

A close-up photograph of a dog's snout, showing the texture of its fur and the details of its nose. The image is slightly blurred, focusing on the central part of the snout.

# **Olfactory navigation: using odors to orient in space and time**

***Deconstructing the  
Sense of Smell  
June 19, 2015***

**Lucia Jacobs**

**Department of Psychology & HW Institute of Neuroscience  
University of California, Berkeley**

*“Far better an approximate solution to the right question than an exact answer to the wrong question, which can always be made more precise.”*

John Tukey



The background of the slide is a photograph of an underwater scene. Sunlight filters down from the surface, creating a shimmering, dappled light effect on the water. The water is a clear, vibrant blue-green color. The overall atmosphere is serene and natural.

# **SPATIAL MAPPING EVOLVED UNDERWATER**



**In a world  
defined  
by chemicals**

**first  
universal  
only remote  
still expensive**





# **Spatial orientation**

## **Egocentric**

Learned reaction to objects

Beacon; turning algorithm

Unanchored; cumulative errors

## **Allocentric**

Self is object in landscape

Anchored in absolute space

Expensive but resilient



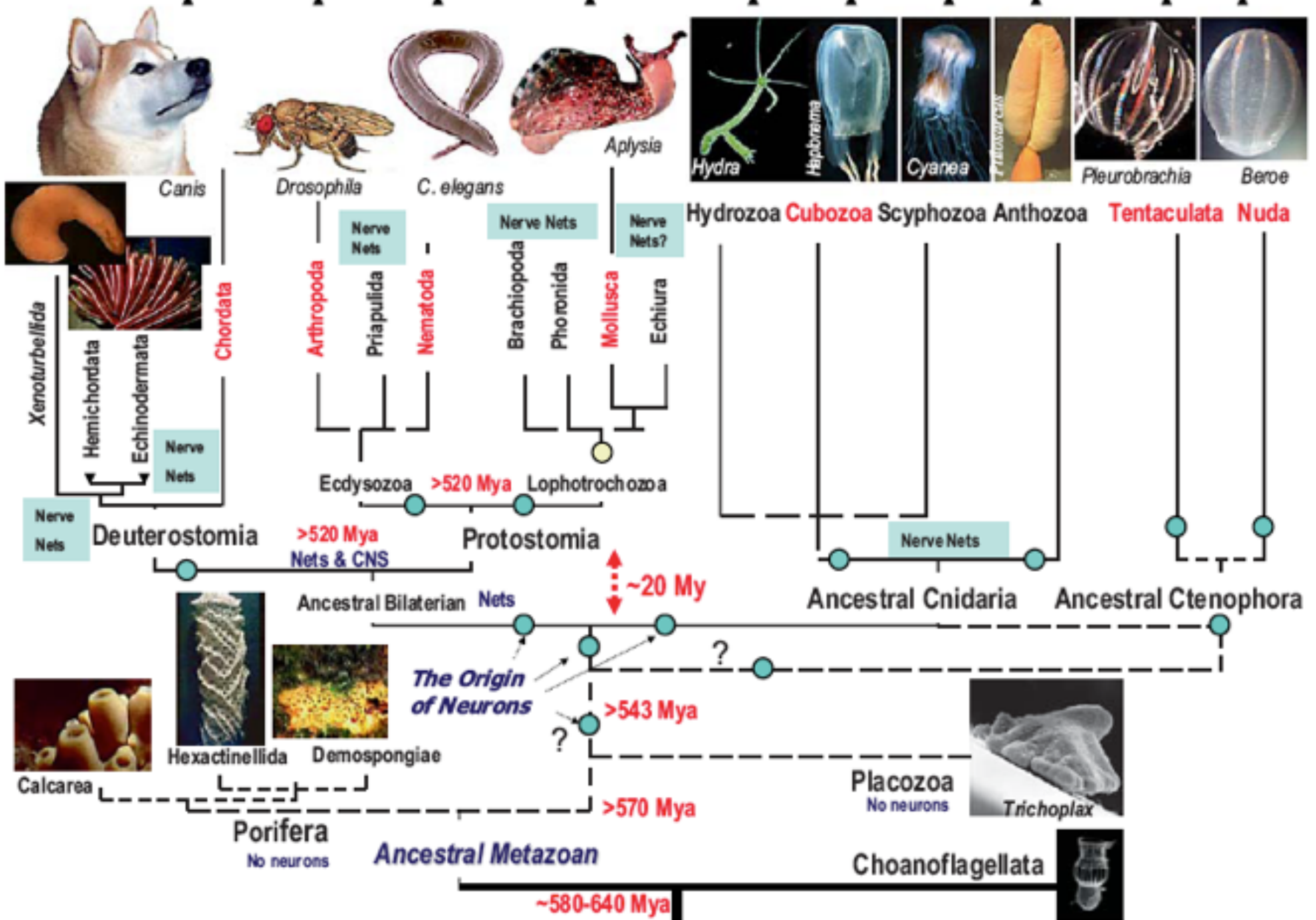
**When did this  
evolve?**



# Brains, Centralized Nervous Systems & Nets

# Diffuse Nerve Nets

# Nets & "Brain"



Moroz, L. 2009 On the independent origins of complex brains and neurons  
Brain Behav Evol 74: 177-190



**Why did this  
evolve?**



# Cambrian explosion



[www.johnsibbick.com](http://www.johnsibbick.com)

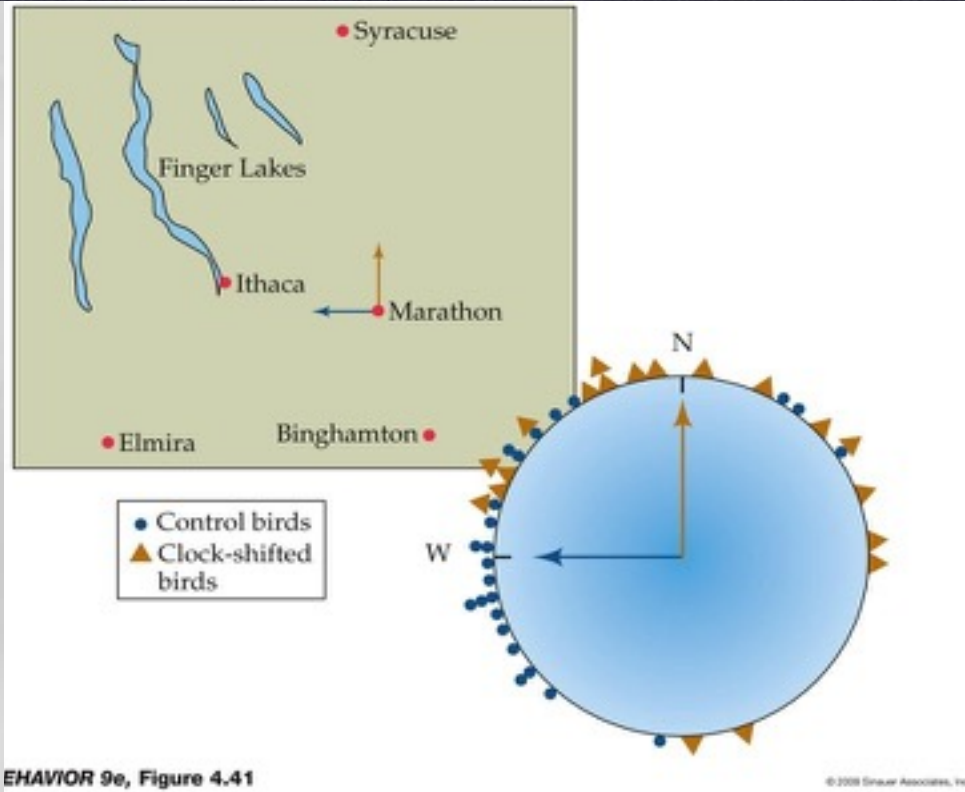
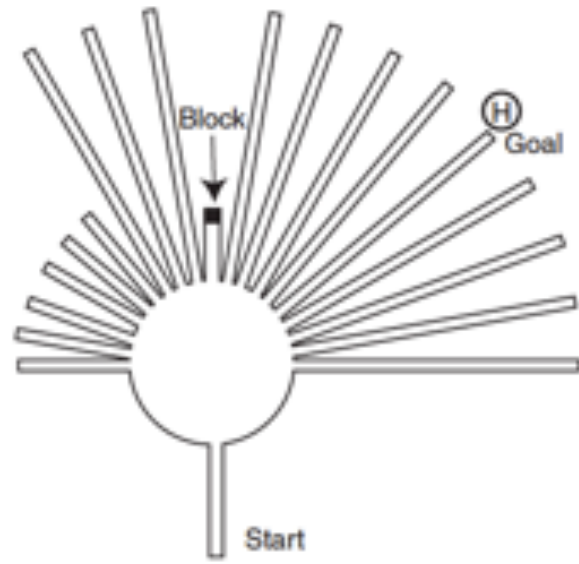
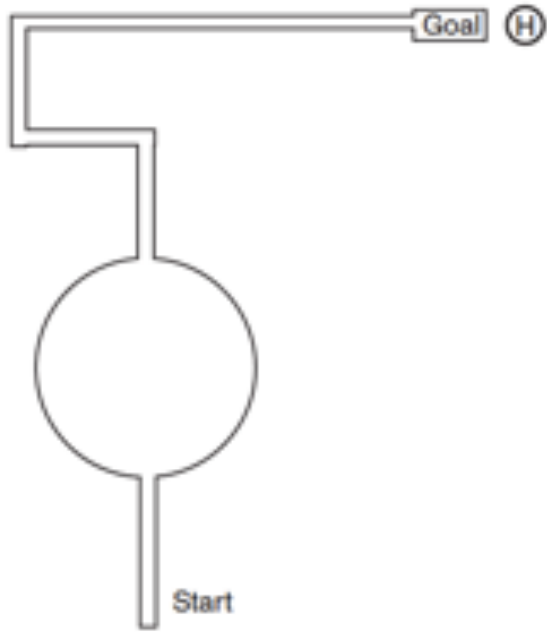
# What is true navigation?

Not egocentric (S-R)

Not memorized allocentric (route)

