L14. Sound Localization 2

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BioN84240
C. D. Hopkins

Jeffreys' Model (1948)

- Suppose Right & Left neural inputs from opposite sides converge.
- Delays, from neuronal conduction.
- Output cells (A-E) fire only if there is coincident inputs from both R and L.
- Delay-Line + coincidence detector produces a map of azimuth.

Barn Owls

Roger Payne established that barn owls hunt in total darkness by using passive listening (Payne, 1971)*. Later work by Masakazu Konishi established the owl as an experimental model system in Neuroethology.

* Payne, R. S. (1971) Acoustic location of prey by barn owls (Tyto alba).
In barn owls, asymmetric ear placement converts IID into a map of elevation.

Head turning does not depend on feedback:
- Short sounds: head turn begins after the sound.
- Magnitude of turn is correct for sounds of different directions.
- Accuracy is 1 to 2 degrees.
- Ballistic movement, no feedback needed.

Map of ITD

Discovery:
“A Neural Map of Auditory Space”

ERIC I. KNUDSEN
MASAKAZU KONISHI
SCIENCE, VOL. 200, 19 MAY 1978
Individual neurons in inferior colliculus are “space-tuned”. Their receptive fields are oval shaped, tuned for sound direction.

Knudsen & Konishi (1978)

Tuning is determined by two different sensory cues: ITD and ILD.

Knudsen & Konishi (1978)

A map of auditory space

Knudsen & Konishi (1978)

Single Cells in the IC

• space-tuned receptive fields
• arranged in a map of auditory space
• map is a “computational map” not a map of a sensory surface.

Top Down Case in Point

While I was waiting for the large anechoic room that was to be assembled in my laboratory, I worked on the owl’s visual Wulst with Jack Pettigrew. After one year of exciting research with Jack, he asked me what I was going to do with the auditory system. Since I was impressed by the selectivity of visual neurons for space, I told him that I would like to map the spatial receptive fields of auditory neurons. He enthusiastically endorsed this idea and paid for the necessary instruments to be built by the legendary designer and machinist Herb Adams. The idea was to deliver sounds from various directions to plot the distribution of neuronal responses in space. About this time, Eric Knudsen asked me if he could join me as a postdoc. Eric and I met in a café or hamburger joint in Manhattan to discuss our project. When he asked me what I was looking for, I answered “a map of auditory space,” because the owl can rapidly pin point sound sources as if it were using a look-up table. Eric said that he would expect a map without any reason. We were naive and ignorant because we did not know Arnold Starr’s review* in which he pointed out that neither spatial receptive field or maps should exist in the auditory system because space is not mapped in the inner ear.

Mark Konishi

ISN Newsletter March 1999

http://www.neurobio.arizona.edu/isn/Newsletters/isn.news.mar99.sec2.html#2

We did find neurons with spatial receptive fields first in the forebrain auditory area. We could not, however, recognize any map of auditory space. Eric suggested that we go to the inferior colliculus. Since we could not afford to kill an owl to make a brain atlas, we used the head of a frozen owl. We cut it with a band saw and look at unstained sections to determine the coordinates of the inferior colliculus. In the first multiunit recording, we saw a cluster of neurons responding only to sound coming from a particular direction. As I was leaving for somewhere, Eric continued to record further. He later reported to me that the preferred sound direction changed systematically as he moved the electrode. We worked very hard for about three months to find a map of auditory space. Eric and I celebrated this occasion with a bottle of champagne. - Mark Konishi


Neurophysiological mechanisms of sound localization.
Behavioral Test of ILD

- Trained owls
- Right ear plugged: owl turns down
- Left ear plugged, turns up

Behavioral Test of ITD

- Owl presented with an artificial ITD from two earphones.
- Owl turns head after training to locate sounds at different azimuths
- Main cue: ongoing disparity of sound times (ITD)

ITD Test

- Behavioral test, trained owl
- ITD manipulated with stereo headphones.
- Owl turns toward time-advanced sound.
- 10 microsec sensitivity.

Hypothesis

- Vertical axis coded by IID
- Horizontal axis coded by ITD

Time pathway in the owl (blue)

Cells in nucleus magnocellularis project to nucleus laminaris both ipsilaterally and contralaterally. Ipsilateral axons enter dorsally, contralateral axons enter ventrally.

NL: azimuth maps onto depth in nucleus
NL analogous function to MSO in mammal

Carr, CE & Konishi, M 1988
C. Carr and M. Konishi find cells in *nucleus magnocellularis* that could generate a map of azimuth.


Map of Interaural Level Differences?

Injections of tracer in the Right VLVp reveals terminals in the left dorsal VLVp

Time and Amplitude Pathways Converge in the IC

The two cochlear nuclei specialized for either time encoding or amplitude encoding

- N. magnocellularis:
  - TIME PATHWAY
  - thick axons; heavy myelin
  - endbulb of Held
  - adendritic cell

- N. angularis
  - AMPLITUDE PATHWAY
  - small boutons
  - diffuse arbor

Vision guides plasticity

Q? How does the ITD map get calibrated in development?
Head size is changing

The Auditory Map is Plastic

1. Earplugs cause localization errors toward plugged ear.
2. These errors are temporary: after 2-3 weeks with earplugs, owls learn correct sound location.
3. After removal of ear plugs, owls again make errors.
4. These post-removal errors are also reversible (in young owls)
5. However, adults do not compensate for ear plugs.

Vision is important in re-adjusting the auditory map

- Errors corrected after ear plug removal (A, B)
- No correction if blinders are placed on owl after plug removal (C).
- No correction if vision is displaced using prisms (D)

Knudsen and Knudsen (1985)

When recording from neurons in Optic tectum, ITD from a neuron in the 0 degree azimuth part of the map is tuned to 0 degrees azimuth.

After 8 weeks with L23 prisms, a neuron in the zero degree part of map is now tuned to 50 microsecond ITD. (the map has become displaced)

Vision guides plasticity

Vision guides plasticity

E. Knudsen, 1999
Spectral cues (used for vertical localization by humans) are shifted by modified pinna (using ear molds).

Relearning sound localization with new ears.

Plot shows monaural sensitivity as function of frequency and sound elevation (control listening above, with modified pinna shape (ear mold)).

Errors in elevation estimation caused by insertion of earmolds are gradually corrected (over 39 days).
Removal of earmold results in instantaneous recovery of elevation accuracy.

Lessons from Owls
1. Barn owls are "champions" at sound localization. Their auditory system is specialized for this function both in terms of accuracy and the fact that it is a 2-D system that uses cues for both azimuth and elevation.
2. There are two parallel auditory systems in the owl: one specialized for analysis of ITD, the other for analysis of IID. These parallel pathways are specialized. Far for encoding and preserving time one for encoding and preserving amplitude.
3. Combined in the midbrain, the owl generates an computational map of auditory space. (Computational: does not exist in the periphery)
4. ITD pathway generates a place map using delay-line + coincidence detectors. The place map was predicted by L. Jeffress (1948).
5. Alignment of the auditory map with the visual map in the optic tectum is plastic. In young owls it can be re-aligned by early experience.
6. Realignment of the map requires re-wiring of the neurons in the optic tectum by growth of dendrites and formation of new synapses.