Owls: Acoustic Space

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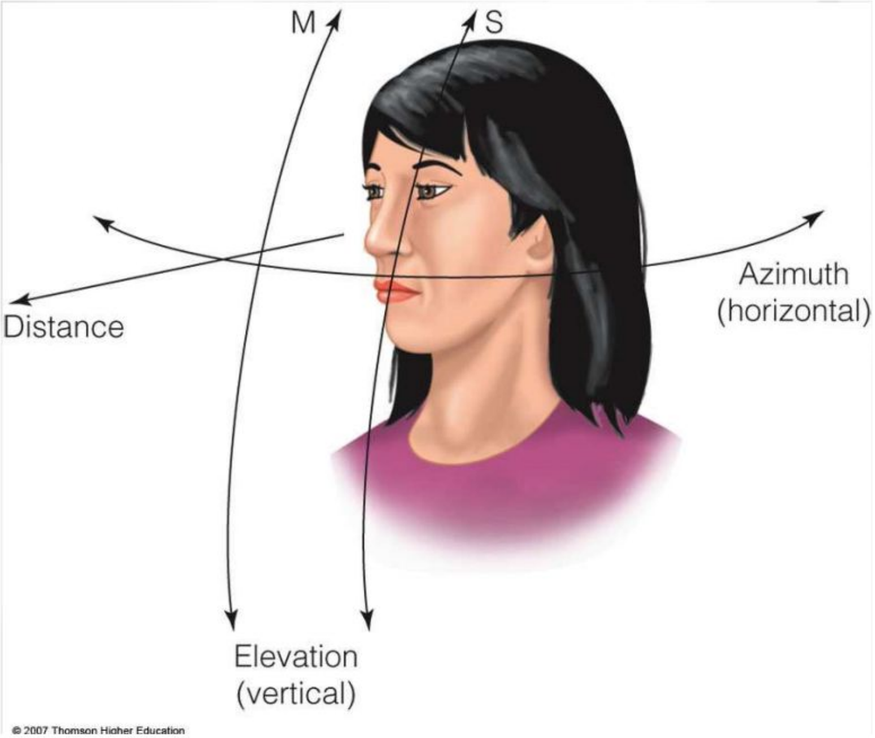
Review: Auditory cartography

Auditory space: field of sound surrounding an observer

Coordinates for describing auditory space:

- Distance: location in space relative to the observer
- Azimuth: horizontal location, calculated as angular distance
- Elevation: vertical location, also angular distance



Owls: Expert listeners

Some owl facts:

- Generally nocturnal/crepuscular and hunt mostly at dusk/night, therefore don’t rely on vision
- Can locate prey in total darkness using only hearing, with an error >1° in both planes
- Can ‘hear’ where prey is before taking off
- Hunt the source of the sound, not the actual prey

Acoustic Location of Prey by Barn Owls (Tyto Alba)
ROGER S. PAYNE
Journal of Experimental Biology 1971 54: 535-573;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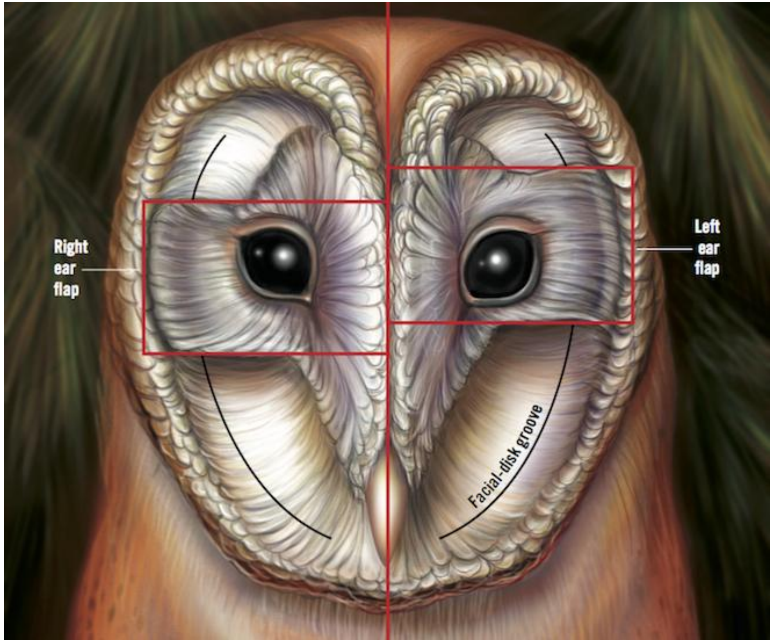
How do owls know vertical and horizontal position?