*Creating novel path across untravelled space, in the absence of beacons.*

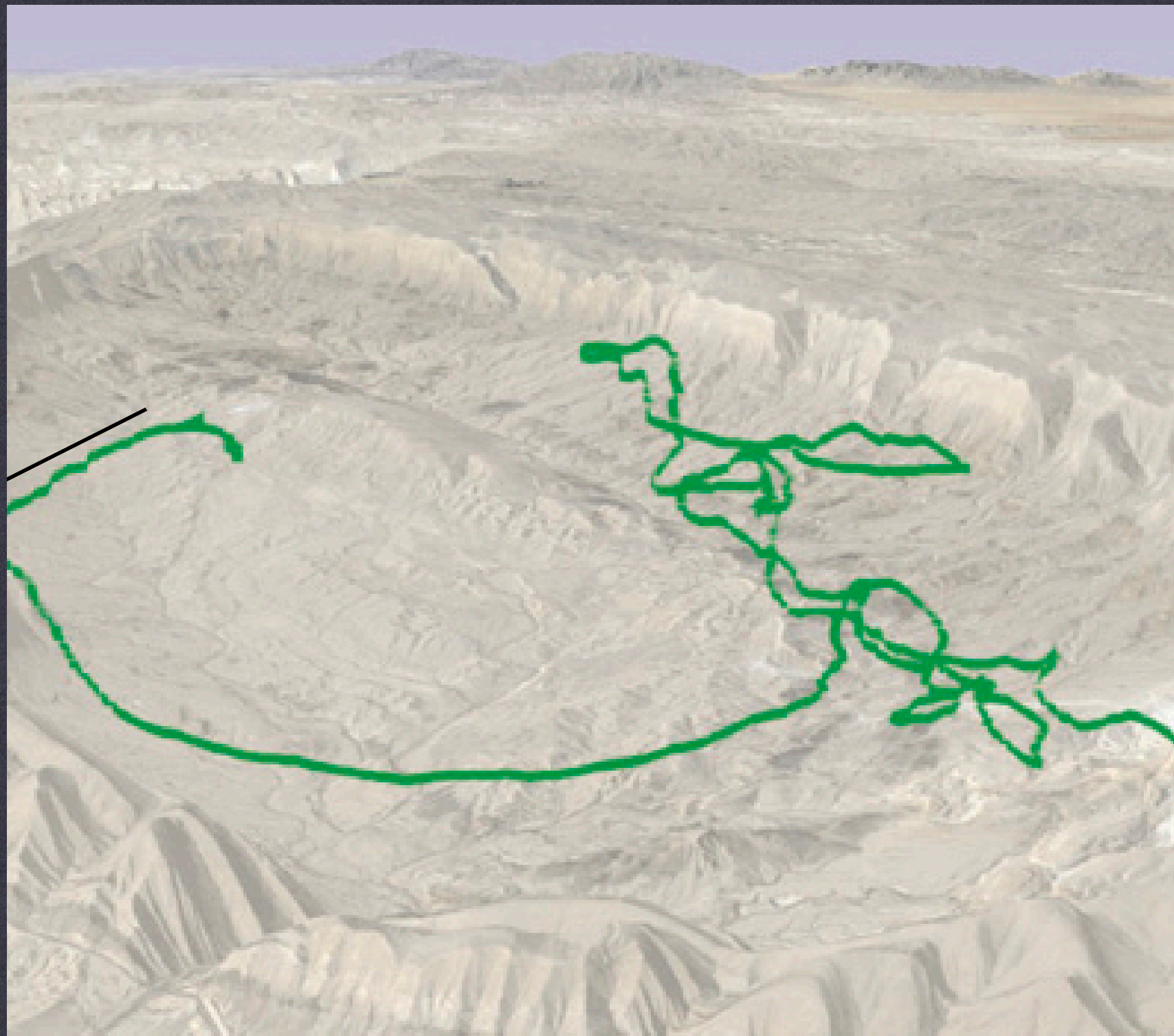




# 1949: ANIMALS MAKE MAPS

EDWARD TOLMAN AT BERKELEY: CONVERGENCE WITH GUSTAV KRAMER IN WEST GERMANY



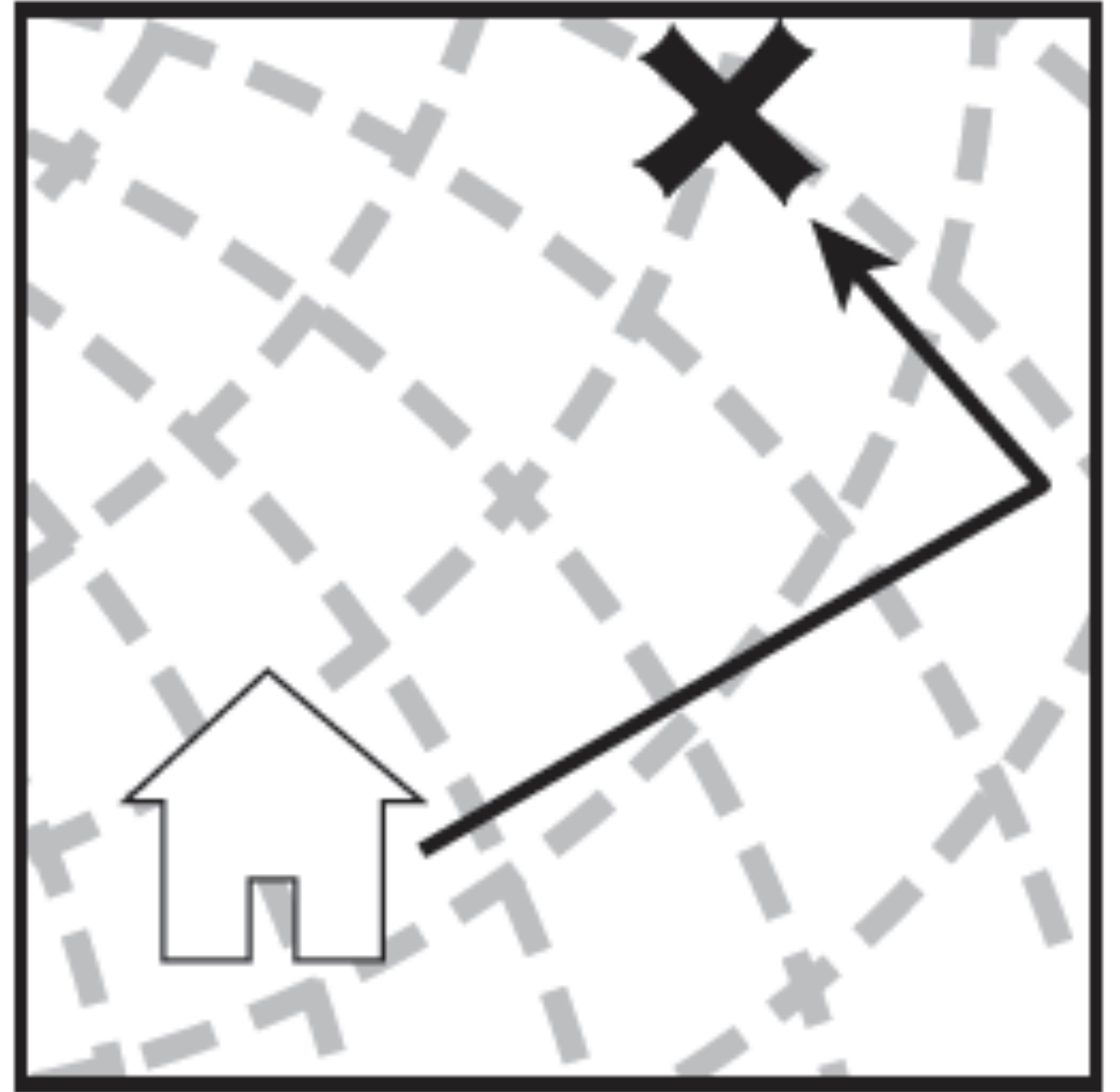
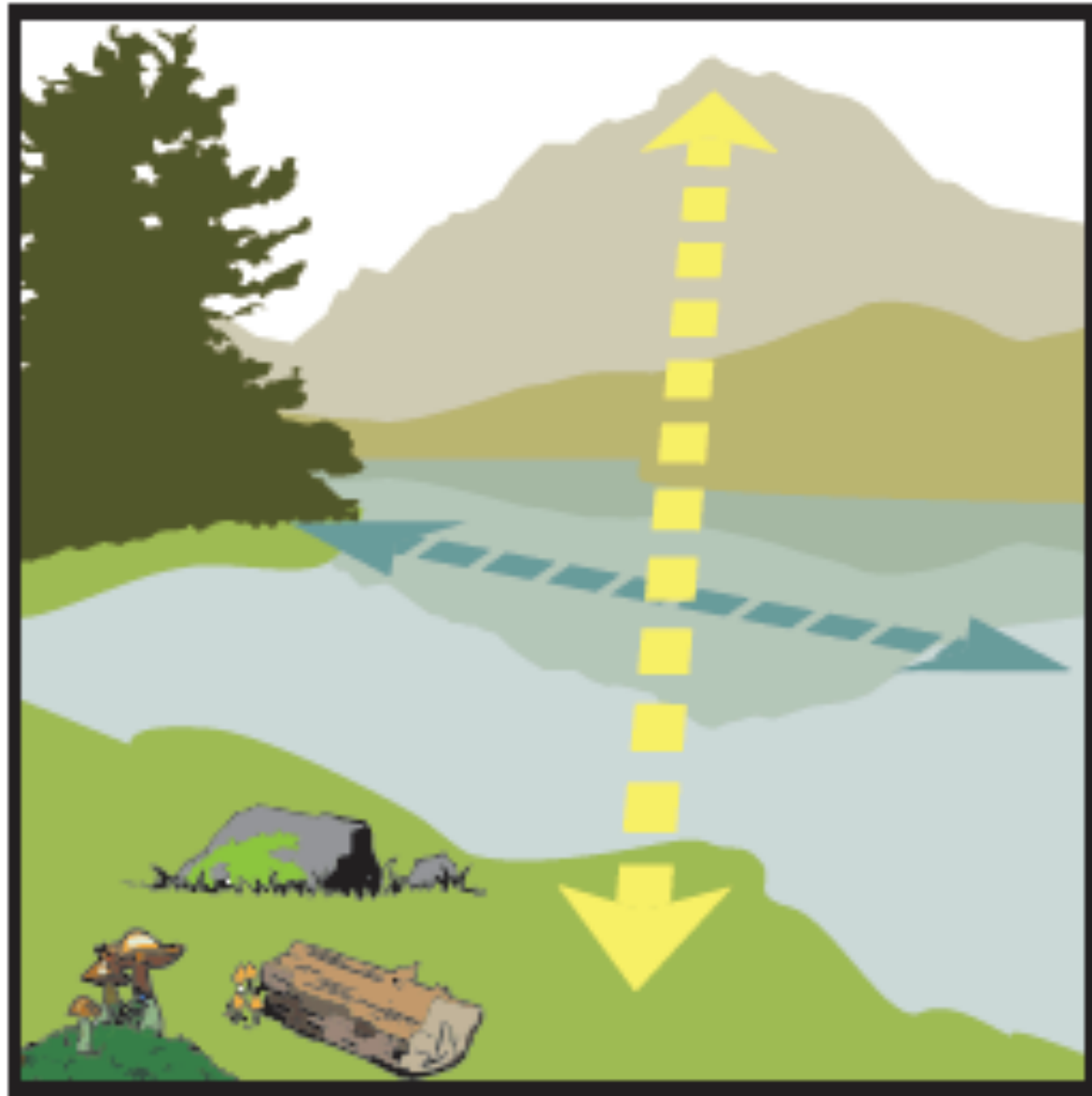


# PIGEON-LIKE NAVIGATION IN A FLYING MAMMAL

EGYPTIAN FRUIT BAT IN THE NEGEV DESERT (TSOAR ET AL. 2011 PNAS)

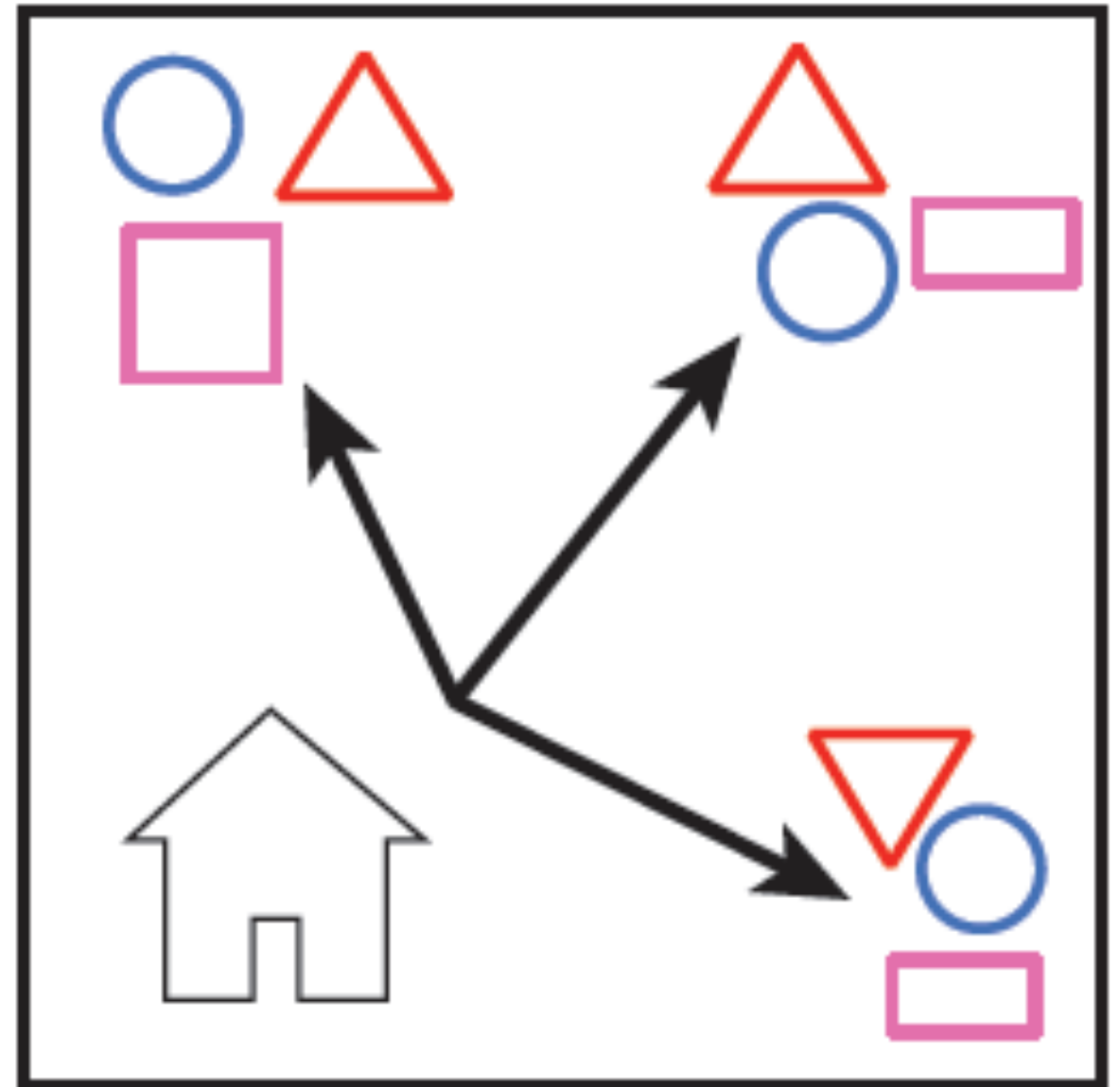


# THE BEARING MAP



**Directional** (gradient) cues - gradients, slope, shapes  
Dentate gyrus subfield

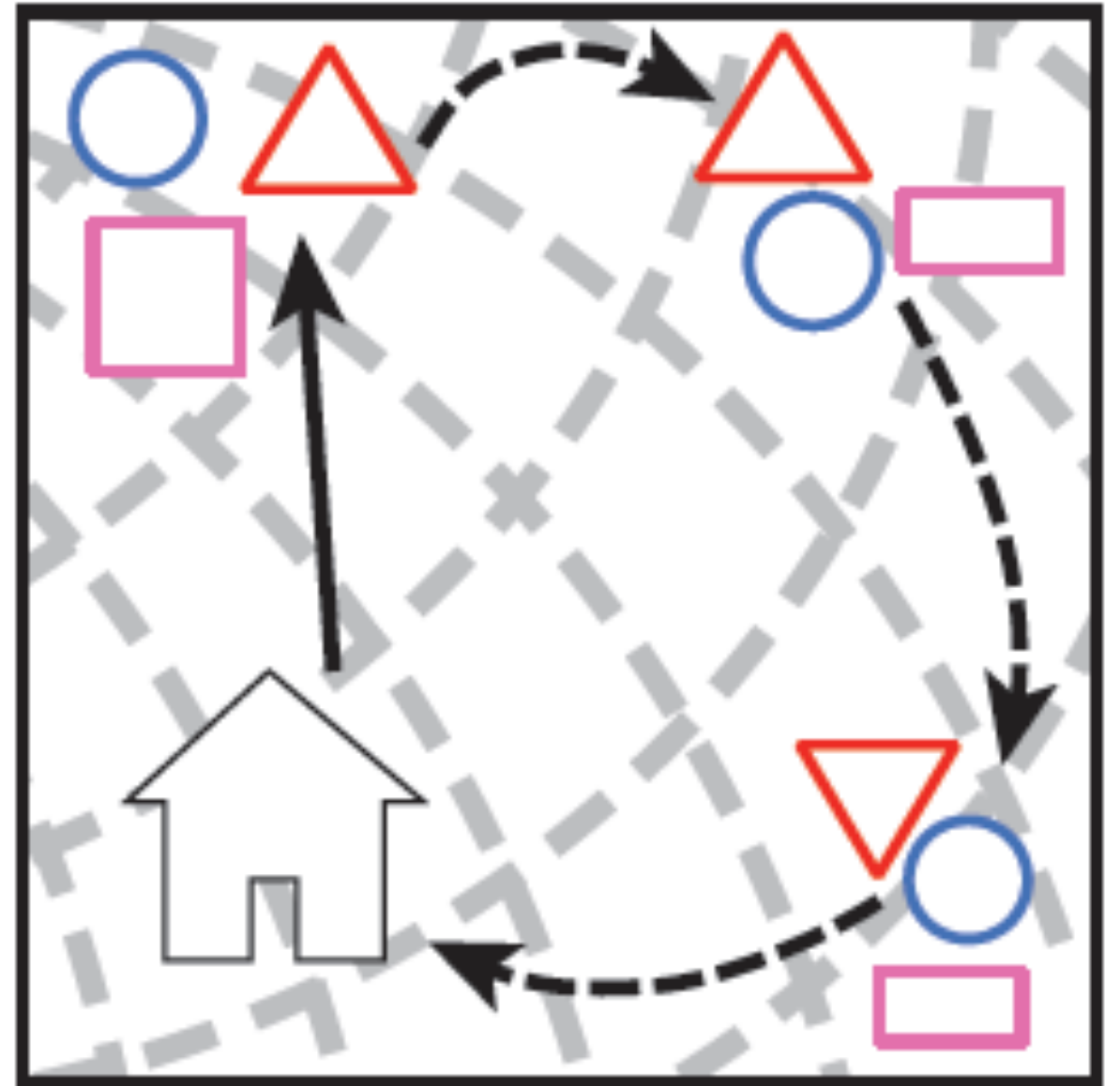
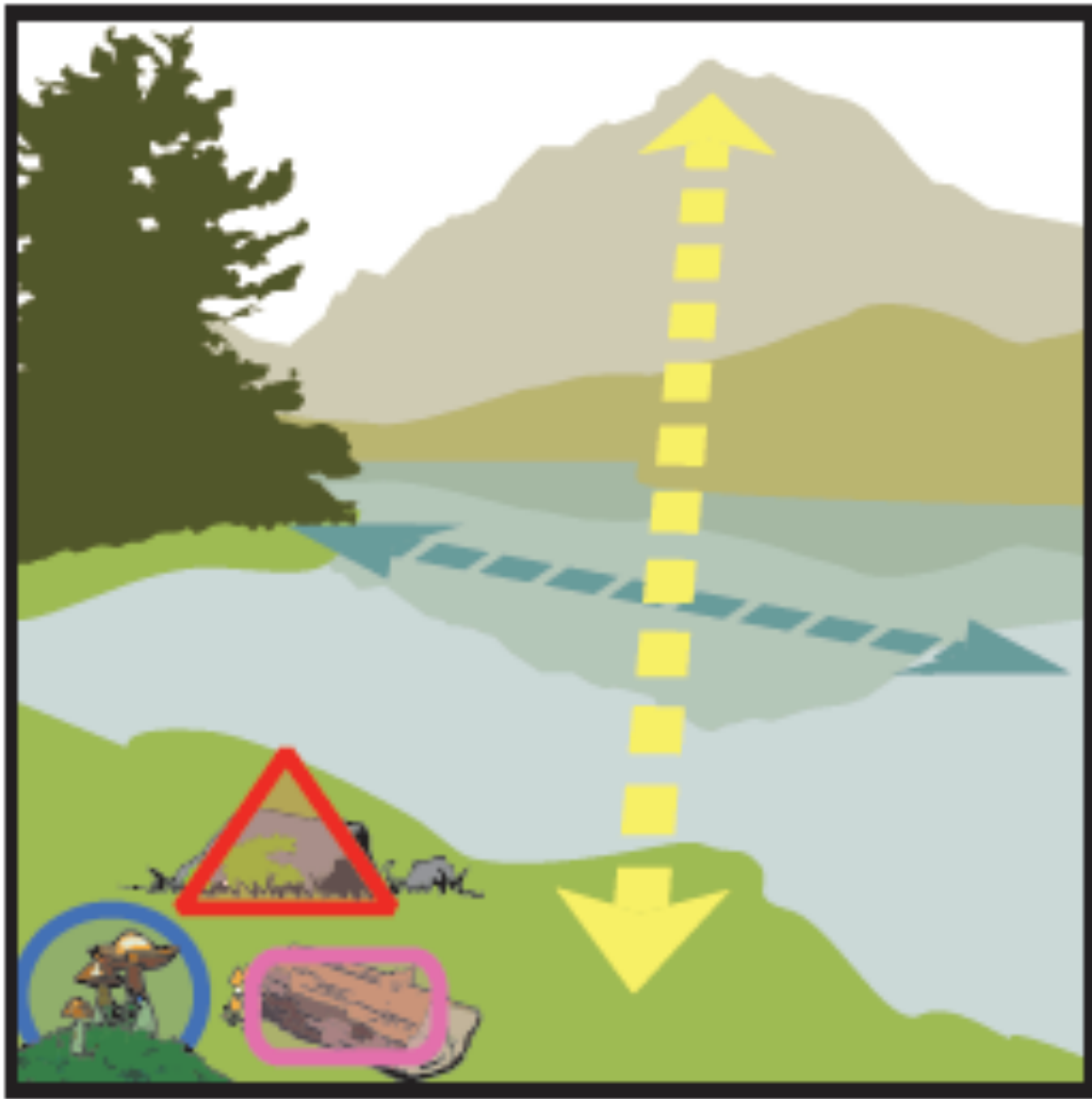
# THE SKETCH MAPS



