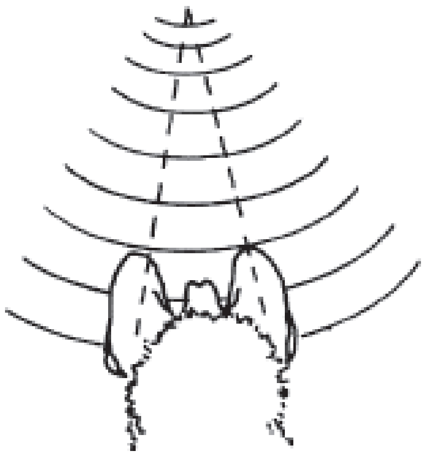


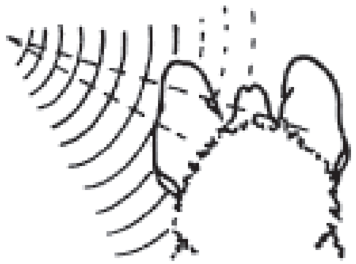
Azimuth indications:

Differences between the ears in intensity and arrival time of sound give the azimuth of the target









Drawings to illustrate generation of interaural time disparities and interaural intensity disparities

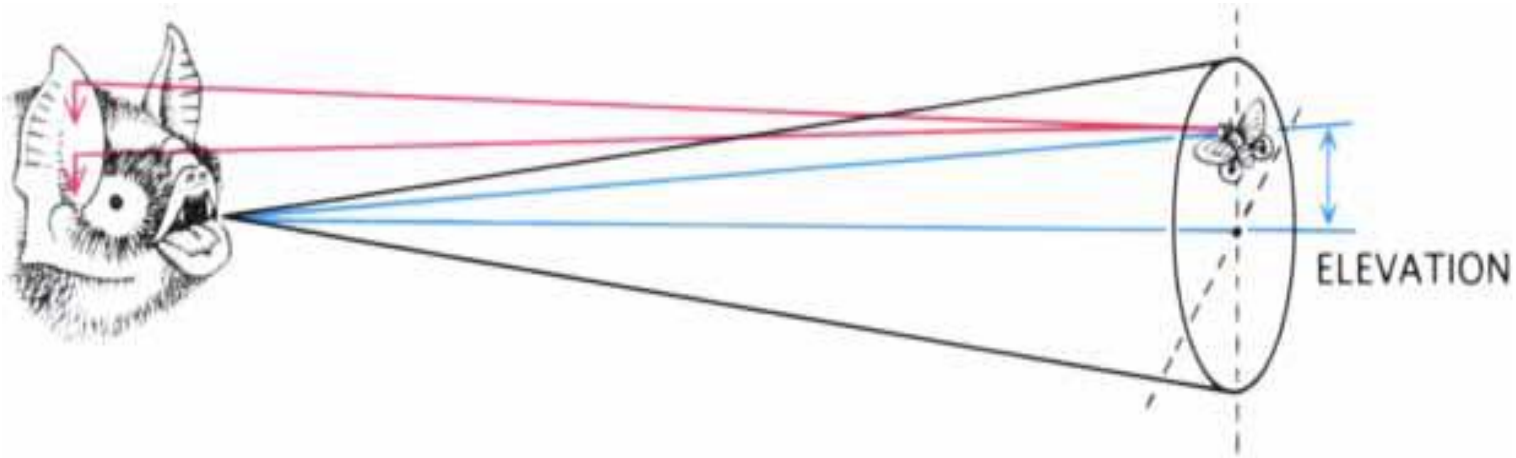
At left sound waves reach the bat's ears from a source directly ahead. In this case the sounds reaching both ears will be of equal intensity and will arrive at the same time since the path lengths, indicated by the *broken lines from the source to the ears, are* equal. If the sound source is displaced to one side, as shown on the *right, the sound waves* reach the closer ear unimpeded, but the head and ears block most of sound to the farther ear. This **acoustic shadow** makes the sound more intense in the closer ear than in the farther ear, and thus creates an **interaural intensity disparity.** In addition, the sound path to the closer ear is shorter than the path to the farther ear thereby creating a difference in the arrival times of the sound at the two ears, indicated by the *different lengths of the broken lines*

Elevation indication:

✓The interference pattern of sound waves reflected within the structure of the outer ear gives the elevation

✓Many bats determine the vertical angle (elevation) of targets by interpreting interference patterns caused by sounds reflecting from the **tragus**, a flap of skin in the external ear

✓Horseshoe bats move their ears up and down independently, and may calculate elevation from intensity differences received at each ear



Horseshoe bat

Biosonar pulses can be classified into three types

1. **Constant frequency (CF)-** consist of a single frequency, or tone
2. **Frequency modulated (FM)-** FM pulses sweep downward and sound like chirps
3. **Combined CF-FM-** CF –FM pulses consist of a long, constant tone followed by a downward chirp, iiiiiiu.

The little brown bat, ***Myotis lucifuqus*, is an "FM" bat**; it emits FM pulses lasting between 0.5 and 3 milliseconds and sweeping downward by about one octave

The mustached bat, *Pteronotus parnellii*, is a "CF-FM" bat; it emits long CF pulses lasting between 5 and 30 milliseconds followed by a short FM sweep lasting between 2 and 4 milliseconds

The fish catching bat, ***Noctilio leporinus***, for example, **emits CF and CF - FM** pulses while **cruising in flight** but emits **FM pulses while hunting prey**

The Diversity of Echolocation Signals

- **Narrowband signals** span a narrow range of frequencies, and are relatively **long in duration**
- They allow **ranging of distant targets**, and are well adapted for the detection of acoustic glints from flying insects

✓ **Broadband calls** span a wide range of frequencies and are typically short — **often <5 milliseconds** — in duration

✓ They are well adapted for **localization**.

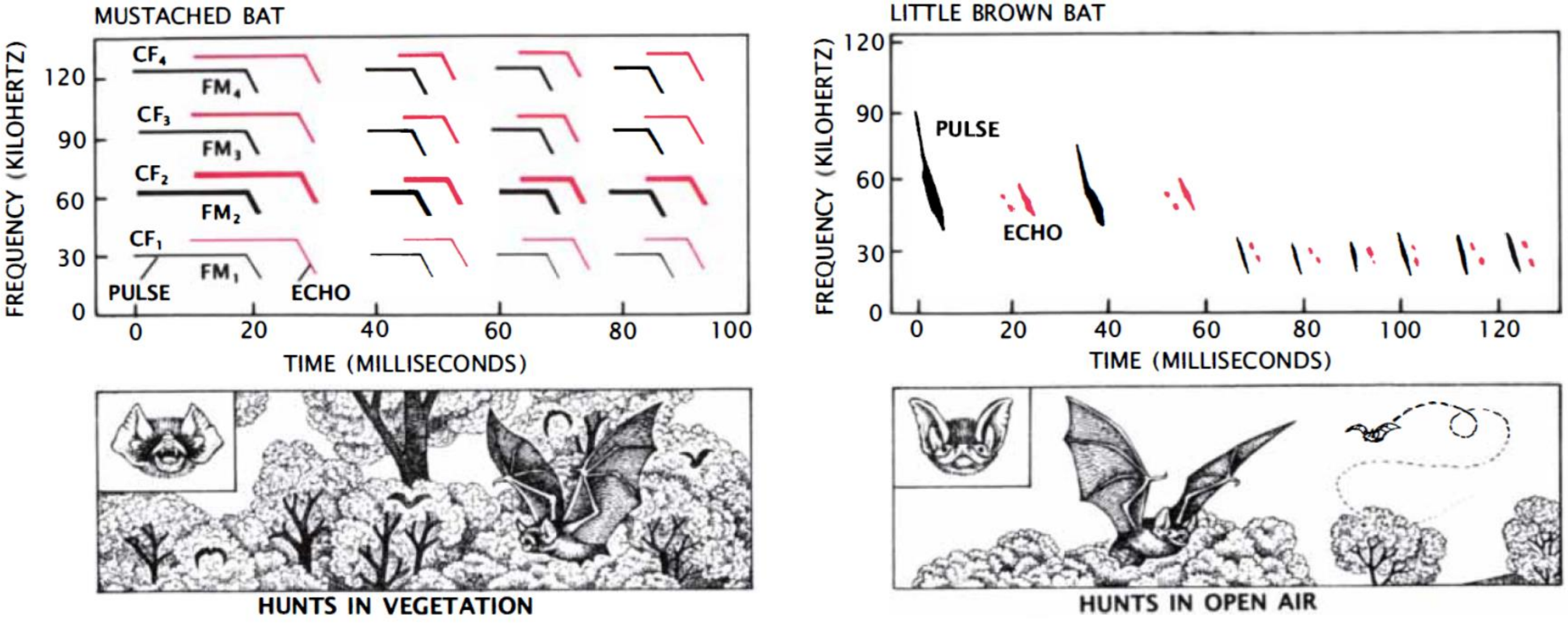
Detection and localization performance are traded off against one another

