Bees & the Cognitive Map Debate

By: Paige Leerssen; Chuyu Yang, Dan John, & Mark Bailey

Based on the review "The internal maps of insects" by Barbara Webb, 2019

Bees & the Cognitive Map Debate

Not about the existence of ‘a centralized mental metric representation'

Rather, whether it remains implicit and ‘at any one time, the animal knows where to go rather than where it is on some kind of cognitive map’

Implicit or Metric Representation?

Knows where to go

Knows where it is on a map

Base Model for Insect Navigation

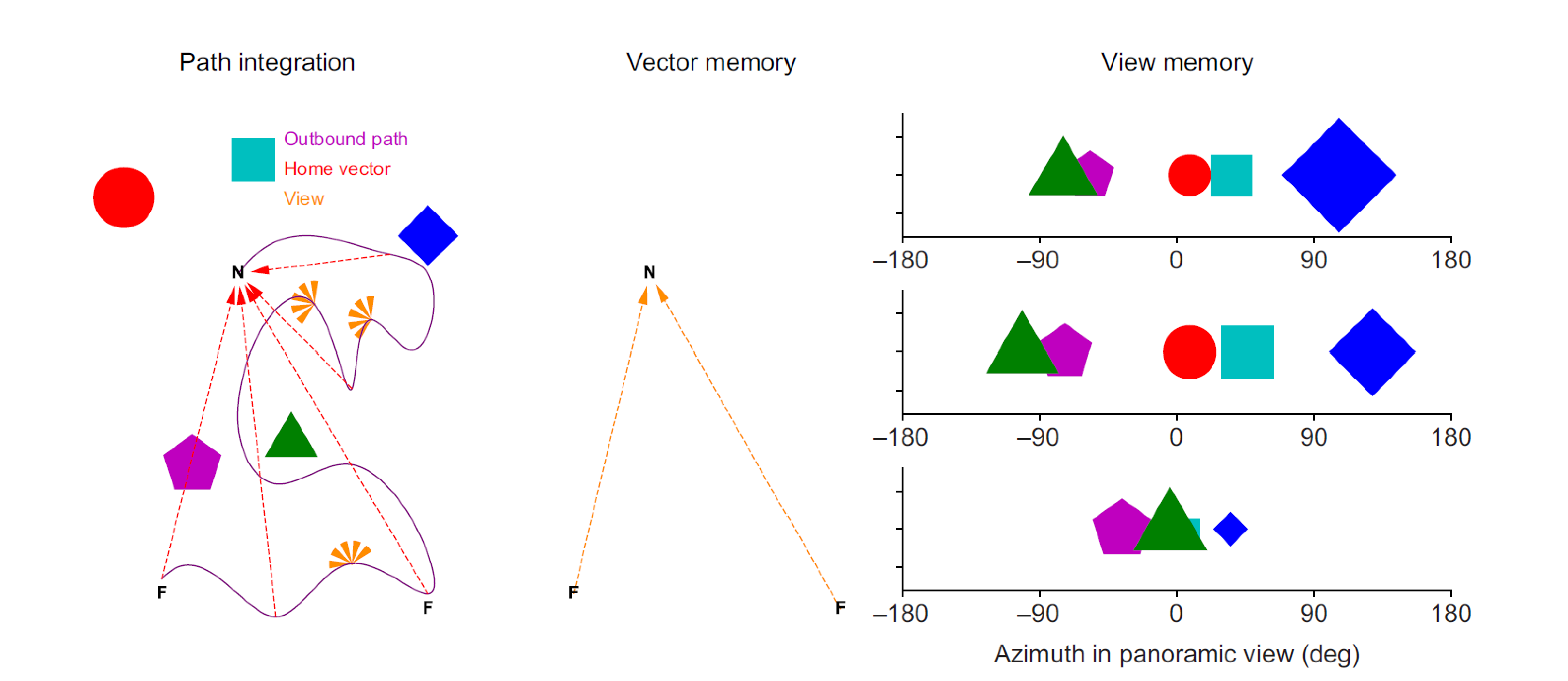
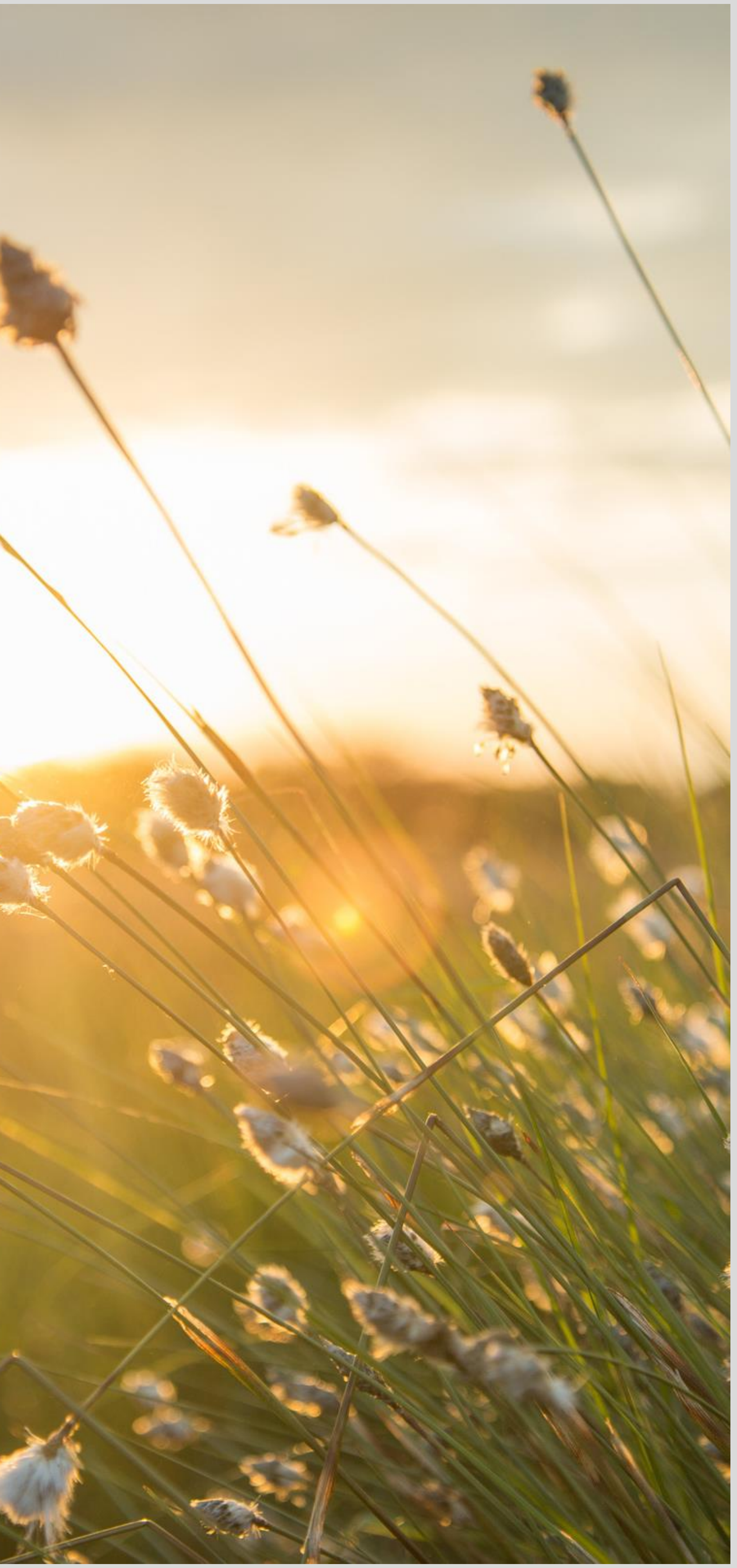


Figure adapted from Webb (2019)



Allothetic vs. Idiothetic Information

- Allothetic: The use of external cues for navigation (i.e., celestial cues like polarized light from the sun, landscape cues, etc.)

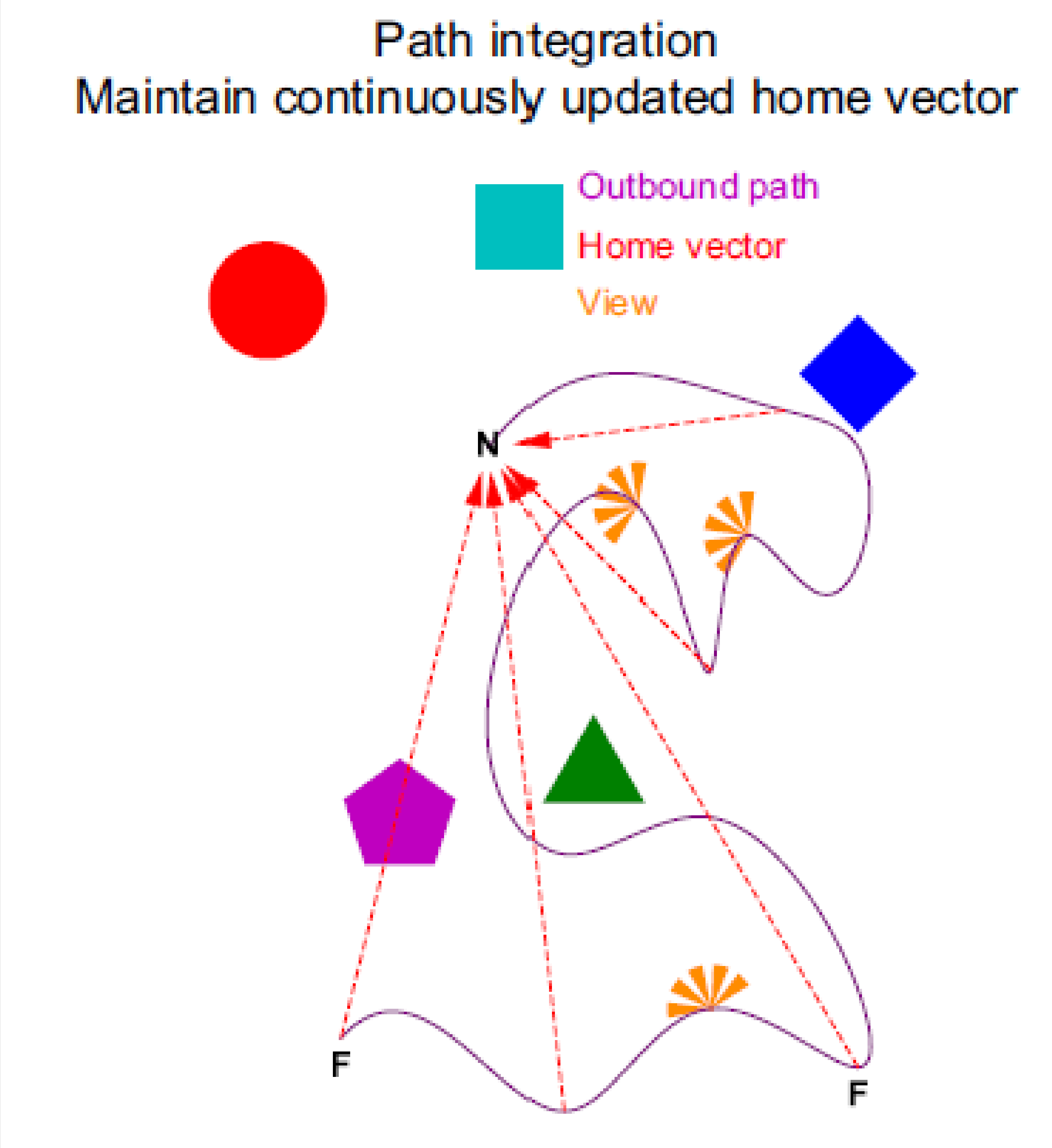
- Idiothetic: The use of self-motion cues for navigation (i.e., heart beats, wing beats, muscle cues, etc.)

Path Integration

Aka dead reckoning

Capacity to use idiothetic cues to calculate the updated position of the animal by monitoring its trajectory in relation to a start location

(cues generated by the animal's movements)



Byrne, J. H. (2017). Learning and memory: a comprehensive reference. Academic Press.

Figure adapted from Webb (2019)

Path Integration

Evidence for Path Integration in Bees

After being displaced, control bees continue following the PI vector that they believe will take them home.

