Cicadas (Order Homoptera)

• Medium to large insects with two pairs of membranous wings, prominent compound eyes, and three simple eyes (ocelli).
• Many produce loud sounds by vibrating membranes (tymbals) near base of abdomen
• Rythmical ticks, buzzes, whines, or musical sounds
• Congregational and courtship “songs”

Cicada sound production

Tymbal
• Most complex insect sound-producing mechanism known
• Circular membrane surrounded by heavy rings on cicada’s abdomen
• Contraction of tymbal muscle causes tymbal to spring back, producing loud click or pulse (120-480 per second); amplified by resonating cavity in the abdomen

Dog-day Cicada

Tibicen resh

Periodical Cicada

Kingdom: Animalia
Phylum: Arthropoda
Subphylum: Hexapoda
Class: Insecta
Order: Hemiptera
Family: Cicadidae
Genus: Magicicada
Species: septendecim
Cicada sound production

**Tymbal**
- Loudest known insect sound: up to 100 decibels at close range
- Most likely females detect and prefer males with the loudest “songs”

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Cicada sound production

- **Phonotaxis** – orientation toward sound
- Song choruses
- Synchrony or alternation
- “Domino effect” (first song triggers others)
- “Last word effect” (competition for last song)

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Sound production in animals

1. Beating a substrate
2. Rubbing of appendages
3. Respiratory structures

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Sound power and body size

- Total sound power depends on the size of the animal (animals with small body mass tend to produce sounds with low acoustic power).
- Some exceptions to this rule: cicadas
Modes of sound production

- **Monopole** - sound alternately contracts and expands in concentric circles around source.
  - alternating compression and rarefaction used by some fish (pulsating air sac)
- **Dipole** - sound source that vibrates back and forth
  - E.g. **stridulation** in crickets
  - Efficiency of sound transmission?

Sound waves

- Sound waves produce pressure fluctuations in the air that are small relative to atmospheric pressure.

![Waveform](http://resource.ierv.soton.ac.uk/pag/tutorial/tutorial_files/Web-bio-in-nature.htm)

Sound waves

- Sound waves travel at a speed of around 340 meters per second at room temperature.
- Human hearing extends from about 20 to 20,000 cycles/second (20 Hz to 20 kHz).
- The corresponding wavelengths range from about 17 mm (at 20 kHz) to 17 m (at 20 Hz).

Waveform

- The **waveform** of a sound is a representation of sound pressure (amplitude or displacement) versus time.
Spectrum

- The amplitude spectrum of a sound is a representation of amplitude by frequency.

Properties of sound

- Complex sounds
  - Most sounds in nature
  - e.g., human voices, bird and insect songs, frog calls
  - Complex sound types
    - Periodic (tonal, repeating pattern in the waveform)
    - Aperiodic (noise, with no repeating pattern)

Properties of sound

- Sine wave
- Complex wave (periodic)

Primate vocal tract

Specialized vocal resonators

- Howler Monkey (*Alouatta*)
- Gibbon (*Hylobates*)

Human vocal tract
Respiratory structures

**Larynx**
- Main source of sound production by mammals
- Controls airflow during breathing and sound production

Vocal fold oscillation

- One-mass model
  - Air flow through the glottis during the closing phase travels at the same speed because of inertia, producing lowered air pressure above the glottis.


Source-Filter Theory

Speech production

- **Source**: during normal (voiced) speech the vocal folds vibrate at a frequency that depends on their length and mass as well as the amount of tension in the muscles that control them.
- **Filter**: the vocal tract is a complex resonant filter system that amplifies certain frequencies and attenuates others.

Speech terminology...

- **Fundamental frequency** (Fo): lowest frequency component in voiced speech sounds, linked to vocal fold vibration.
- **Formants**: resonances of the vocal tract.

Audio demo: the source signal

- Source signal for an adult male voice
- Source signal for an adult female voice
- Source signal for a 10-year child
Helium speech

• Inhaling helium during speech changes the frequencies of the vocal tract resonances but keeps the pitch the same. Why? Because sound travels faster in a helium mixture than in air. The vocal tract resonances are shifted up, but the vocal folds vibrate at the same rate and the voice pitch is relatively unaffected.

