Animal Navigation:
Behavioral strategies, sensory cues, and brain mechanisms

Nachum Ulanovsky
Department of Neurobiology, Weizmann Institute of Science
Outline of today’s lecture

• Introduction: Feats of animal navigation

• Navigational strategies:
  • Beaconing
  • Route following
  • Path integration
  • Map and Compass / Cognitive Map

• Sensory cues for navigation:
  • Compass mechanisms
  • Map mechanisms

• Brain mechanisms of Navigation (brief introduction)

• Summary
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• Summary
Shearwater migration across the Pacific

Population data from 19 birds

←3 pairs of birds

Recaptured at their breeding grounds in New Zealand

Some other famous examples

- **Wandering Albatross:** finding a tiny island in the vast ocean
- **Salmon:** returning to the river of birth after years in the ocean
- **Sea Turtles**
- **Monarch Butterflies**
- **Spiny Lobsters**
- ... And many other examples (some of them we will see later)
Mammals can also do it… Medium-scale navigation: Egyptian fruit bats navigating to an individual tree

Tsoar, Nathan, Bartan, Vyssotski, Dell’Omo & Ulanovsky (PNAS, 2011)
GPS movie: Bat 079
A typical example of a full night flight of an individual bat released @ cave
Characteristics of the bats’ commuting flights:

- Long-distance flights (often > 15 km one-way)
- Very straight flights (straightness index > 0.9 for almost all bats)
- Very fast (typically 30–40 km/hr, and up to 63 km/hr)
- Very high (typically 100–200 meters, and up to 643 m)
- Bats returned to the same individual tree night after night, for many nights

With Y. Yovel & I. Borisov

Tsoar, Nathan, Bartan, Vyssotski, Dell’Omo & Ulanovsky (PNAS, 2011)
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**Visual Beaconing in Wasps (Tinbergen)**

**Beaconing:** Navigation towards a directly-perceptible sensory cue.

Training

- Sandpatch
- Pinecones

Nest

- 17 wasps
- 5-12 choices each

Dummy nest

- 17 wasps
- 5-12 choices each
Visual Beaconing in Ants that inhabit cluttered environments

Olfactory Beaconing in Pacific Salmon

Olfactory Beaconing in Pacific Salmon

(1) Age 0+: emergence from gravel and migration to lake

(2) Age 0–3: lake residence

(3) Age 2–3: smolting and migration to sea

Outflow

Iliamna Lake

Dittman and Quinn, JEB 1996
Olfactory Beaconing in Pacific Salmon

(4) Age 4–6: ocean distribution prior to homing migration
Olfactory Beaconing in Pacific Salmon

(5) Age 4–6: homing migration to lake

(6) Homing to natal site for spawning

Iliamna Lake

Outflow

Kilometers

0 10 20
Olfactory Beaconding in Pacific Salmon

Olfactory Imprinting: experimental manipulations of artificial odorants using laboratory- or hatchery-reared salmon have shown that the fish navigate up-gradient towards the odor with which they were imprinted (in the wild: the odor of their stream).
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Route following (route guidance) in ants

20 m long corridor of 1-m wide with cues at every 2 m interval

cylinder: 60 cm height
: 16 cm diameter

Ants trained for 14 days (~300 trials)

Route following (route guidance) in ants

Information from path integrator is used, but it is not essential!

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Definition of Path Integration:
“...a running computation of the present location from the past trajectory”

(term coined by Horst Mittelstaedt)

• A continuous process of computation/integration
• Provides an estimate of present location
• Trajectory/motion cues are required
• Requires no landmarks or trails
Most famous path-integrator: The desert ant, *Cataglyphis fortis*

Lives in extremely flat and featureless salt planes in the Sahara
Backup strategy in the desert ant: Systematic Search
Outline of a Path Integration system

Distance:
per unit time

Direction
Rotation per unit time

Path Integration system

“Home vector”
(estimates the vector pointing towards home)

Need mechanisms for:

- Measuring **distance** (per unit time)
- Measuring **direction** (per unit time)
Manipulating the Sun’s direction by using a mirror showed that ants use a sun compass.
Insects can see the polarization pattern of the sky in the Dorsal Rim Area of their compound eyes. Experiments with rotating polarization filters have shown that desert ants indeed functionally use a polarization compass.
When sun and polarization directional cues are unavailable, the desert ant uses a wind compass.
Distance measurement (odometer) in desert ants: Step Counter


Measuring distance ("odometer"):

- In desert ants = step counter
- In honeybees = optic flow
BUT: Path integration is error prone

- Systematic errors sometimes $> 20^\circ$ in direction
- Random errors sometimes $\sim 10^\circ$ in direction
BUT: Path integration is error prone

- The problem: Path integration accumulates (integrates) the errors.
- Mammals are less good path integrators than the desert ant. Random errors are even larger in rodents than in ants (Etienne et al., *Nature* 1998)
- Path integration in mammals is likely most useful for “filling the gaps” when reliable external sensory information is *not* available.