The **most sophisticated type of echolocation calls** is used by **horseshoe bats in the Old World**, and was evolved independently by **Parnell's mustached bat *Pteronotus parnellii*** in the New World

These bats emit signals with a long constant frequency component that allows efficient detection, and also allows the bats to classify targets; for example, they can distinguish a mosquito beating its wings rapidly from a beetle with slower wing beats

The bats also achieve excellent localization performance by using broadband sweeps at the end of the calls

Echological Signals are Niche Based



BIOSONAR PULSE of the mustached bat consists of a long, constant-frequency (CF) component followed by a short, frequency-modulated (FM) component. Each pulse contains four harmonics (indicated by subscripts). When closing in on a target, the bat emits shorter pulses at a higher rate, while keeping the same tones. The little brown bat emits only FM chirps. When nearing a target, it emits shorter, lower chirps at a faster rate. Each species emits pulses suited to its behavior.

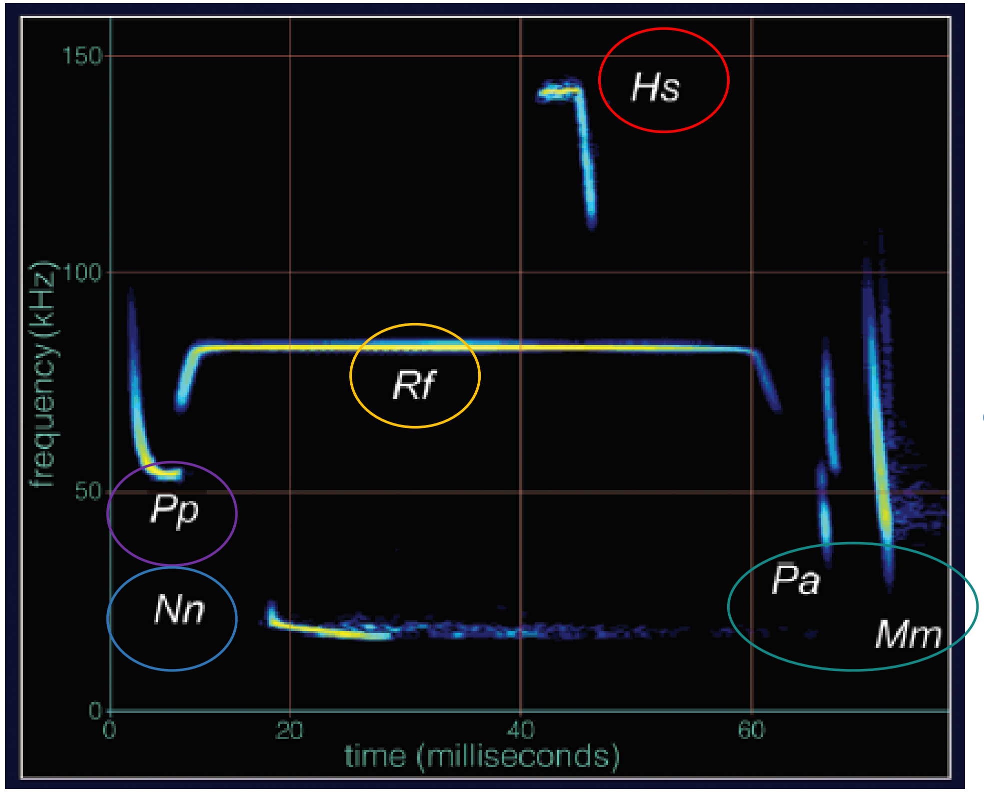


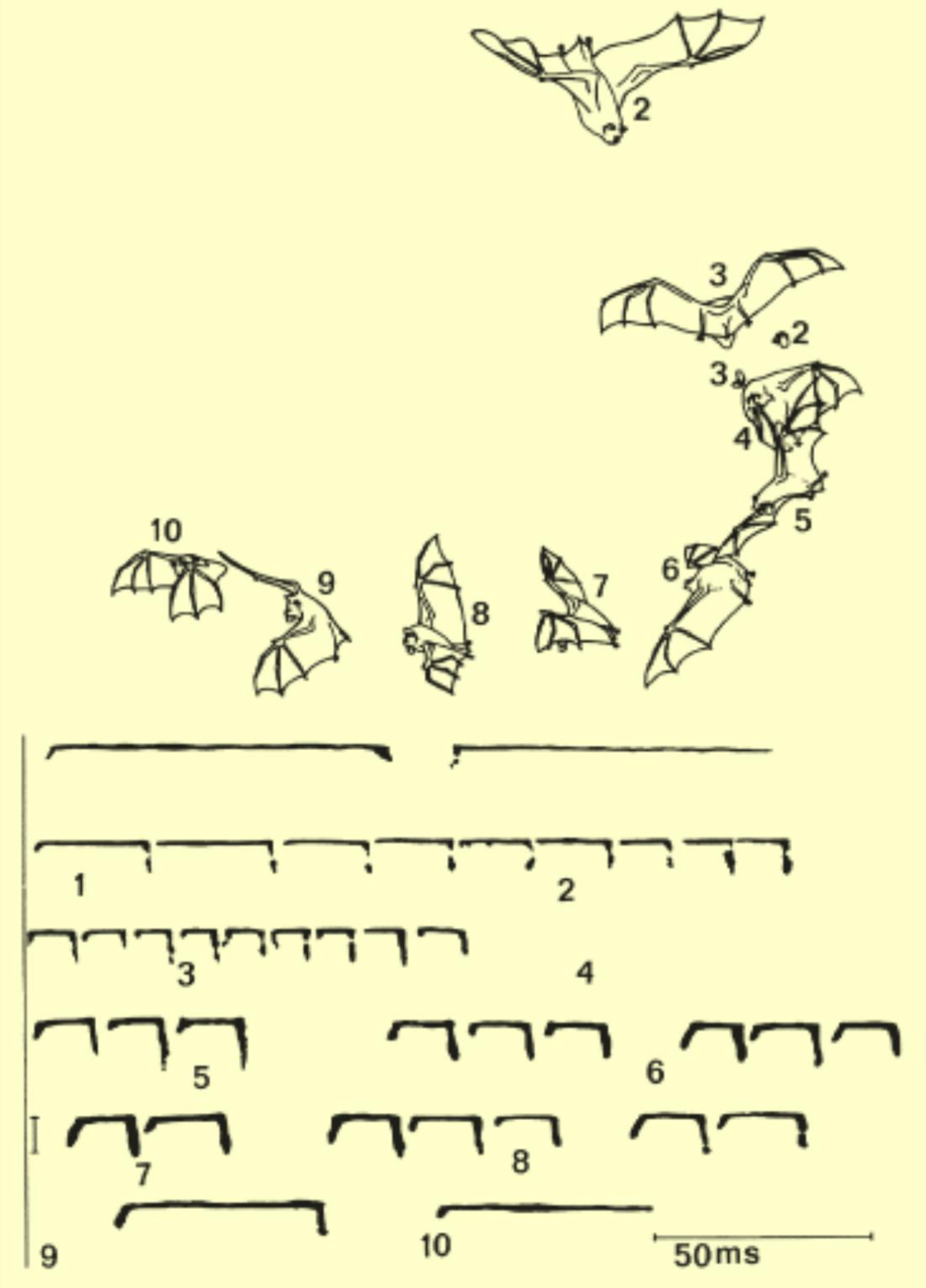
Figure 2. Echolocation calls from a selection of bat species.