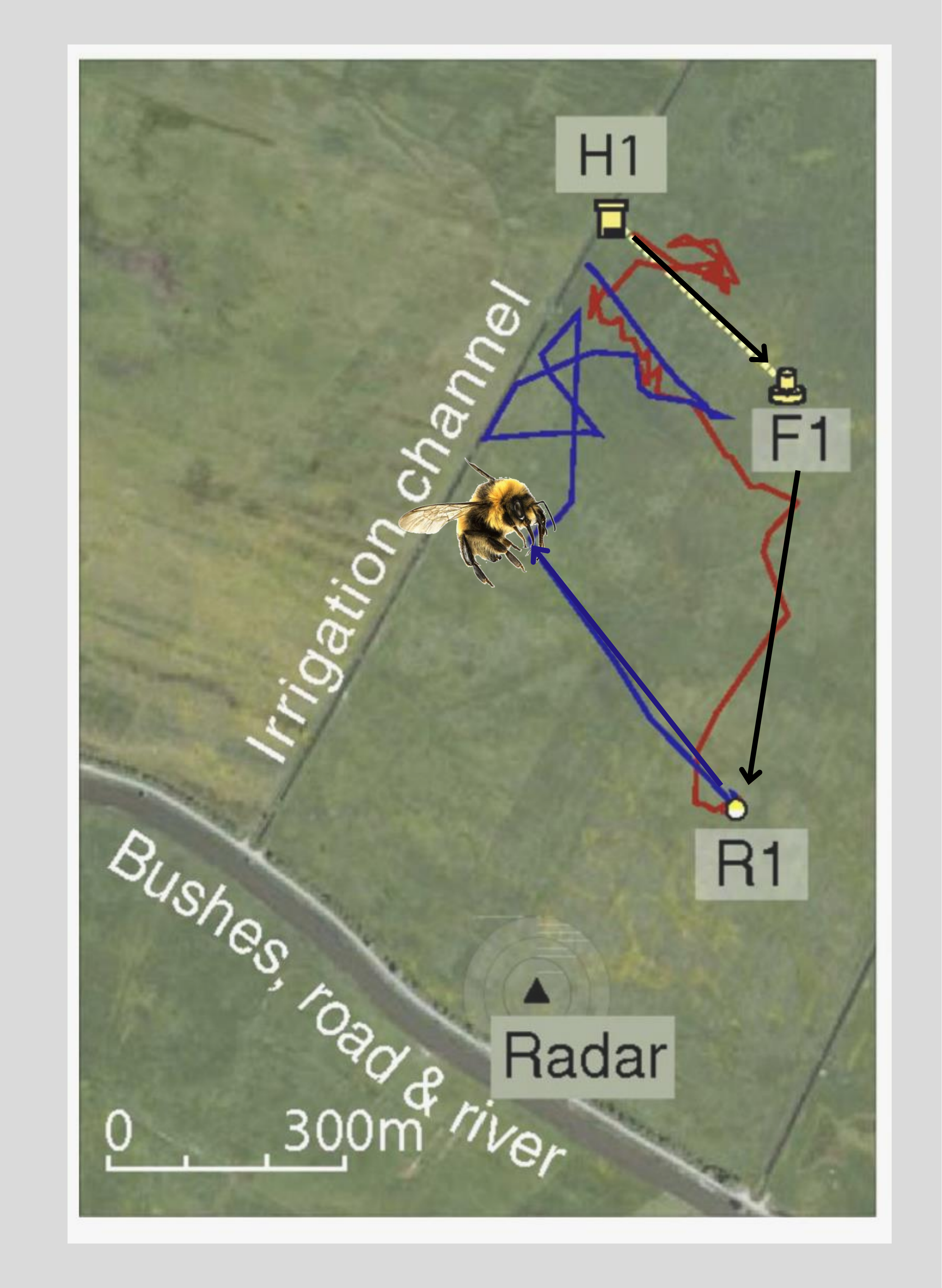


Figure adapted from Cheeseman et al., 2014

Vector Memory

The state of the PI system on reaching a goal can be stored

Later activation of that memory (by an internal motivation to return to a different goal) can interact with PI to produce a return to this goal

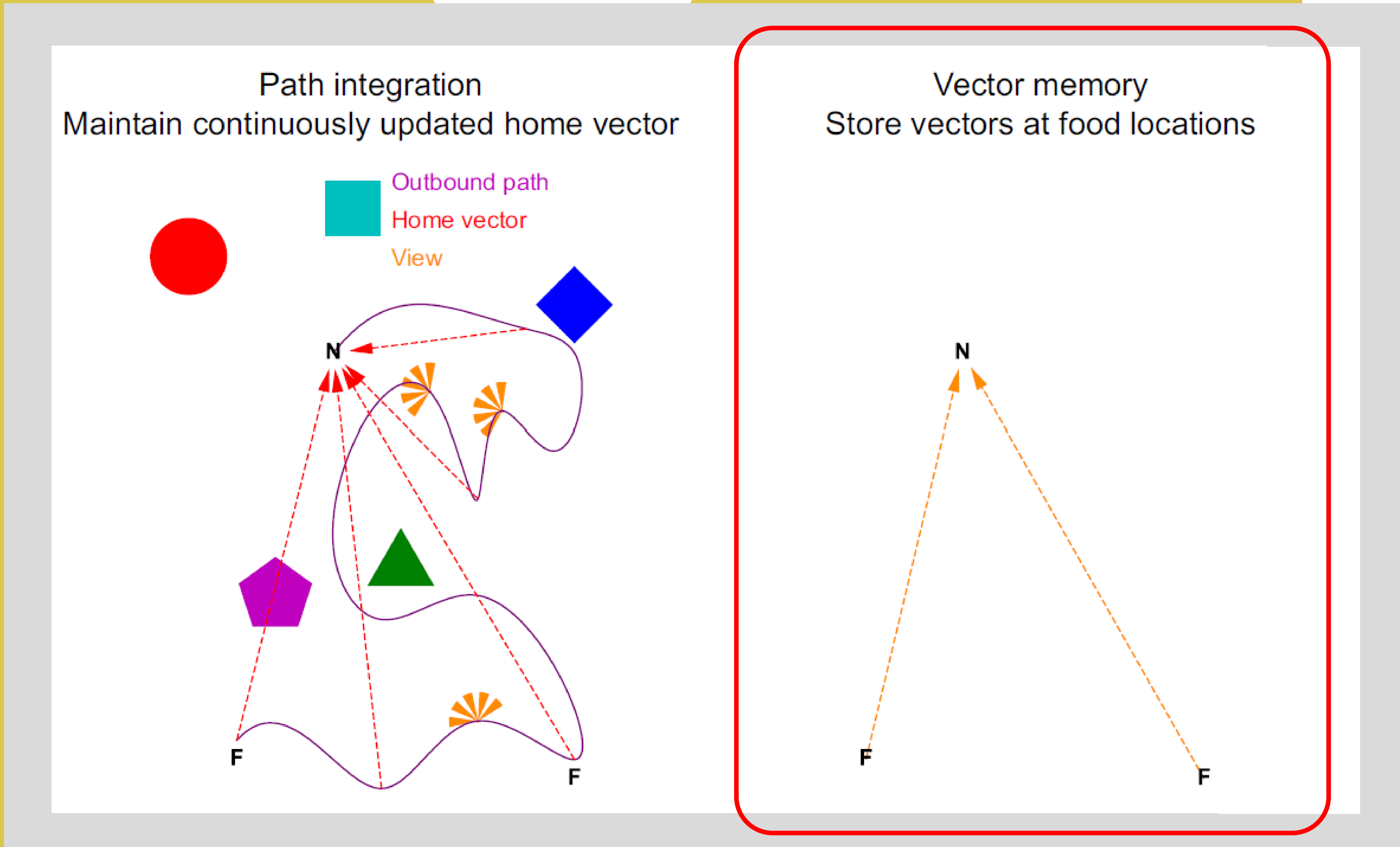


Figure adapted from Webb (2019)

Evidence for Vector Memory in Bees

1.) Bees follow PI

2.) Search for vector towards home

3.) Find active vector memory towards home when they near a goal they've visited before

Steering is driven by PI – VM → 0

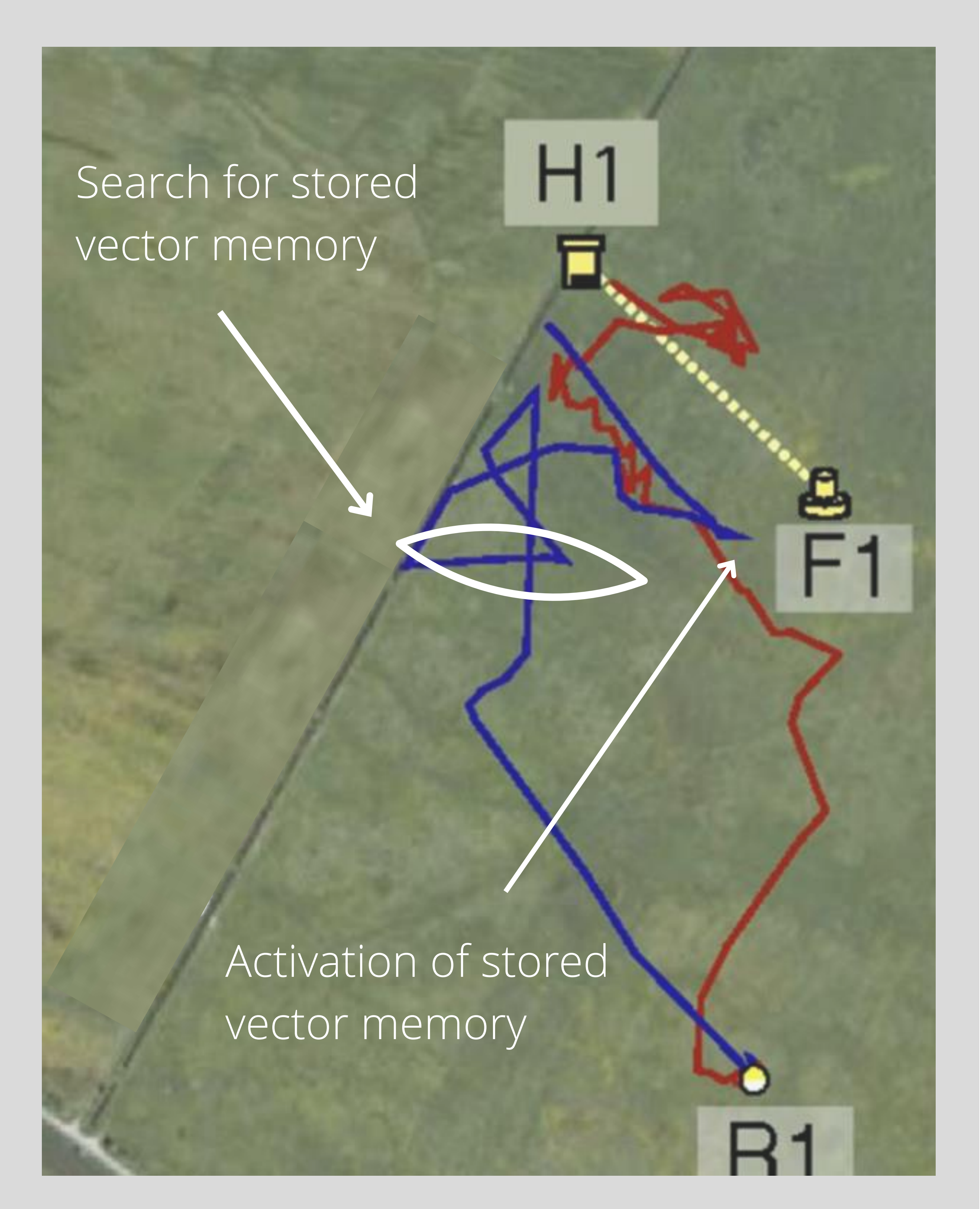


Figure adapted from Cheeseman et al., 2014

Q. What if they're using allothetic cues to navigate home instead of vector memory?

A.1. No memorable landmarks in view

A.2. They wouldn't need to search for a homeward vector

A.3. Home vector is a single, consistent, geocentric frame of reference as celestial compass cues are fixed in orientation relative to the terrain, as is the origin