**Positional** (landmark) cues – local objects in unique constellations

**CAI** Subfield

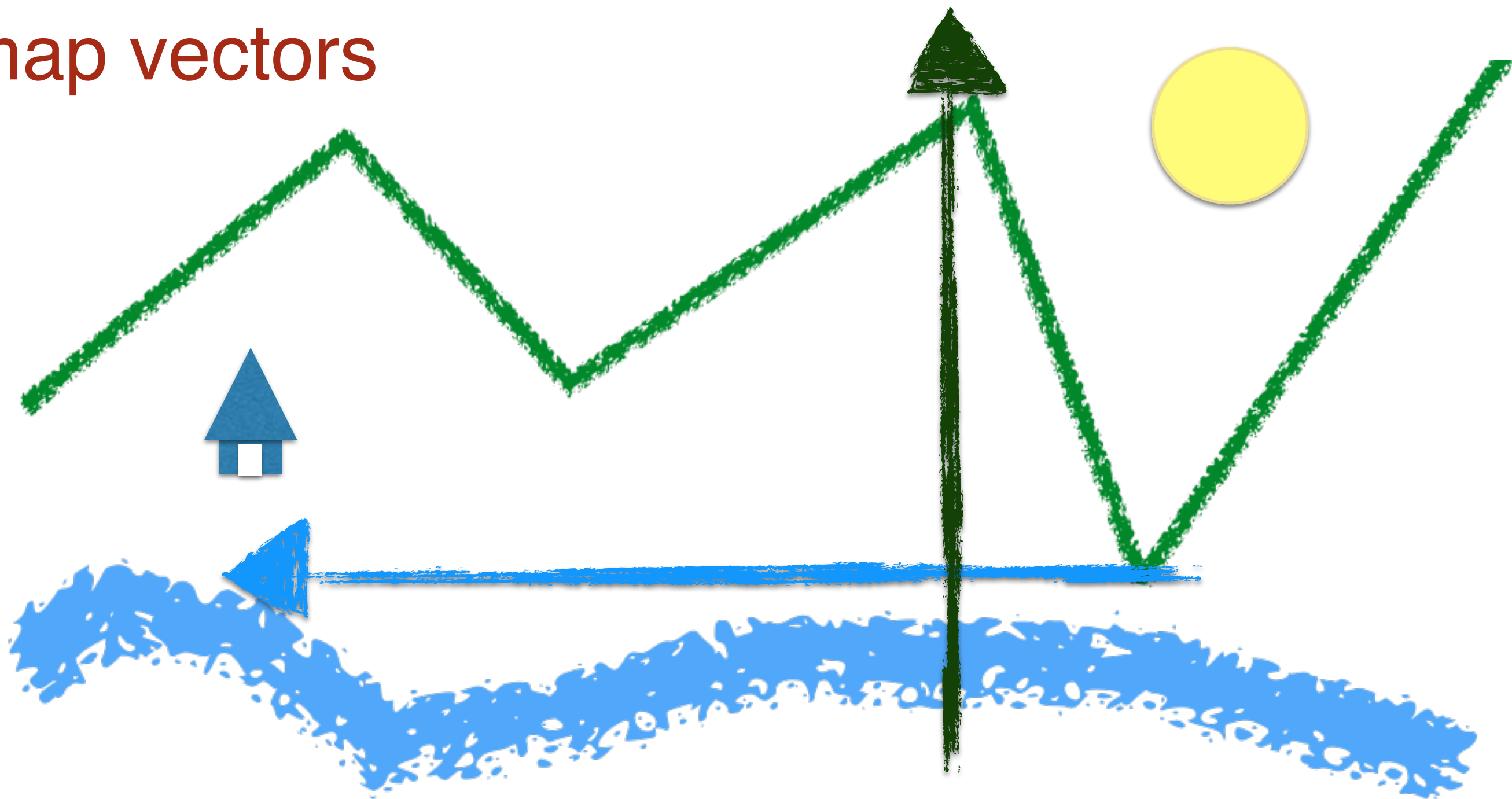
# THE INTEGRATED (COGNITIVE) MAP



Sketch Maps recoded in Bearing Map coordinates  
CA<sub>3</sub> Subfield of Ammon's Horn



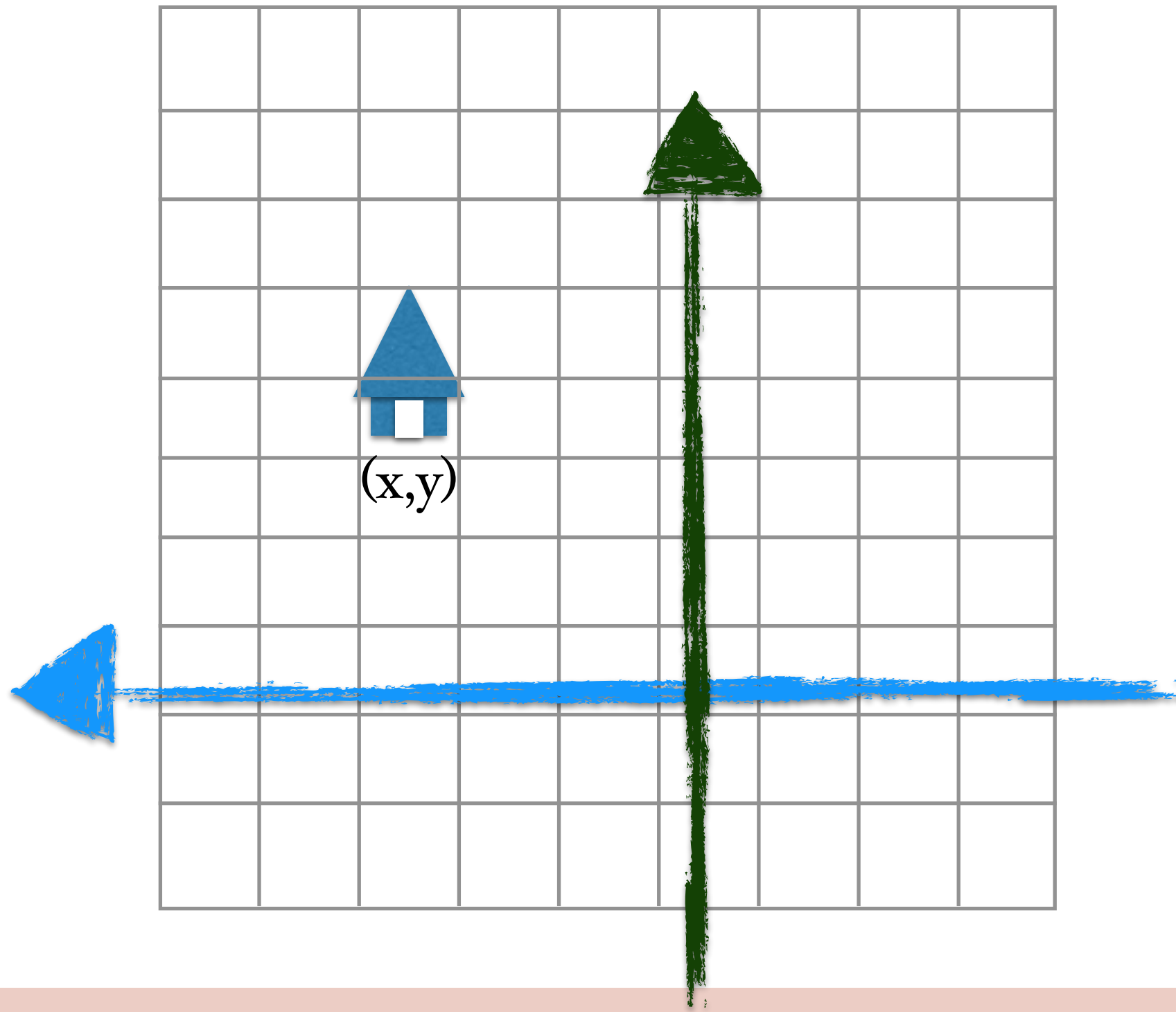
# map vectors



## COMPASS or DIRECTIONAL CUES

- **gradients:** odor, sound, magnetic field
- **polarization:** landscape shapes, objects, slope