A spectrogram plotting frequency against time, with signal amplitude coded in colour (higher amplitudes are yellow or red, lower amplitudes more blue). The noctule *Nyctalus noctula* (*Nn*) produces calls that are relatively low in frequency, long in duration, and narrowband. These calls are well suited for the detection of distant targets, and the noctule hunts in open habitats. The brown long-eared bat *Plecotus auritus* (*Pa*) and the whiskered bat *Myotis mystacinus* (*Mm*) emit brief broadband signals adapted to localizing targets in cluttered habitats such as woodland where these bats hunt. The soprano pipistrelle *Pipistrellus pygmaeus* (*Pp*) uses calls starting with a broadband sweep and terminating in a narrowband tail: it hunts for insects along treelines. The greater horseshoe bat *Rhinolophus ferrumequinum* (*Rf*) produces long constant frequency calls that allow powerful potential for detecting and classifying insect prey in clutter. The bat adds broadband sweeps at the start and end of the calls, and the terminal sweep functions in localization. The greater horseshoe bat uses Doppler shift compensation, and separates pulse and echo in frequency when flying. Schneider's leaf-nosed bat *Hipposideros speoris* (*Hs*) uses a shorter version of the horseshoe bat-type signal, and compensates for Doppler shifts partially when flying. Time-expanded versions of these calls can be heard at www.biosonar.bris.ac.uk

ADVANCED TOPIC

Biosonar and Neural Computation in
Mustached Bat

Pteronotus parnellii



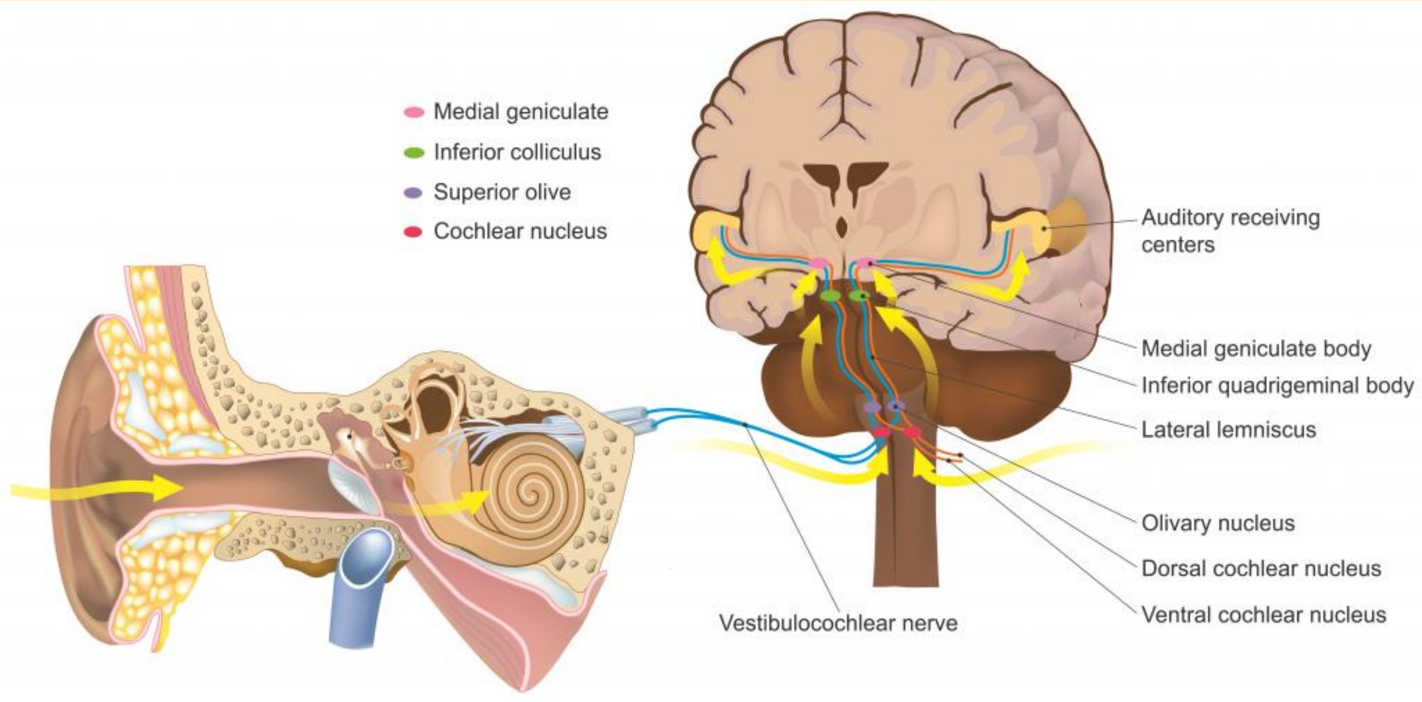
A *Pteronotus* in action…

Few Fundamentals About *Pteronotus*…

- ✓ A mustached bat at rest emits a **fundamental tone of around 30.5 kilohertz**, along with **three higher harmonics**
- ✓ The "**resting**" frequency of the second harmonic (CF2) is around **61 kilohertz**
- ✓ If the bat detects a Doppler-shifted echo at 63 kilohertz from a stationary object, it reduces the frequency of emitted pulses by about 1.8 kilohertz, so that subsequent echoes are stabilized at a "**reference**" frequency of around **61.2 kilohertz**

1. *These bats turn out to be **specialized to analyze tiny differences** in frequencies near the **reference frequency***
2. *Hence, **Doppler-shift compensation brings the echo CF2 into the range** at which the bat can most **easily detect ripples from beating insect wings***

Specialization Begins in the Bat's Ear…



Neurobiology of hearing in mammals (hence Pteronotus!)

The neural signal produced at the cochlea must contain all the information vital to the bat, the physical properties of an acoustic signal-**amplitude, time and frequency**

Acoustic Information Decrypting in *Pteronotus*…

- ✓ **Amplitude** is expressed by the rate at which the auditory nerve fibers discharge impulses: the greater the amplitude, the higher the discharge rate

- ✓ The **duration** of signals and the intervals between them are mimicked by the pattern of the nerve impulses

- ✓ The **frequency** of the signal is expressed by location on the basilar membrane: high frequencies vibrate the portion nearest the eardrum, whereas lower ones stimulate portions farther in. A certain portion of the mustached

Sensory adaptation

- ✓ Bat's basilar membrane is unusually thick

- ✓ This thickness is related to extreme sensitivity to frequencies of between **61.0 and 61.5 kilohertz** (the CF2 of the Doppler shift-compensated echoes) as well as insensitivity to frequencies of around 59.5 kilohertz (the CF2 of the Doppler shift-compensating pulses)

- ✓ In other words, the **membrane is strongly stimulated by the echoes but poorly stimulated by the animal's own vocalizations**

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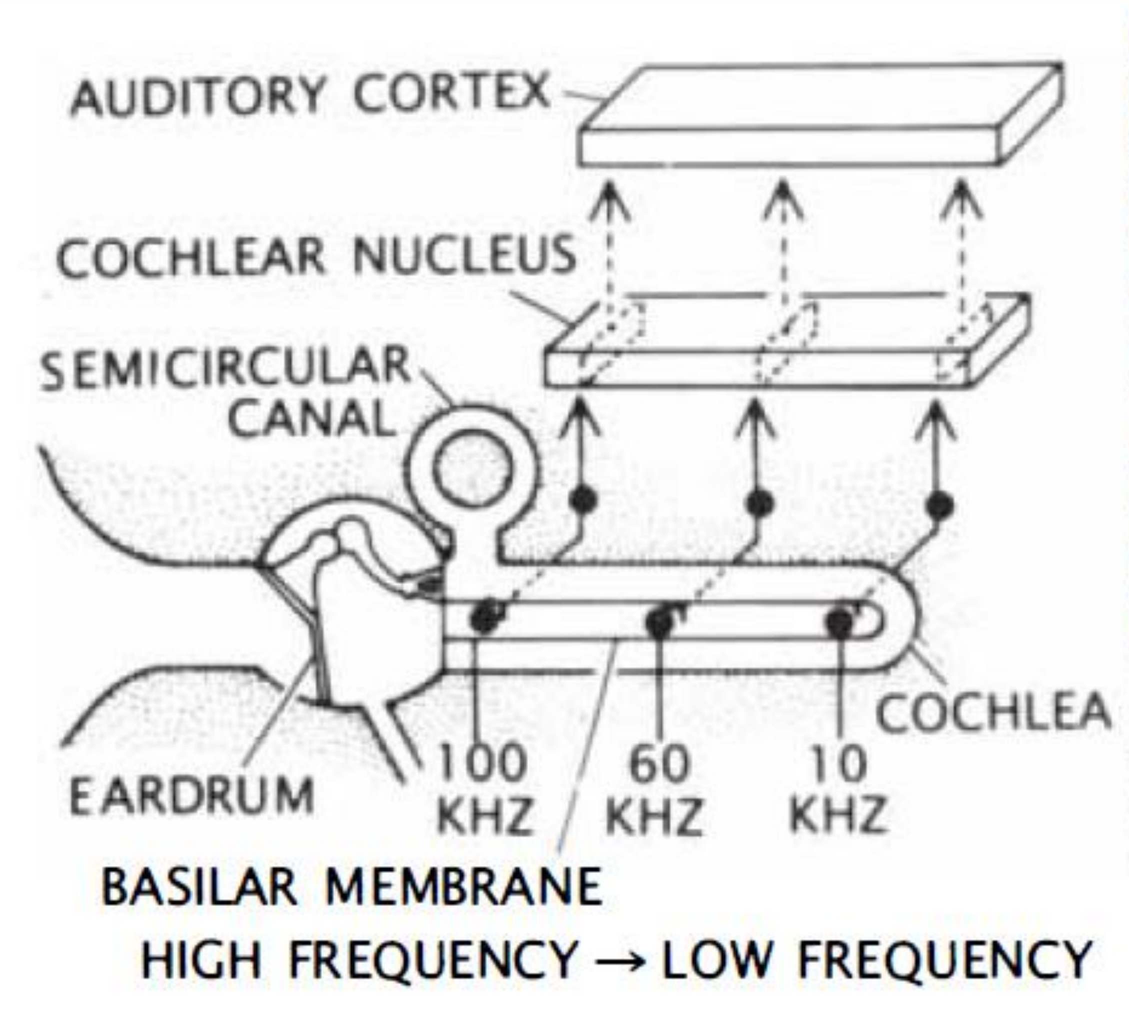