Space isn't mapped by the inner ear-- so how can an animal locate via hearing?



https://www.birdwatchingdaily.com/news/science/owl-behavior-hunting/

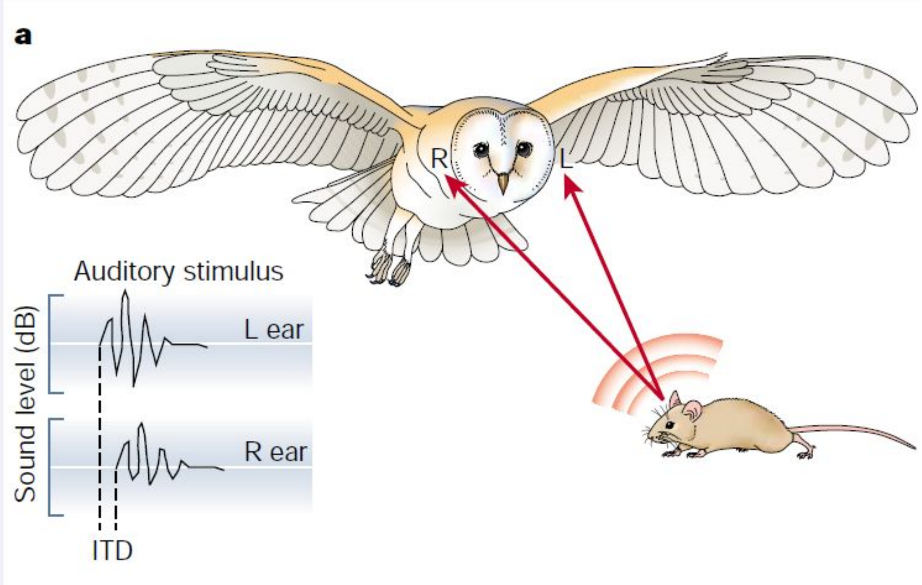
Interaural level difference (ILD)

Asymmetry between ears

- Vertical plane of sound differentially reaches each ear
- Allows owl to tell sounds **elevation**

How do owls know vertical and horizontal position?

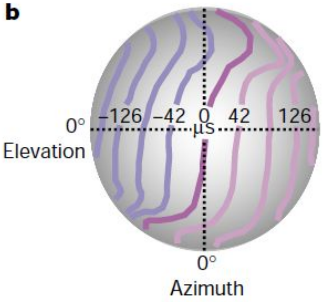
Space isn’t mapped by the inner ear-- so how can an animal locate via hearing?



Knudsen, 2002

Interaural Time difference (ITD)

- Sound will (generally) reach either the left or the right ear first
- Difference between arrival of sound is used to tell where the sound originated along the horizontal plane
- Allows owl to determine the sound’s **azimuth**



(ITD values for 6kHz sound)

How is space represented in the auditory system?

Sound localization in owls: Theories (Knudsen & Konishi, ‘78)

Population theory of sound localization

Idea:

‘sound location is encoded by the relative activation of two populations of neurons’

- One population → right ear
- Other population → left ear

Holds that the interaural disparities to which neurons are sensitive are too broad to explain owl behavioral acuity