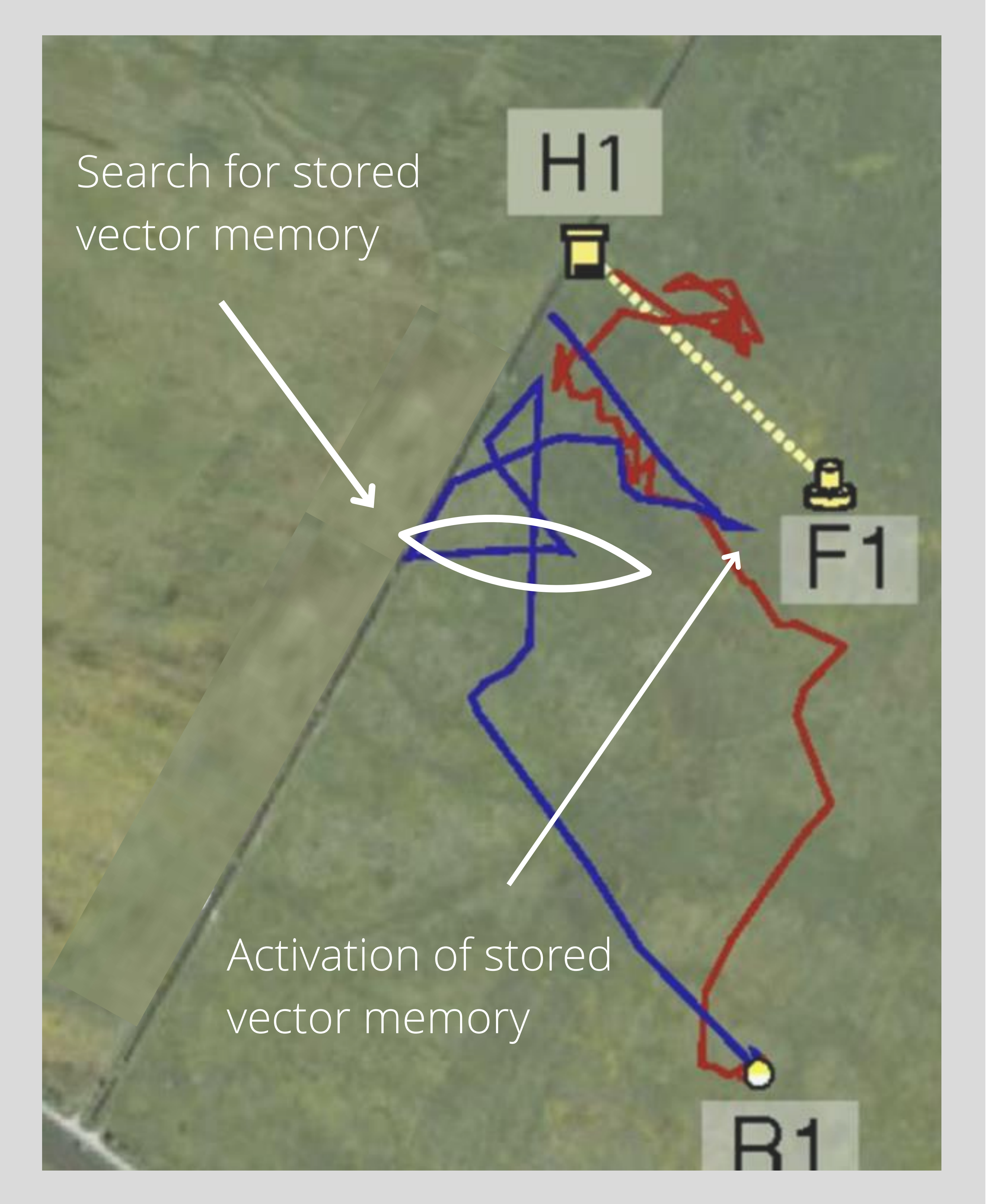


Figure adapted from Cheeseman et al., 2014

View Memory

Multiple images when facing or moving along a route to a goal can be stored, allowing the familiarity of the current view to guide movement

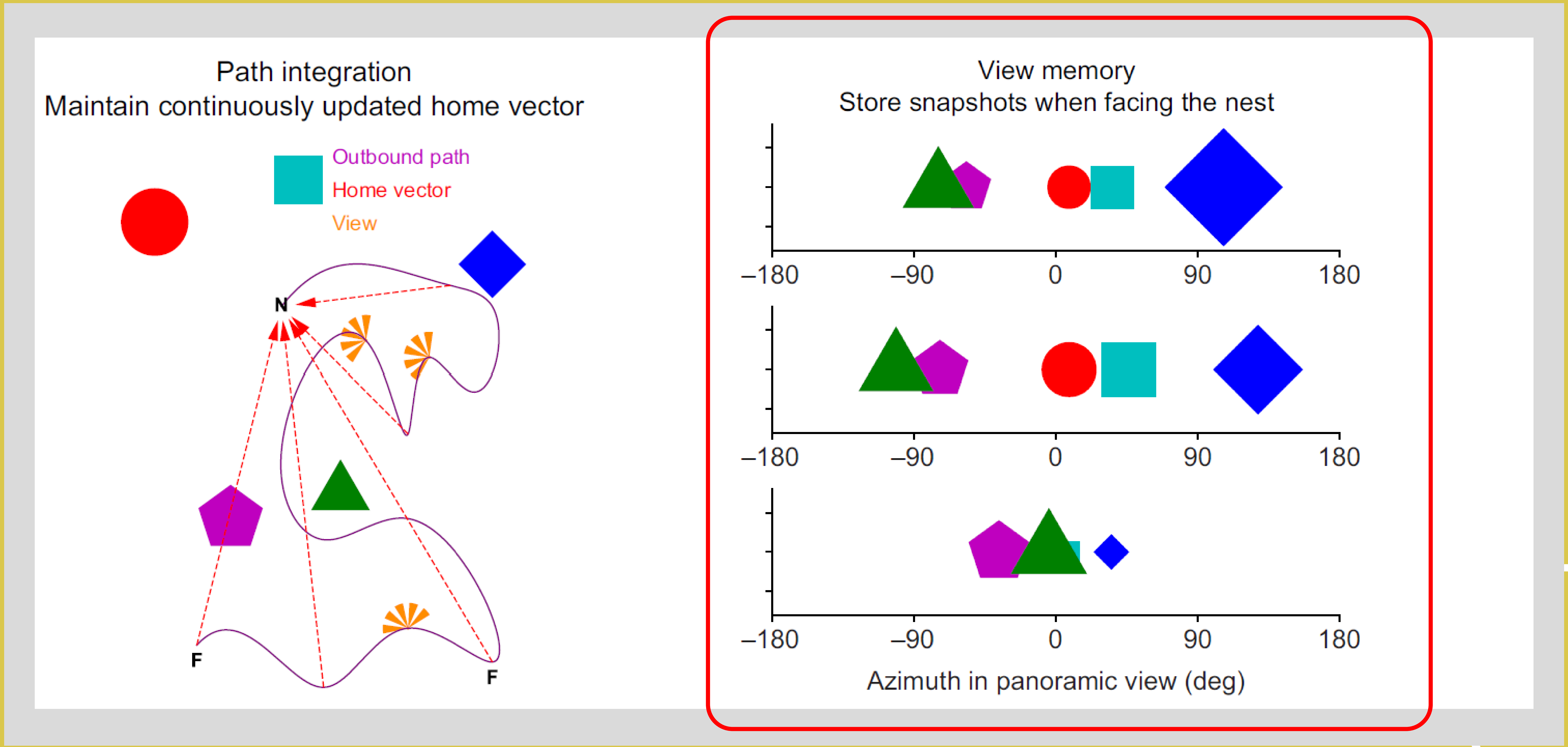


Figure adapted from Webb (2019)

View Memory cont.

View memory follows the 'snapshot model' by assuming the memory is of a retinotopic, panoramic view, rather than of individual and identifiable landmarks and their estimated spatial locations

*Optic Flow

Figure from Max Planck Institute for biological intelligence

Evidence for View Memory in Bees

1.) Bees follow PI

2.) Use snapshots of bushes/road/river to orient themselves towards home

3.) Follow vector memory home

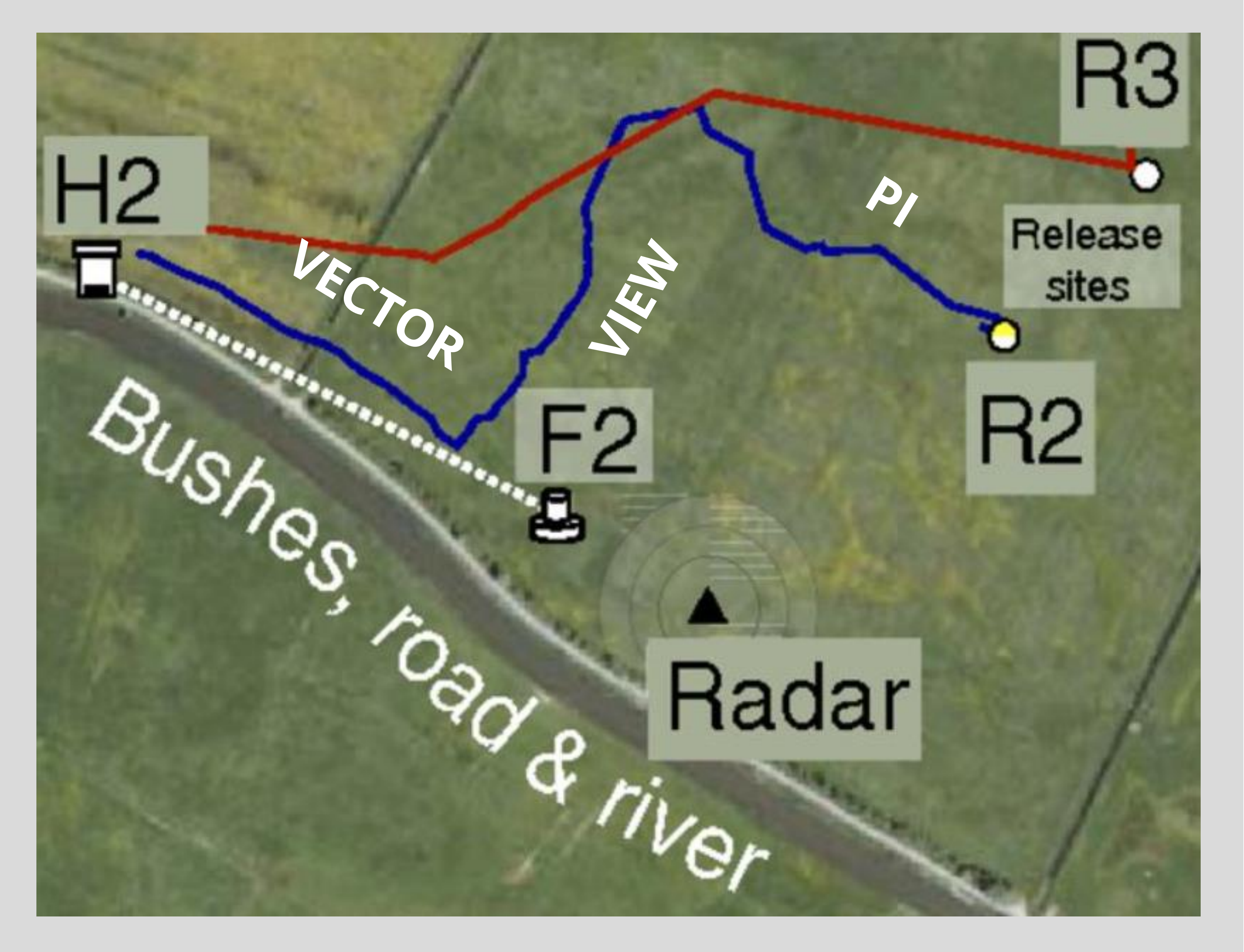


Figure adapted from Cheeseman et al., 2014

Interaction Proposal # 1

PI and vector memory determine which images are stored in view memory.

Learning excursions: bees store images when PI indicates it is facing home

Route following: first trip home from food is guided by PI and first trip back to feeder guided by vector memory to learn relevant views.

Thereafter could use view alignment alone.

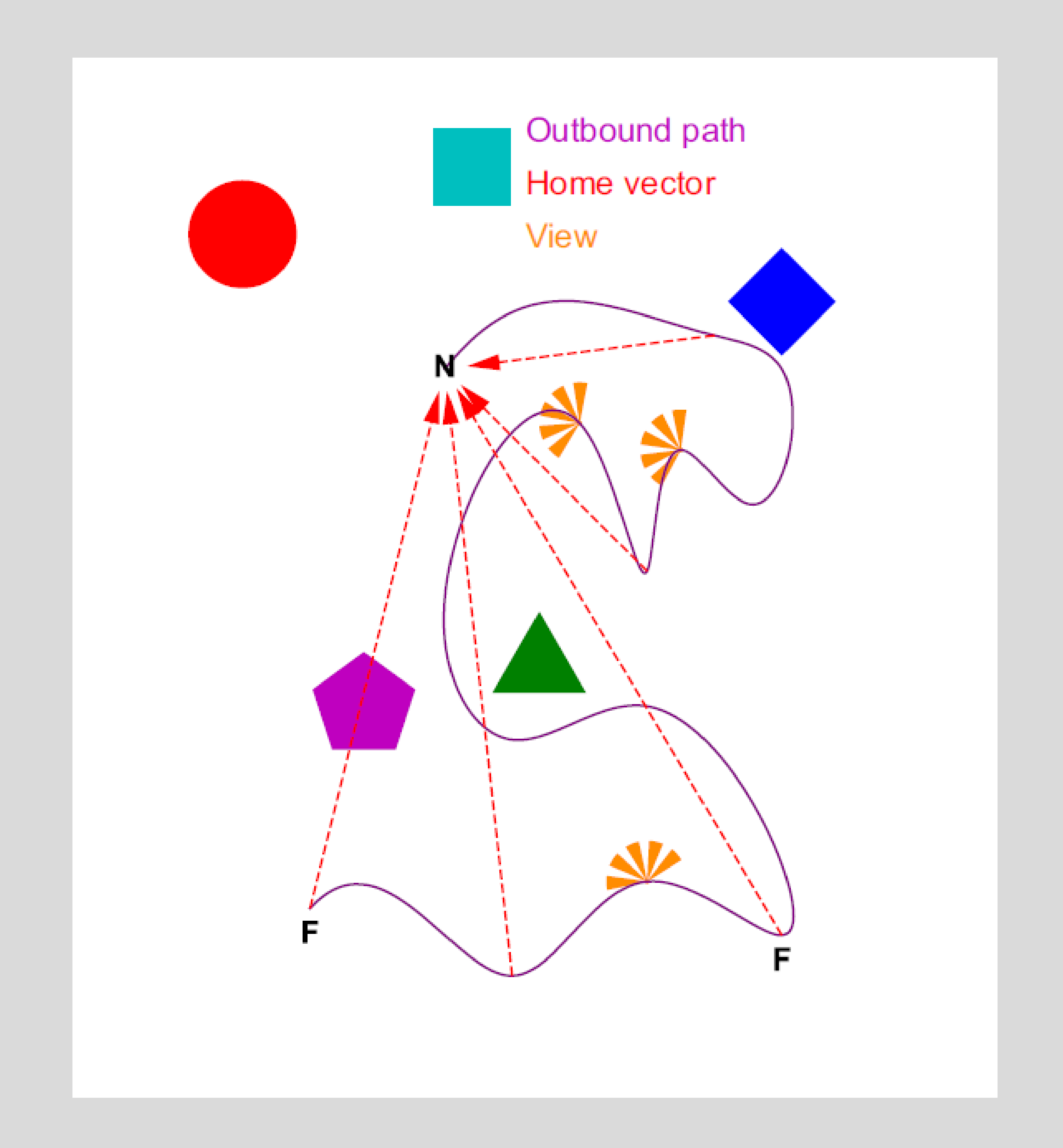


Figure adapted from Webb (2019)