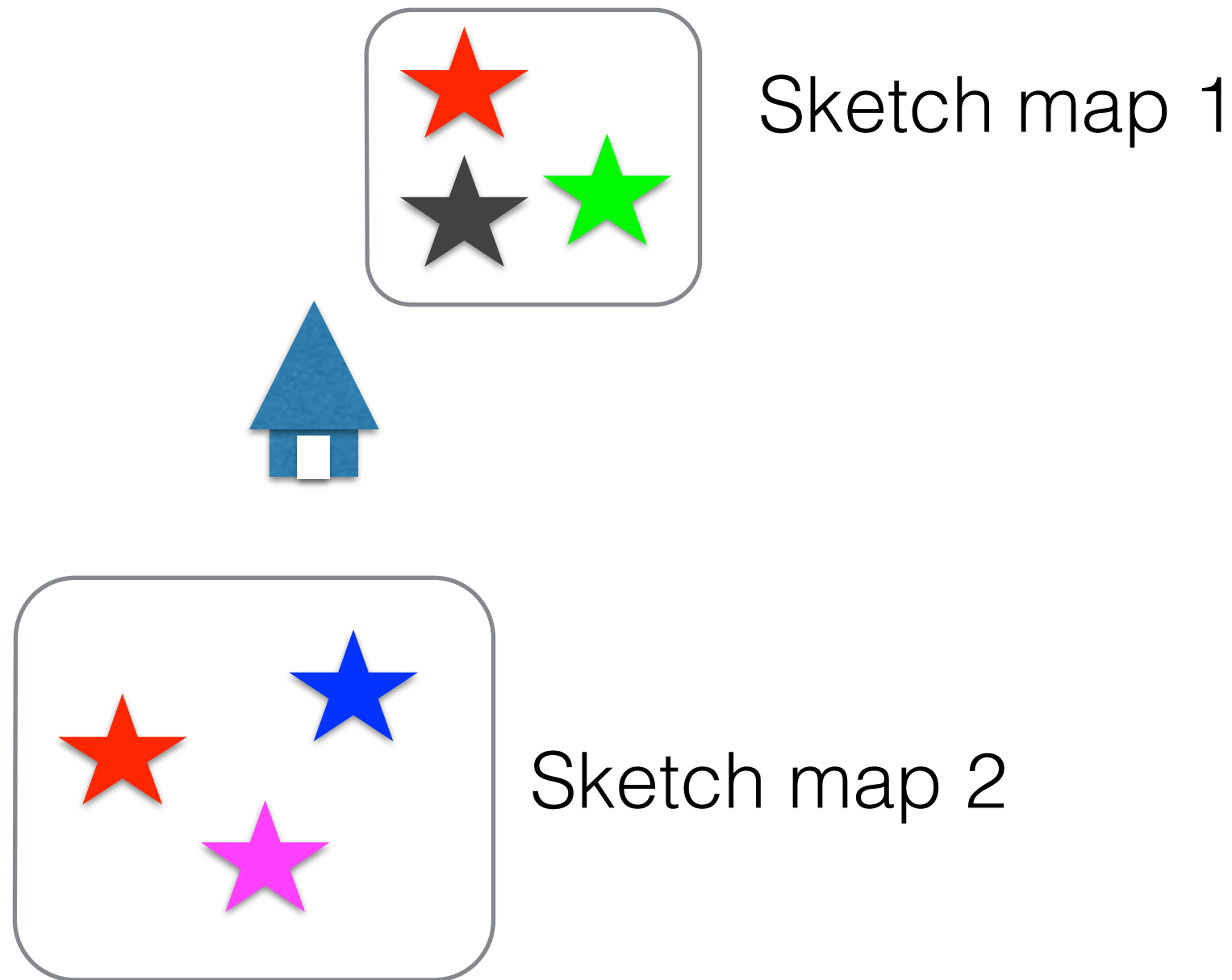
# Construct grid from vectors



**Location defined in absence of unique landmarks**



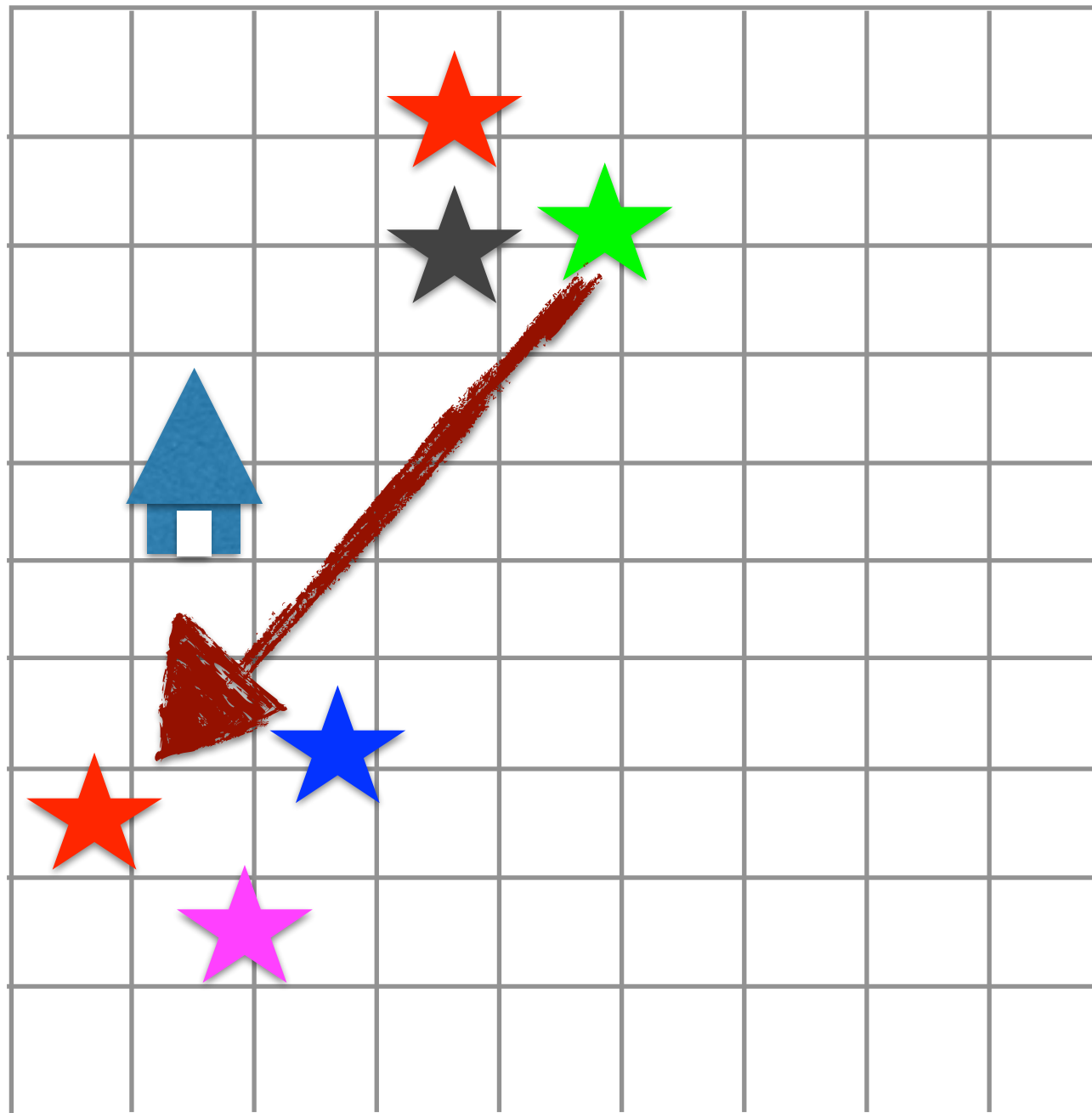
# Add positional cues



**ARRAYS of positional cues form SKETCH MAPS**  
close arrays of unique learned objects

# Integrate directional and positional cues

Encode positional cues in directional cue coordinate system

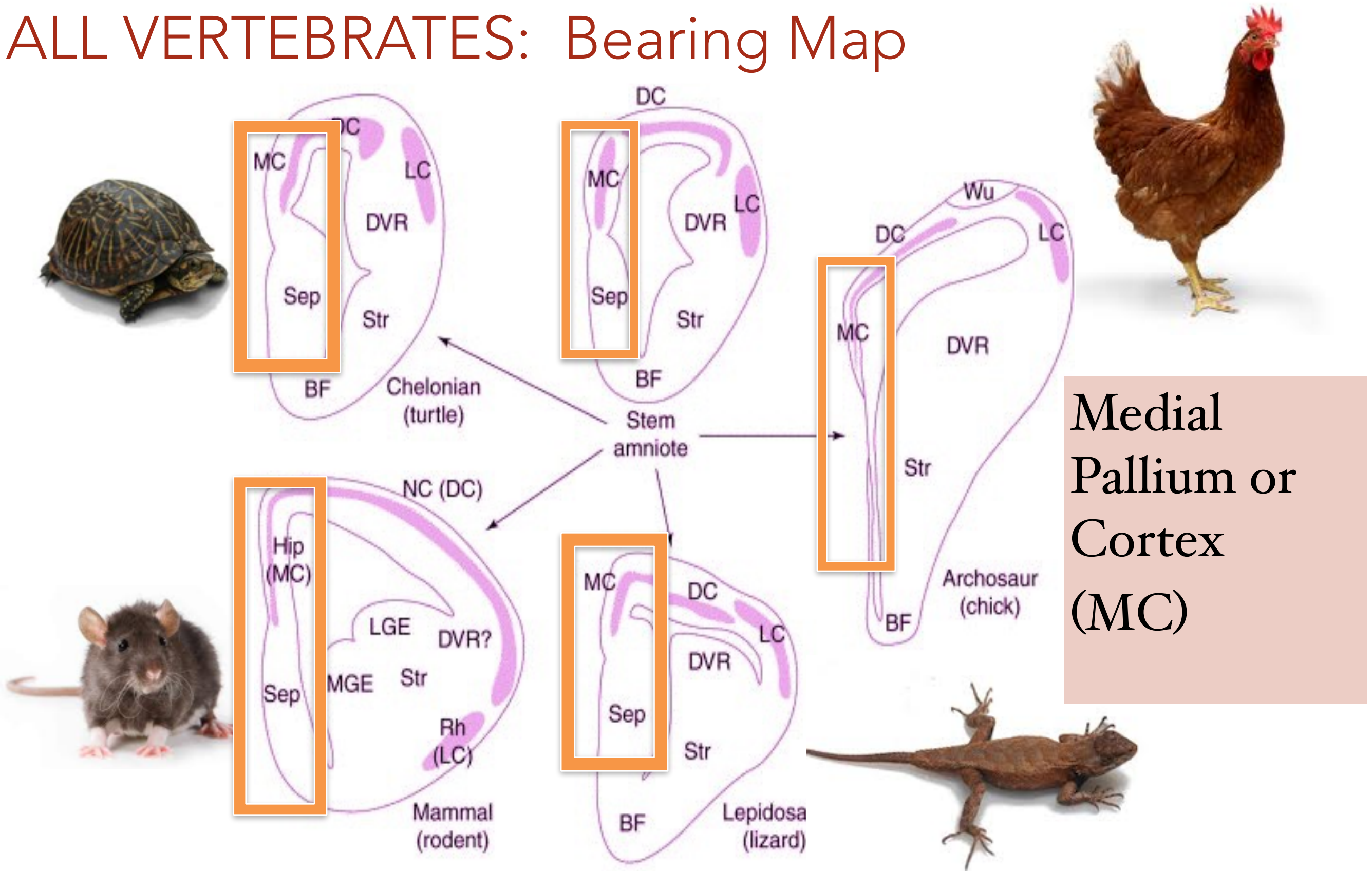


Compute **novel** shortcut to **imperceptible** goal

Parallel map theory



# ALL VERTEBRATES: Bearing Map



# Bird Maps

Standard model (Wallraff 2005)

**Navigational Map**

HP independent; need olfaction

**Familiar Area Map**

HP dependent; need vision

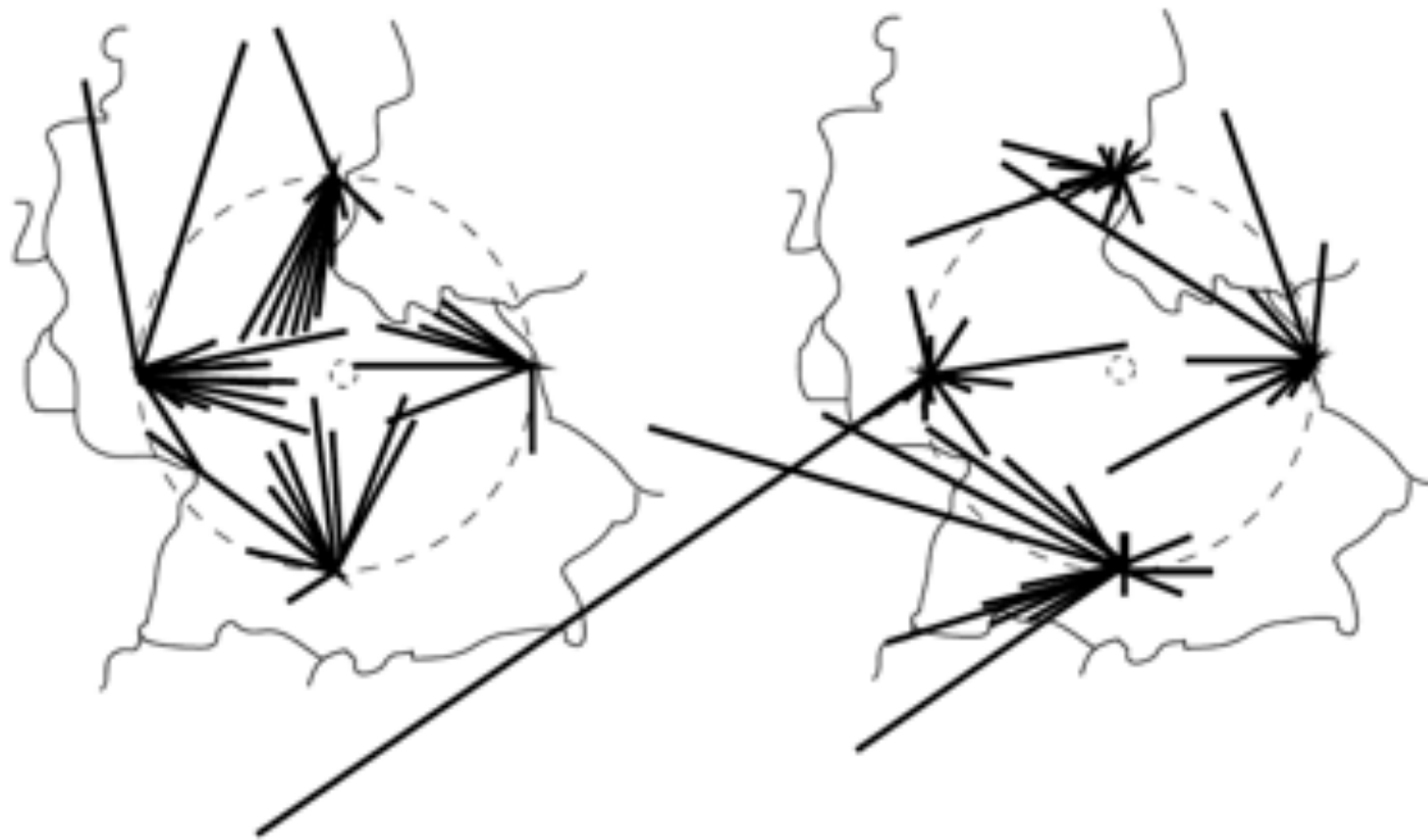
*Floriano Papi (1970); Hans Wallraff, Anna Gagliardo, et al.*

Domestic Pigeon, trained artificially

Olfaction > Magnetic

Wild Catbird, natural migration

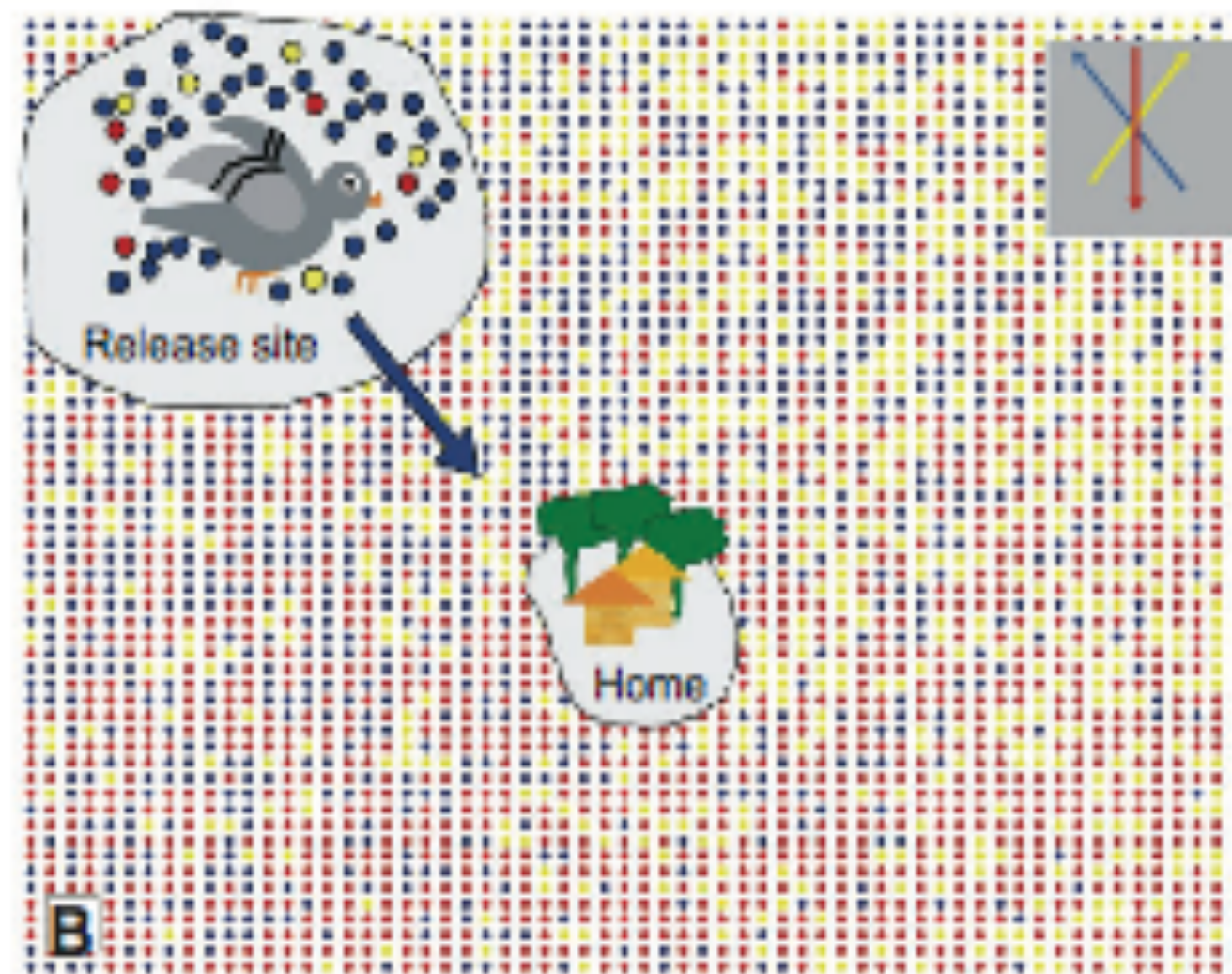
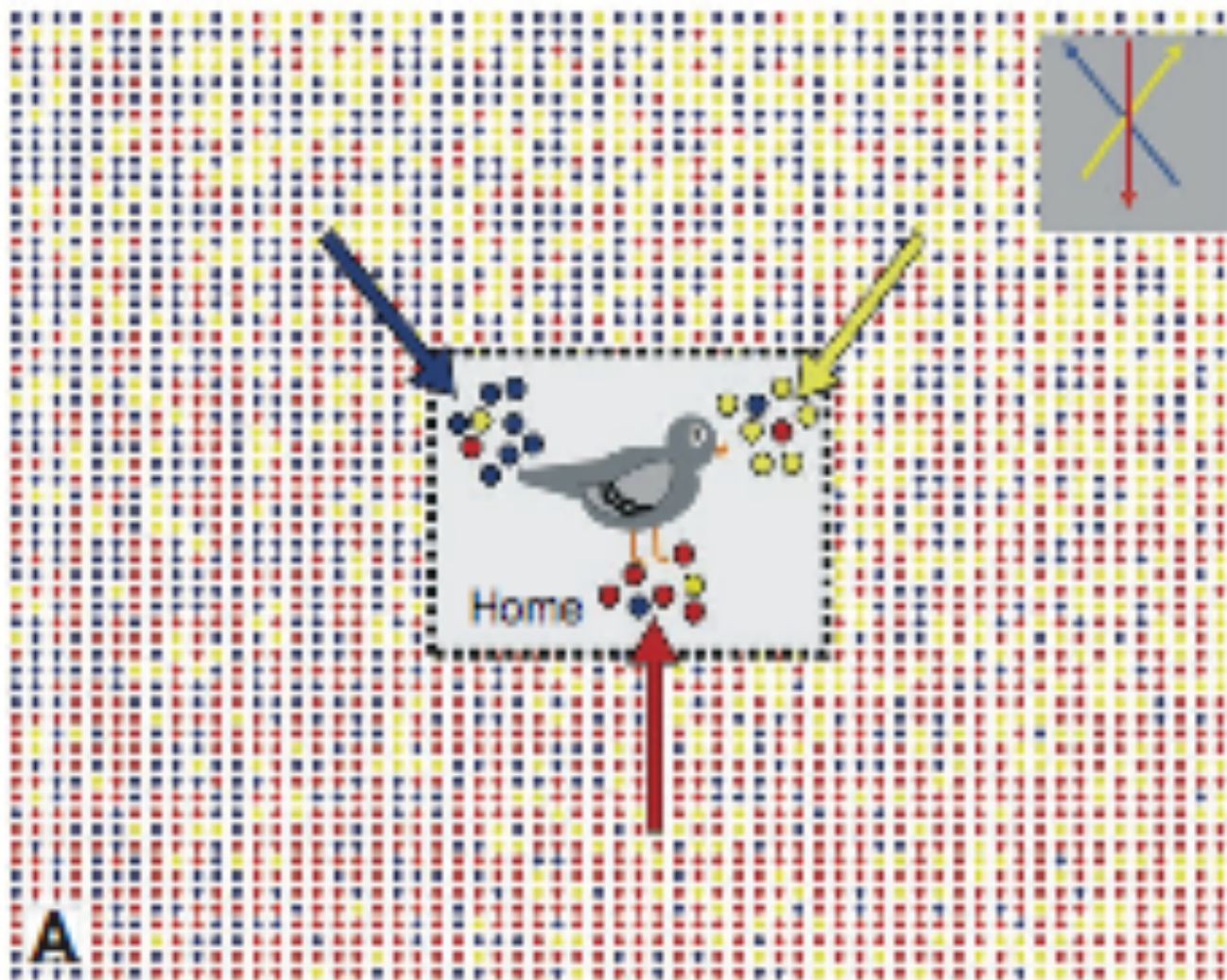
Olfaction > Magnetic



**Mehlhorn, J., & Rehkämper, G.** (2009). Neurobiology of the homing pigeon—a review. *Naturwissenschaften*.

**Holland, R. A., Thorup, K., Gagliardo, A., ...& Wikelski, M.** (2009). Testing the role of sensory systems in the migratory heading of a songbird. *Journal of Experimental Biology*.