In another experiment:
Random errors of ~25% in *distance*

Merkle, Knaden, Wehner (2006)
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The cognitive map: A concept that arose historically (Tolman 1948) from laboratory work in rats = small scale navigation. The “neuropsychological” approach.
Kramer (1953) suggested that long-distance homing (in the field) occurs in two steps:

1. The Map step: computing your location.
2. The Compass step: computing the direction to home.

This is the basic framework to this day in studies of animal navigation in the field.

*The map-and-compass*: A concept very close to that of the cognitive map; arose historically (Kramer 1953) from a very different research community, that of people doing field work in birds = large scale navigation. The neuroethological approach.
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Honeybee navigation and the use of the sun compass

Movie (M. Srinivasan)
Honeybee navigation and the use of the sun compass

The waggle dance:
A symbolic ‘language’
(Karl von Frisch)
Honeybee navigation and the use of the sun compass

Round dance
(feeder distance < 50m)

Waggle dance
(feeder distance > 50m)
You can use the waggle dance to ask how far the bee *thinks* that it flew ... just like you can use the directed search of a desert ant to ask how far the ant *thinks* that it walked.

Srinivasan used this to show that the honeybee odometer is based on *optic flow*. 
Optic flow is important for honeybees.

I. Optic flow controls their flight speed

Speed of flight is regulated by holding the global image velocity constant

Srinivasan, Zhang, Lehrer & Collett
II. Honeybees use optic flow to measure distance

How do the recruits respond to the dancing tunnel bees?

Scouts returning from 6 m tunnel signal a distance of 200 m

Recruits search at 200 m

Esch, Zhang, Srinivasan & Tautz
Nature (2001)
**Hypothesis:** Hatchling sea turtles use wave direction to keep course into the open sea and away from shore

![Wave direction diagram]

*Sea turtle hatchlings use the direction of waves as a compass*
Sea turtle hatchlings use the direction of waves as a compass.

Lohmann and Lohmann (1996)
Compass mechanisms in birds

- **Celestial compass:**
  - **Stars** (in night-migratory birds): Can be manipulated in a planetarium, e.g. if rotating the simulated starry sky by 90°: birds rotate by 90°
  - **Sun:** Can be manipulated by clock-shifting

- **Magnetic compass** (based on the geomagnetic field)

(note that the geomagnetic field can be used both for **compass** and for **locational** information – as we’ll see later)
Demonstrating sun compass in pigeons
Demonstrating magnetic compass navigation in migratory birds in captivity

These laboratory experiments rely on the behavioral phenomenon of Zugunruhe (migratory restlessness)

Funnel cage by Emlen & Emlen (1966)

Funnel cage lined with coated paper
Demonstrating magnetic compass navigation in migratory birds in captivity
Demonstrating magnetic compass navigation in migratory birds in captivity

- Local geomagnetic field
- Magnetic North turned 120° to ESE

- $N = mN$
- $SE = mN$

European Robins
Mechanism of magnetic compass in night-migratory birds (e.g. European robins): Light- and magnetic-field-dependent radical-pair reaction?