Interaction Proposal # 2

Weighted Interaction

The output of the three systems can be combined to control behavior

Weighting of PI, vector memory and view memory components can vary

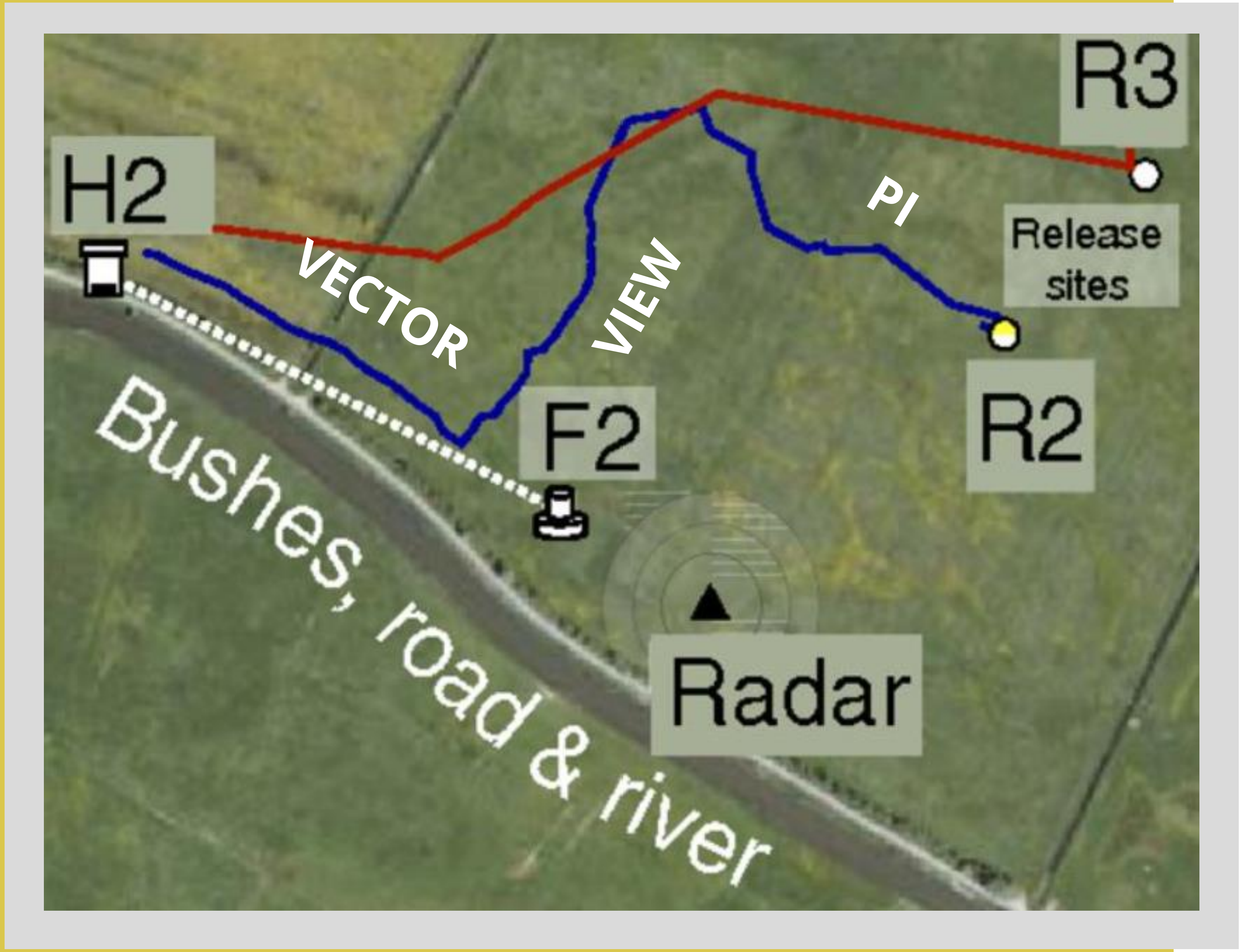


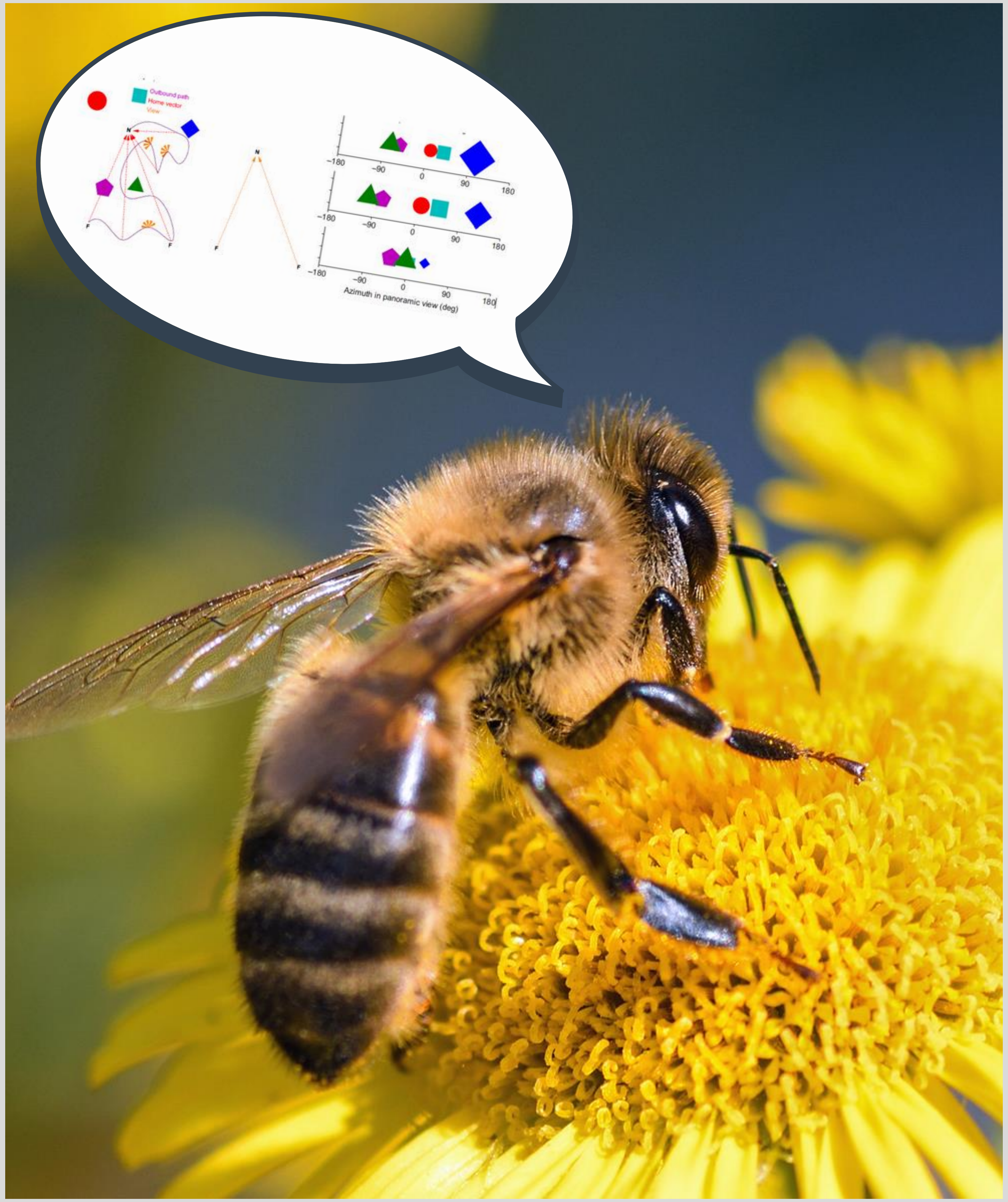
Figure adapted from Cheeseman et al., 2014

Is the Base Model a Cognitive Map?

Evidence for insects recovering PI information from views or noticing a discrepancy between their PI and view memory would appear (ipso facto) to be evidence that they have attached PI coordinates to their views, and thus effectively have a map

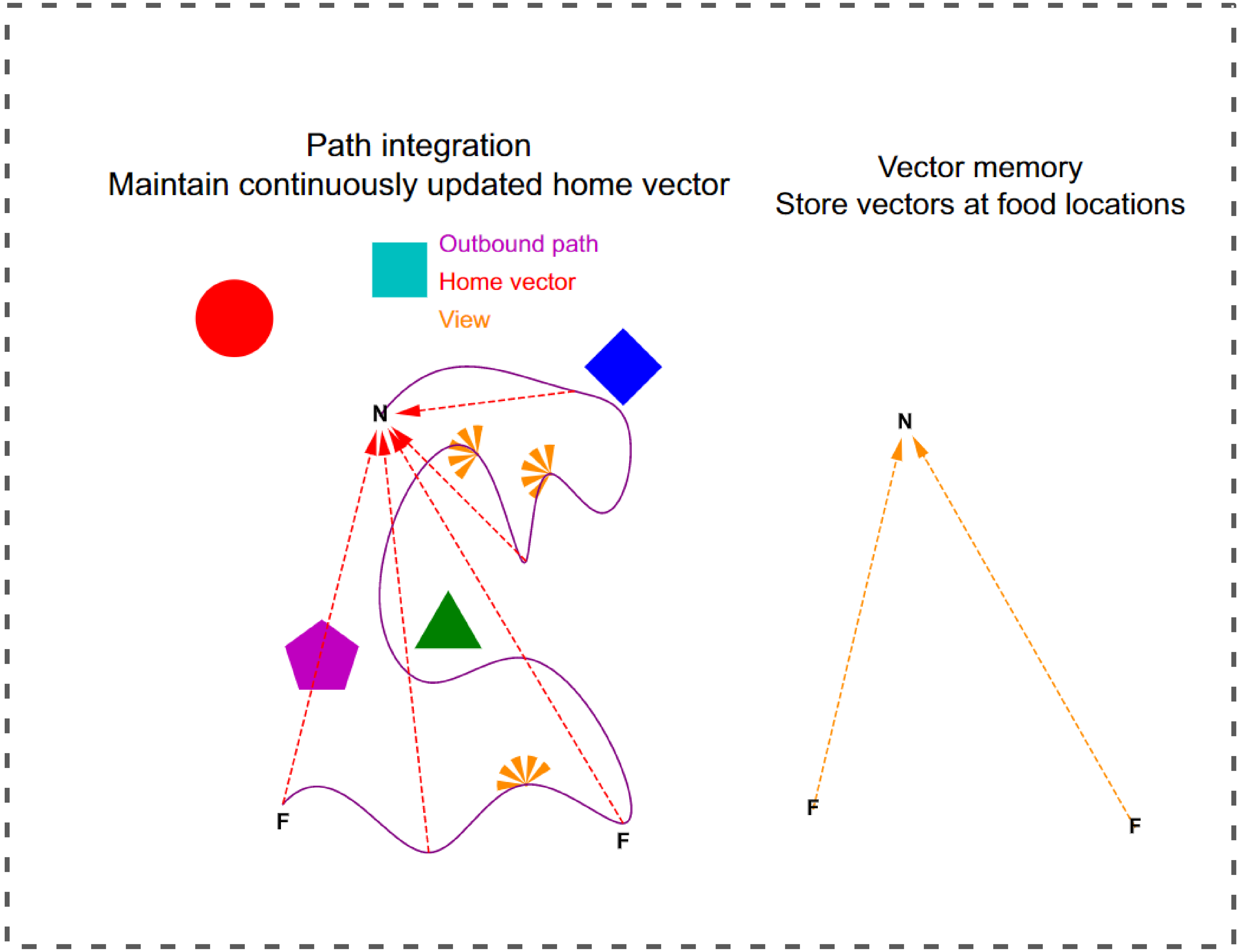
View Memory -> Embedded in PI = Cognitive Map