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Neuronal Adaptations of *Pteronotus*…

- ✓ The frequency selectivity of the **spiral ganglion cells** is extremely high within the key range of **61.0 to 61.5 kilohertz**.
- ✓ **They are tuned to single frequencies**. That is, each neuron has a "best" frequency (the frequency that evokes the largest response), **which differs slightly from that of its neighbors**.
- ✓ Indeed, these neurons are so sharply tuned to their best frequencies that they can detect **shifts as small as 0.01 percent**.
- ✓ Flying insects can easily evoke frequency shifts an order of magnitude greater
- ✓ The auditory periphery is also highly tuned to analyze frequency shifts near CF1 (30-kilohertz) and CF3 (92-kilohertz) signals.

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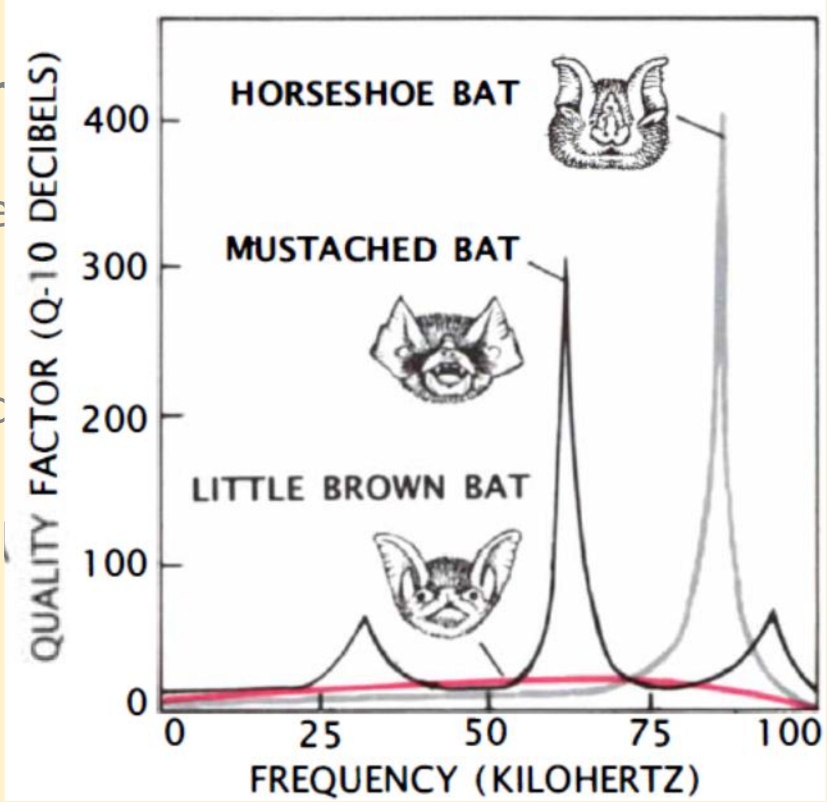


In the mustached bat the great sensitivity and sharp tuning of the auditory periphery to the CF2 frequency are combined with Doppler-shift compensation to proffer three advantages

1. First, the auditory periphery is exquisitely sensitive to the CF 2 echo (near 61 kilohertz) but is insensitive to the bat's emitted CF2 pulse (near 59 kilohertz) during Doppler-shift compensation; hence, masking of the echo by the emitted pulse is minimal

2. Second, the sharply tuned neurons are well able to detect the signal even if it is embedded in background noise

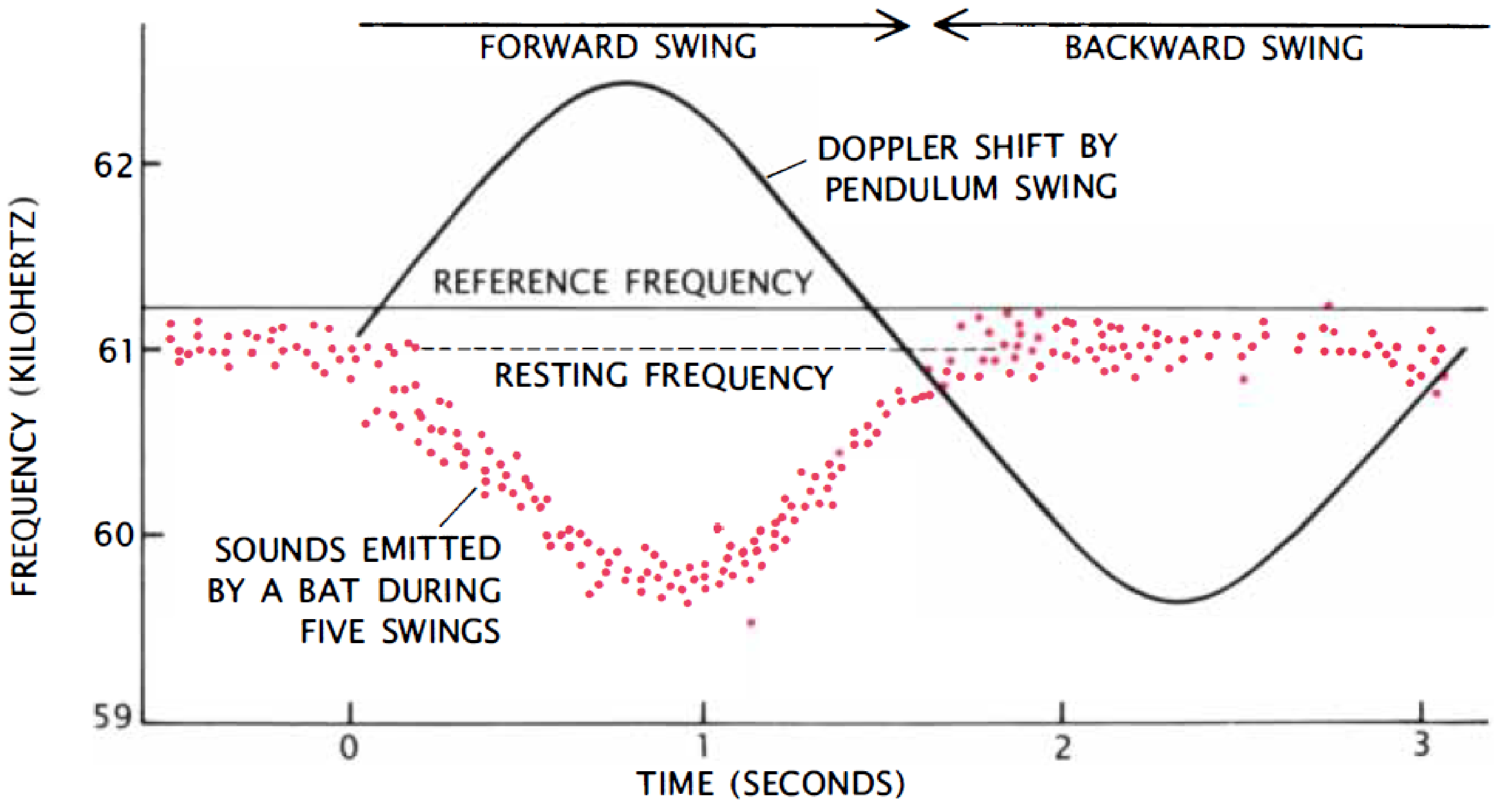
3. Third, the array of sharply tuned neurons has a high likelihood of picking up the echo from the beating wings of a flying insect as the echo sweeps up and down in frequency.