Candidate molecules: Cryptochromes, which are located in the bird’s retina.
Testing the radical pair model

Magnetoreception is light-dependent

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Compass Mechanisms: Summary

• ‘Compass’ from path integration (integrating vestibular cues: semicircular canals)
• Distal visual cues (e.g. mountains)
• Polarization compass: In insects
  • Wind
  • Sun
  • Waves
  • Stars
  • Magnetic
• Others...
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Map mechanisms

Three main map mechanisms:
- ‘Mosaic map’ based on visual landmarks
- Magnetic map
- Olfactory bi-gradient map
The concept of ‘Mosaic Map’ based on familiar landmarks

- Self-triangulation.
The magnetic field of the earth
Magnetic Inclination provides information about Latitude

- **Magnetic Declination** (deviation of magnetic north from true north) provides some information about *Longitude* (at least close to the poles).
Magnetic Anomalies might provide detailed local map information.
Evidence for usage of magnetic map information in sea turtles

Trigger effect in young marine turtles, *Caretta caretta*

The magnetic conditions in specific areas elicit different directional tendencies

(Lohmann & Lohmann, Nature 2002)
Mechanism for sensing magnetic intensity in birds

**Magnetite** is found in the upper beak of birds:

*Caveat:* Raging arguments for years between proponents of **magnetic map** and proponents of **olfactory map**: The key reason that these arguments rage is that both the nostril and the upper beak are innervated by the same nerve, so invasive experiments that are done to show causality (and many such experiments have been done) are very difficult to interpret unequivocally as supporting one sensory system or another.

(from Fleißner et al. 2003)
Mechanism for sensing magnetic intensity in birds

**Magnetite** is found in the upper beak of birds:

In addition, a recent paper (Treiber *et al.*, *Nature* 2012) has cast doubt that the magnetite particles are located in sensory neurons, and proposed instead that the magnetite is concentrated in immune-system cells, and thus cannot be related to navigation!

(from Fleißner *et al.* 2003)
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Brain Mechanisms of Navigation – Outline

• Hippocampus and spatial memory: early discoveries
• Hippocampus and large-scale navigation
• Back to small-scale navigation in the laboratory:
  • Place cells
  • Head direction cells
  • Grid cells
  • Other brain areas involved in navigation
Brain Mechanisms of Navigation – Outline

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The hippocampus

Egyptian fruit bat

Echidna
(ancient egg-laying mammal)

Rat
The hippocampus

- Highly conserved brain structure across all mammals, including humans (exists also in birds, but looks quite different)
- The most important brain region, clinically

(Amaral and Witter 1989)
Hippocampal place cells in rats

(O’Keefe & Nadel 1978)
(O’Keefe & Dostrovsky 1971)

John O’Keefe

Spike count
Time spent
Firing-rate map

‘Place field’ of a pyramidal cell in rat hippocampus

(Muller et al. 1987)
Movie of a rat hippocampal place cell in action
Bilateral hippocampal lesions impair allocentric navigation

These deficits of spatial memory occur after lesions in dorsal hippocampus – not ventral hippocampus.
Rat navigation in a watermaze is thought to be similar to the concept of ‘Mosaic Map’ in birds: self-triangulation based on distal landmarks.
Neuroethology and the discovery of place cells

O’Keefe & Nadel, “The hippocampus as a cognitive map” (1978)
Neuroethology and the discovery of place cells

O’Keefe & Nadel, “The hippocampus as a cognitive map” (1978)

question, even with a good bit of luck and insight.* We suggest that during the exploratory phases of research into the function of a structure it is necessary to use a more information-rich methodology, the neuroethological one.

The neuroethological approach differs from the neuropsychological one in several respects. First, it seeks to study the activity of single units in as naturalistic a setting as possible, in the belief that an animal’s behaviour in its natural environment maximizes the possibility of producing changes in unit activity that are meaningfully related to that unit’s function. It thus embodies the reasonable assumption that the brain of a particular animal is built to operate in a specific environment. At the very

4.7.1. A NEUROETHOLOGICAL STRATEGY
The strategy used in our own work on single-unit activity in the hippocampus of the freely moving rat leans towards the neuroethological, rather than the neuropsychological, approach. The following is a general outline of this procedure.
Brain Mechanisms of Navigation – Outline

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Hippocampal volume correlates with navigational load in rodents

A  Male and female range size
polygamy: *meadow vole*  monogamy: *pine vole*

B  Relative hippocampal volume

![Graph showing hippocampal volume in meadow and pine voles](image-url)
Hippocampal volume correlates with navigational load in humans

Volume of posterior hippocampus in humans (equivalent to dorsal hippocampus in rats):

- Larger in London taxi drivers than in age-matched controls.
- Correlated with time spent as a taxi driver.
- Larger in Taxi drivers than in experience-matched Bus drivers.
- In Bus drivers, no correlation with experience was found.

