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

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**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 10³</td>
<td>1 x 10⁻³</td>
<td>0.0003 x 10⁴</td>
</tr>
<tr>
<td>Water</td>
<td>1.5 x 10³</td>
<td>1</td>
<td>1.5 x 10⁴</td>
</tr>
<tr>
<td>Rock</td>
<td>2-5 x 10³</td>
<td>2-3</td>
<td>4-5 x 10⁴</td>
</tr>
</tbody>
</table>


**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

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**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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  - Use short-range signals (most insects)
Exploiting resonance

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


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. Allows sound waves to bend around small openings and barriers and spread out past the obstacle.

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

Factors affecting acoustic signal transmission

- **Scattering** - signal contacts an obstruction and undergoes a complex multidirectional change in the transmission direction

Sound examples

- **Gray wolf (Canis lupus)**

- **Musical Wren (Cyphorhinus aradus)**

Examples: vocal sounds

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

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

Joseph Fourier (1768-1830)

Complex wave

Simple sine waves

Frequency and pitch

- Physical property: Frequency
- Psychological property: Pitch

Frequency analysis

Sine wave

Complex wave

Intensity

Frequency

Intensity

Frequency

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
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).
Temporal coding

Phase Locking

Source: http://www.neurophys.wisc.edu/animations/

Sound localization

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 localization

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

Sound localization

• **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.

Sound localization

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

• Marler (1955) first studied **alarm calls** in different species of small passerine birds and found important acoustic similarities:
  – Single, brief duration “seet” call
  – Low amplitude
  – High frequency (narrowband)
  – Gradual onset

• 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

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

• 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 “see” alarm call

– American Robin “whinny” call
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.

Learning fine-tunes a specific response of nestlings to the parental alarm calls of their own species.


Davies NB, Madden JR, Butchart SH.

Parent birds often give alarm calls when a predator approaches their nest. However, it is not clear whether these alarms function to warn nestlings, nor is it known whether nestling responses are species-specific. The parental alarms of red warbler, Acrocephalus scirpaceus (“churr”), dunnocks, Prunella modularis (“tseep”), and robins, Erithacus rubecula (“see”)) are very different. Playback experiments revealed that nestlings of all three species ceased begging only in response to conspecific alarm calls. These differences between species in response are not simply a product of differences in raising environment, because when newly hatched dunnocks and robins were cross-fostered to nests of the other two species, they did not develop a response to their foster species’ alarms. Instead, they still responded specifically to their own species’ alarms. However, their response was less strong than that of nestlings raised normally by their own species. We suggest that, as in song development, a neural template enables nestlings to recognize features of their own species’ signals from a background of irrelevant sounds, but learning fine-tunes the response to reduce recognition errors.
Parental alarm calls suppress nestling vocalization. 

Platzen D, Magrath RD.

Evolutionary models suggest that the cost of a signal can ensure its honesty. Empirical studies of nestling begging imply that predator attraction can impose such a cost. However, parents might reduce or abate this cost by warning young of the presence of danger. We tested, in a controlled field playback experiment, whether alarm calls cause 5-, 8- and 11-day-old nestlings of the white-browed scrubwren, Sericornis frontalis, to suppress vocalization. In this species, nestlings vocalize when parents visit the nest (begging) and when they are absent (non-begging), so we measured effects on both types of vocalization. Playback of parental alarm calls suppressed non-begging vocalization almost completely but only slightly reduced begging calls during a playback of parental feeding calls that followed. The reaction of nestlings was largely independent of age. Our results suggest two reasons why experiments ignoring the role of parents probably overestimate the real cost of nestling vocalizations. Parents can warn young from a distance about the presence of danger and so suppress non-begging vocalizations that might otherwise be heard, and a parent’s presence at the nest presumably indicates it is safe to beg.

Example exam question
• Marler (1955) identified some important acoustic differences between alarm calls and mobbing calls in song birds. What were these differences, and how did Marler link these properties to the different functions that these calls serve?

Example exam question
• Organize your answer in terms of Tinbergen’s four questions:
  1. Mechanism
  2. Function
  3. Ontogeny
  4. Phylogeny

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
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.

Vocal signals and body size

FIGURE 12.6: Toad size and croaks