In the mustach… ry to the CF2 frequency are c…

1. First, th… s insensitive to the bat's … isking of the echo by the …

2. Second, … background noise

3. Third, th… the beating wings of a fl…



DOPPLER-SHIFT COMPENSATION is demonstrated by placing a mustached bat on a pendulum. During the forward swing the animal lowers the frequency of its emitted pulse (*red*) such that the echo stays at a "reference" frequency. The animal does not compensate for Doppler shift during the backward swing. O'Dell W. Henson, Jr., of the University of North Carolina at Chapel Hill first performed the experiment.

Extraction of Information from Auditory Signal Coded Nerve Signals
(as the Velocity or Distance of Prey)

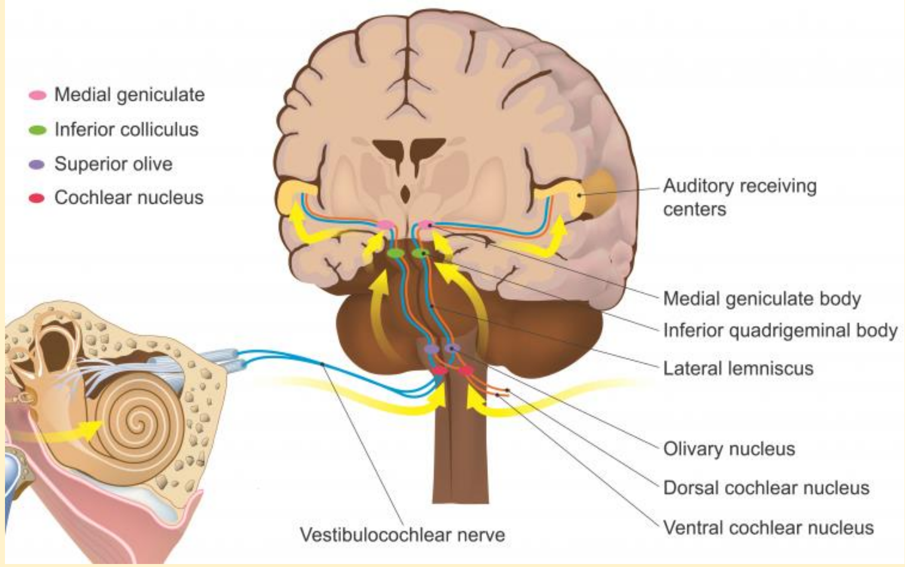
- Auditory signal coded nerve signals must be further analyzed occurs in the central auditory system

- From the cochlea, signals are processed sequentially, beginning at the **cochlear nucleus** and proceeding to the **lateral lemniscus**, **inferior colliculus**, **medial geniculate body** and finally to the **auditory cortex**

- One region of the auditory cortex contains neurons that **respond only to certain frequencies** and **amplitudes of echoes**

- A second region responds only to **frequency differences** between **pulses and echoes**

- A third region is sensitive to the **time interval** between **pulses and echoes**



- The **largest of the specialized regions** in the mustached bat's **auditory cortex** is the one **that processes Doppler-shifted CF 2 signals**

- This region, called the **DSCF area**, represents only a narrow sliver of the frequency range, **between 60.6 and 62.3 kilohertz** (when the bat's resting frequency is 61.00 kilohertz), yet it occupies **30 percent** of the **primary auditory cortex**

- The **exact frequencies overrepresented differ among individual bats according to their resting frequencies**

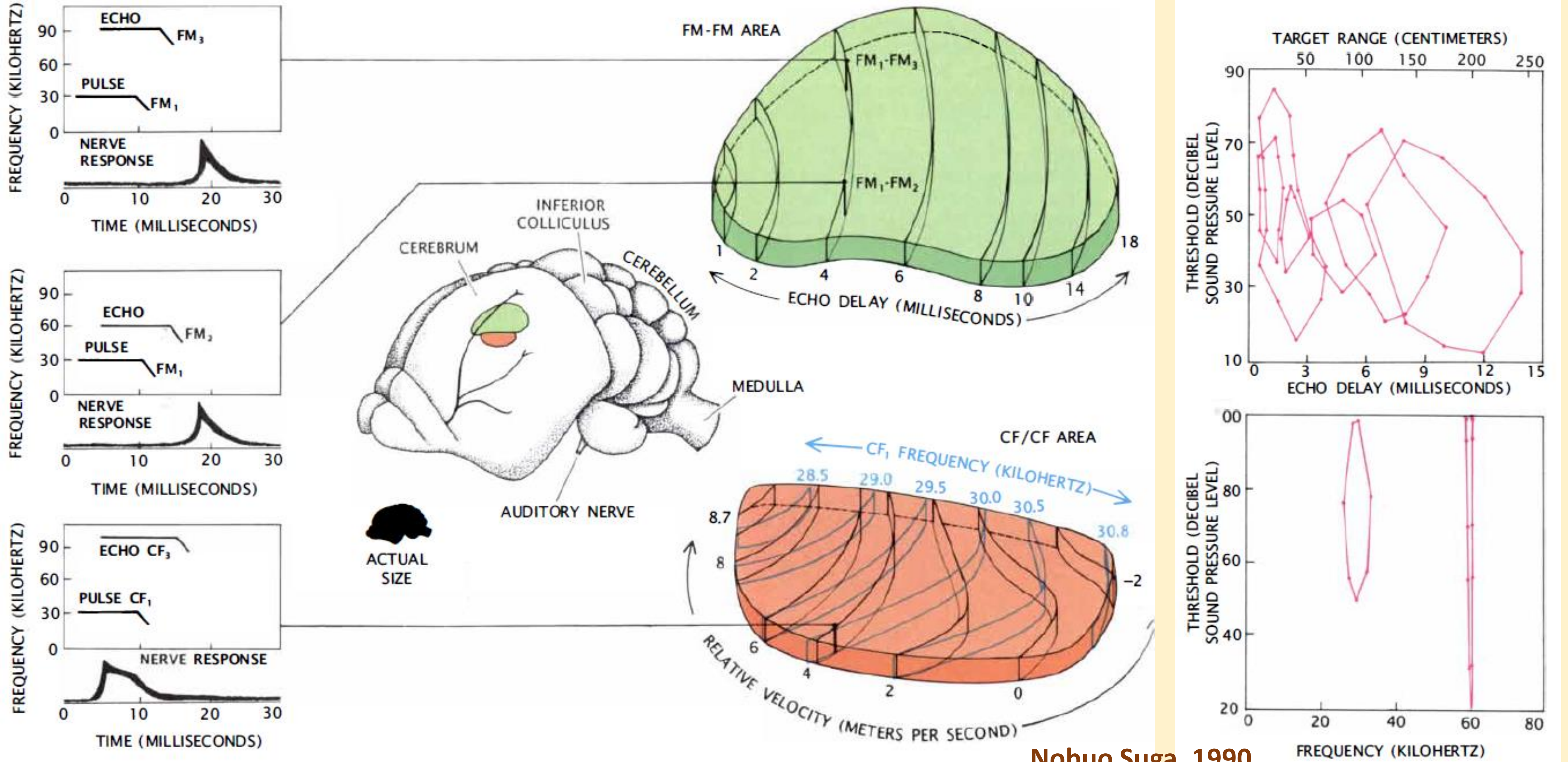
- In other words, **each bat's auditory system is personalized**

Similar overrepresentation is found in the brain wherever the signal being processed is critical to an animal's Behavior (e.g. in cats and monkeys the **visual cortex over represents the fovea**, the area of the retina where visual acuity is highest; the primate **somatosensory cortex over represents the tactile sense of the fingers**)

- Neurons in the DSCF area are sharply tuned to particular frequencies (even more so than neurons in the auditory periphery)
- They are also tuned to the amplitude of a signal- hence, each DSCF neuron has a particular frequency and amplitude to which it responds best
- This sharpening of the response is apparently the result of lateral inhibition, a ubiquitous mechanism in sensory systems by which inhibitory signals from adjacent neurons enhance the selectivity of a neuron to a particular stimulus

- The auditory cortex of the mustached bat is about 900 microns, or some 40 to 50 neurons, thick
- All of the neurons perpendicular to the surface are tuned to an identical frequency and amplitude
- Hence, the DSCF area has a **"columnar organization“** ***(****Such columnar organization was*

first discovered in 1959 in the somatosensory cortex of monkeys by Vernon B. Mountcastle of Johns Hopkins University)



Nobuo Suga, 1990

COMPUTATIONAL MAPS in the auditory cortex of mustached bats represent echo delay (or distance) and Doppler shift (or relative velocity). In the FM-FM area (*green*), neurons along each black line respond to a specific echo delay. The top graph (*right*) shows the delay-tuning curves of six FM-FM neurons; each neuron responds to a specific echo delay and amplitude. In the CF/CF area (*tan*), neurons along the blue lines respond to a specific CF_1 combined with varying CF_2. Neurons along the black lines respond to Doppler shifts corresponding to a specific relative target velocity. The bottom graph (*right*) shows the frequency-tuning curves of a CF_1/CF_2 neuron. This neuron is most responsive when stimulated by a CF_1 of 29.38 kilohertz at 63 decibels combined with a CF_2 of 60.52 kilohertz at 45 decibels.

