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

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**Why study animal navigation?**

- Navigation is a higher brain function that is:
  - Important for the animal’s survival (behaviorally relevant)
  - **Quantifiable** (spatial accuracy, straightness, time...)
  - Closely related to learning and memory (spatial memory)

For this reason, many researchers who are interested more generally in learning and memory, study the case of navigation and spatial memory.

- A meeting place of the neuroethological and neuropsychological approaches.
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

GPS Movie
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

The bats relied on spatial memory.

Tsoar, Nathan, Bartan, Vyssotski, Dell’Omo & Ulanovsky (PNAS, 2011)
Homing experiments

Bats displaced 45 km south

Bat 157

Bat 160
Homing experiment – bat #160

From displacement (night 1)

From cave (night 3)

Foraging at same two familiar trees (night 2)
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• Next week: Brain mechanisms of navigation
**Visual Beaconing in Wasps (Tinbergen)**

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

- **Training:**
  - *Nest*
  - *Dummy nest*

- **Mocking the Visual Beaconing Effect:**
  - *Nest*
  - *Dummy nest*

- **Graph:**
  - 17 wasps, 5-12 choices each.
Visual Beaconing in Ants that inhabit cluttered environments

View-based Homing:
The problem of visual ambiguity

Extreme example: Repetitive structures.
Animals (e.g. birds) have difficulties with repetitive structures in the world.

Animal Architecture.
Hutchinson, London
Olfactory Beaconing in Pacific Salmon

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

Kilometers

0  10  20
Olfactory Beaconsing 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

Training stage

PI Routemarks

FvRm+

PI ONLY

FvRm-

Routemarks ONLY

ZvRm+

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

Homing Pigeons sometimes follow highways & exits

Lipp et al. (2004)
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Path integration

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

Rudiger Wehner
Outline of a Path Integration system

Distance: per unit time

Direction: Rotation per unit time

Path Integration system

“Home vector” (estimated location = vector relative to 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

(BEES: Srinivasan et al., will appear in your reading material)

Path integration only in X,Y, not in the third dimension


Wohlgemuth et al., Nature (2001)
BUT: Path integration is error prone

• Systematic errors sometimes > 20° in direction

• Random errors sometimes ~ 10° in direction

• Systematic errors (underestimation) of ~20% in distance

• Random errors (variability) of ~10% in distance

Sommer & Wehner (2004)
BUT: Path integration is error prone

Mammals are less good path integrators than the desert ant. Random errors are even larger in rodents than in the ant (Etienne et al, *Nature* 1998).

In another experiment:
Random errors of \(\sim 25\%\) in distance

Merkle, Knaden, Wehner (2006)
Backup strategy in the desert ant: Systematic Search
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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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Compass Mechanisms

• ‘Compass’ from path integration (integrating vestibular cues: semicircular canals)
• Distal visual cues (e.g. mountains)
• Polarization compass: In insects, and possibly by Vikings (‘sun-stone’, Cordierite?)
• Wind
• Sun
• Waves
• Stars
• Magnetic

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

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

Round dance  
(feeder distance < 50m)

Waggle dance  
(feeder distance > 50m)
Sea turtle hatchlings use the direction of waves as a compass.

**Hypothesis:** Hatchling sea turtles use wave direction to keep course into the open sea and away from shore.
Sea turtle hatchlings use the direction of waves as 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 magnetic compass navigation in migratory birds in captivity

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

Funnel cage lined with coated paper

Funnel cage by Emlen & Emlen (1966)
Demonstrating magnetic compass navigation in migratory birds in captivity
Demonstrating magnetic compass navigation in migratory birds in captivity

- Local geomagnetic field
- Control
- $N = mN$

- Magnetic North turned 120° to ESE
- $SE = mN$

European Robins
Mechanism of magnetic compass in night-migratory birds (e.g. European robins): Light- and magnetic-field-dependent radical-pair reaction?
According to the model: Pattern of radical-pair reactions on the bird's retina is modulated by the geomagnetic field as the bird flies to different directions.

(from Ritz et al. 2000)
Testing the radical pair model

The first step - absorption of a photon - would make magnetoreception light-dependent.
Testing the radical pair model

Magnetoreception is light-dependent

LED - Spektra

Wavelength (nm)

Austr. Silvereye
European Robins
Garden Warbler
Carrier Pigeon
Domestic Chicken

Testing the radical pair model
Testing the radical pair model

High frequency electromagnetic (radio) waves in the MHz frequency range should interfere with the singlet-triplet transition!
Testing the radical pair model

Candidate molecule that can form the crucial radical pairs: **Cryptochrome**. Was found in the retina of European Robins, in cells that project into a brain area involved in magnetic processing (“Cluster N”).