*From Gagliardo et al. (2013) J. Exp. Biol. 216: 2165-2171; Figure 1.*

**Distort** olfactory learning during development  
(add baffles; add odors)

**Lesion or anesthetize** (OE, OB, piriform)

# An alternative to the 'Navigational Map'

HP lesioned bird could

- use reference memory for odor
- this supplies initial bearing
- only disoriented in familiar area  
(working memory required)

Jacobs & Menzel, R. (2014). Movement Ecology.



*Suggested by the only two exceptions to HP-pigeon orienting from UNFAMILIAR SITE:*

Bingman, & Yates. (1992). Behavioral Neuroscience

- raised in Maryland, tested in Ohio
- 800 km displacement

**WRONG MAP**

Bingman, et al. (1990). Behavioral Neuroscience, 104(6), 906–911.

- HP lesioned before learning loft area odors

**NO MAP**



# If correct...

Hippocampal function homologous in birds (natural scale, olfactory) and rodents (small scale, olfactory also?)

Parallel map architecture general solution

Jacobs & Menzel, R. (2014). Movement Ecology.

# Olfactory navigation in mammals?

Rat HP place fields controlled by  
spatial array of odors; rotation.

Zhang & Manahan-Vaughan (2015). *Cerebral  
Cortex*.

# Humans?



*Porter, J., et al. (2006).  
Mechanisms of scent-  
tracking in humans.  
Nature Neuroscience, 10,  
27–29.*

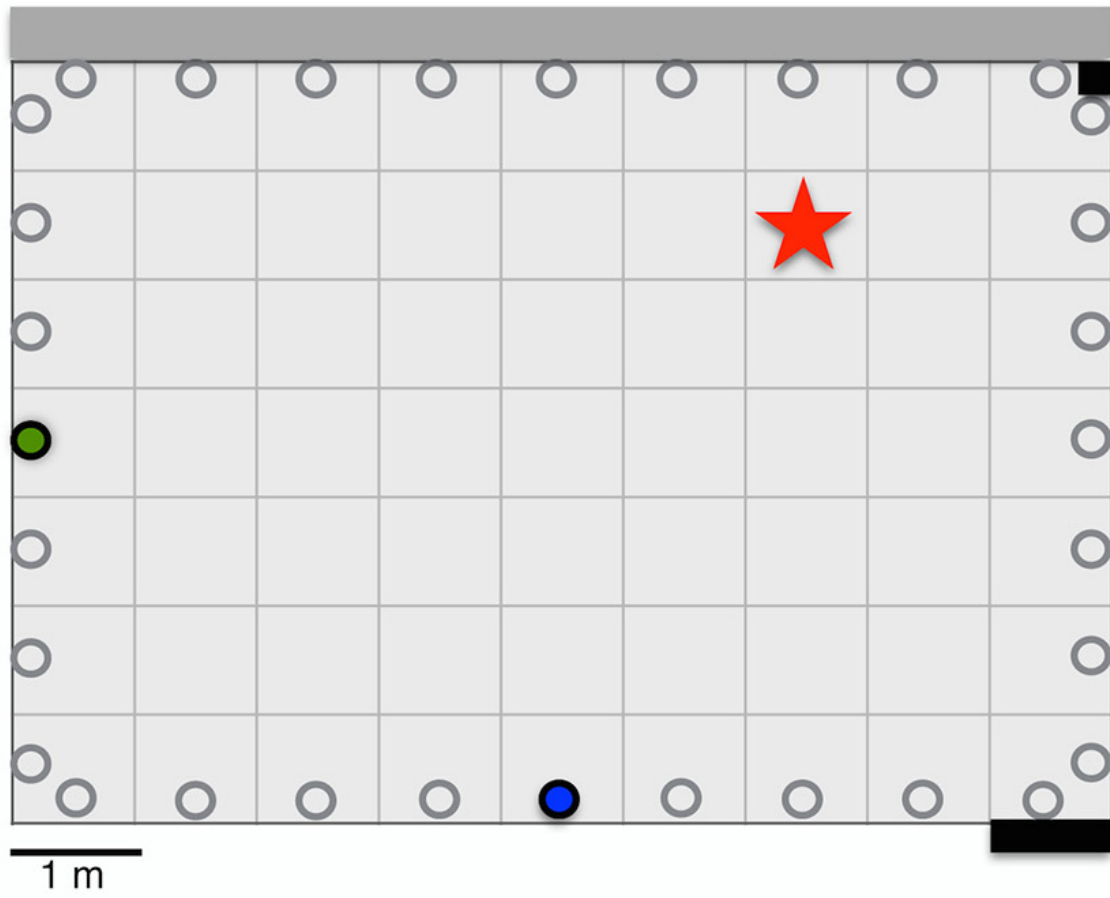
But can humans using **working memory** to map an **arbitrary location** in a purely **olfactory** landscape?



# Procedure

- **Olfaction condition:** Mask vision, audition.
- Disorient enroute to location.
- One minute sampling.
- Disorient and return to start.
- Remove masks.
- Return to sample location.
- **Task validation:** vision only
- **Control condition:** no sensory input.
  - Within subject, fixed order

A



B



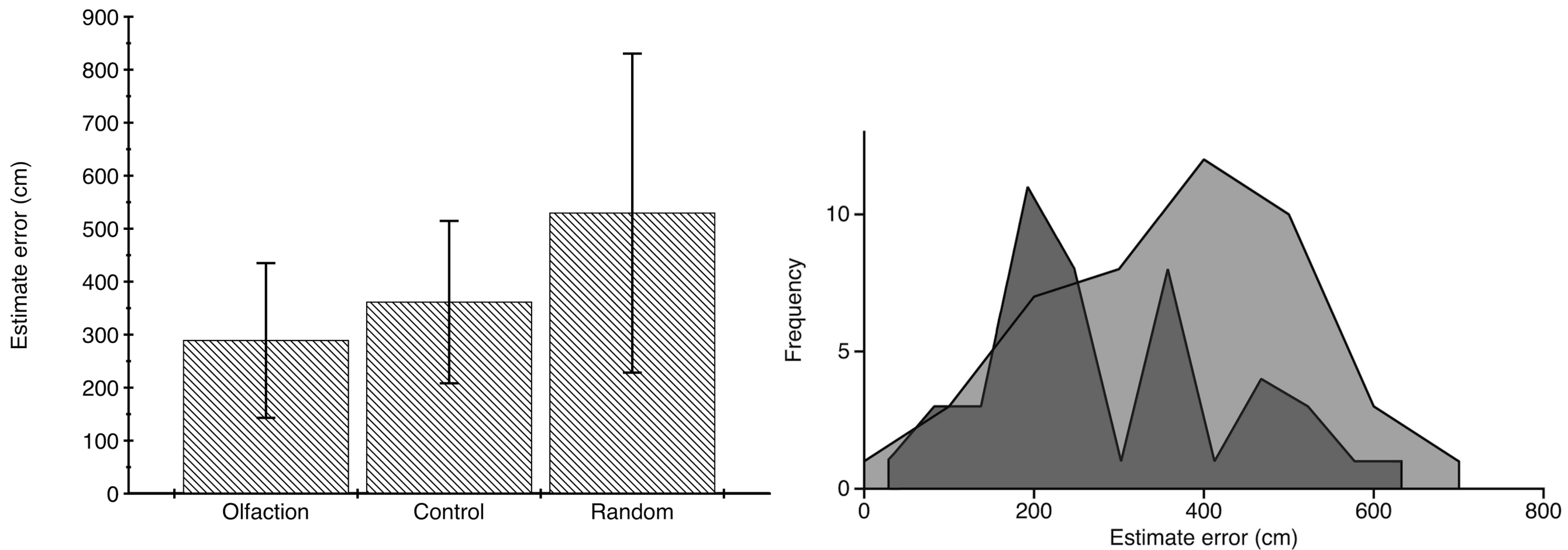
C



D



# Humans can map an arbitrary location using only odor





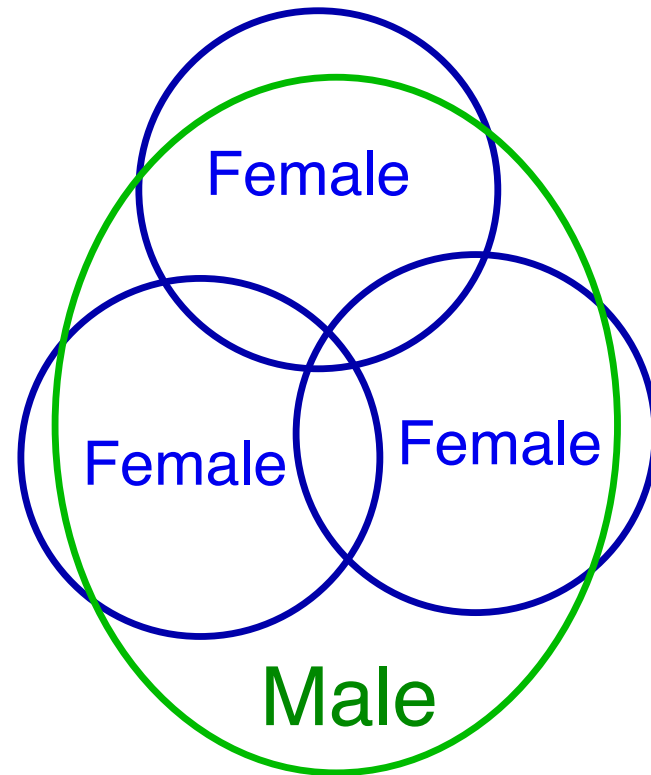
# Implications

- First demonstration of olfactory orientation to arbitrary location, in any species.
- Assume pigeons use this for navigation.
- If in humans, could be a general mechanism for orientation.

# So far

- Hippocampus may be homologous in structure and function in birds and mammals.
- Elements of olfactory navigation can be demonstrated in birds, rats and humans.
- Do olfactory systems scale with navigational demand, as does hippocampus?

# Hippocampal size larger when creating flexible new routes





# DATA FROM DIFFERENT VERTEBRATE GROUPS

Correcting for brain size and phylogeny

## **Olfactory bulb size increases with**

Home range size, terrestrial carnivores (*mammals*)

Predatory theropod species (*dinosaurs*)

Secondary nocturnality (*birds*)

Navigational ability

(*domesticated pigeons*)



**Gittleman, J. L.** (1991). Carnivore olfactory bulb size: allometry, phylogeny and ecology. *J. Zoology*.

**Zelenitsky, D., Therrien, F., & Kobayashi, Y.** (2009). Olfactory acuity in theropods: palaeobiological and evolutionary implications. *Proc Roy Soc B*.

**Healy, S. D., & Guilford, T.** (1990). Olfactory-bulb size and nocturnality in birds. *Evolution*.

**Mehlhorn, J., & Rehkämper, G.** (2009). Neurobiology of the homing pigeon—a review. *Naturwissenschaften*.

# MOSAIC EVOLUTION OF OLFACTORY SYSTEM

Finlay & Darlington analyses:

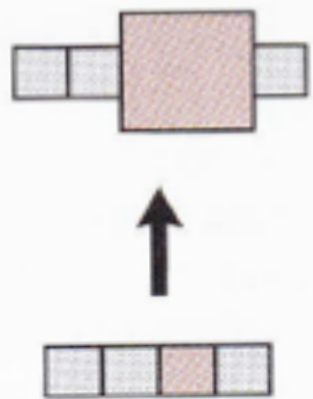
Mammals

Sharks (basal vertebrate)

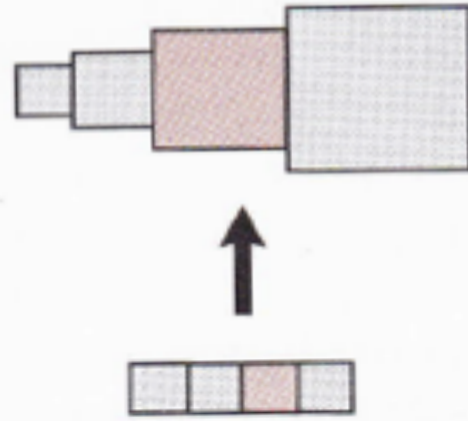
**90-97%** variance brain structure size explained by size of whole brain

**3-10% olfactory system**

Purely mosaic evolution



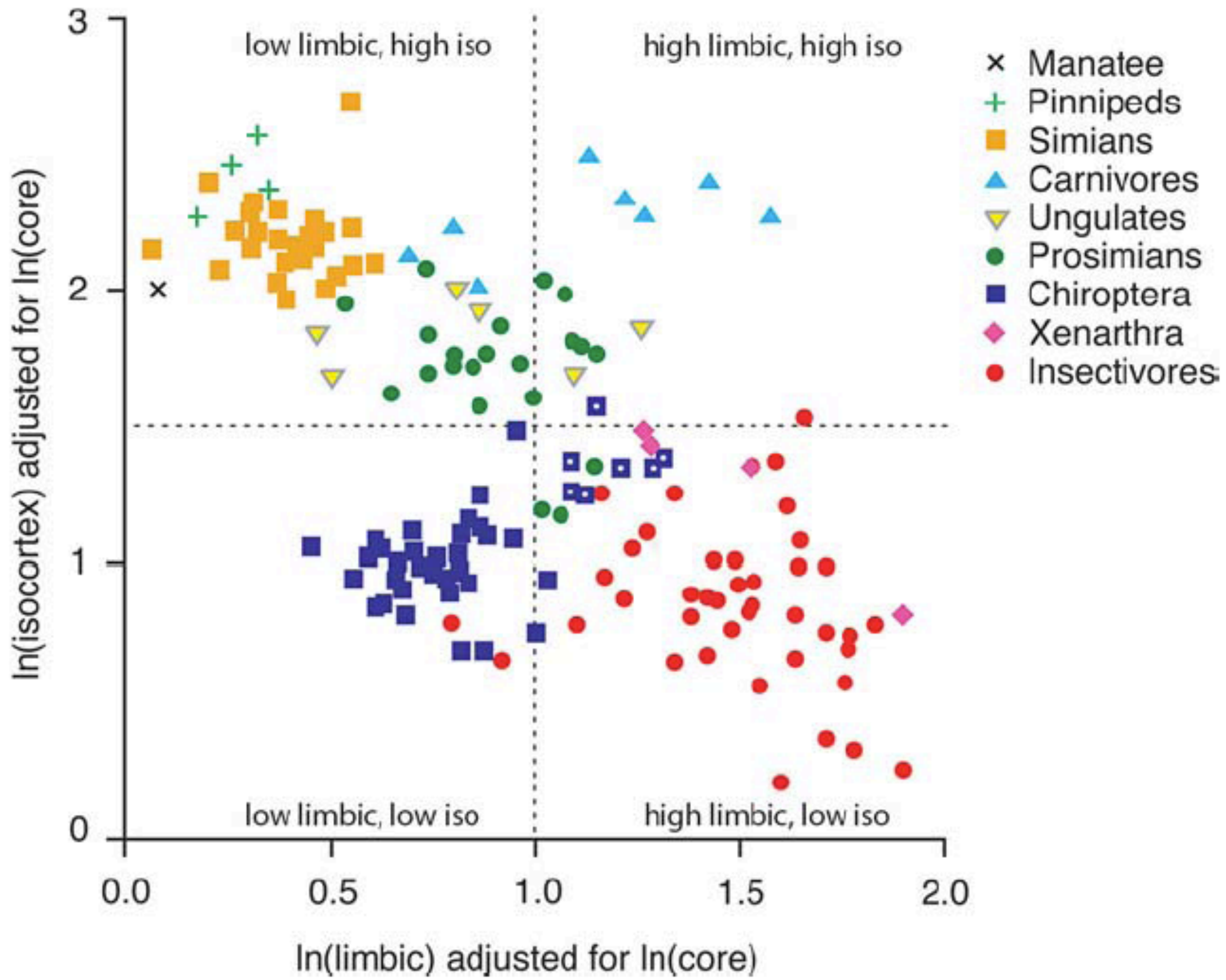
Purely concerted evolution



Finlay, B. & Darlington, R. 1995. Linked regularities in the development and evolution of mammalian brains. *Science*.