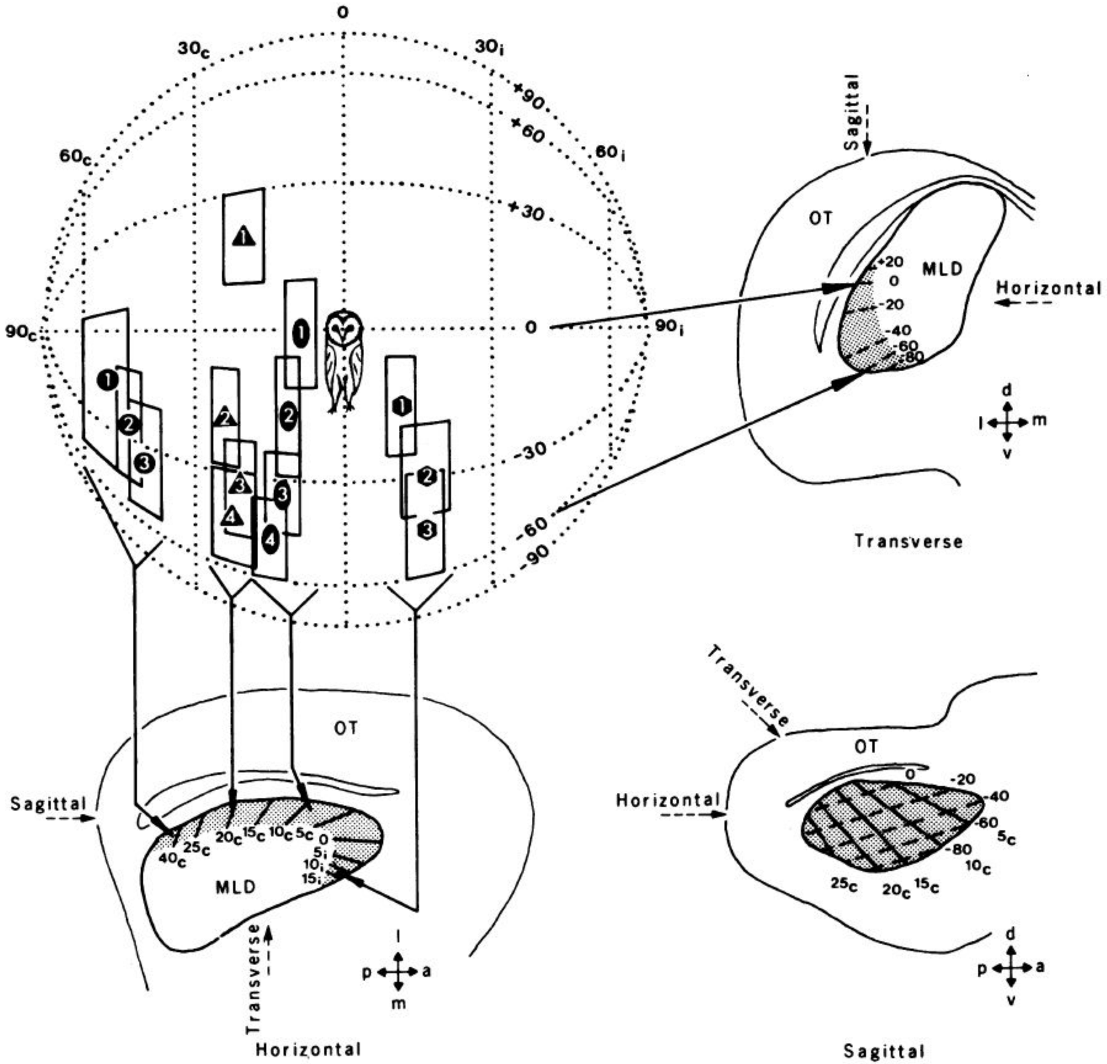
Place theory of sound localization

Idea:

‘Sound location is encoded as ‘place’ in the nervous system, with individual neurons being sensitive only to restricted portions of auditory space’

However,

Neurophysiology shows that auditory units can have specific and sensitive receptive fields (RF)...



Knuden & Konishi, 1978

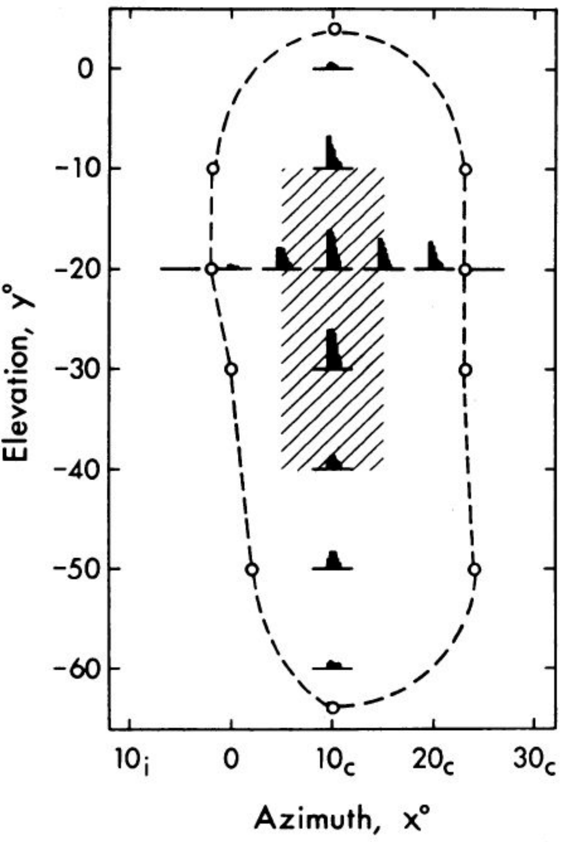
Test the influence of sound source location on the response properties of central auditory neurons