Size variation in speech

Fundamental Frequency

Adults’ voices ← Children’s voices

Formant Frequencies

Anuran vocal communication

• Similar to mammals, anurans (frogs and toads) produce sounds by forcing air through a narrow opening (glottis).
• They also have a second pair of membranes, upstream from the glottis, that vibrate at a higher frequency.

Examples: vocal sounds

Bullfrog (Rana catesbeiana)

Sound spectrogram
Anuran sound production

Examples: vocal sounds

Bullfrog (*Rana catesbeiana*)

Anuran vocal communication

• Each species of frog produces distinctive (species-specific) calls that play an important role in mate choice.
• Many species form groups called *leks*, where males call simultaneously to attract females to breeding sites.

Anuran vocal communication

• Males compete with each other by calling and sometimes by physical aggression.
• Sexually receptive females locate and choose a single male as mate based on properties of the call.

Anuran vocal communication

• Some frogs have an inflatable throat sac that selectively amplifies certain frequencies in the source signal and also serves as a visual signal.

Syrinx

• Found in birds
• Located at the base of the trachea where the two bronchial tubes converge
• Contains two separate oscillating membranes that allow generation of two different sound sources (modulated frequencies) simultaneously
Syrinx

- Sound production is controlled separately for each side of the syrinx by several muscles that are innervated by motor neurons in the hypoglossal nerve coming from the same side of the brain. The right side of the syrinx seems to produce a higher range of frequencies than the left side.

- The Cardinal video shows how birds can switch rapidly and seamlessly from one side of the syrinx to the other. Upward sweeps start on the left and switch to the right; downward sweeps reverse this pattern.
- Some birds can produce harmonically unrelated sounds simultaneously from the two sides of the syrinx (catbirds, thrashers).

Bird songs

- Bird songs often include frequency-modulated notes that sweep through a wide range of frequencies.
- In cardinals, frequencies below 3500 Hz are generated using the left side of the syrinx; higher frequencies use the right side.

Zebra Finch song

- Sound spectrogram

Song development in birds

- Chaffinch (Fringilla coelebs)
Examples: vocal sounds
- Woodhouse’s Toad (*Bufo woodhouseii*)
- Brazilian Free-tailed Bats (*Tadarida braziliensis*)
- Javelina
- Coyote

Examples: bird vocal sounds
- Ferruginous Pygmy Owl
- Pileated Woodpecker
- Rufous Mourner
- Three-wattled Bellbird
- Winter Wren
- Song Sparrow

Non-vocal sounds
- Rattlesnake (*Crotalus*)
- Fruit fly (*Drosophila melanogaster*) “wing song”
- Mosquito (*Aedes*) wing sounds

Whale songs
Large body size allows whales and elephants to produce high intensity, low frequency sounds. Both properties increase the range (distance) for communicating with conspecifics.

Functions of sound communication
1. To bring animals together
2. Identification (species, group, individuals)
3. Synchronization of physiological states
4. Monitoring the environment
5. Maintenance of special relationships

Ecological constraints
1. energy costs
2. overcoming environmental obstacles
3. locatability of the source
4. rapid fading
5. range of physical complexity
Communication by sound

1. **Sound production**
   - Production and modulation of acoustical energy
   - Coupling of vibrations to the medium

2. **Transmission through medium**
   - Impedance matching
   - Sources of distortion

3. **Sound reception**
   - Coupling of vibrations to sound receptors
   - Mechanical-to-neural transduction

---

Acoustic properties of the medium

<table>
<thead>
<tr>
<th>Medium</th>
<th>Speed of sound (cm/sec)</th>
<th>Density of medium (g/cm³)</th>
<th>Acoustic Impedance (rayls)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air</td>
<td>0.3 x 10⁸</td>
<td>1 x 10⁻³</td>
<td>0.0003 x 10⁵</td>
</tr>
<tr>
<td>Water</td>
<td>1.5 x 10⁸</td>
<td>1</td>
<td>1.5 x 10⁵</td>
</tr>
<tr>
<td>Rock</td>
<td>2.5 x 10⁸</td>
<td>2.3</td>
<td>4.5 x 10⁵</td>
</tr>
</tbody>
</table>


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Ecological constraints on acoustical communication systems

