Learning in the auditory system: Lessons from the barn owl

Yoram Gutfreund
The Technion, Haifa, Israel
Which model system?

While humans are good for generating hypotheses, animals are good for testing them.

Which animals?

Animals that lend themselves to combined behavioral and neurophysiological work.

Specialists or Generalists?
• Sound localization
• Sensory maps plasticity and development
• Spatial attention
• Multisensory integration
Barn owls as model system for sound localization

- Facial ruff serves as a sound amplifier
Barn owls as model system for sound localization

• Facial ruff serves as a sound amplifier

• Asymmetric ears allow for an increased spatial resolution in the vertical plane
Barn owls as model system for sound localization

- Facial ruff serves as a sound amplifier
- Asymmetric ears allow for an increased spatial resolution in the vertical plane
- Comb-like structures at the leading edge of the wing reduce noise during flight
Barn owls as model system for sound localization

Facial ruff serves as a sound amplifier

Asymmetric ears allow for an increased spatial resolution in the vertical plane

Comb-like structures at the leading edge of the wing reduce noise during flight

Brain structures involved in the analysis of sound are enlarged
Performing a psychoacoustic experiment with an owl
Sound-localization with free-field stimuli
• The auditory localization cues:

• ITD - horizontal

• ILD - vertical

location producing
ITD = 0 μsec

location producing
ITD = 100 μsec
Precision of sound localization in barn owls may be as good as 3 deg which corresponds to 6-10 $\mu$s.
These signals are the “language” of neural processing.
Durations of events

- Typical duration of action potential: 1 ms
- Typical duration of post-synaptic potentials: 5-10 ms
- Precision of sound localization by interaural time difference: 6-10 μs

What has to be explained is

Factor of 500-1000
The principle of phase locking as a means to conserve time

Sinusoidal signal

Presumed resulting postsynaptic potential

Registered signal in computer

Note that in this example the response always occurs at a phase of 180 degrees.
Phase locking in the barn owl

Phase locking can be measured by plotting spike arrival times with respect to the period of the stimulus tone.

5 kHz  Period 200 μs  9 kHz  Period 111 μs

Precision of phase locking is 35 μs at 5 kHz (Koeppel (1997)).
Visual and auditory maps in the OT
Computational map

Transducing sound to action-potentials

Computing auditory localization cues

Integrating cues from specific locations

Associating with external space

Sound

Frequency
Intensity
Time
Side of ear

Frequency
Binaural localization cues

Space tuned
Computational maps
The matching problem

location producing
ITD = 0 μsec

location producing
ITD = 100 μsec
Computational maps
The matching problem

location producing
ITD = 0 μsec

location producing
ITD = 100 μsec
Effect of prism experience on auditory tuning

Normal

Immediate effect
of prisms

Knudsen and Brainard, Science (1991)
Effect of prism experience on auditory tuning

**Normal**

**Immediate effect of prisms**

**After 8 weeks of prism experience**
Quantification of learning

1. Behavioral test

2. Physiological test
Decline in learning with age

Increased capacity for learning in adults that have had appropriate experience as juveniles

Effects of juvenile experience on adult learning

Incremental learning
Incremental learning

Rich and lively experiences increase learning capacity in adults

Bergan et al., Journal of Neuroscience (2005)
Summary

• Decline in learning with age
• Increased capacity for learning in adults that have had appropriate experience as juveniles
• Incremental training improves learning
• Rich and lively experiences increase learning capacity in adults
Where is the site of plasticity?

Forebrain:
- Sensory/Association Areas
- Archistriatum (FEF)

Thalamus:
- Ovoidalis (MGN)
- Rotundus (Pulvinar)

Midbrain:
- Inferior Colliculus central n.
- Inferior Colliculus external n.
- Optic Tectum (SC)
- Brainstem Tegmentum
- Motor Nuclei for gaze control

- VLVp (LSO/DNLL)
- LAM (MSO)
- left cochlear n.
- right cochlear n.
Horizontal section through the tectal lobe

Visual input from Retina and Forebrain

ICC

OT

ICX

0°

20°

40°

0°

20°

40°

Visual input from Retina and Forebrain
Site of plasticity in the ICX

Debello et al., J. Neurosci. 2001
After prism learning

Visual input from Retina and Forebrain

ICC

OT

ICX

20°

40°

60°

20°

40°

60°

Visual input from Retina and Forebrain
The instructive signal

- Operates in the ICX
- Visually based
Where is the instructive signal coming from?
BDA injection site in ICX
Topography of the OT-ICX projection
Restricted lesion of the optic tectum
How can a visually based instructive signal act in an auditory structure?
Horizontal section through the tectal lobe

Visual input from Retina and Forebrain

- ICC
- ICX
- OT

- 0°
- 20°
- 40°
bicuculline

recording

ICC

OT

ICX

0

50

50

100

µsec

100

r

m

l

c

recording barrel

iontophoresis barrels

bicbic

recrec
Light responses in the ICX
Visual Receptive Fields in the ICX
Properties of visual responses in ICX

- Arrive from the OT
- Display spatially restricted visual receptive fields
- Form a map of space
- Align with auditory spatial representation
Bimodal Stimulus

- light
- right ear
- left ear
Visual and auditory interactions in the ICX
Average

![Graph showing ITD (μs) vs. Post stimulus time (ms) with AV-A (spikes) as the y-axis.]

- **ITD (μs)**: -60, -30, 0, 30, 60
- **Post stimulus time (ms)**: 50, 100, 150, 200
- **AV-A (spikes)**: 0, 4, 8, 12

![Graph showing AV-A (spikes) vs. ITD (μs) with error bars.]

- **AV-A (spikes)**: 6, 10, 14
- **ITD (μs)**: -80, -60, -40, -20, 0, 20, 40, 60, 80
Bimodal stimulus

Normal

Visual input
Bimodal stimulus

Normal

With prisms

Visual input

ICC

ICX

OT

Visual input

ICC

ICX

OT
Bimodal stimulus

Normal

With prisms

Visual input

ICC
ICX
OT

ICC
ICX
OT

Bimodal stimulus
Summary

An inhibitory gate controls the flow of visual information into the auditory system.
Summary

• An inhibitory gate controls the flow of visual information into the auditory system

• The visual signals are appropriate to serve as the instructive signal for auditory plasticity
• Eric Knudsen
  Daniel Feldman
  Michael Brainard
  Will Debello
  Peter Hyde
  Brie Linkenhoker
  Joe Bergan

Stanford University

Hermann Wagner - AACHEN University