- Large, anechoic chamber
- Total darkness
- Moveable speakers, directed in sphere centered on owl head

Auditory units:

- Recorded from mesencephalic lateral dorsal nucleus (MLD), homolog to IC
- In general, MLD units exhibit spatial specific responses, and are arranged according to azimuth/elevation of RFs

Auditory Receptive Fields



Units defined by 3 properties:

- Respond only when a sound is in a particular area
- Respond independently of type and intensity of the sound
- Tuned to high-frequency end of owl's audible range

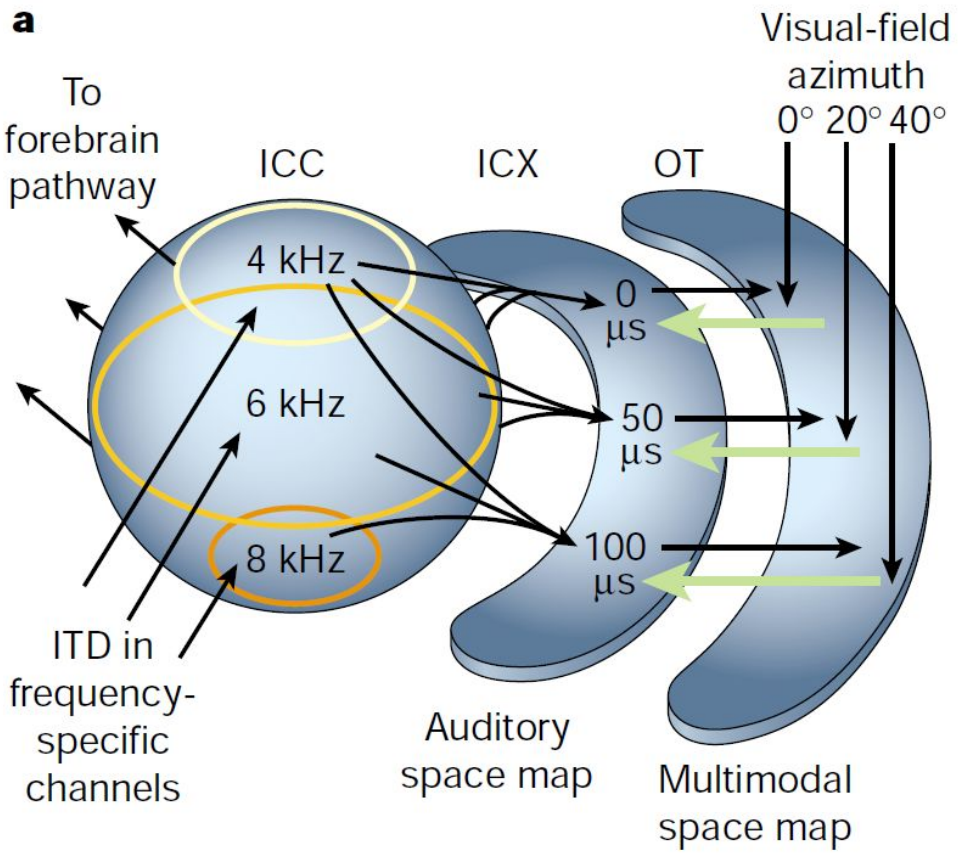
Characteristics of auditory RFs:

- Oval or band-shaped ellipsoids
- Always have a 'unit's best area' (hash marks in image)
- Insensitive to intensity level or kind of stimulus
- Spatial transitions and sizes of RFs are highly variable
- **But,** unit best areas shift very predictably and smoothly
  - Unit's best are can be expressed as a single azimuth-elevation bicoordinate
  - Via unit's best area, can create a detailed map of auditory space representation

Map of Auditory Space

Although auditory space exhibits RFs and can be mapped, it still differs from other sensory representations