Yopak, K. E., ...and Finlay, B. L. (2010). A conserved pattern of brain scaling from sharks to primates. *PNAS*

Striedter, G 2005. PRINCIPLES OF BRAIN EVOLUTION. Sinauer.





# BEHAVIORAL HYPOTHESIS

## Detector Strategy

prey location either obvious or impossible to predict

## Predictor Strategy

with sufficient data, prey location can be predicted in space and time – *increase isocortex size*

*Predict using odorants - increased limbic size*

*Emphasize other sensory - decreased limbic size*

### Detector



Limbic

Iso  
cortex

### Predictor

Limbic

Iso  
cortex

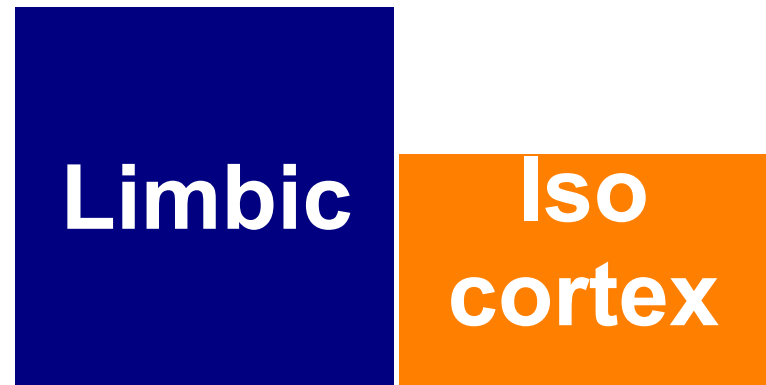


# PATTERNS IN LIMBIC ALLOCATION COINCIDE WITH OLFACTION AND PREDATORY STRATEGY

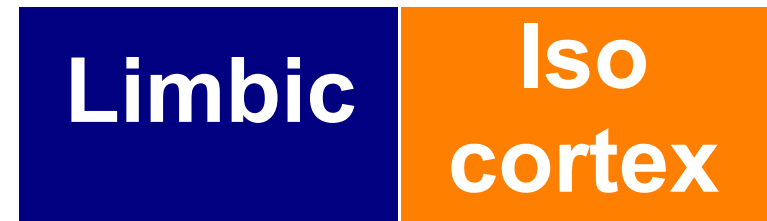
Olfactory

Non-olfactory

Detectors



**Shrew – spatial olfaction**



**Microbat- spatial audition**

Predictors



**Wolf – spatial olfaction**



**Ape - spatial vision**

# HIPPOCAMPAL NEUROGENESIS COVARIES WITH SPATIAL OLFACTION, NOT JUST SPATIAL BEHAVIOR

ONLY two locales of adult neurogenesis found in **all vertebrates...**

**Olfactory Bulb (OB)**

**Hippocampus (HP)**

*Echolocating microbats and whales/dolphins (sonar)*

**small/absent OB size, low/absent HP neurogenesis**

*Simple/non-echolocating (mega) bats:*

**intermediate OB size, intermediate HP neurogenesis**



Amrein, I., Dechmann, D. K., Winter, Y., & Lipp, H.-P. (2007). Absent or Low Rate of Adult Neurogenesis in the Hippocampus of Bats (Chiroptera). *PLoS ONE*.

Gatome, C. W., Mwangi, D. K., Lipp, H.-P., & Amrein, I. (2010). Hippocampal neurogenesis and cortical cellular plasticity in Wahlberg's epauletted fruit bat: a qualitative and quantitative study. *Brain, Behavior and Evolution*.

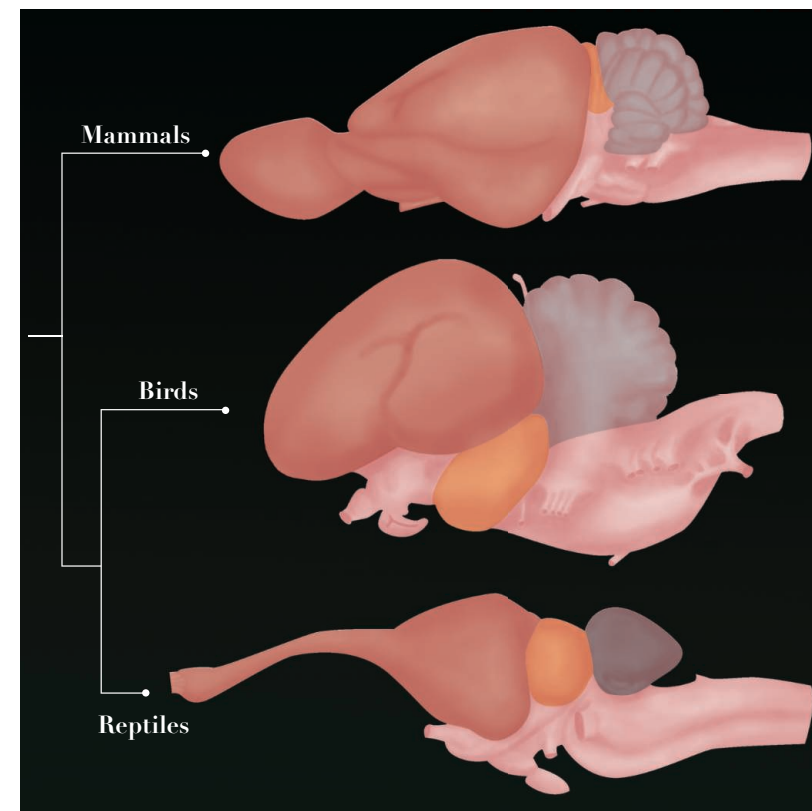


# BRAIN EVOLUTION REVOLUTIONS

*“The mammalian neocortex with its protean powers has evolved from the olfactory forebrain of primitive vertebrates. Perhaps because olfaction demands a neural architecture preadapted to learning complex input patterns.”*

Daniel Osorio, Wayne Getz and Jurgen Rybak. 1994. Insect vision and olfaction: different neural architectures for different kinds of sensory signal? From animals to animats 3. MIT Press.

3 ‘pulses’ of olfactory enhancement preceded increases in total brain size in Early Jurassic



Rowe, T. B., Macrini, T. E., and Luo, Z.-X. (2011). Fossil Evidence on Origin of the Mammalian Brain. *Science* 332, 955–957.

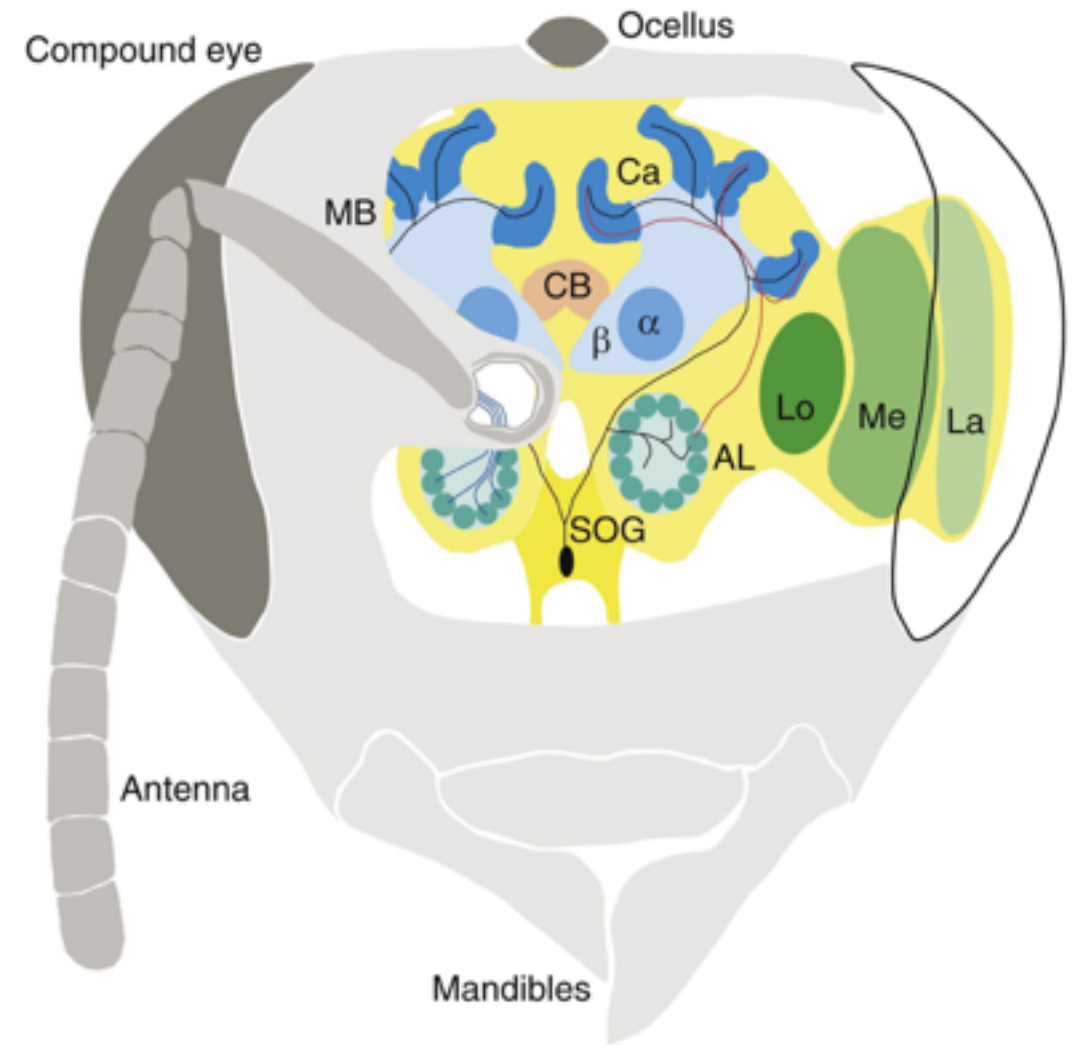
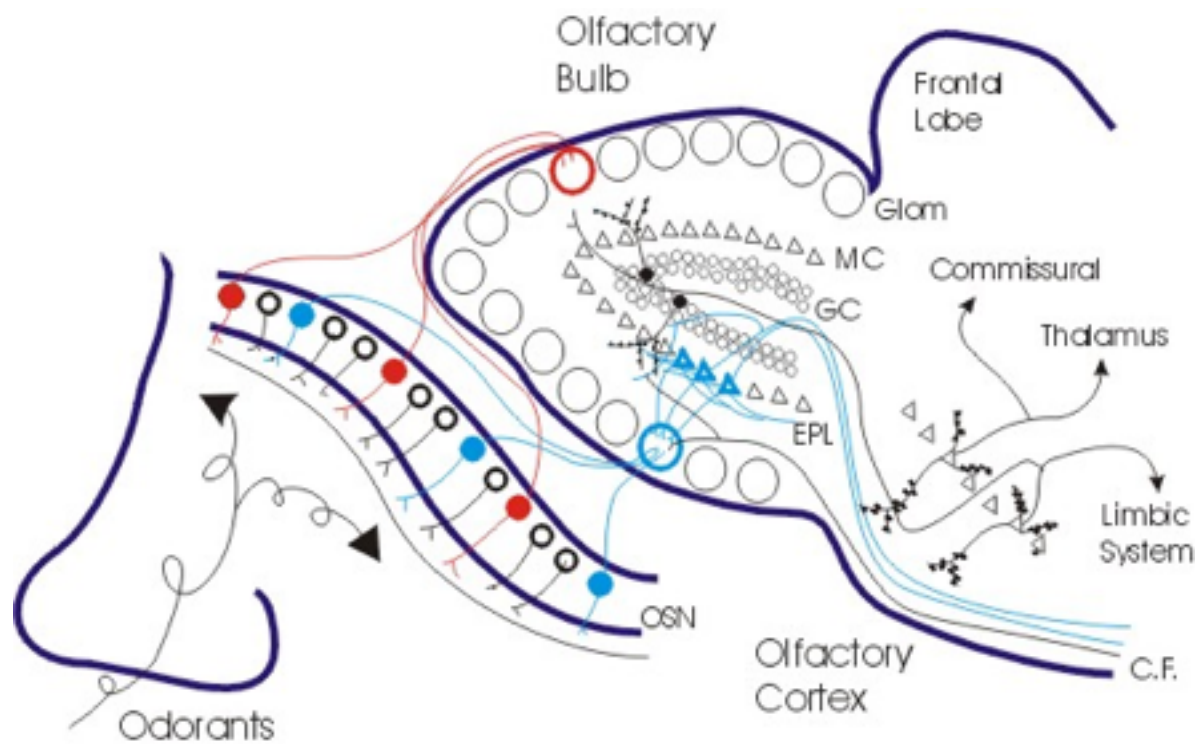


Is this more general?





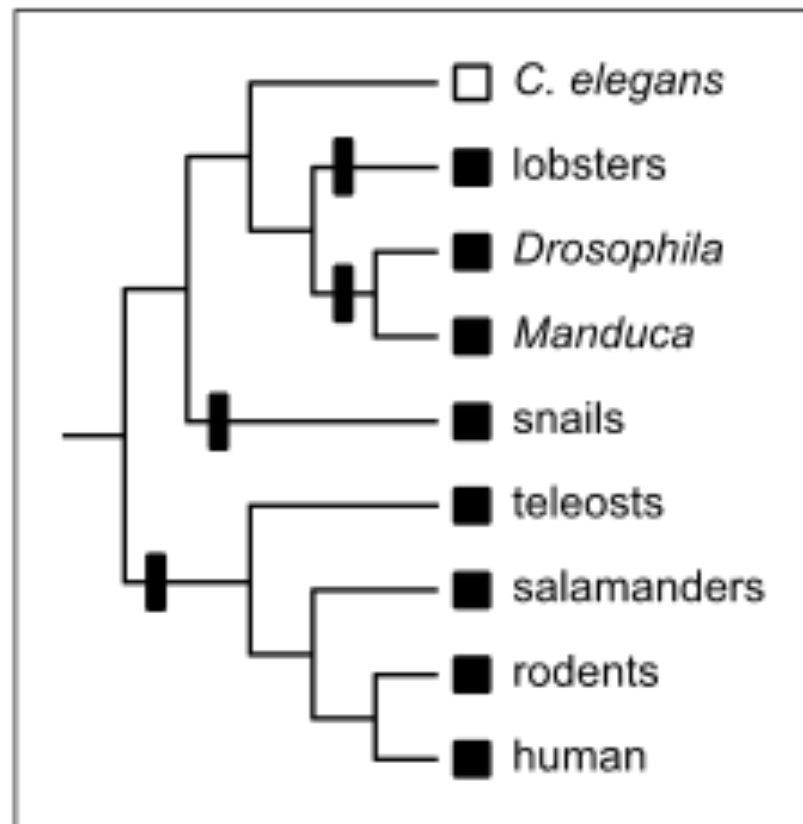
# SIMILARITIES IN OLFACTORY SYSTEMS



Olfactory Glomerulus Present

Nematode  
Crustacean  
Insects  
Mollusk  
Bony Fish  
Amphibian  
Rodent  
Human

Eisthen BBE  
(2002)





## Honey bees navigate according to a map-like spatial memory

Randolf Menzel<sup>1\*</sup>, Uwe Greggers<sup>1\*</sup>, Alan Smith<sup>2,5</sup>, Sandra Berger<sup>1</sup>, Robert Brandt<sup>1</sup>, Sascha Brunke<sup>1</sup>, Sandra Hülse<sup>1</sup>, Tobias Plümpe<sup>1</sup>, Frank Schaupp<sup>1</sup>, Elke Schüttler<sup>1</sup>, Silke Stach<sup>1</sup>, Jan Stindt<sup>1</sup>, Nicola Stol<sup>1</sup> and Sebastian Watzl<sup>1</sup>

<sup>1</sup>Institut für Biologie, Neurobiologie, Freie Universität Berlin, Königin-Luise-Strasse 28/30, 14195 Berlin, Germany; and <sup>2</sup>Plant and Invertebrate Behaviour, Rothamsted Research, Harpenden, Herts AL5 2JQ, United Kingdom

Communicated by Charles R. Gallistel, Rutgers, The State University of New Jersey, Piscataway, NJ, November 25, 2004 (received for review October 15, 2004)



.....