1. energy costs
2. overcoming environmental obstacles
3. locatability of the source
4. rapid fading
5. range of physical complexity

---

Production and coupling of vibrations

- **Stridulation** – sharp blade (*plectrum*) is rubbed against a row of small teeth (*file*)
- **Dipole** – sound source that vibrates back and forth
  - Acoustical short-circuit: cancellation of waves makes it difficult to produce loud sounds
  - Frequency multiplier (multiple teeth)
  - Sound baffle (tree crickets)
  - Use short-range signals (most insects)

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Exploiting resonance

**Bornean tree-hole frogs** (*Metaphrynella sundana*) seek out tree trunks partly filled with water. They tune their vocalizations to the resonant frequencies of the cavity.


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Factors affecting acoustic signal transmission

- **Absorption** - loss of energy due to contact with medium, which may convert signal's energy into another form (e.g. heat)
Factors affecting acoustic signal transmission

- **Attenuation** - decline in signal intensity due to absorption, scattering, distance from source; particularly high frequencies

Factors affecting acoustic signal transmission

- **Diffraction** - redirection of the signal because of contact with an absorbing or reflecting medium

Factors affecting acoustic signal transmission

- **Geometric spreading** - signals radiate in several directions from the source; not perfectly directional; result = energy loss

Factors affecting acoustic signal transmission

- **Interference** - signals reflected from the substrate later interact with the originally transmitted signal

Factors affecting acoustic signal transmission

- **Reflection** - signal bounces back in the direction of the emitting structure as a result of striking a reflective medium

Factors affecting acoustic signal transmission

- **Refraction** - signal direction/speed is altered/perturbed by medium or climatic changes like temperature gradients
Factors affecting acoustic signal transmission

- **Reverberation** - multiple scattering events produce a time delay in the arrival of the signal, perceived as an echo; blurring

Obstacles and sound transmission

- Vegetation (tree trunks, leaves) and other obstacles can obstruct sound transmission.
- **Echoes** are produced when sounds are reflected from an obstacle and follow an indirect path to the ear of the receiver.

Examples: vocal sounds

- Woodhouse’s Toad (*Bufo woodhouseii*)
- Brazilian Free-tailed Bats (*Tadarida brasiliensis*)
- Javelina
- Coyote

Sound examples

- **Gray wolf** (*Canis lupus*)
- **Musical Wren** (*Cyphorhinus aradus*)
Examples: bird vocal sounds
- Ferruginous Pygmy Owl
- Pileated Woodpecker
- Rufous Mourner
- Three-wattled Bellbird
- Winter Wren
- Song Sparrow

Non-vocal sounds
- Rattlesnake (*Crotalus*)
- Fruit fly (*Drosophila melanogaster*) “wing song”
- Mosquito (*Aedes*) wing sounds

Whale songs
Large body size allows whales and elephants to produce high intensity, low frequency sounds. Both properties increase the range (distance) for communicating with conspecifics.

Hearing
- Particle detector (near field)
  - row of hairs on antenna or abdomen of insects
  - selective to species-specific frequency range
- Pressure detector (far field)
  - membrane (tympanum) stretched over a closed cavity; vibrates in response to sound pressure fluctuations

Mammalian hearing

Human auditory system
Frequency analysis

- Fourier analysis: mathematical decomposition of any complex waveform into simple sinusoidal components

- Fourier synthesis: any complex waveform can be reconstructed (synthesized) from sine waves.

Joseph Fourier (1768-1830)

Frequency and pitch

- Physical property: Frequency
- Psychological property: Pitch

Place theory of hearing

- Cochlear fibers vary in length
- Tuned to vibrate at specific frequencies
- Different positions along the cochlea respond selectively to different frequencies to determine what pitch we hear

Response to a low-frequency sound
Response to a high-frequency sound

Mechanical-to-neural transduction

- The inner ear converts the *mechanical* vibration into a sequence of *electrical* signals called **action potentials**.

Place coding in the cochlea

- **Tonotopic map** of frequency:
  - Different positions along the cochlea respond selectively to different frequencies

Place coding in the cochlea

- **Action potentials** are generated in the auditory nerve and propagated to the central nervous system.
- Intense (loud) sounds generate high levels of neural activation.
  - **Place ↔ Frequency**
  - **Neural firing rate ↔ Intensity**

Temporal coding

- In addition to place coding, information is coded in the temporal synchronization of nerve spikes (**temporal coding**).
Q: Why do animals generally have two ears?