Base Model ≠ Cognitive Map

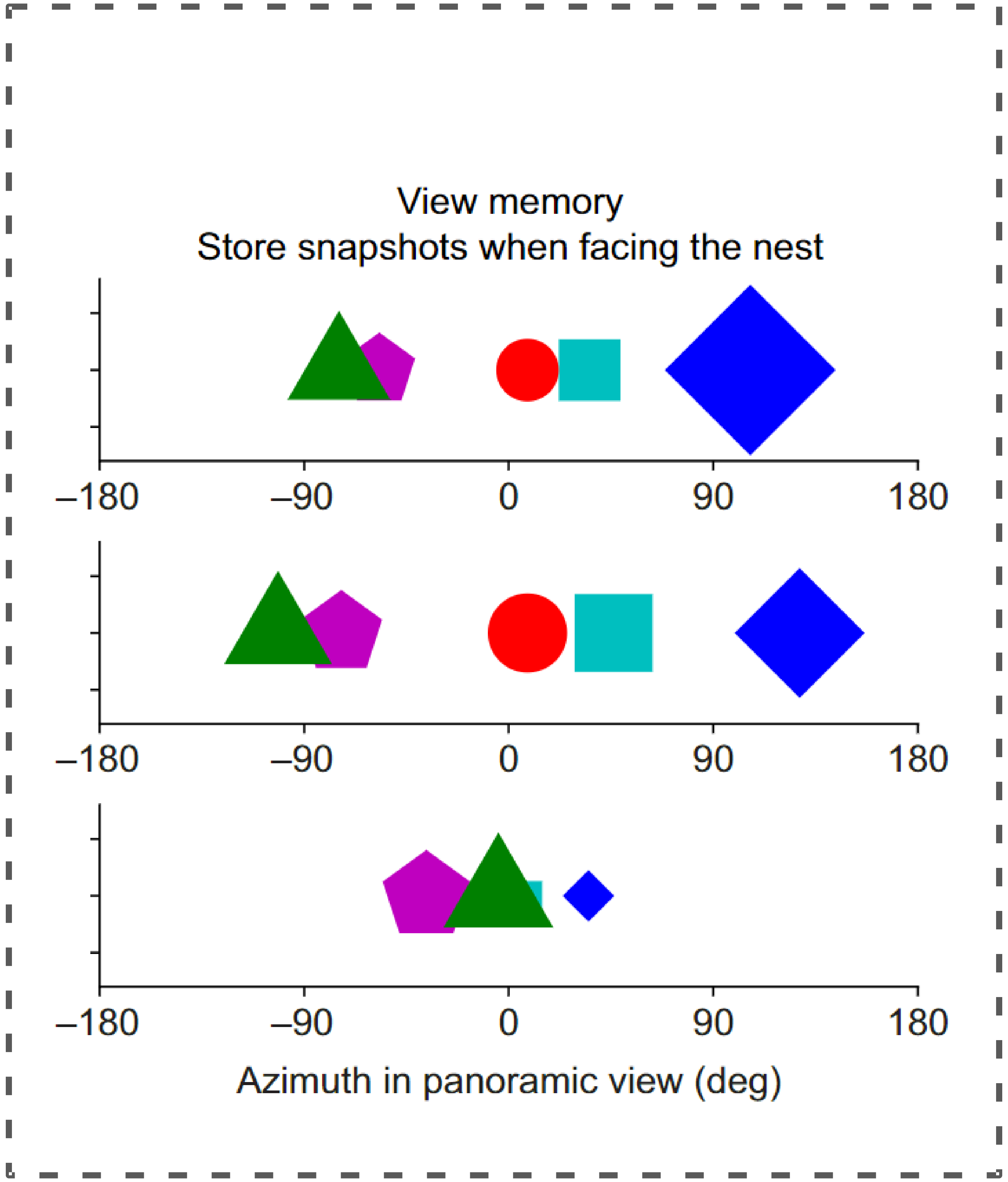


Base model

Vector system -> Central complex

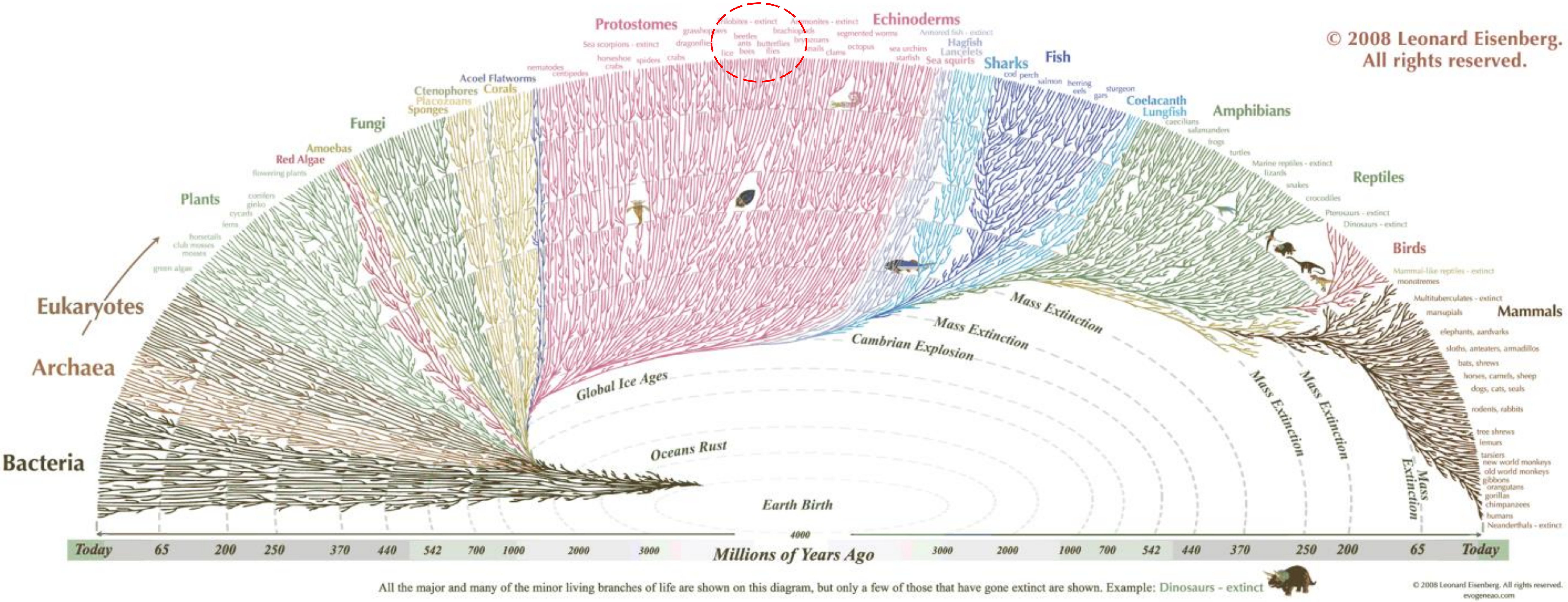


View memory -> Mushroom body

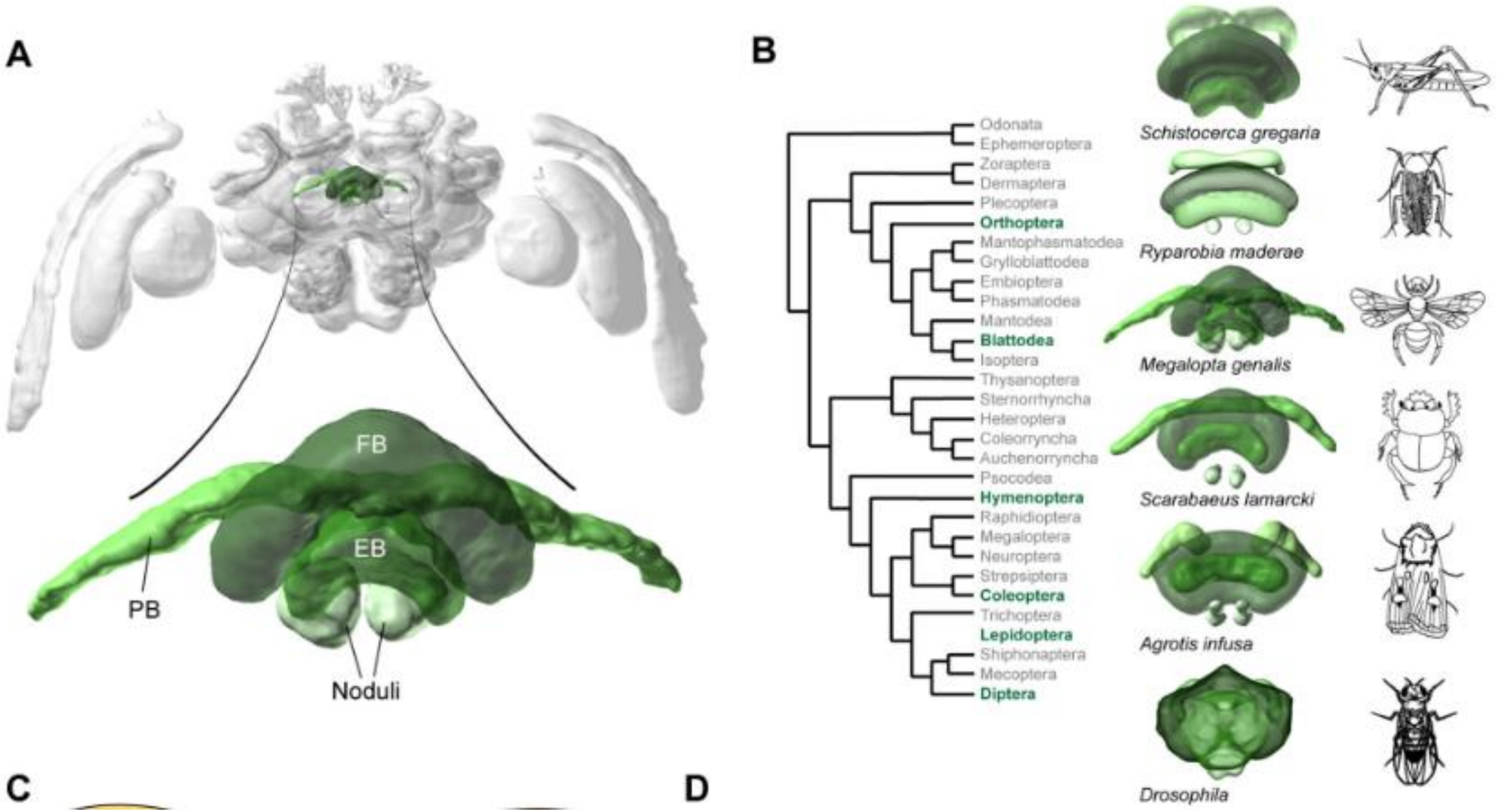


Webb (2019)

How far are we from insects?