*Caveat*: According to the model, Cryptochrome molecules need to be anchored perpendicularly to retina, which was not shown yet, and it’s unclear how this could occur.

0.65 – 7.0 MHz radio waves indeed interfere!
Demonstrating sun compass in pigeons

Controls

Clock-shift 6 h slow
Sun compass in pigeons is Learned

Establishing the sun compass in young homing pigeons:

(1) Takes place spontaneously in the 3‘rd month of life and can be advanced by early flying experience.

(2) The pigeons must observe large portions of the sun's arc at different times of the day to be able to use the sun compass during the entire day.

(3) The geomagnetic field serves as reference system to assess the changes in sun azimuth.
Sun compass in pigeons is Learned

After observing the sun in an altered magnetic field for 10 days:

The magnetic field serves as reference for learning the sun compass.

Indicates a sensitive phase (critical period)

Young pigeons

Old, experienced pigeons
Sun compass seems to dominate over magnetic compass in pigeons
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Map mechanisms

Three main map mechanisms:

• ‘Mosaic map’ based on landmarks
• Magnetic map
• Olfactory bi-gradient map
The concept of ‘Mosaic Map’ based on familiar landmarks
The magnetic field of the earth
Magnetic Inclination provides information about Latitude
Magnetic Anomalies might provide 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 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.
Mechanism for sensing magnetic intensity in birds

Magnetite is found in the upper beak of birds:

(from Fleißner et al. 2003)

In addition, a very recent paper (Treiber et al., *Nature*, April 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!
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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)

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

(Courtesy of Colgin, Moser & Moser)
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.

Large-scale navigation by birds

Small-scale navigation by rats in a watermaze
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 and brain volume for meadow vole and pine vole.](image)
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)

Note flight over the sea

4 Controls
4 hippocampus lesioned birds

1 km

HFA15
HF410
HF377
HF493
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) move much larger distances than 10 meters.
Brain Mechanisms of Navigation – What I will talk about

- Hippocampus and spatial memory: early discoveries
- Hippocampus and large-scale navigation
- Back to small-scale navigation in the laboratory:
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Place fields increase in size along the dorso-ventral (septo-temporal) axis in the hippocampus.

Hypothesis: very large-scale place fields here, at the temporal pole??

Place fields increase in size along the dorso-ventral (septo-temporal) axis in the hippocampus.
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.

Tetrode recording of 80 neurons simultaneously.

Putative pyramidal neuron (place cell)

Interneuron (very little spatial modulation)

Wilson and McNaughton, Science (1993)
Place cells in bat hippocampus

A single cell

More examples of place fields from 6 neurons

Ulanovsky & Moss,
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)
How would 3-D space be represented by place cells?
Previous attempts to address the question of 3-D spatial representation in the mammalian brain

**Problem**: Animals were moving on 2-D planes → could not provide answers regarding TRUE 3-D space.

**Solution**: Use an animal that can move freely in 3-D space.
Telemetric recordings from the hippocampus of a crawling bat

Telemetry system weighing 10–15 gr total – *Rousettus* bats (~150 gr) can easily carry it.

→ Extensive testing of the telemetry system in our lab showed: (i) high bandwidth, (ii) linearity, (iii) very low noise.
Telemetric recordings from the hippocampus of a flying bat

Wing-beat artifact

Spikes

Michael Yartsev
Nachum Ulanovsky

% of artifact time during flight

1-3 4-6 7-9 10-12 13-15 16-18

Recording days

200 ms
3-D place fields in the hippocampus of flying bats

Example 1
3-D place fields in the hippocampus of flying bats

Example 2

Michael Yartsev
Nachum Ulanovsky
3-D place fields in the hippocampus of flying bats

MOVIE

3D_PF_CA1_movie.wmv
Gap in spatial scales and in dimensionality in lab experiments vs. real-life navigation

- Spatial scales and heights studied to date in hippocampal brain studies
- Spatial scales & heights that need be studies to relate to real-life navigation
Outline of today’s lecture

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  • **Head direction cells**
  • Grid cells
  • Other brain areas involved in navigation
• Summary
Head direction cells in dorsal presubiculum of rats

- 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”.

![Graphs showing firing fields of head direction cells](image)
Is there a representation of 3-D head direction in the mammalian brain?