- Notably, **auditory space is an emergent property of higher-order neurons, as opposed to other sensory maps that are direct projections of the sensory surface (retina RFs, mechanoreceptors, nociceptors…)**
- Auditory map is constructed a few steps down the auditory pathway from the relative patterns of auditory nerve input from each ear



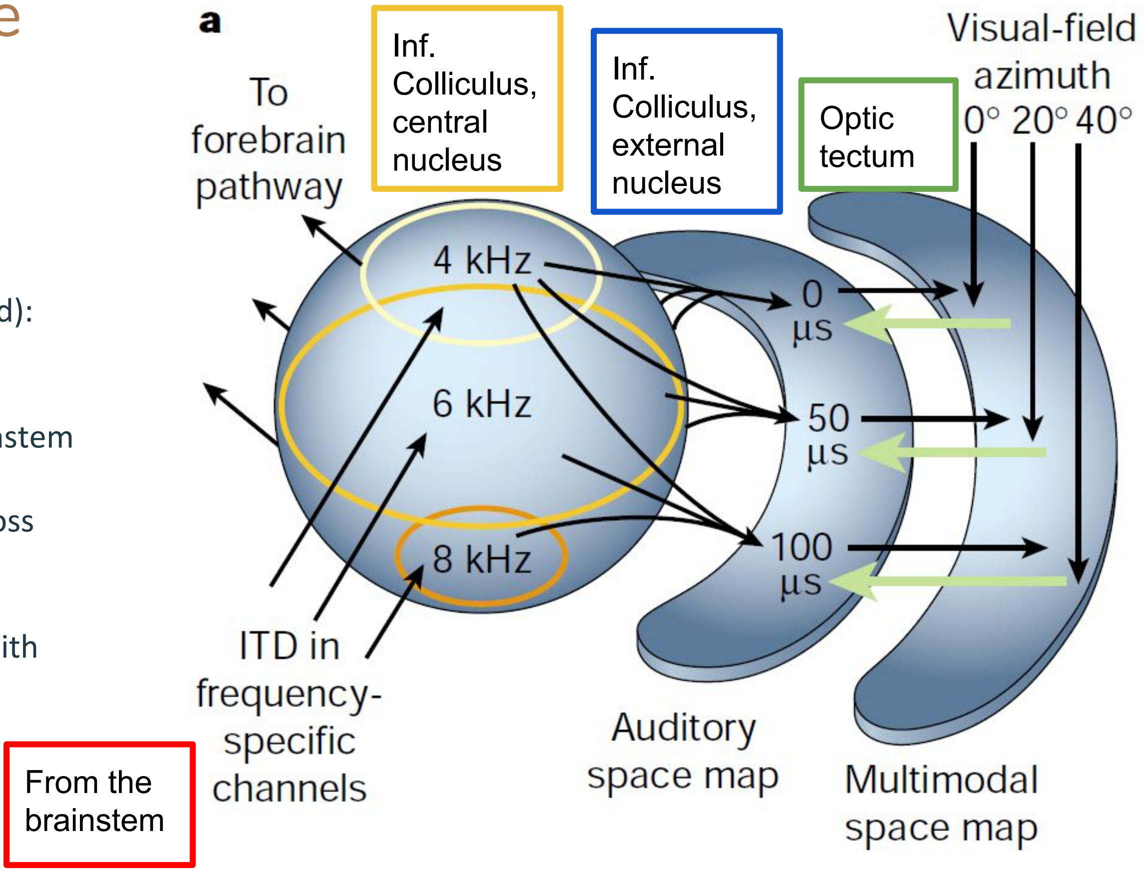
Knudsen, 2002

Map of Auditory Space

- ITD, ILD, and sound intensity are all processed in parallel pathways in brainstem

In **midbrain localization pathway** (pictured):

- ITD is measured and mapped into frequency specific channels in brainstem
- ICC is tonotopically organized
- ITD /sound cue infor combined across frequency channels and sent to ICX
- Map emerges in ICX,
- And conveyed to OT, and merges with **visual** map of space