## True navigation and magnetic maps in spiny lobsters

Larry C. Boles & Kenneth J. Lohmann

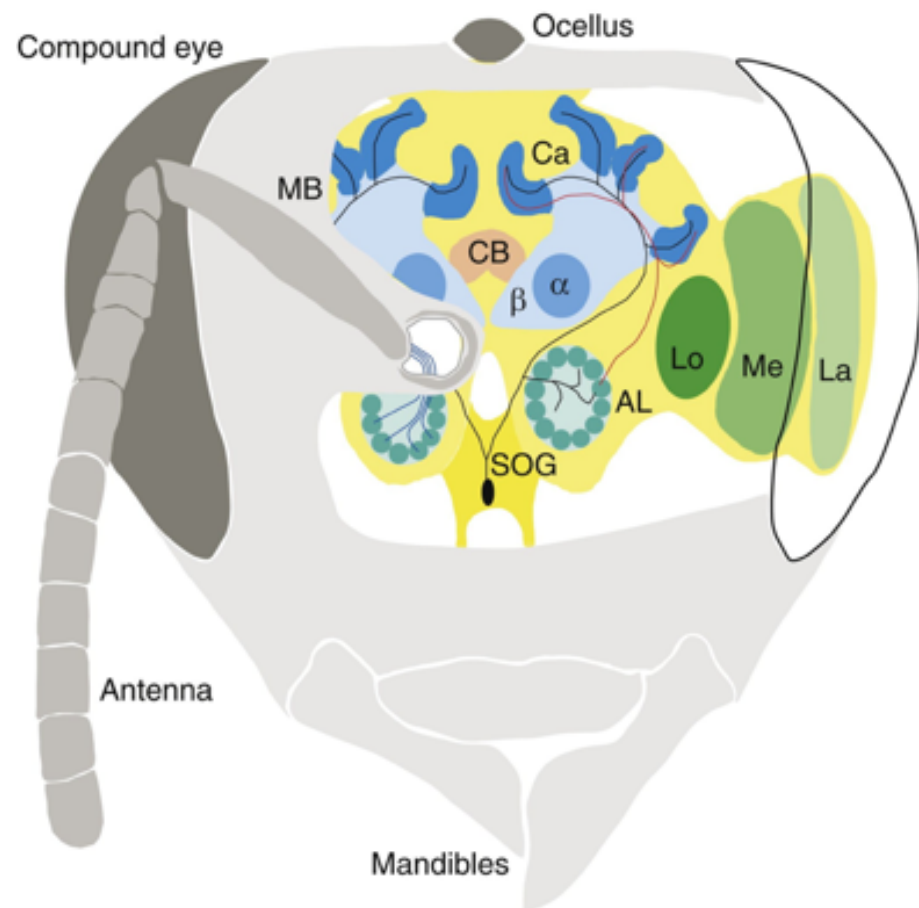
*Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27599, USA*



**HONEY BEES AND LOBSTERS MAP...SANS HIPPOCAMPUS**

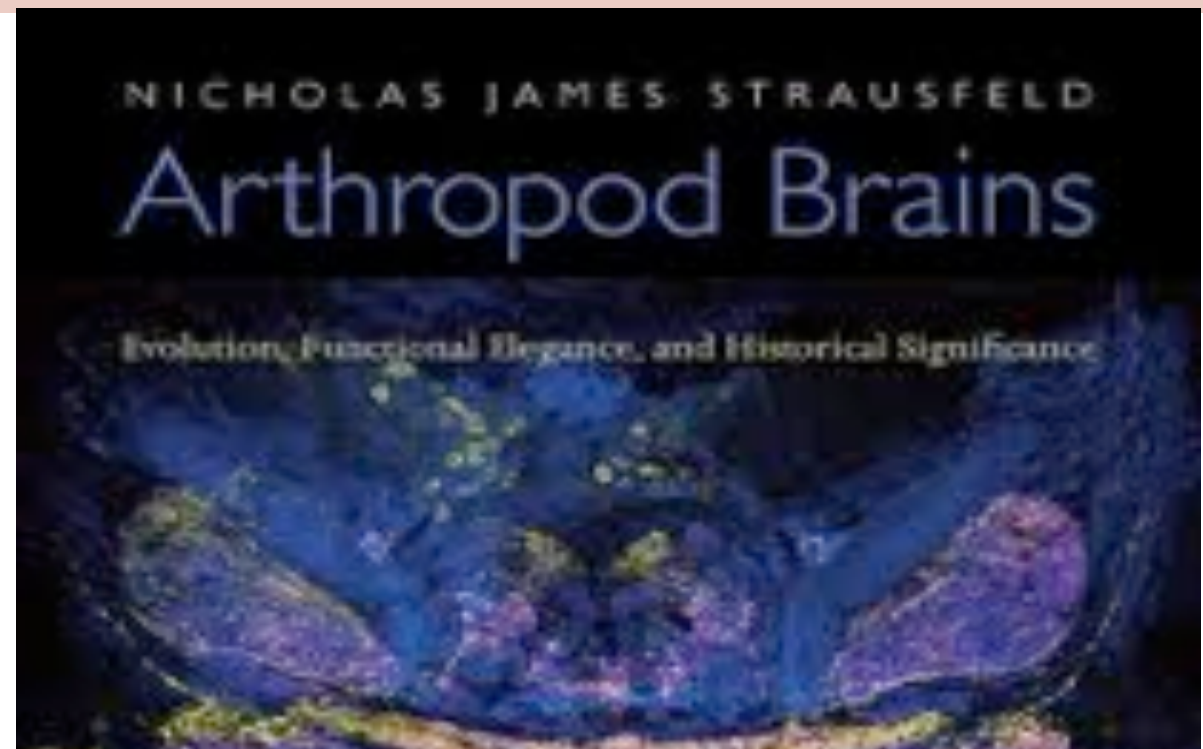


# INSECT BEARING MAP?



Insect MUSHROOM BODY primarily olfactory, input from ANTENNAL LOBE

Water-Striders: reduced AL, robust MB: sensory substitution



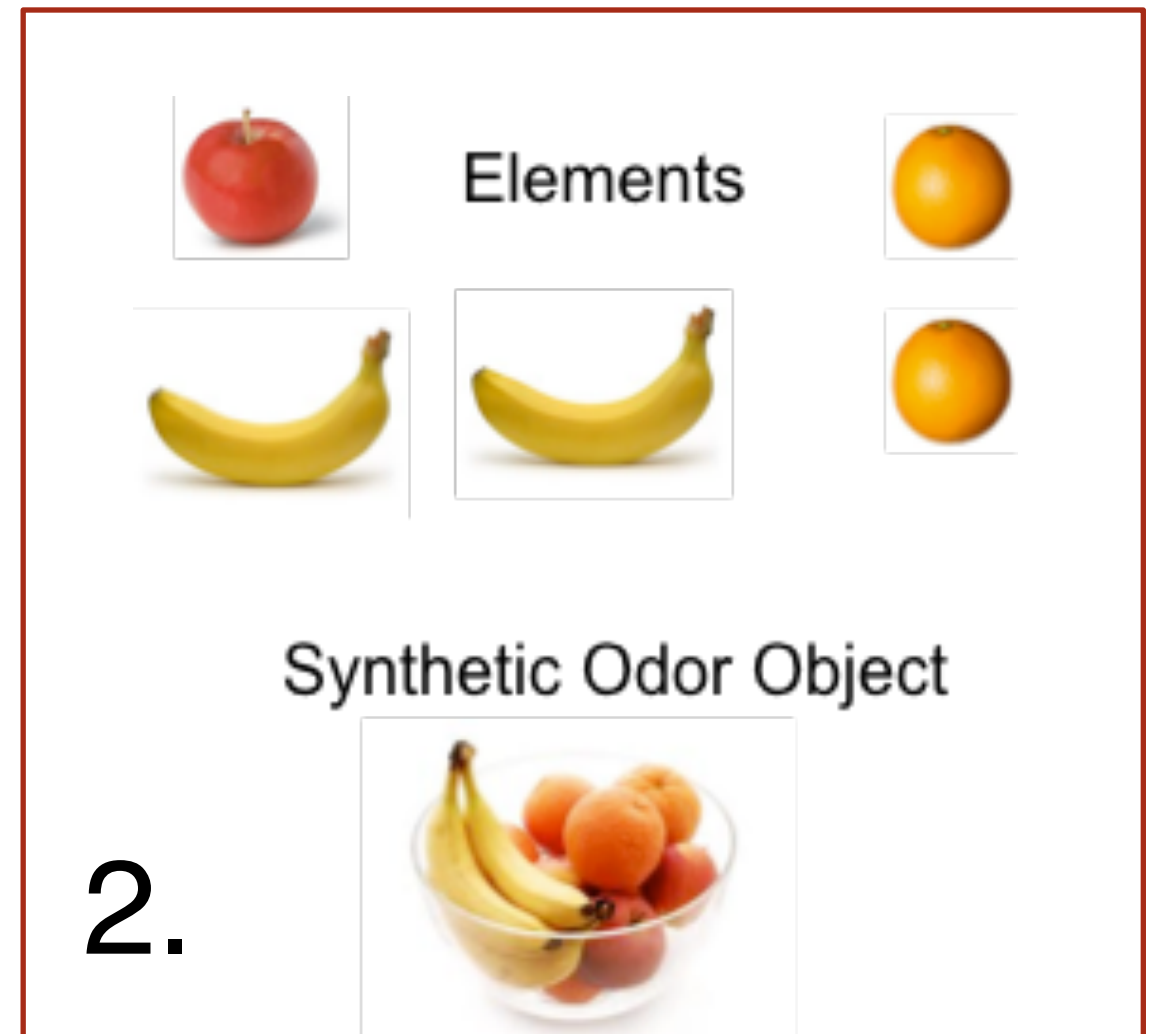
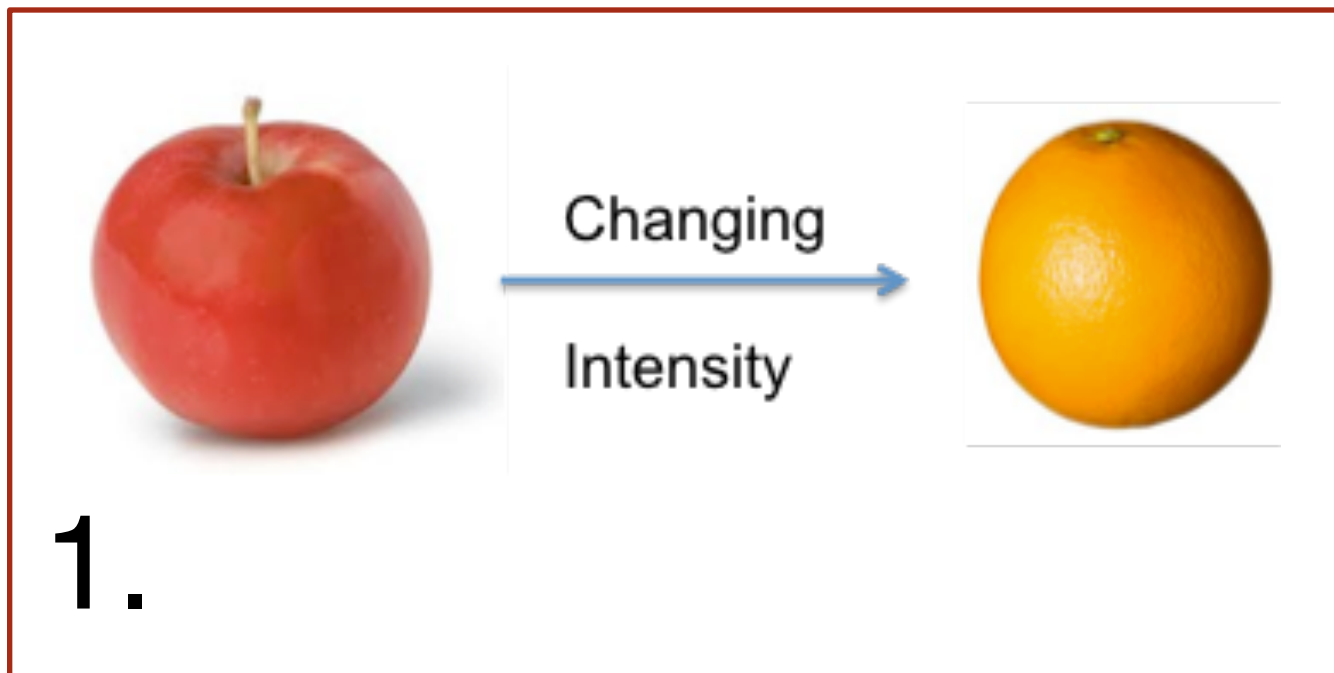
Strausfeld, N. J., Sinakevitch, I., Brown, S. M., & Farris, S. M. (2009). Ground plan of the insect mushroom body: Functional and evolutionary implications. *J. Comp. Neurol.*

# Implications

- Demand for spatial olfaction may explain patterns of allometry and plasticity across diverse taxa.
- Olfactory circuits could thus be constructed not only to identify but also to map odors for the purpose of spatial navigation.