Maguire et al., *PNAS* (2000)

Interpretations:

- The hen and the egg problem: Does posterior hippocampus grow with experience (plasticity), or is a large hippocampus needed in order to do well and "survive" for many years in the demanding profession of a London taxi driver?
- Navigation based on a cognitive-map strategy (taxi drivers) requires/causes a larger hippocampus than route-based navigation (bus drivers)?
Lesions in the hippocampus of homing pigeons affect navigation.

- Regular release
- Clock-shifted (requires re-orientation)

4 Controls

4 hippocampus lesioned birds

Note flight over the sea →
Lesions in the hippocampus of homing pigeons affect navigation

- **Interpretation**: The map is not stored in the hippocampus, since hippocampus-lesioned birds could home; only re-orientation seems to depend on the hippocampus

- **Caveat**: Bird hippocampus differs substantially in morphology from mammalian hippocampus

Extraordinary flight of a hippocampus-lesioned bird above the sea: Never occurs in normal birds
CAVEAT: No studies of place cells were done on this scale...

... and not even on this scale
... Largest place fields demonstrated to date: ~10 meters

Still not large enough… Rats in the wild (real rats, not laboratory rats) navigate distances of up to 1–2 km per night = much larger distances than 10 meters.
Brain Mechanisms of Navigation – What I will talk about

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Neural basis of map-and-compass navigation?

1. Map

2. Compass

Head-direction cells
Presubiculum (PrS)

Place cells
Hippocampus

Courtesy of Menno P. Witter

Movie courtesy of Tor Kirkesola, 2010

Ranck & Taube
JNS 1990

Movie courtesy of Dori Derdikman, 2010
Brain Mechanisms of Navigation – What I will talk about

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Place fields increase in size along the dorso-ventral axis in the hippocampus: A gradient of spatial resolutions


2 cells in dorsal hippocampus

2 cells in ventral hippocampus
Place fields increase in size along the dorso-ventral axis in the hippocampus: A gradient of spatial resolutions

Hypothesis: very large-scale place fields here, at the temporal pole??
The place fields of hippocampal place cells tile the environment
The rat’s location can be reconstructed from the activity of an ensemble of simultaneously-recorded place cells.

Putative pyramidal neuron (place cell)

Interneuron (very little spatial modulation)

Tetrode recording of 80 neurons simultaneously

Multiple maps are stored simultaneously in rat hippocampus

“Remapping” between representations of square and circular environments.

Wills et al., Nature (2005)
Place cells in bat hippocampus

A single cell in big brown bat

More examples of place fields from 6 neurons

And in another bat species: Egyptian fruit bat.

Examples of hippocampal place fields from our current study species, the Egyptian fruit bat.

As in rats, these place fields tile the environment, and represent the animal’s spatial location.

Yartsev, Witter, Ulanovsky
Nature (2011)
Telemetric recordings from the hippocampus of a flying bat

Yartsev & Ulanovsky
Science (2013)
3-D place cells in bats

- 3-D place fields are spherical in shape: Same resolution in all directions (isotropic).
- 3-D place fields Tile space uniformly.

Yartsev & Ulanovsky
Science (2013)
Many mammals navigate through 3-D complex environments.

Open question: How is 3-D space represented in mammalian brains across species?
Outline of today’s lecture

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  • **Head direction cells**
  • Grid cells
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• Summary
Head direction cells are found in the dorsal presubiculum, anterior thalamus, medial entorhinal cortex, and in several other brain areas adjacent to the hippocampus.

These cells are tuned to head direction, but *not* to place – i.e. they serve as neural “compasses”.

---

**Head direction cells in dorsal presubiculum of rats**

![3 Head Direction Cells Firing Fields](image)

- Head direction cells are found in the dorsal presubiculum, anterior thalamus, medial entorhinal cortex, and in several other brain areas adjacent to the hippocampus.
- These cells are tuned to head direction, but *not* to place – i.e. they serve as neural “compasses”.
Is there a representation of 3-D head direction in the mammalian brain = “3-D neural compasses”?  