Why mustached bat also produces an FM sound at the end of the CF component?

❖ The FM Signal provides the primary cue for measuring the time interval between a pulse and echo- **the distance to a target**

❖ A one-millisecond echo delay corresponds to a target distance of **17.3 centimeters**.

❖ Simmons found that several species of bats can detect a difference in distance of between **12 and 17 millimeters**,

(discriminate a difference in echo delay of between 69 and 98 millionths of a second!)

❖ There neurons respond poorly if a pulse, echo, CF tone or FM sound is presented individually

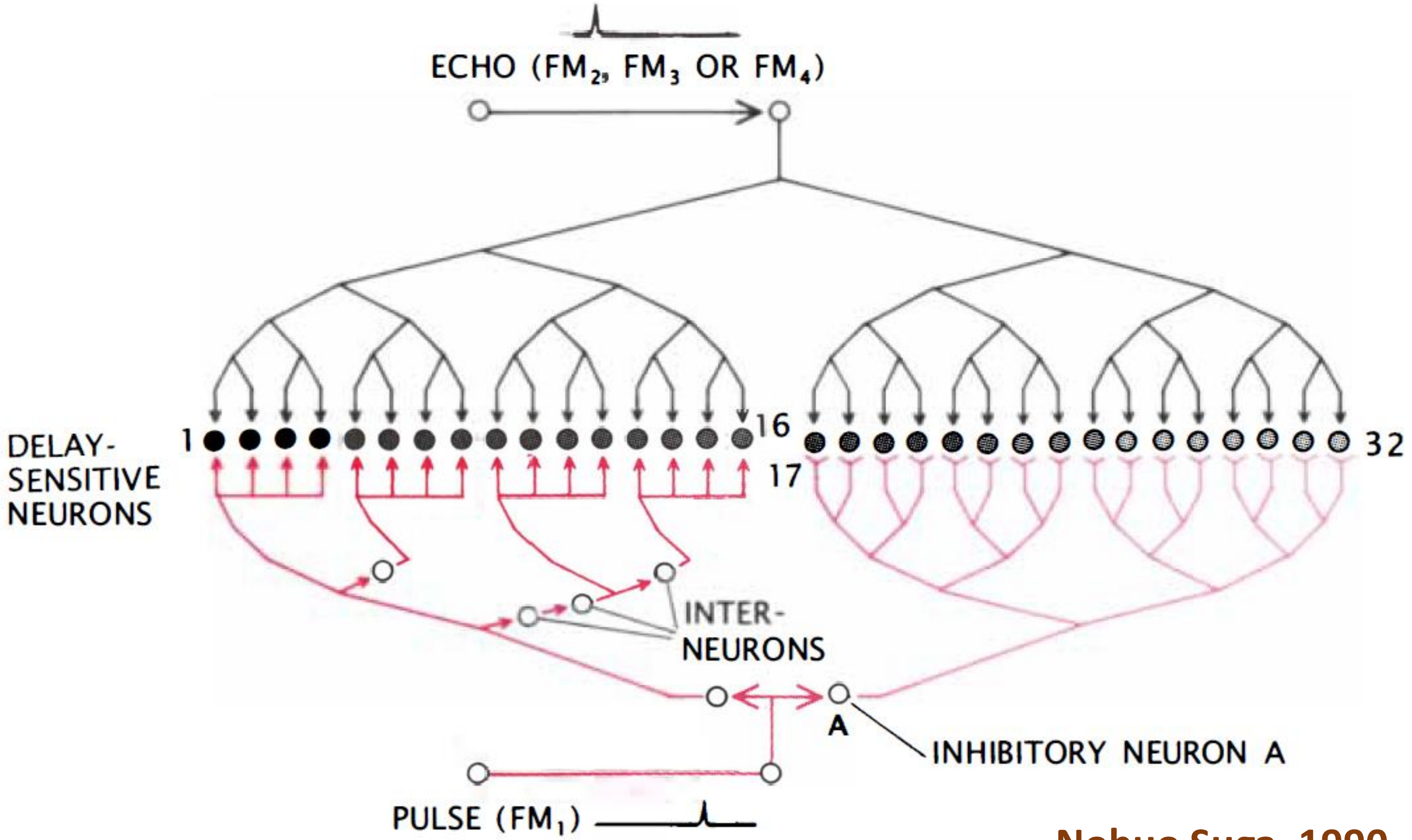
❖ They respond strongly if a pulse is followed by an echo having a particular delay time

❖ FM-FM neuron can be **28,000** times more sensitive to a **pulse-echo pair** than it is to either **signal alone**

- Each column of neurons responds to a particular echo delay, and the columns are arranged so that the preferred delay increases along one axis

- This axis represents delays **from .4 to 18 milliseconds**, or target ranges of from **7 to 310 centimeters**

- The **resolving power** of this neuron array is presumably such that an animal can detect a difference in target distance of about **10 millimeters**