# COULD THESE PERCEPTUAL PHENOMENA HAVE SPATIAL FUNCTIONS?

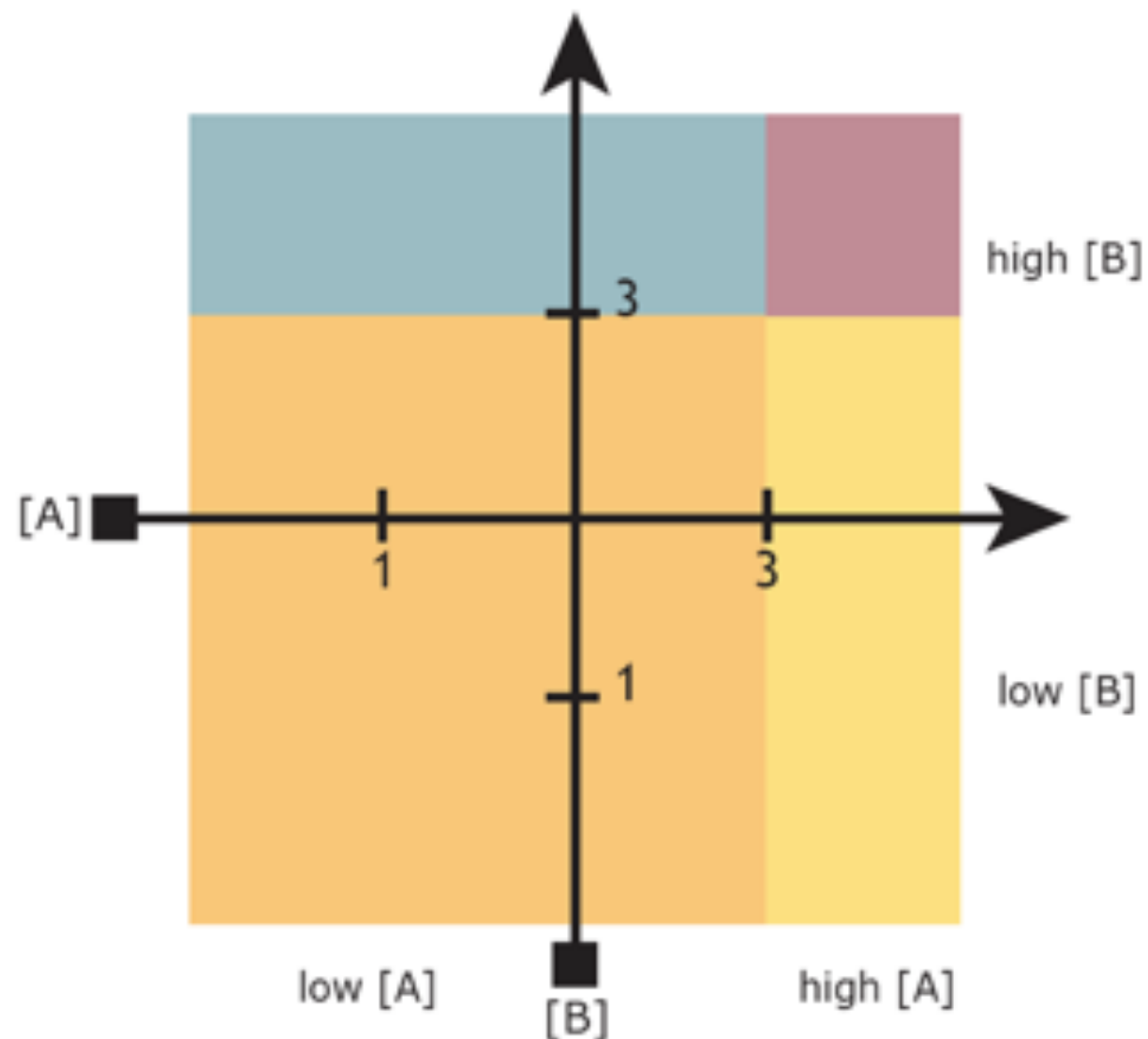


# ODOR PERCEPT COULD CREATE GLOBAL ORGANIZATION

Intensity gradients demarcated

High and low concentration percepts

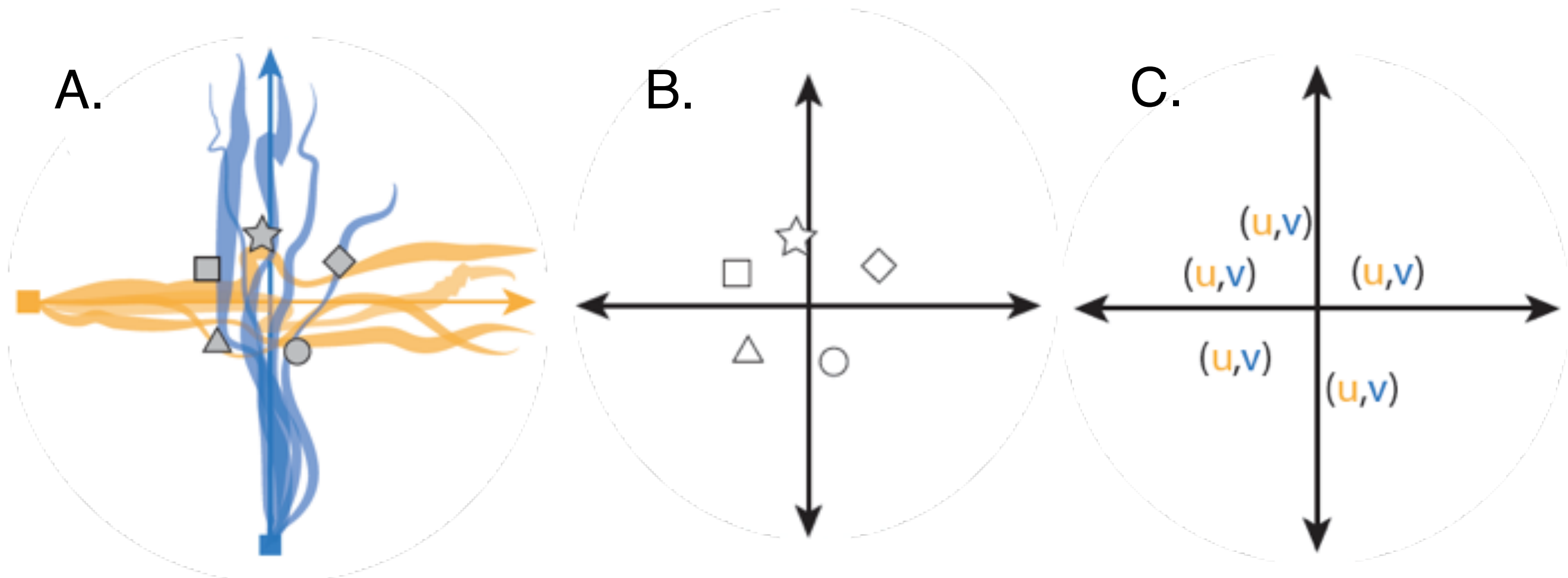
Creates neighborhoods in olfactory space



# ODOR OBJECTS COULD BE PERCEIVED AS POSITIONAL CUES (LANDMARKS)

Confluence of odorant plumes

- A. Unique ratios located in olfactory space
- B. Perceived as Synthetic Odor Object
- C. Perceived as Mixture of Elements



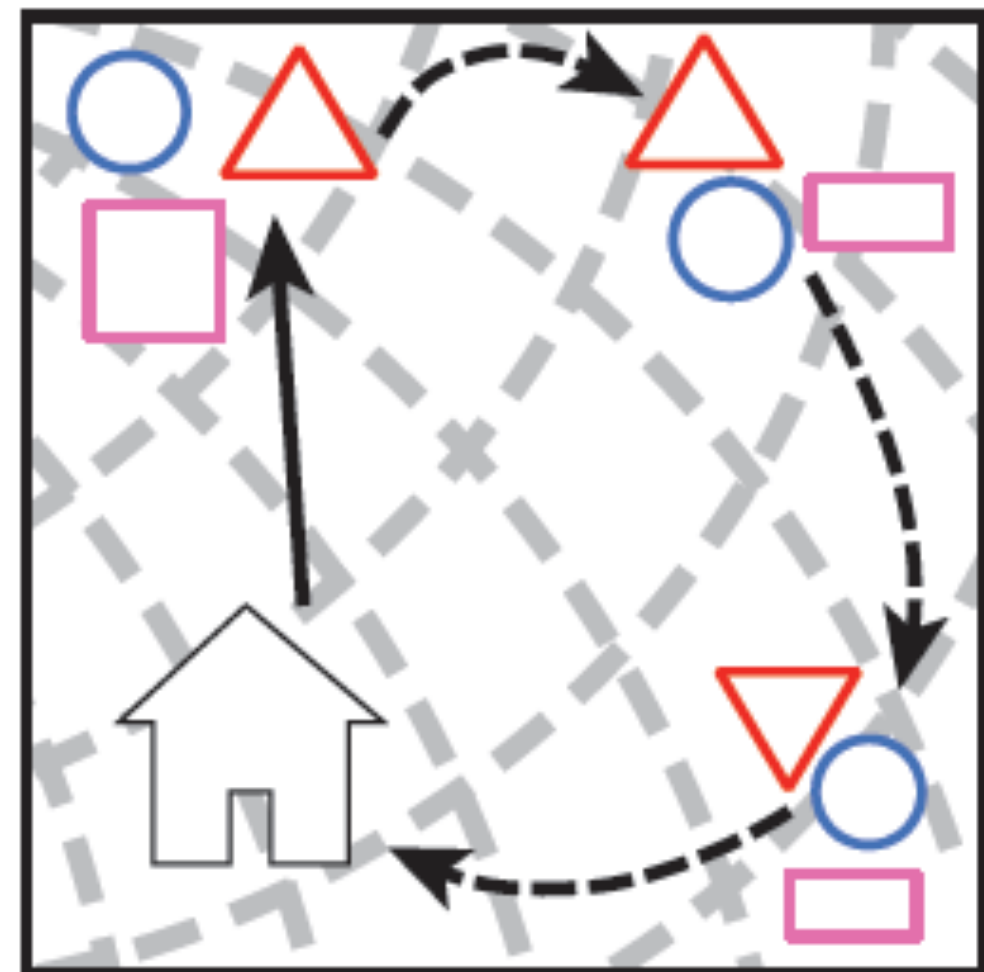
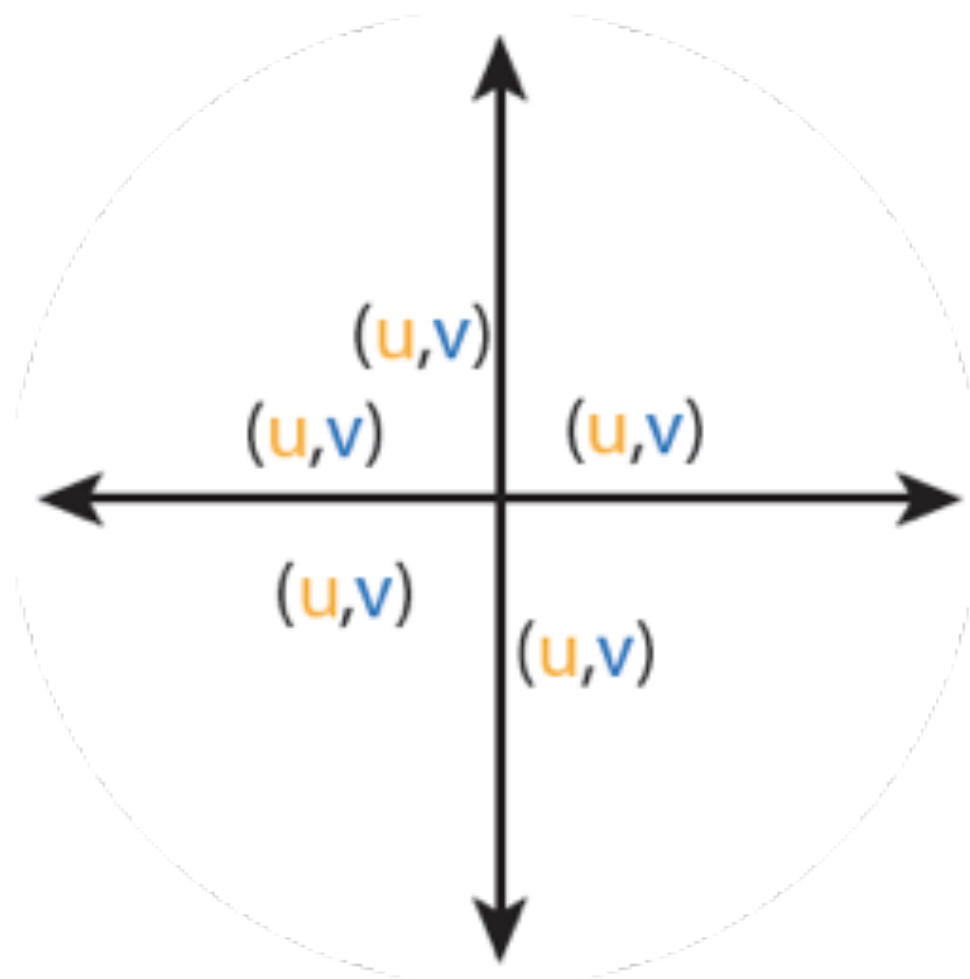


# OLFACTION COULD USE PARALLEL MAP STRUCTURE TO STORE AND EXTRAPOLATE

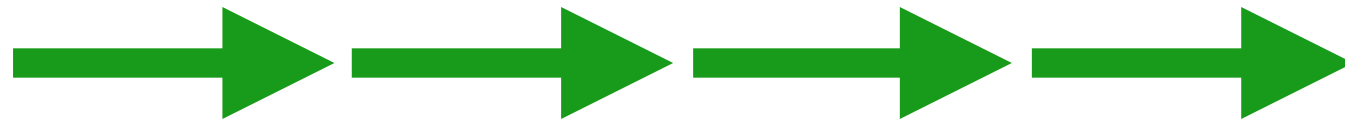
Has necessary information – origin of hippocampal logic?

Objects re-coded in grid coordinates

Flexible short-cutting



# What other properties are needed to map gradients?



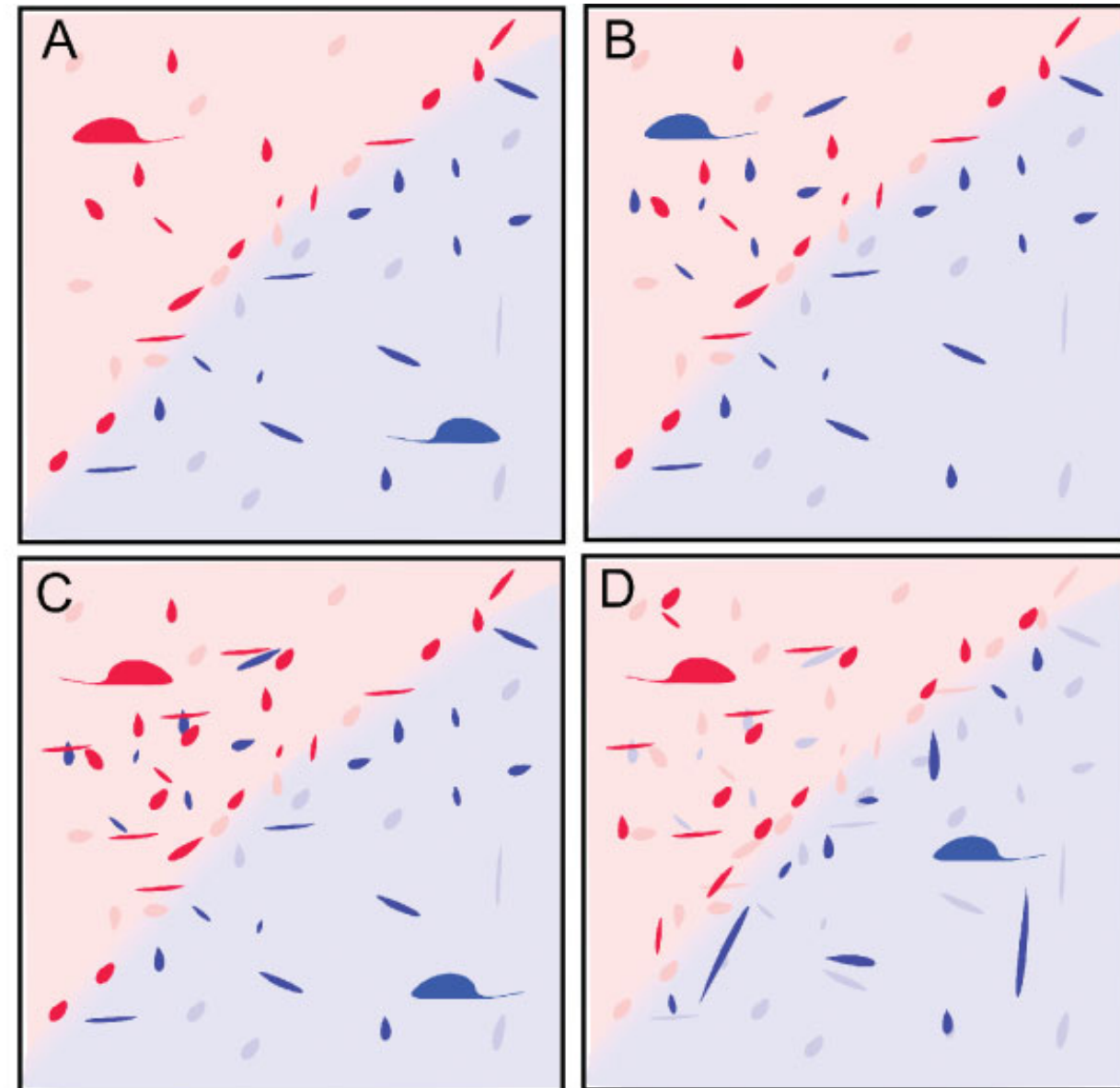
- **MUST KNOW**
  - **Rate of locomotion**
  - **Rate of sampling (respiration)**
- **DECODE fluid direction and speed, using measurements from other systems (vibrissae, rhinarium, etc.)**

# Space and Time

Review articles

## Scent wars: the chemobiology of competitive signalling in mice

Jane L. Hurst\* and Robert J. Beynon



©Witnes Photographic



# ACKNOWLEDGEMENTS



**Randolf Menzel**, Freie Universität Berlin

**Françoise Schenk**, University of Lausanne

**Frank Sulloway**, **Mimi Koehl**, **Barbara**

**Meyer**, **Tom Cline** UC Berkeley

**Berkeley CogBio Lab**: **Mikel Delgado**,

**Jennifer Arter**, **Amy Cook**, **Judy Jinn**, **Molly**

**Nicholas**, **Zoe Burr** and **Scott Bradley**

**Funding**: NSF EECS 1028319