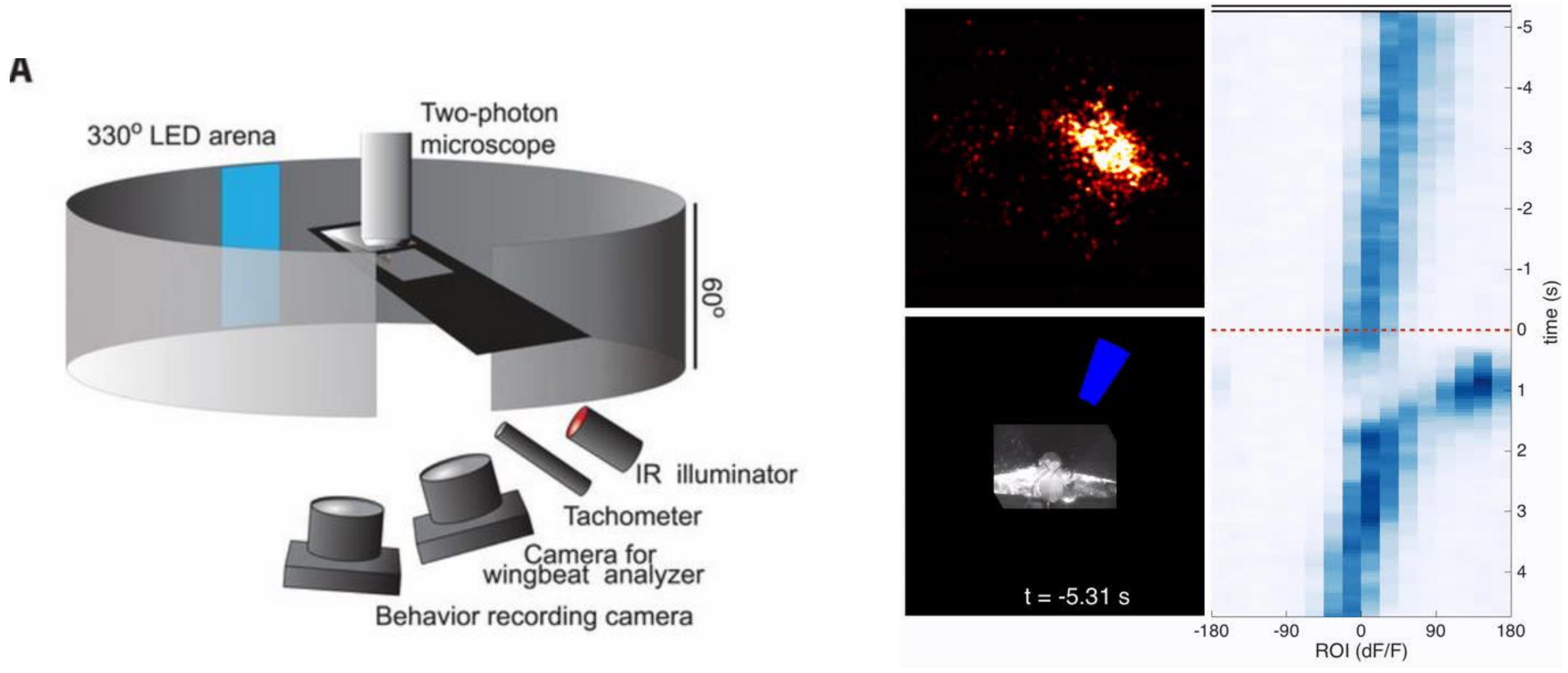


Central complex is conserved across a wide range of insects

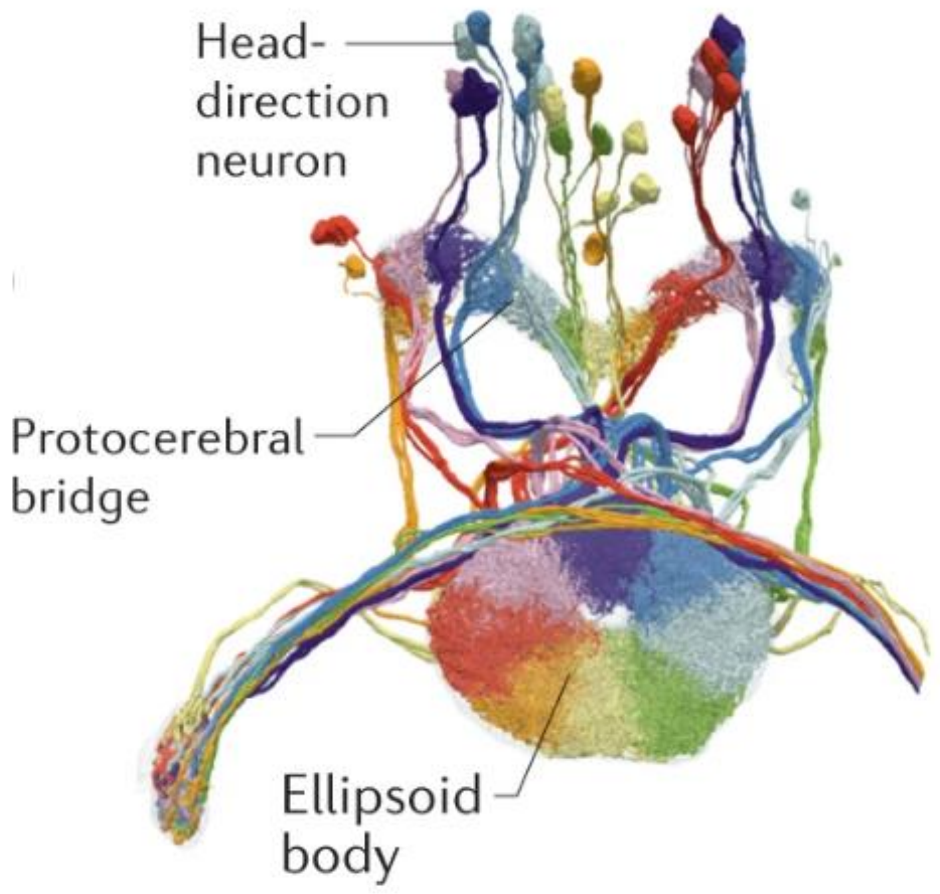


Honkanen et al. (2019)

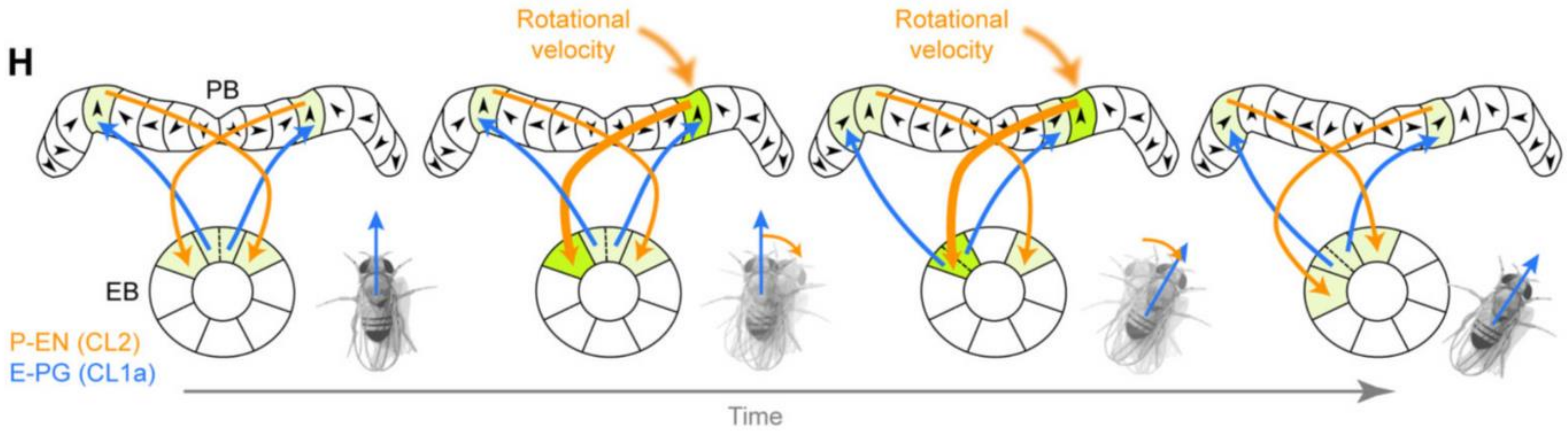
Ring attractor for head direction cells



Kim et al. (2017)



Khona et al. (2022)



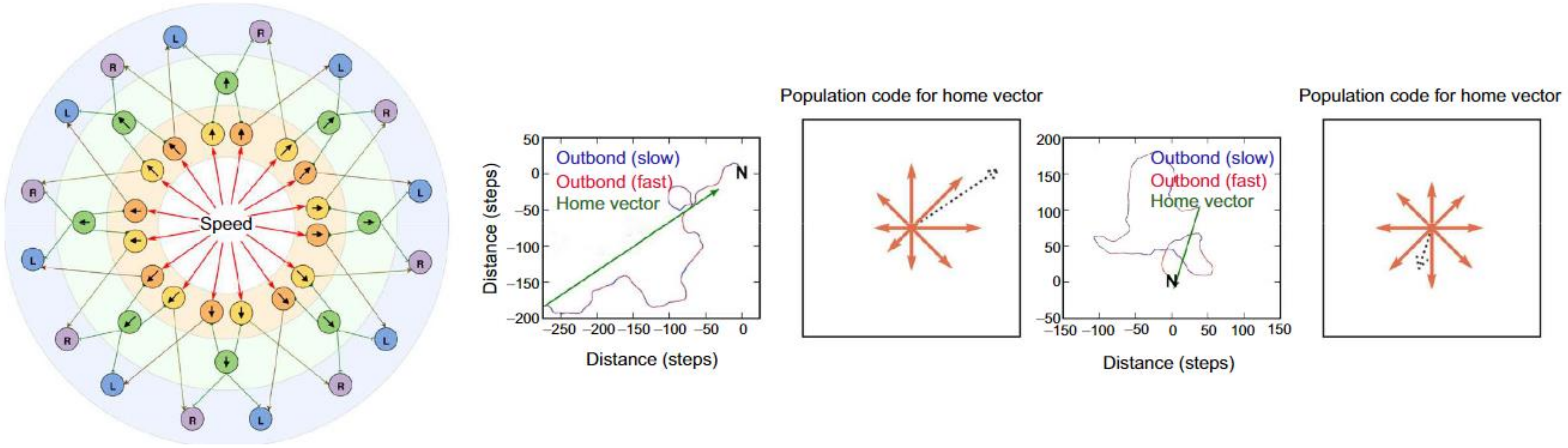
Honkanen et al. (2019)

Possible neural implementation for the vector system

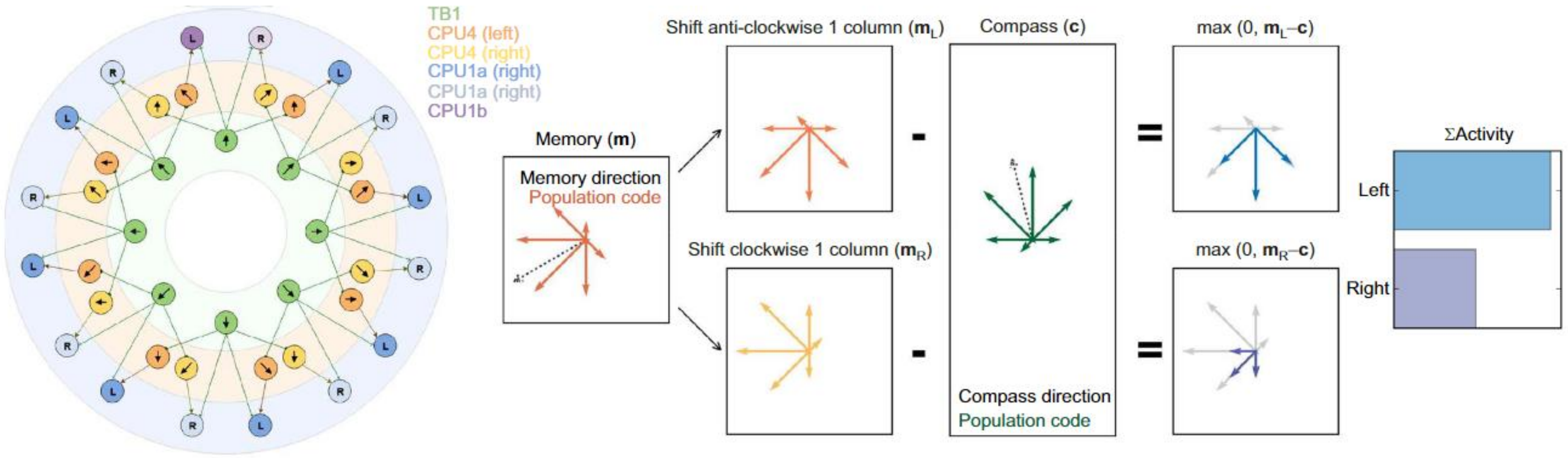
--inspired by connections
--activity of individual CX neurons can reliably predict intended movement directions in freely walking cockroaches

TB1: directional tuning
CPU4: vector memory
CPU1: steering

Update PI
Each CPU4 cell modulates the accumulation of speed in its preferred (inhibited) direction.



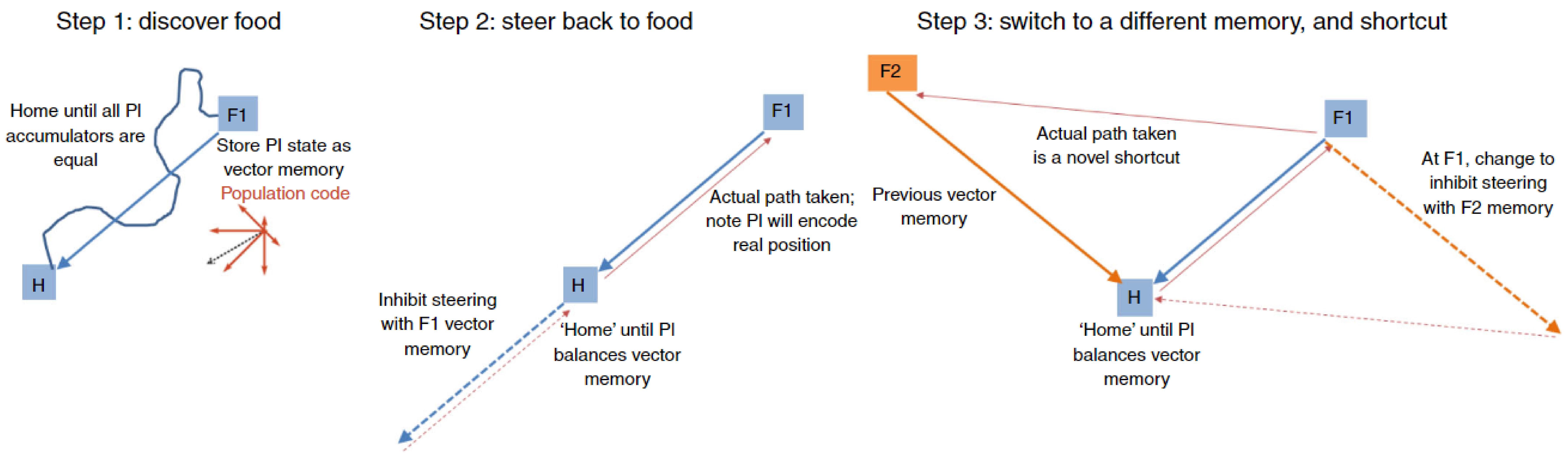
Homing steering
Compare TB1 with CPU4 column by column. The resulting imbalance in CPU1-neuron activity between the right and left side causes steering.