Knudsen, 2002

Map of Auditory Space

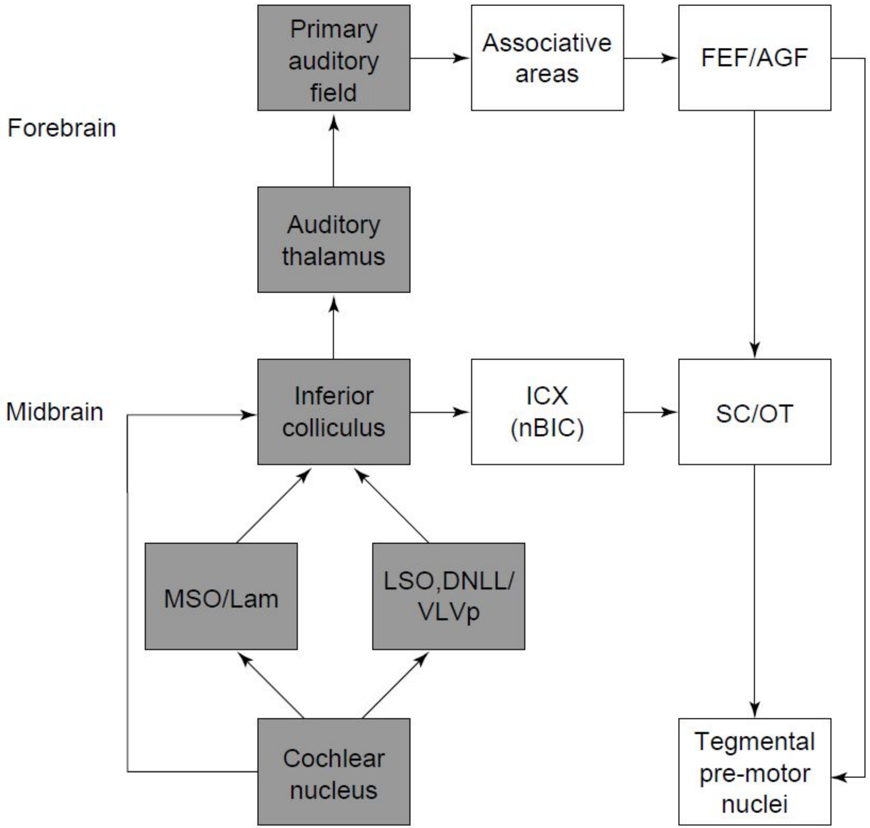
Midbrain pathway → space encoded as **map**
Forebrain pathway → space encoded in **clusters**

In **forebrain pathway:**

- No global topography, although neighboring neurons are tuned to similar localization cues
- Contributes to higher-order functions
    - Working memory
    - Planning complex motor sequences
    - Executive control of orientation

Difference may reflect the different roles each area has in guiding behavior

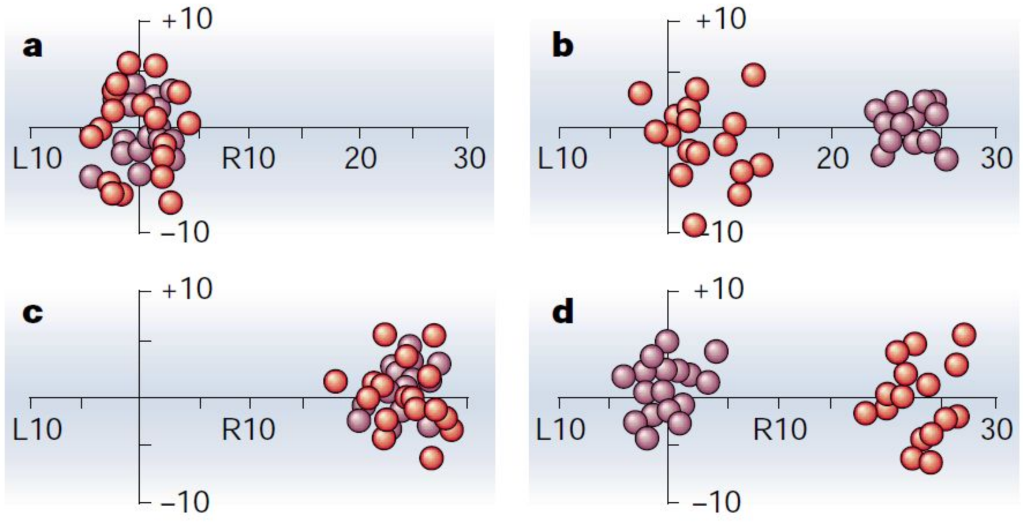
What happens if the visual input gets weird?



Cohen & Knudsen, 1999

Adjusting behavioral response with optical displacement

After several weeks, owls learn to adjust orienting behavior so that sound source matches visual source.