Head-direction cells
In rats

Head-direction cells
In bats

Solstad et al.
Science 2008

Yarcev, Witter, Ulanovsky
Nature 2011
Tracking the rotation angles (Euler angles) of the bat’s head in 3-D

Euler Angles

Roll

Pitch

Yaw

4-LEDs tracking head-stage

Arseny Finkelstein
Dori Derdikman
Nachum Ulanovsky

Bat looking up (positive pitch)

Bat looking straight (0 pitch)

Bat looking down (negative pitch)
Recording from bat dorsal presubiculum
Example cell: 3-D tuning to yaw, pitch and roll

1st session:

About 30% of yaw-tuned cells were also tuned to pitch or roll: “3-D compasses”.
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Grid cells in medial entorhinal cortex (MEC)
Nearby grid cells have the same grid spacing and orientation, but 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
The Mystery: How are the grids formed?

Two major models of grid-cell formation:

1. Network interactions

2. Path integration using continuous theta oscillation (‘from oscillations in time to oscillations in space’)

Rat grid cell

McNaughton et al., 2006

Burgess et al., 2008
The Mystery: How are the grids formed?

Two major models of grid-cell formation:

1. Network interactions

2. Path integration using continuous theta oscillation (‘from oscillations in time to oscillations in space’)

Rat grid cell

Theta oscillation in rats

(Hollup et al. 2001)
The Mystery: How are the grids formed?

Two major models of grid-cell formation:

1. Network interactions

2. Path integration using continuous theta oscillation (‘from oscillations in time to oscillations in space’)

The Problem:
- In rodents, grid cells and theta oscillation are not dissociable

Rat grid cell

McNaughton et al., 2006

Burgess et al., 2008
Place cells in bat hippocampus

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)
Theta oscillation occurs in short intermittent bouts (~1-2 sec)

Example of a theta-bout

Like in humans...

(Cantero et al. 2003)

... and unlike in rats

(Hollup et al. 2001)
The Mystery: How are the grids formed?

Two major models of grid-cell formation:

1. Network interactions
2. Path integration using continuous theta oscillation (‘from oscillations in time to oscillations in space’)

Rationale of our experiments:

- In rodents, grid cells and theta oscillation are not dissociable
- If we find in the bat grid cells without theta oscillation, this will contradict the second class of models
- Unusual logic: Studies in bats could allow dissociating the two major theories of grid-cell formation in rats.
First grid cells in a non-rodent species

One of the first grid cells that we recorded in bat entorhinal cortex

Another example
First grid cells in a non-rodent species

Another example: A grid x head-direction conjunctive cell

Yartsev, Witter, Ulanovsky
Nature (2011)
Properties of grid cells in bat medial entorhinal cortex

Grid vertices are at 60° angles

Grid cells recorded simultaneously show clustering in orientation and spacing

Co-localized grid cell have different phases

Yartsev, Witter, Ulanovsky
*Nature* (2011)
• N = 25 grid cells in medial entorhinal cortex (MEC) of Egyptian fruit bats: very similar to grid cells in rats, in many of their detailed properties.
• We found also head-direction and border cells in bat MEC – similar to rats.
Theta oscillation in the rodent entorhinal cortex

Theta in the bat entorhinal cortex...

Grid cell autocorrelation

Theta oscillation in the rodent entorhinal cortex

Theta in the bat entorhinal cortex...
Bat grid cells show virtually no theta modulation of their firing.
Theta bouts are not required for creating the grids

Yartsev, Witter, Ulanovsky
Nature (2011)
But how are the grids formed?

Two major models of grid-cell formation:

1. Network interactions

2. Path integration using continuous theta oscillation (‘from oscillations in time to oscillations in space’)

Conclusion:
Theta oscillations are not required for the grids → Argues against the “oscillatory interference models” of grid cells
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).

Graphs from last week:

In desert ants:
Random errors of \(~25\%\) in distance
Hypothesized role of grid cells in large-scale navigation


*BUT*: No such huge grids were found yet (and it is difficult to look for them).
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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 – posterior parietal cortex?
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• Brain mechanisms of Navigation (brief introduction)

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Summary: Take home messages

• 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 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!
Spatial cell types in the hippocampus and entorhinal cortex: The basic elements of the rat’s “brain navigation circuit”

**Medial entorhinal cortex**

- **Border Cells**
  - Solstad et al., Science 2008

- **Head-direction cells**
  - Solstad et al., Science 2008

- **Grid cells**
  - Hafting et al., Nature 2005

**Hippocampus**

- **Place cells**
  - Fyhn et al., Science 2004
Summary of some caveats regarding studies of the neural basis of animal navigation

- 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 “you are here” component): How do animals compute the Home Vector? Trajectory planning? Decision making?

Thank you!