Sensory Worlds: Hearing in Barn Owls

Dr. Katie Lucas
Learning in Retirement
Carleton University
Winter 2018
Readings

Textbooks

BEHAVIORAL NEUROBIOLOGY
An Integrative Approach
SECOND EDITION
GÜNTER K. H. ZUPANC

THE NEUROETHOLOGY OF PREDATION AND ESCAPE
Keith T. Silk | Laurence D. Pittor | William J. Herber

WILEY Blackwell

Popular science books

• Sensory exotica: A World beyond Human Experience
  Howard C. Hughes

*Available in library reserves

https://carleton.ca/linr/winter-2018-session/class-notes/
Hearing in Barn Owls

- Our understanding of the underlying neural mechanisms have been greatly advanced by focusing on a ‘simple’ behaviour.

https://www.youtube.com/watch?v=8SI73-Ka51E
(0-2:00)
The stimulus - Sound
Analyzing sounds

A

B

1 wavelength ($\lambda$)

Particle displacement

Amplitude

0

Pressure

1 period (T)
Analyzing sounds

• Amplitude (decibels)
  • “Loudness”

• Frequency (Hz, cycles per second)
  • “Pitch”

Sound localization in the barn owl - behaviour

- Able to capture prey in complete darkness
  - Adaptation to field mice
- Behavioural response
  - Head flick
  - Swoop and strike
• Used dummy experiments to rule out olfactory and infrared sensing (Roger Payne, 1962 and 1971)
  • Replace mouse with wad of paper rustling through leaves
  • Mouse on sand (silent)...towing a leaf
  • Owl doesn’t locate mouse by smell or body heat
Experimental setup

Measureable behaviour:
Head tick

Electromagnetic angle detector system
-Owl trained not to attack, but simply turn head

Figure 7.12 (Zupanc)
Experimental setup

- Barn owl can locate sound within one or two degrees in both azimuth and elevation
- High frequencies (5-9 kHz) necessary
- 60 ms delay
  - Head movement determined under *open-loop conditions*
- Error range 9 cm

**Measureable behaviour:**
Head tick

Figure 7.12 (Zupanc)
Cues for sound localization

• Interaural time difference (ITD)
  • Sound arrives to each ear at a different time

• Interaural intensity difference (IID)
  • Sounds arrive to each ear with a different intensity
    • Sound attenuates with distance

Figure 7.16 (Zupanc)
Cues for sound localization

- Adaptations in the facial ruff
  - Troughs
    - Collect high frequency sounds
    - Divert to ear canals
  - Preaural flap
    - Asymmetrical
      - Left higher than right
      - Tilted in opposite directions

Asymmetries lead to differently perceived intensities of sound

Figure 7.15 (Zupanc)
Cues for sound localization

Figure 7.14, 7.15 (Zupanc)
Cues for sound localization

Figure 6.13, 6.14 (Zupanc)

Up-Down (elevation) affected more than Left-Right (azimuth)

Uses IID to localize in the elevation plane

Figure 6.13, 6.14 (Zupanc)
Cues for sound localization

- Playback experiments, altering the time difference between Left and Right ears.

- Behaviour (head turn) is predicted by L-R disparity.

Knudsen and Konishi (from Carew 2000)
Cues for sound localization

• Interaural time difference (ITD)
  • Localization cue for the horizontal plane

• Interaural intensity difference (IID)
  • Localization cue for the vertical plane
Why have both?

Physical space can be mapped in terms of ITD and IID (bicoordinate system)

**BICOORDINATE SYSTEM**

ITD
~42 µsecs every 20°

IID
~8 dB every 20°

Figure 7.17 (Zupanc)
Encoding sound: spike trains

Stimulus  Sensory transduction  Neural coding
Neural coding

(a) Cat pressure receptor

(b) Intensity coding

Fig. 3.7 (Zupanc)
Extracellular recordings: multi-unit activity

an “electrical antenna” that monitors voltage changes outside (extracellular) the neuron

Fig. 3.2 (Zupanc)
Extracellular recordings: multi-unit activity

Extracellular action potential varies with neuron and its relative location
Encoding sound: spike trains

Information being encoded:
• Frequency
• Intensity
• Timing
Encoding sound: spike trains

Figure 6.17 (Zupanc)
Encoding sound: spike trains

Figure 6.17 (Zupanc)
Neural basis for sound localization

• Neural circuit involved in sound localization in the owl brain
  • Processes **Time** and **Intensity** information separately
  • Spike train incoming from auditory nerve
    • Nerve divides into *contralaterals*
    • Separating time and intensity information to processed *in parallel*

Figure 7.19 (Zupanc)
Neural basis for sound localization

We consider the ‘neural algorithm’…what the brain is doing at each stage

Figure 7.19 (Zupanc)
Neural basis of a delay line
Computing interaural time differences

Tonotopic, bilateral

Left

NL

Right

NL

NM

NM

Phase-lock tonotopically

NM: magnocellular cochlear nucleus
NL: nucleus laminaris (avian homologue of the superior olivary nucleus)
Delay lines and coincidence detection

- Jeffress’s model for encoding Interaural Time Differences
  - **Coincidence detectors**: fires maximally when it receives simultaneous (coincident) excitation from its input elements
  - **Delay line**: slow down input from one side to allow for simultaneous arrival at coincidence detector, maximizing time differences
Without a delay, the coincidence detector receives information from the right ear before receiving information from the left ear. Since the inputs are temporally offset, they do not summate, so the coincidence detector fires weakly.
Delay lines and coincidence detection

