Sound production in animals

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

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

Sound examples

- **Gray wolf (Canis lupus)**
- **Musical Wren (Cyphorhinus aradus)**
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 (ipsilateral) side of the brain. The right side of the syrinx seems to produce a higher range of frequencies than the left side.

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.

Syrinx

http://www.indiana.edu/~songbird/multi/songproduction_index.html

http://hyperphysics.phy-astr.gsu.edu/hbase/sound/soucon.html#soucon

Bird songs

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Lateralization of song

• The syrinx is a bilateral structure located at the point where the two bronchial passages converge in the trachea.
• Bird sound is produced when air passes through the medial and lateral labia on each side of the syrinx.
• Song is produced bilaterally except when air is prevented from flowing through one side of the syrinx.

Patterns of syringeal lateralization

• Different species of birds produce sounds in different ways.
• Northern Cardinals produce frequency sweeps that abruptly switch from one side to the other in mid-stream.
• Brown-headed Cowbirds alternate from one side to the other, producing discrete sounds on different pitches without a silent gap or frequency slur (glide) between them.
Two sound sources

- Birds like Brown Thrashers can produce two sounds on each side of the syrinx at the same time that are not harmonically related to each other. The right side generally produces higher frequencies than the left.

Syrinx

- 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).

Northern Cardinal - vocal production

Brown-headed Cowbird

Lateral dominance of motor control

- Fernando Nottebohm has shown that the two sides of the syrinx are independently controlled by specific regions in the brain.
- These areas are larger in males than females in Canaries and Zebra Finches, consistent with the greater use of song by males.
- Pacific Coast Marsh Wrens have song repertoires that are three times larger than Atlantic Coast birds, and also have 30-40 percent larger song control areas in their brains.
Lateral dominance of motor control

• A lesion in the tracheosyringeal branch of the hypoglossal nerve disables the left or right syrinx (on the same side as the lesion).
• In canaries, the number of song elements in the birds’ repertoires was reduced when the left side was cut, but only slightly affected by cutting the right side, indicating left syringeal dominance of song production.

Lateral dominance of motor control

• Laterality of song control has been observed all the way into the higher vocal center (HVC) brain region; unilateral lesions to HVC produce lateralized effects in the temporal patterning of song in the zebra finch.

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.

Zebra Finch song

• Sound spectrogram

Song development in birds

• Chaffinch (Fringilla coelebs)

Sound production in animals

1. Beating a substrate
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3. Respiratory structures
Stridulation in crickets

https://www.youtube.com/watch?v=PbBvfhbHwBM

Stridulation in birds

- Specialized adaptations of wings for sound production
- Secondary wing feathers are enlarged and hollow with regular, raised ridges; neighboring feather tapers abruptly to a thin, stiff, blade.

https://www.youtube.com/watch?v=7FHSQQMnOlko

Stridulation in birds

- Tick–Tick–Ting sound: fundamental frequencies of 1590 and 1490 Hz with harmonics at integer multiples.
- Feather oscillations = 106/second
- Frequency multiplier: 106 x 14 ≈ 1490 Hz

https://www.youtube.com/watch?v=7FHSQQMnOlko

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.

8x normal speed

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 10⁴</td>
<td>1 x 10⁻³</td>
<td>0.0003 x 10⁵</td>
</tr>
<tr>
<td>Water</td>
<td>1.5 x 10⁴</td>
<td>1</td>
<td>1.5 x 10⁵</td>
</tr>
<tr>
<td>Rock</td>
<td>2-5 x 10⁴</td>
<td>2-3</td>
<td>4-5 x 10⁵</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

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)

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.

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

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

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

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)

- **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

  - Sine wave
  - Complex wave

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*).

Temporal coding

Source: [http://www.neurophys.wisc.edu/animations/](http://www.neurophys.wisc.edu/animations/)
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.

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

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

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

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

- 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.