Testing:

- Present auditory (red) or visual (purple) stimulus, randomly
- Measure head orientation response, relative to actual presentation

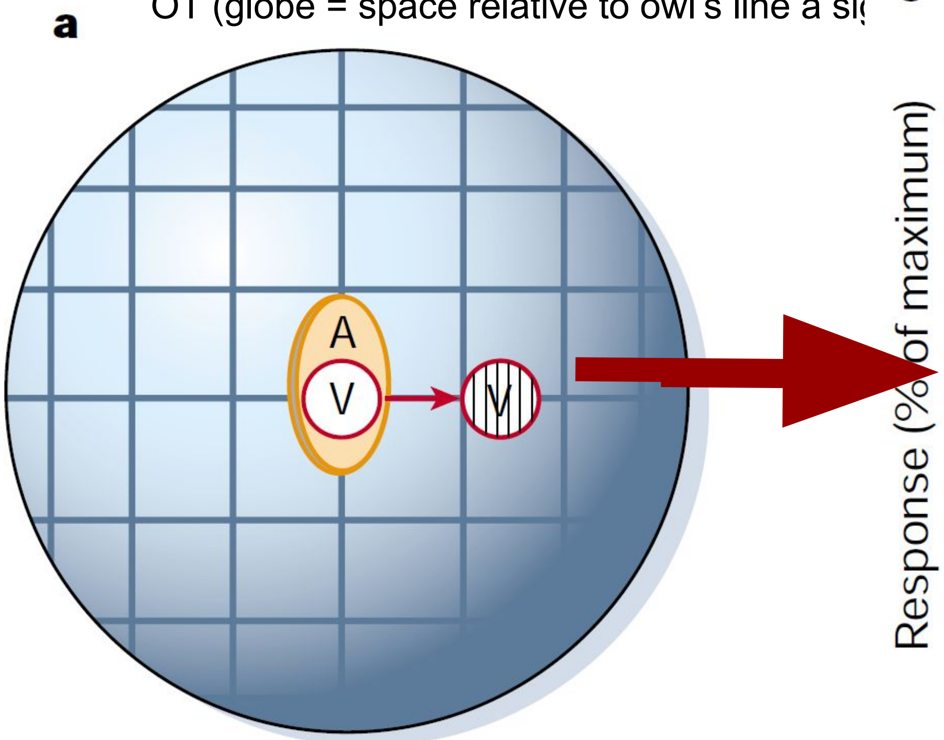
A. Before prism goggles
B. + 1 day, with 23° displacement of the visual field
C. + 42 days with goggles
D. Goggles removed

So, owls also model system for plasticity and adaptive learning.