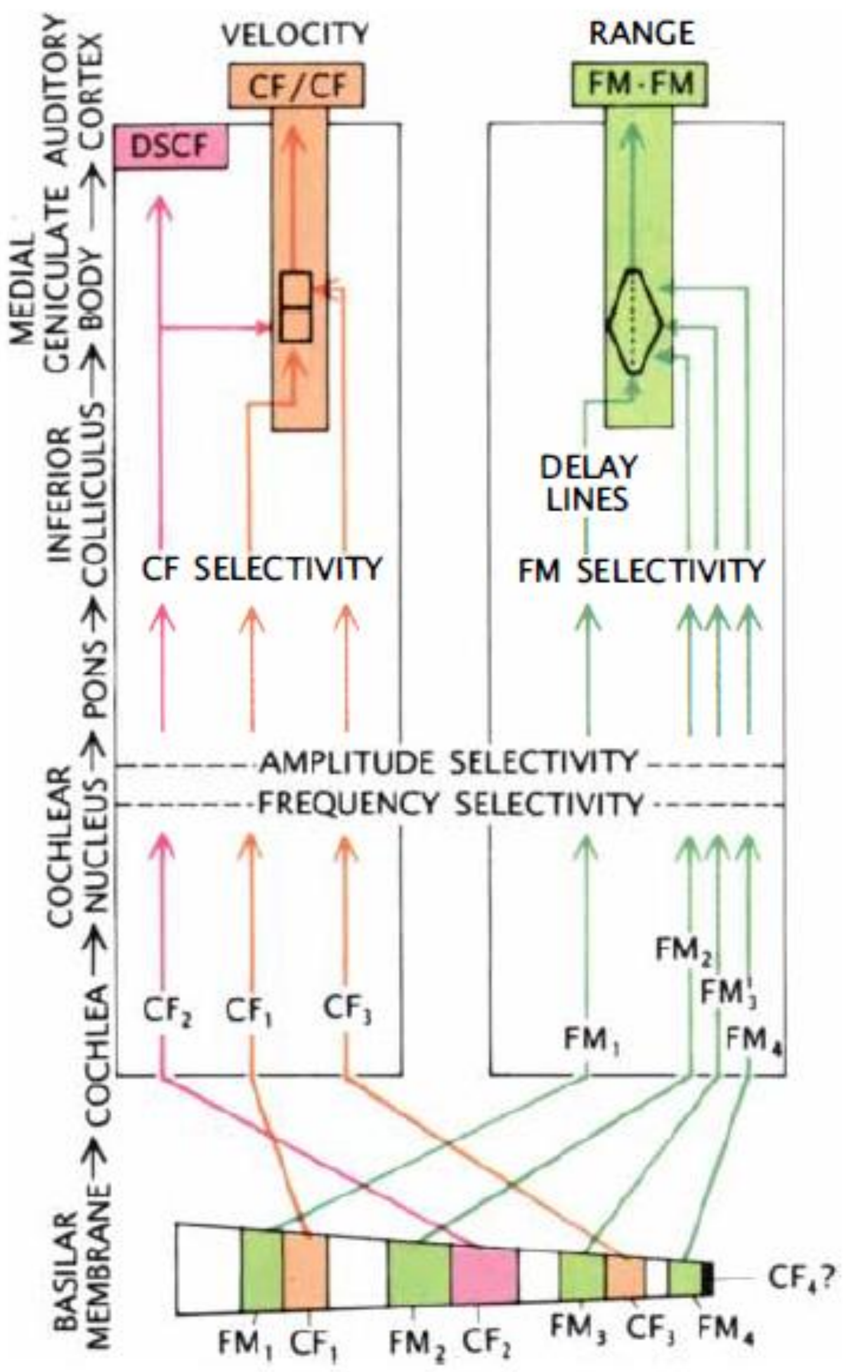


Nobuo Suga, 1990

NEURAL NETWORK creates neurons that respond to specific echo delays. The network delays the response to a pulse FM_1, so that it arrives at a neuron at the same time as the response to a higher harmonic of the echo FM, triggering a response from that neuron. The pulse response is slowed by a combination of axonal delays (because it takes time for a nerve impulse to travel along an axon) and synaptic delays. Even longer delays can be created by inhibition. Neuron *A* inhibits neurons 17 through 32; after a time, the inhibition wears off, beginning with neuron 17, and the neurons become briefly excited. (Paler colors indicate longer delays.) The response to the echo, on the other hand, spreads to all of the neurons simultaneously.

How do pathways in the auditory system give rise to neurons that are sensitive to pulse-echo delays?

- **Two groups of collicular neurons**, one group tuned to the pulse **FM1** and the other to **higher harmonics** in the echo FM
- They **converge on a single group of neurons** in the **medial geniculate** to create neurons sensitive to combinations of FM components
- This **combination sensitivity** is mediated by the receptor for **N-methyl-D-aspartate (NMDA)** to a large extent
- The receptor's biophysical properties cause the neuron's response to be **amplified when neural inputs coincide**
- Hence, the receptor performs the **logical AND operation** (as in "IF A AND B, THEN on)



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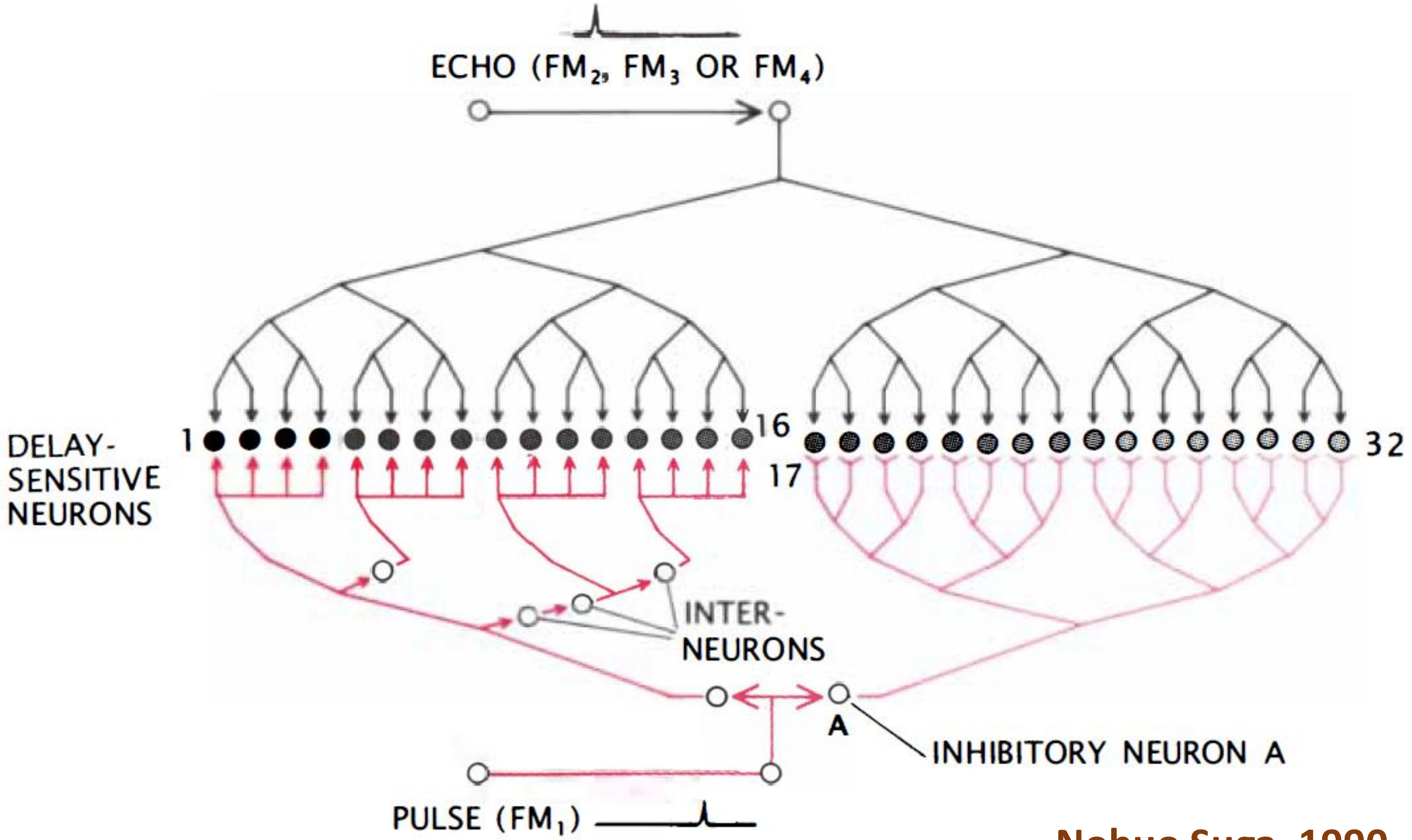

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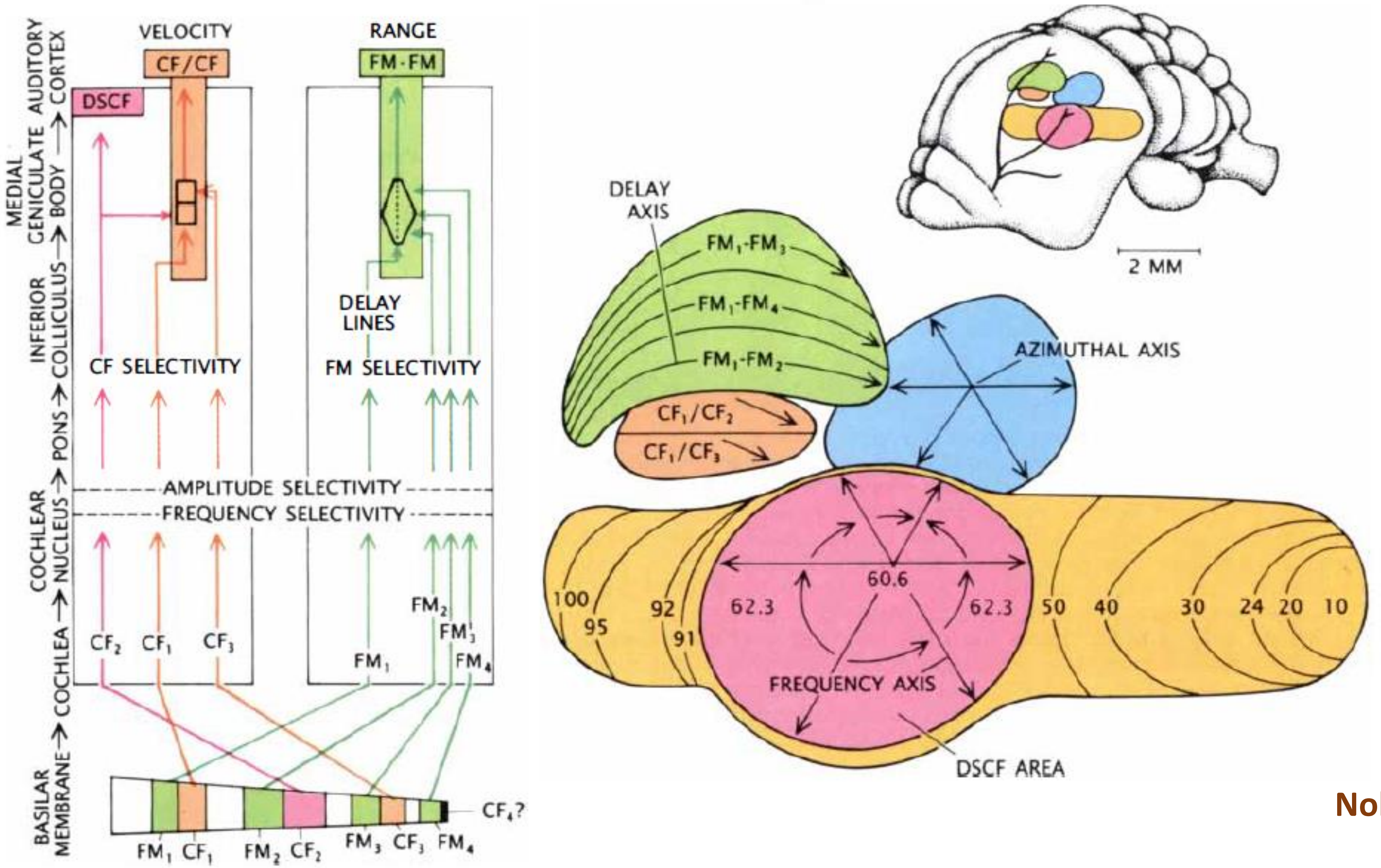