Webb (2019)

Novel shortcuts without explicit vector addition

The goal is (PI - vector memory) -> 0



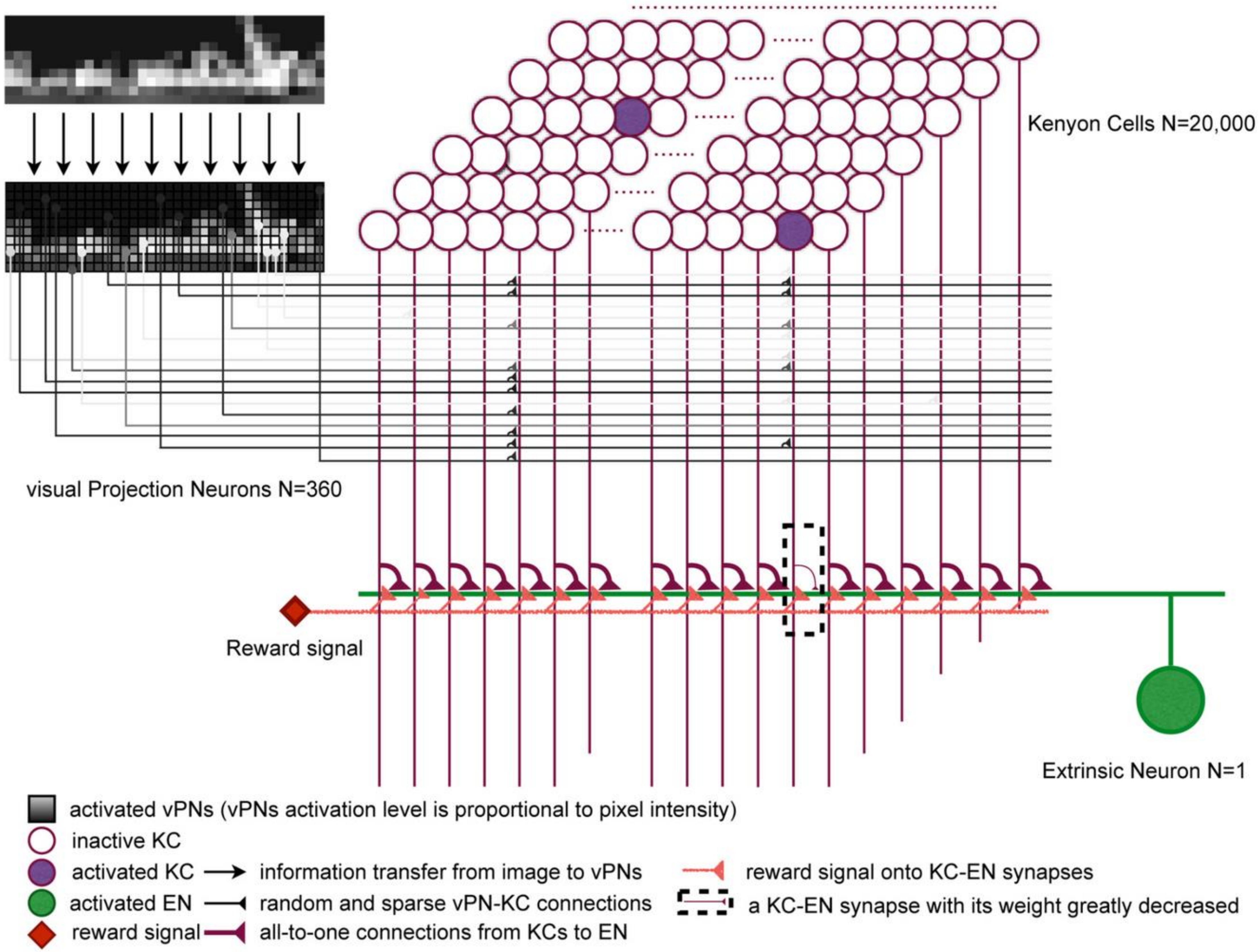
Webb (2019)

Vector memory of honey bee

Possible neural implementation for the view memory: mushroom body

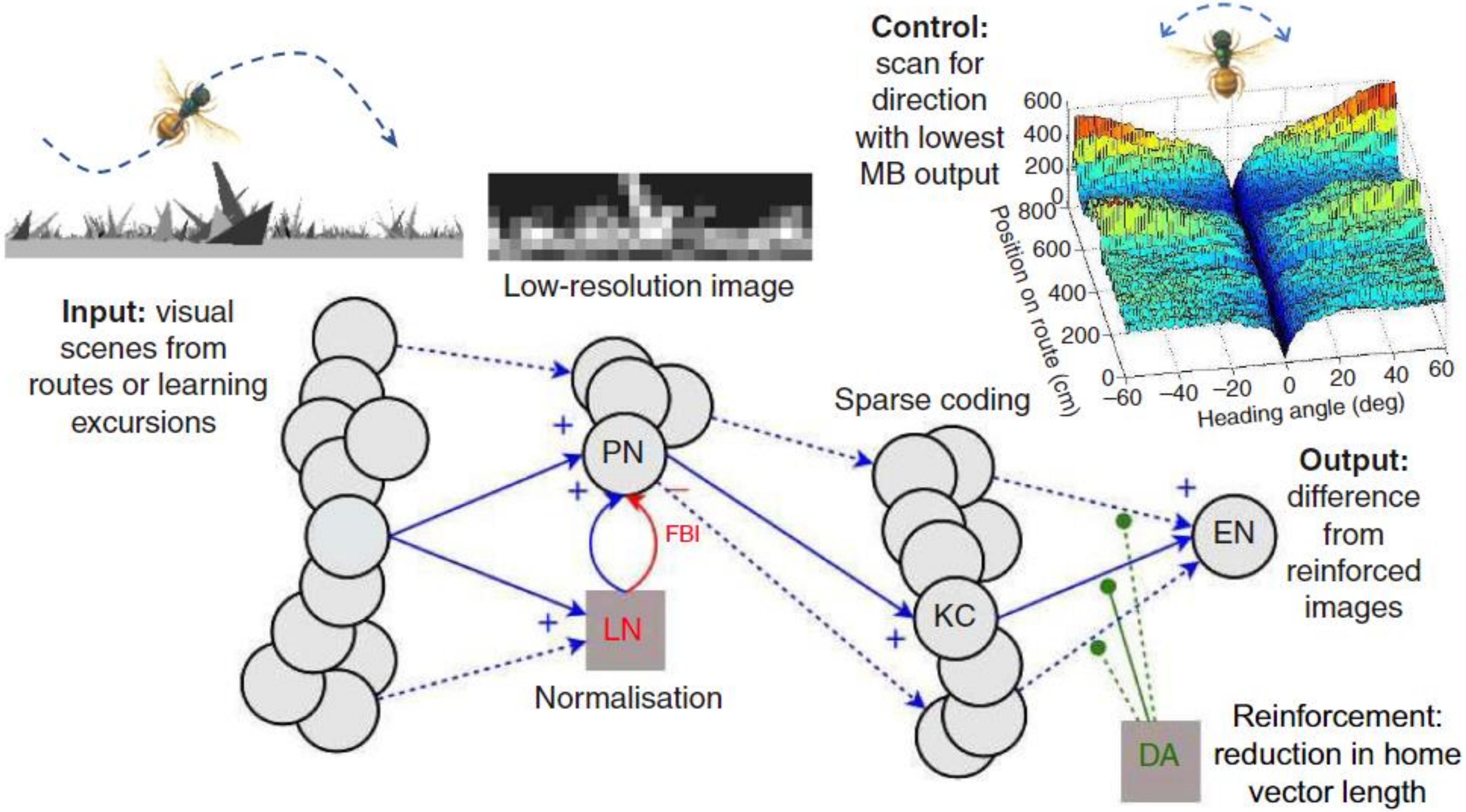
-- visual input to the MB
-- divergent connectivity from the antennal lobe to the much larger number of KCs
-- reward-dependent learning

- Sparse connection between images and KC cells
- Sparse firing of Kenton Cells
- When Kenton Cells and Extrinsic neuron fire together, decrease the weight
- After training, when a stored scene is shown, Extrinsic neuron will have low activity

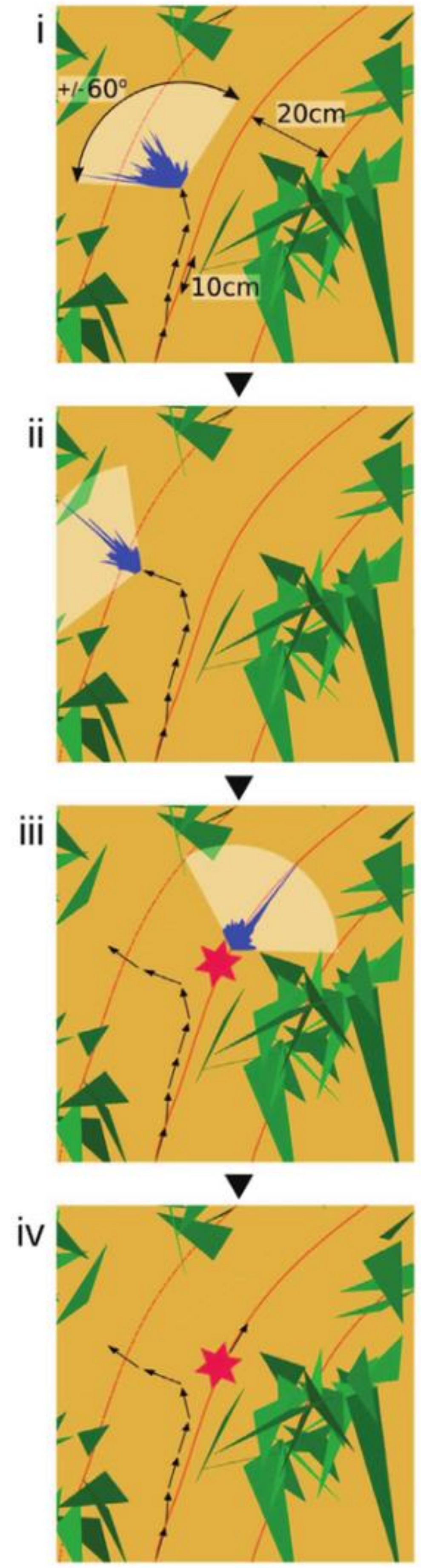


Ardin (2016)