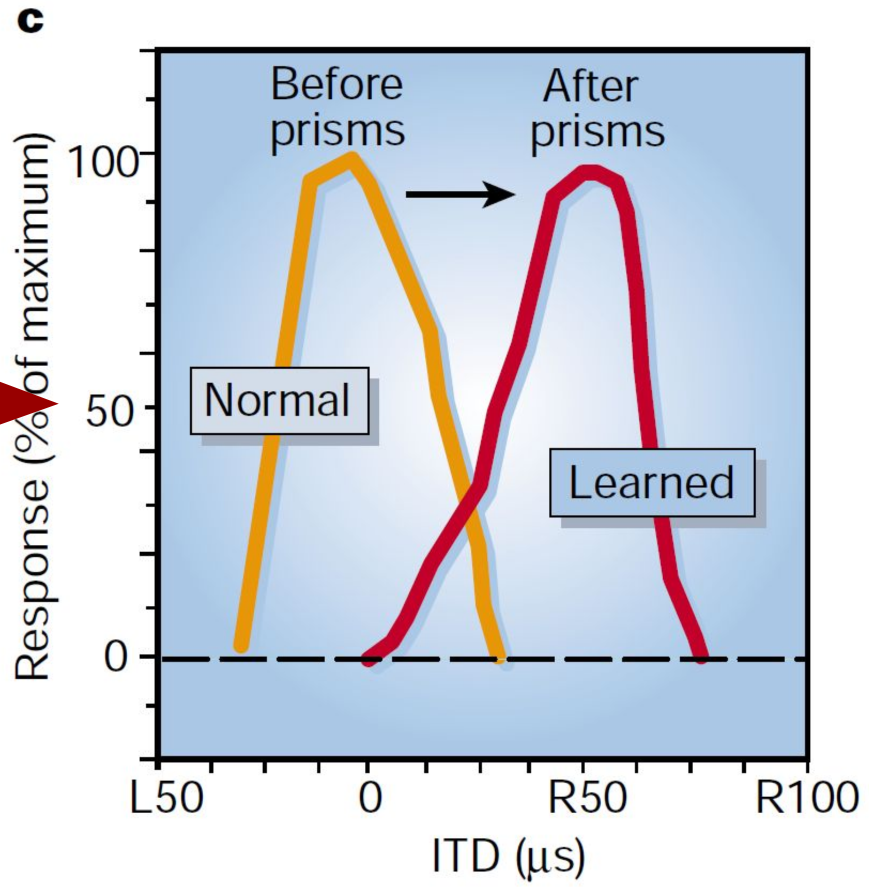
Knudsen, 2002

Sites of plasticity in auditory space

OT (globe = space relative to owl's line a si



A/V RFs, chick with prism goggles



Knudsen, 2002

Sites of plasticity in auditory space

While ICX/OT undergo large-scale adaptive plasticity, ICC does not

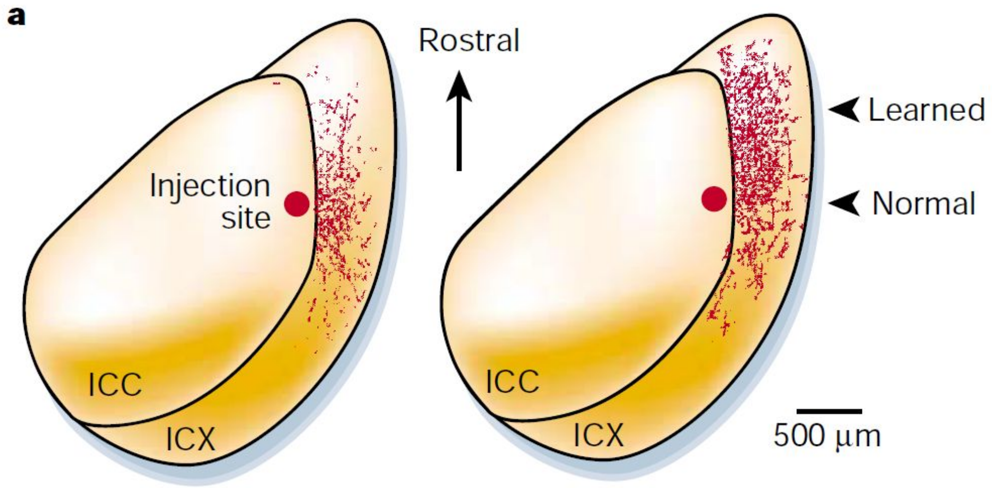
Tuning of neurons in ICC does not change with altered visual RFs

But,
Along with functional changes in the ICX, the axonal projections from ICC → ICX change

- ICC → ICX projections become broader
- Normal (non-prism) projections remain, while new projections form
- Assumed that these new projection carry newly learns ITD tuning

‘Prism experience must induce the formation of learned circuitry in the ICX at least in part through axonal sprouting and synaptogenesis’

- Knudsen, 2002



Knudsen, 2002

Owl facts, revised:

- Owls rely on differences in interaural cues for time and sound level, like mammals
  - So, can apply discoveries in these expert listeners beyond birds

- Although auditory receptive fields are not direct projections of external stimulus, they can be linked to the external world with his acuity
  - Auditory cues are extracted and re-combined downstream into perceptual information
  - Thus, the owl is not only a physiological animal model, but also one for neural computation in general (Takahashi et al., 2003)

- Selective functional properties and anatomical structures are subject to experience-based plasticity
  - Normal projections and anatomical features are preserved when visual RFs are altered

Literature

- **Cohen & Knudsen.** Maps versus clusters: different representations of auditory space in the midbrain and forebrain. (1999) Trends in Neurosciences.
- **Eric Knudsen.** Instructed learning in the auditory localization pathway of the barn owl. (2002) Nature.
- **E. Knudsen-M Konishi.** A neural map of auditory space in the owl. (1978) Science.
- **T. Takahashi-A. Bala-M. Spitzer-D. Euston-M. Spezio-C. Keller.** The synthesis and use of the owl's auditory space map. (2003) Biological Cybernetics.

Questions?