PARALLEL PATHWAYS process different streams of biosonar information (*left*). Various CF and FM harmonics excite different parts of the basilar membrane, and signals are sent to the auditory cortex via several subcortical nuclei. Higher up in the auditory pathway, the neurons become more narrowly selective for frequency and amplitude. In the primary auditory cortex, frequencies from 10 to 100 kilohertz are tonotopically organized (*yellow*); the large area (*pink*) at the center represents 60.6 to 62.3 kilohertz. CF and FM signals are integrated in the medial geniculate body, giving rise to neurons that respond to specific combinations of CF or FM signals. These combination-sensitive neurons project axons to the CF/CF or FM-FM areas of the auditory cortex, creating maps that correspond to the relative target velocity (*tan*) or distance (*green*).

Nobuo Suga, 1990

Why is one harmonic not enough?

- The first harmonic is the weakest component of the emitted pulse, the pulse is so feeble that other bats can barely hear it
- About all a flying bat hears from its roostmates are the higher harmonics
- Combinations of the higher harmonics, however, cannot excite FM-FM or CF /CF neurons
- When a bat emits a pulse, however, it can hear its own first harmonic, which is conducted from its vocal cords to its ear through the surrounding tissue
- This sound, in combination with higher harmonics that are delayed or Doppler-shifted, can then stimulate FM-FM and CF / CF neurons
- In this way, the neural processing of biosonar signals is shielded from the cacophony of echoes generated by the colony

- By suppressing the first harmonic, which is between 24 and 31 kilohertz, a mustached bat can approach moths closely without alerting them

Echolocation jamming

- Echolocation (or sonar) systems of animals, like human radar systems, are susceptible to interference known as echolocation jamming or sonar jamming
- Jamming occurs when non-target sounds interfere with target echoes
- Jamming can be purposeful or inadvertent, and can be caused by the echolocation system itself, other echolocating animals, prey, or humans

Self jamming

- Bats produce some of the loudest sounds in nature and then they immediately listen for echoes that are hundreds of times fainter than the sounds they emit
- **To avoid deafening themselves**, whenever a bat makes an echolocation emission, a small muscle in the bat's middle ear (the stapedius muscle) clamps down on small bones called ossicles, which normally amplify sounds between the ear drum and the cochlea
- **Jamming can occur if an animal is still producing a sound when an echo returns**
- Bats avoid this type of jamming by producing short sounds of 3-50 ms when searching for prey or navigating
- Bats produce progressively shorter sounds, down to 0.5 ms, to avoid self-jamming when echolocating targets that they are approaching
- Another form of jamming occurs when an echolocating animal produces many sounds in succession and **assigns an echo to the wrong emission**
- To avoid this type of jamming, bats typically wait enough time for echoes to return from all possible targets before making the next sound
- Another way bats overcome this problem is by producing successive sounds with unique time-frequency structures.
- This allows bats to process echoes from multiple emissions at the same time, and to correctly assign an echo to its emission using its time frequency signature.

Reference

Biosonar and Neural Computation in Bats

Bats extract remarkably detailed information about their surroundings from biosonar signals. Neurons in their auditory systems are highly specialized for performing this task

by Nobuo Suga

It used to be a common misconception that bats' use of sound pulses to navigate and locate prey is a crude system, the acoustic equivalent of feeling one's way in the dark with a cane. But biosonar has since been shown to be anything but crude: an echolocating bat can pursue and capture a fleeing moth with a facility and success rate that would be the envy of any military aerospace engineer.

In addition to providing information about how far away a target is, bat sonar can relay some remarkable details. Doppler shifts—changes in the frequency of the echo relative to the original signal—convey information not only about the relative velocity of a flying insect but also about its wingbeat. The amplitude of the echo, combined with the delay, indicates the size of the target. The amplitudes of the component frequencies correspond to the size of various features of the target. Differences between the ears in intensity and arrival time of sound give the azimuth of the target, whereas the interference pattern of sound waves reflected within the structure of the outer ear gives the elevation.

The complex neural computations needed to extract this information occur within a brain the size of a large pearl. For the past 27 years my colleagues and I have been exploring the neural mechanisms that underlie the echolocating abilities of bats. The well-defined characteristics of a bat's auditory world make the animal ideal for elucidating the information processing that goes on in its auditory system. Similar mechanisms are undoubtedly shared by other animals.

There are some 800 species of Microchiropteran bats in the world today, all of which are presumed to echolocate. These species live in diverse habitats and vary greatly in behavior and physical characteristics. Their biosonar pulses also differ, even among species within the same genus. Nevertheless, these pulses can be classified into three types: constant frequency (CF), frequency modulated (FM) and combined CF-FM. CF pulses consist of a single frequency, or tone. FM pulses sweep downward and sound like chirps. Combined CF-FM pulses consist of a long, constant tone followed by a downward chirp, *iiiiiiu*. In many bats the tones are not pure but rather consist of a fundamental, or first, harmonic and several higher harmonics (multiples of the fundamental frequency).

Most bat species emit only one type of pulse. The little brown bat, *Myotis lucifuqus*, is an "FM" bat; it emits FM pulses lasting between .5 and three milliseconds and sweeping downward by about one octave. The mustached bat, *Pteronotus parnellii*, is a "CF-FM" bat; it emits long CF pulses lasting between five and 30 milliseconds followed by a short FM sweep lasting between two and four milliseconds. Several species change their pulses, depending on the situation. The fish-catching bat, *Noctilio leporinus*, for example, emits CF and CF-FM pulses while cruising in flight but emits FM pulses while hunting prey.

A long CF pulse is excellent for detecting targets larger than the wavelength of the signal, because the reflected sound energy is highly concentrated at a particular frequency. It is also ideal for measuring Doppler shifts. The CF pulse is not appropriate, however, for locating a target precisely or discerning its details. A larger number of frequencies is needed to obtain more information about target features. Bats broaden their frequency bandwidth by producing harmonics and by emitting FM bursts that sweep over a wide frequency range. FM pulses also contain more information about time and so are used to compute echo delays and thereby determine the distance to a target.

Certain bat species control the energy in each harmonic depending on the distance to a target. If the target is far away, they amplify the lower harmonics, which are less attenuated by the air. But if the target is nearby, they enhance the higher harmonics to obtain finer details of the target. When closing in on prey, Microchiropterans shorten the duration of pulses and increase the rate of pulse emission, up to 200 per second in FM bats and up to 100 per second in CF-FM bats. This adjustment occurs not only because bats need to characterize the prey in greater detail but also because when the distance between a bat and its prey is small, the angular position of the prey changes more rapidly, and so the bat needs to emit more signals to track the prey accurately.

The hunting strategies and behavior of a bat species are directly related to the characteristics of its biosonar. The

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MUSTACHED BAT sweeps in for a midflight drink from a pond. This species' biosonar has been studied extensively.

That's all Folks!