**Head-direction cells**  
*In rats*  
Solstad et al.  
Science 2008

**Head-direction cells**  
*In bats*  
Yarcev, Witter, Ulanovsky  
Nature 2011
Tracking the rotation angles (Euler angles) of the bat’s head in 3-D

Euler Angles

Bat looking straight (0 pitch)
Bat looking up (positive pitch)
Bat looking down (negative pitch)

4-LEDs tracking head-stage

Recording from bat dorsal presubiculum
Example cells:
Azimuth, Pitch, and conjunctive Azimuth x Pitch

Finkelstein et al.
• About 35% of Azimuth-tuned cells were also tuned to Pitch or Roll.
• Tuning to Roll was weaker and much less prevalent.
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Grid cells in medial entorhinal cortex (MEC)

Cell 1

Cell 2

Cell 3

Cell 4
Grid cells are organized in *modules*. Cells from the same module share the same grid spacing and orientation, but have a random grid phase.
Entorhinal grids might be combined to produce hippocampal place fields: Hexagonal Fourier-like decomposition

Model by Solstad et al. (2006)

- Grid cells may provide the basis functions for the representation of space in the mammalian brain.
- Findings in recent years have complicated this picture... Perhaps in fact the place cells generate the grid cells – or maybe it’s a loop.
Grid cells in bats

Yartsev, Witter, Ulanovsky
Nature (2011)
Proposed role of grid cells in path integration (in Rats)

- **Finding:** Grid cells persist after turning off the light (Hafting et al. 2005, see example above).

- **Caveat:** In these experiments, there was no attempt to remove odors (local cues): i.e., the rats could have been using a route-following navigational strategy (via local olfactory landmarks) to know their location – and not necessarily path integration.
Another caveat: Path integration is error prone

Mammals are less good path integrators than the desert ant. Rodents are not able to path-integrate reliably for more than 1–3 m (Etienne et al, *Nature* 1998).

A graph that we have seen earlier.

In *desert ants*: Random errors of ≈25% in distance.

Mammals are less good path integrators that the desert ant.
Hypothesized role of grid cells in large-scale navigation


*BUT*: No such huge grids were studied, to date.
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Other brain areas involved in navigation

* Beaconing / “response strategy” – **striatum**. That is, if you train a rat to always turn left (response strategy): this depends on the striatum. But if you train the rat to reach some *absolute* location in space: this depends on intact hippocampus & entorhinal cortex.

* Route-based navigation, transformations from organism-based (“egocentric”) coordinate frame to absolute-space-based (“allocentric”) coordinate frame – **parietal cortex**?
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Spatial cell types in the hippocampus and entorhinal cortex: The basic elements of the rat’s “brain navigation circuit”

Medial entorhinal cortex

- Border Cells
- Head-direction cells

Hippocampus

- Grid cells
- Place cells

Solstad et al., Science 2008

Hafting et al., Nature 2005

Fyhn et al., Science 2004
Spatial cell types in the hippocampus and entorhinal cortex:
The basic elements of the rat’s “brain navigation circuit”

**SUMMARY:**
- **Place cell** → **Position** (where am I)
- **Grid cells** → **Distance** (“ruler”)
- **Border cells** → **Borders** of the environment
- **Head-direction cells** → **Direction**

\[\text{Map} \quad \text{Compass}\]
Animal navigation is complex and rich, and relies on multiple cues:

- Need to find animal models that allow isolating certain cues or strategies (e.g. path integration in the desert ant)

**Warning:** When studying navigation and spatial memory in the lab, always be mindful of the rich set of strategies that animals could use. Be very careful and suspicious: Perhaps the animal is using another cue, not what you are thinking? Perhaps your animal is ‘cheating’ you? Perhaps you are cheating yourself? ...

The same warning goes for all of animal behavior: When studying a certain behavioral phenomenon, be very careful and make sure you ruled out the possibility that the animal is using an alternative behavioral strategy.

**The good news are:** It’s possible to do it! But you have to be careful.
Future challenges in the study of the neural basis of animal navigation, spatial memory and spatial cognition

- Gap in spatial scale: Even rats (let alone bats) would require in the wild much larger place fields & grid fields than shown to date in the laboratory.

- Too little is known about the neural basis of the “higher” components of navigation (apart of the “map” component and “compass” component) – and this needs to be elucidated:
  - How do animals compute the Home Vector?
  - Trajectory planning?
  - Decision making?
Future challenges in the study of the neural basis of animal navigation, spatial memory and spatial cognition

Our lab is currently investigating directly some of these big open questions:

• How does the brain represent the spatial position of goals?  
  *Answer: we find a vectorial representation of goals (direction & distance).

• What are the neural codes for space on truly large scales (hundreds of meters or 1-km)?

Thank you!