With the addition of a time delay from the right ear to the coincidence detector, both left and right inputs arrive simultaneously, and the detector fires maximally.
Neural basis of a delay line

Figure 2. Drawing of transverse section through dorsal brain stem. This drawing shows the projection from the nucleus magnocellularis (NM) to the nucleus laminaris (NL). Two magnocellular neurons were reconstructed from approximately 23–50-μm sections with the aid of a camera lucida and superimposed upon a drawing of the dorsal brain stem. These arbors were labeled after a small HRP injection in the 5.5-kHz region of the nucleus magnocellularis, and each labeled fiber was traced back to a labeled cell body in the injection site. Because each arbor is 3-dimensional (see Fig. 3-4), the actual mediolateral extent of the nucleus laminaris has been exaggerated to accommodate the full arbor. Similarly, each bundle of afferents in the nucleus laminaris forms a cylinder, not a flat sheet, and the “twisted bundle” of ipsilateral axons above the nucleus magnocellularis has been dorsoventrally compressed. IV, fourth ventricle. Scale bar, 1 mm.

Neural basis of a delay line

**Figure 2.** Drawing of transverse section through dorsal brain stem. This drawing shows the projection from the nucleus magnocellularis (NM) to the nucleus laminaris (NL). Two magnocellular neurons were reconstructed from approximately 25–50-μm sections with the aid of a camera lucida and superimposed upon a drawing of the dorsal brain stem. These arbors were labeled after a small HRP injection in the 5.5-kHz region of the nucleus magnocellularis, and each labeled fiber was traced back to a labeled cell body in the injection site. Because each arbor is 3-dimensional (see Fig. 3A), the actual mediolateral extent of the nucleus laminaris has been exaggerated to accommodate the full arbor. Similarly, each bundle of afferents in the nucleus laminaris forms a cylinder, not a flat sheet, and the “twisted bundle” of ipsilateral axons above the nucleus magnocellularis has been dorsoventrally compressed. IV, fourth ventricle. Scale bar, 1 mm.

Neural basis of a delay line

D-V conduction time of about 130us over 700um (200us over total depth)

Since each cell has a specific *place*, it can code for a specific *time difference*.

From Carew 2000, after Carr and Konishi
Neural basis for sound localization

Figure 6.18 (Zupanc)
Spatial map in external nucleus

Space-specific neurons

Respond to acoustic stimuli only if the sound originates from a restricted area in space – within its receptive field

From Carew 2000
Spatial map in external nucleus

Combination of ITDs and IID endows each space-specific neuron with a unique spatial address in auditory space
Spatial map in external nucleus

Regions near the midpoint of the face are represented by significantly more neurons, providing a higher resolution.
Spatial map in external nucleus

From Carew 2000, after Knudsen and Konishi 1978
Barn Owls have ageless ears

- Published September 2017
- Presbycusis (a.k.a. age-related hearing loss)
Cochlea – the inner ear

- Presbycusis (a.k.a. age-related hearing loss)
  - Loss of hair cells
  - Human hearing range 20 Hz – 20 kHz
  - We lose our high frequency hearing first
  - Also observed in mice, gerbils, chinchillas

Hair cells transduce sound into a neural signal

https://www.youtube.com/watch?v=dyenMluFaUw
Barn Owls have ageless ears

<table>
<thead>
<tr>
<th>Young (less than 2 years)</th>
<th>Old (more than 13 years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ulge</td>
<td>Bart</td>
</tr>
<tr>
<td>Sova</td>
<td>Lisa</td>
</tr>
<tr>
<td>Grün</td>
<td>Weiss</td>
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<td>Rot</td>
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</table>

- Measured *auditory threshold*
  - Lowest sound intensity that they could hear
  - 0.5-12 kHz
Barn Owls have ageless ears

- Go/No Go paradigm

Experimenter plays sound tones at different frequencies and intensities

If the owl hears a sound, it flies to target perch and receives a food reward

No reward for ‘false alarms’, and ended trials if more than 20%
Barn Owls have ageless ears

- Audiogram
  - Plot showing threshold responses for all frequencies tested
- Barn owls are more sensitive than most other birds
- No significant difference between young and old
Barn Owls have ageless ears

- Variation in thresholds in quiet of one barn owl (Weiss), measured between 1994 and 2016
Barn Owls have ageless ears

**HOW?**

- Birds are able to restore auditory function after damage, while mammals are not
  - Can regenerate lost hair cells
  - Mammals can regenerate hair cells in the *vestibular system* (for balance), but not in the cochlea

Basilar Papilla (equivalent to Mammalian Cochlea)
Basilar Papilla in Bengalese Finch

A

B

C
Basilar Papilla in Bengalese Finch - Treated with amikacin
Basilar Papilla in Bengalese Finch - 12 weeks later
Barn Owls have ageless ears

• “The hope and interesting question remains whether, someday, our knowledge on preservation of sensitive hearing in birds will provide new treatment options that could counteract human sensory deficits”.
  • Krumm et al. (2017)
Articles I discussed today

• Why are Barn owls a model system for sound localization?
  • JEB Classics (2010), *Journal of Experimental Biology*
• Acoustic location of prey by Barn Owls (*Tyto alba*)
  • Roger Payne (1971) *Journal of Experimental Biology*
• Watch the secret to why barn owls don’t lose their hearing
• Barn Owls have ageless ears
  • Krumm et al. (2017) *Proceedings of the Royal Society B*
Next week

• Visual feature detection in toads