A: To locate the source of sounds they hear.

Cues for sound localization:
- Interaural intensity (level) differences (IIDs)
- Interaural time (phase) differences (ITDs)

• **Sound shadow effect**: At high frequencies, wavelengths are very short, and an animal's head will partially block the sound waves.

• **Interaural intensity differences**: When a sound comes from a source located to one side of an animal's head, the difference in intensity between the two ears helps to localize the sound source.

• **Interaural time differences**: There is a slight delay in the time of arrival of the sound at the opposite ear that also helps sound localization.

After Sekuler and Blake (1990, p.344)
Sound localization

• Marler (1955) found that **alarm calls** in birds causes others to seek cover. Alarm calls in different bird species have similar structure:
  - Single, brief “seet” call
  - Low amplitude
  - High frequency (narrowband)
  - Gradual onset

**American Robin “see” alarm call**

Sound localization

• Unlike alarm calls, **mobbing calls** are made of:
  - Repeated series of loud “chuck” calls
  - Wide range of frequencies (broadband)
  - Sudden sharp onset and offset

**American Robin “who” mobbing call**

Sound localization

• Marler (1955) found that **mobbing calls** are repeated, loud calls that attract others. Unlike alarm calls, mobbing calls consist of:
  - Repeated series of loud “chuck” calls
  - Wide range of frequencies (broadband)
  - Sudden sharp onset and offsets

**American Robin “whinny” call**

Sound localization

• Marler (1955) found that **alarm calls** in birds causes others to seek cover. Alarm calls in different bird species have similar structure:
  - Single, brief “seet” call
  - Low amplitude
  - High frequency (narrowband)
  - Gradual onset

Sound localization

• Marler suggested that alarm signals are shaped by strong selection pressures. Alarm calls reveal a clear trade-off between **detectability** and **localizability**.
  - **Small** animals are better at detecting high frequencies than larger animals (e.g., predators)
  - Sounds with a narrow band of frequencies and **gradual onsets and offsets** are hard to localize.
Sound localization

- **Narrowband** sounds are harder to localize than broadband sounds. **High frequencies** are linked to fear rather than attack
- **Conclusions:**
  - Use brief, high-frequency sounds without sharp onsets to avoid localization
  - Use longer, more intense, broadband sounds to attract attention

Marler’s hypothesis

1. Small animals are better at detecting high frequencies than larger animals (e.g. predators)
2. Sounds with gradual onsets and offsets are hard to localize
3. Narrowband sounds are harder to localize than broadband
4. High frequencies are linked to fear rather than attack
5. Mobbing calls are repeated in a loud voice to attract others

Alarm call detection

Depends on:
1. Amplitude of signal at the source
2. Attenuation characteristics of environment
3. Signal-to-noise ratio at the receiver
4. Sensitivity and discrimination ability of the receiver

Adaptation hypothesis

- Any given sound in the repertoire of a species has been favored by natural selection because its influence on the behavior of other animals is beneficial (i.e., raises the fitness of) the sender and/or his or her close relatives.

Ecological constraints communicating via sound waves

1. energy costs
2. overcoming environmental obstacles
3. locatability of the source
4. rapid fading
5. range of physical complexity

Advantages of sound

1. Sound bends around objects (leaves, tree trunks) that are **opaque** to visual signals
2. Allows for very rapid changes in pattern
3. Can be more precisely timed than chemical signals
4. Rapid signal decay
5. More precisely localizable than chemical signals
### Advantages of sound

6. Useful for small or cryptically colored species (grasshoppers, crickets, frogs, birds), animals that are nocturnal, or live in dimly lit environments.

7. Large body size allows whales and elephants to produce high intensity, low frequency sounds. Both of these properties increase the range (distance) over which they can communicate with conspecifics.

### Design features for long distance communication

- Calling individuals select particular depths and channel sounds so that they are detectable over a range as much as 100 miles.
- High intensity, low frequency sounds, large body size, good signal-to-noise ratio.