Possible neural implementation for the view memory: mushroom body



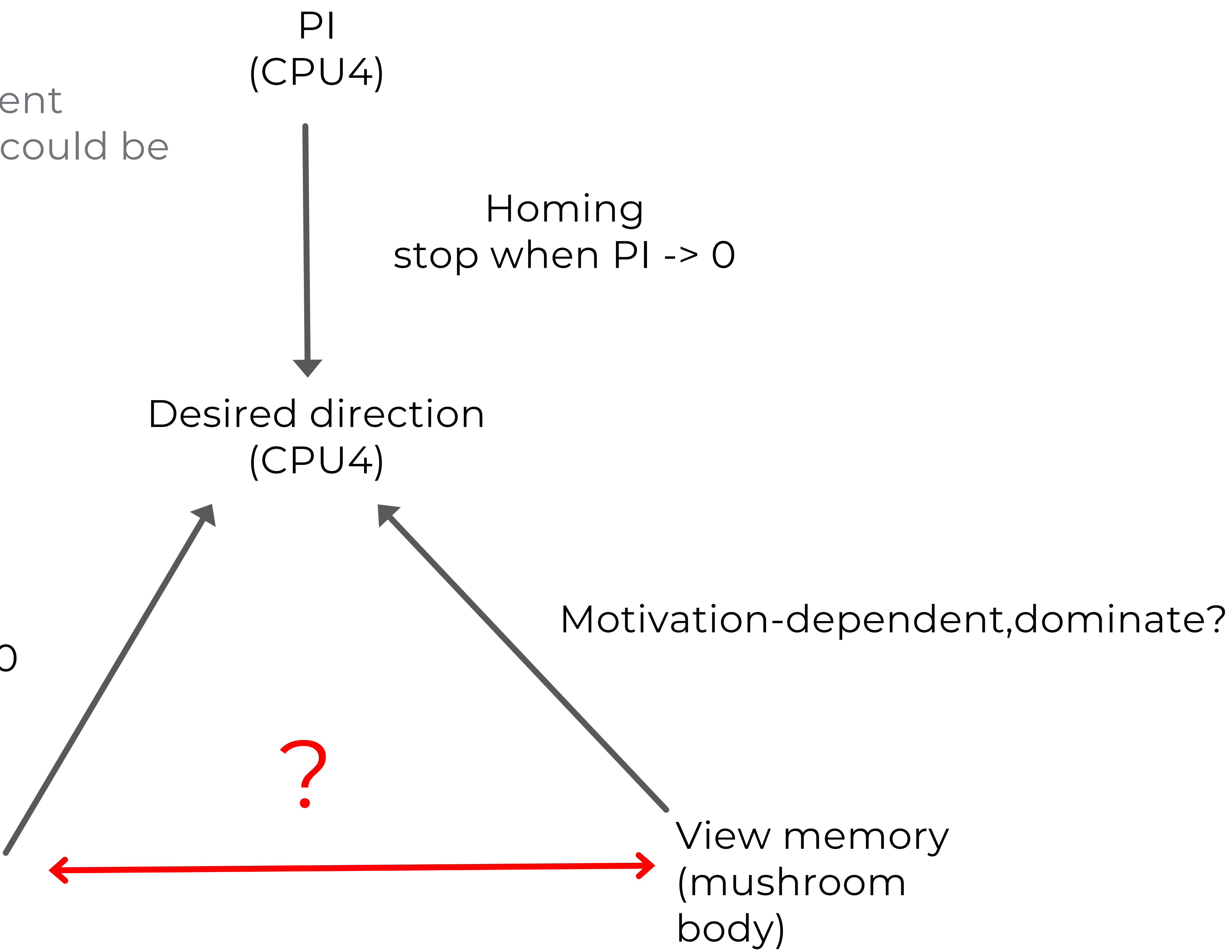
Webb (2019)



Ardin (2016)

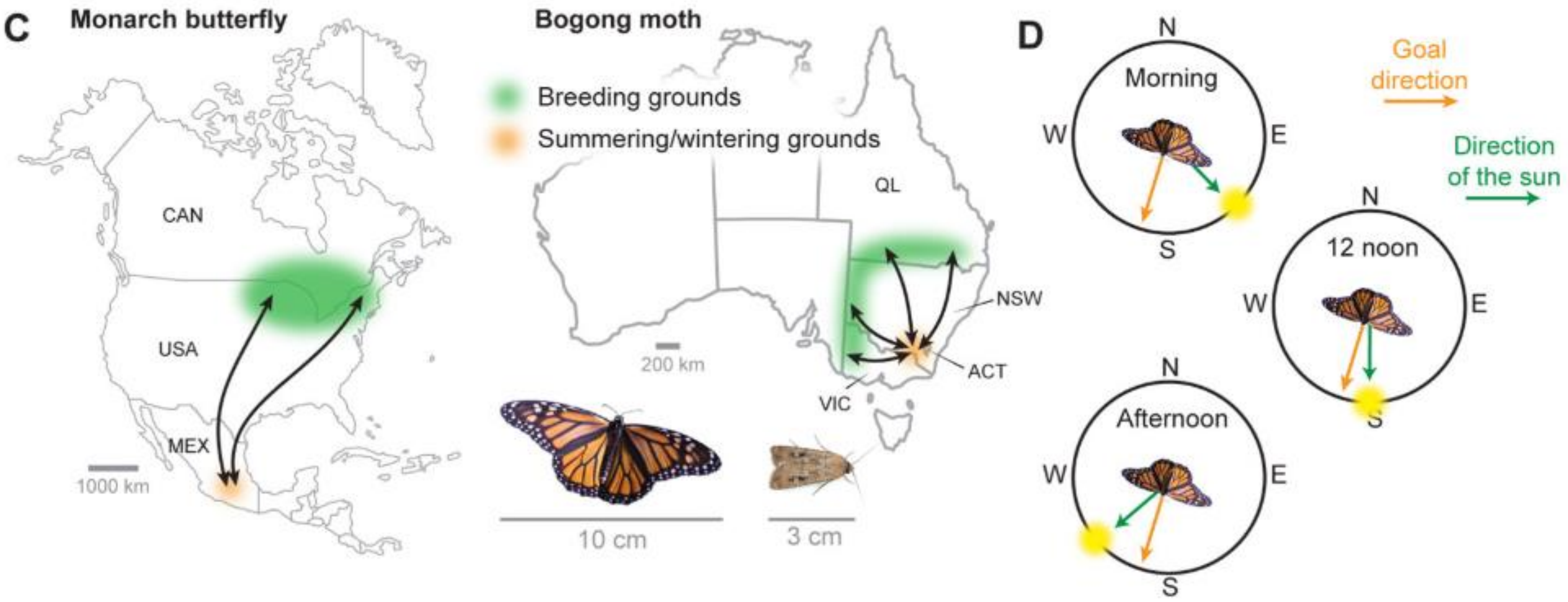
Is there a map?

Even though they seem to be different navigational strategies, the circuits could be overlapping.



Dung beetle use celestial cues to set rolling direction

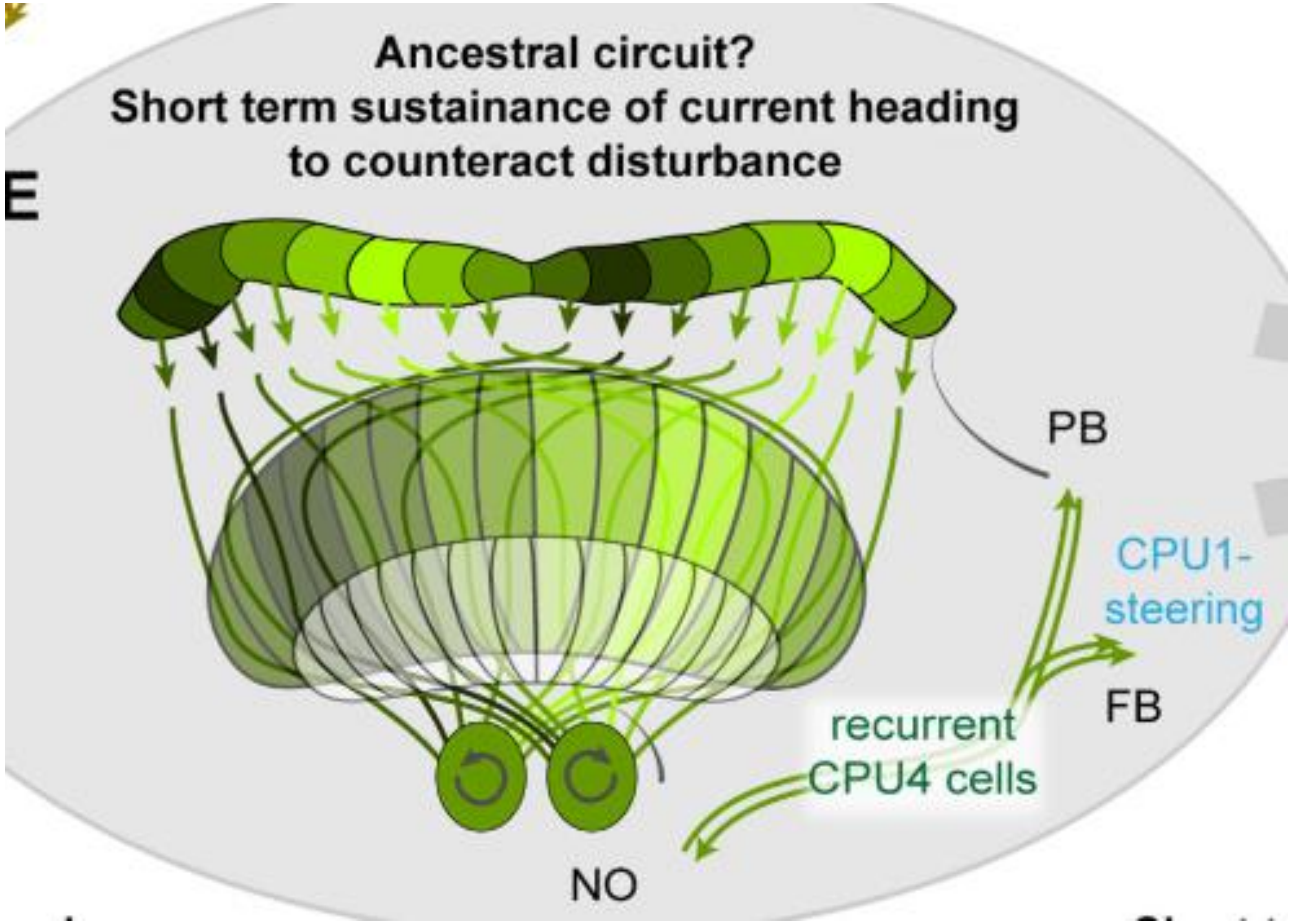
The Monarch butterfly and the Bogong moth migratory routes



Honkanen et al. (2019)

A common framework for encoding navigational decisions in the insect CX

-- Mediating the animal's next move during target directed behaviour?



Honkanen et al. (2019)

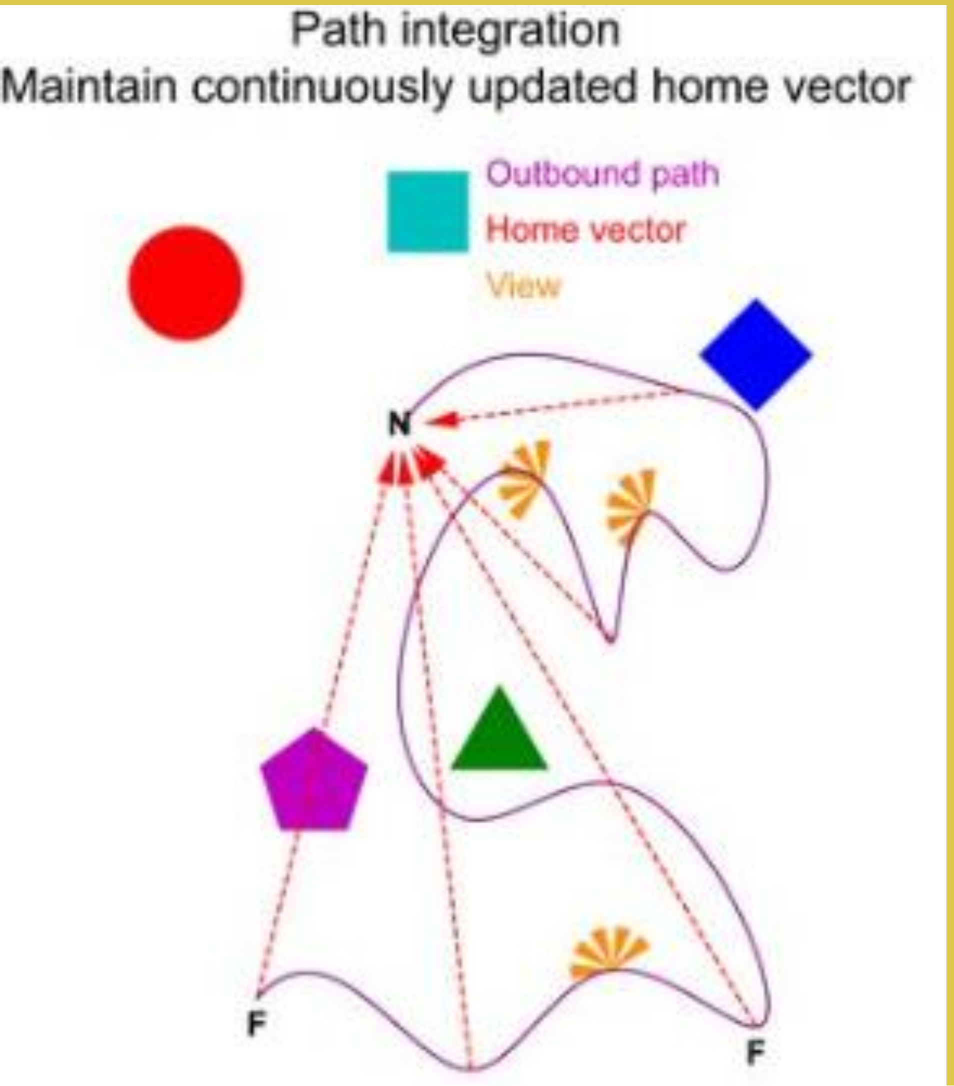
Multisite imaging of neural activity using a genetically encoded calcium sensor in the honey bee

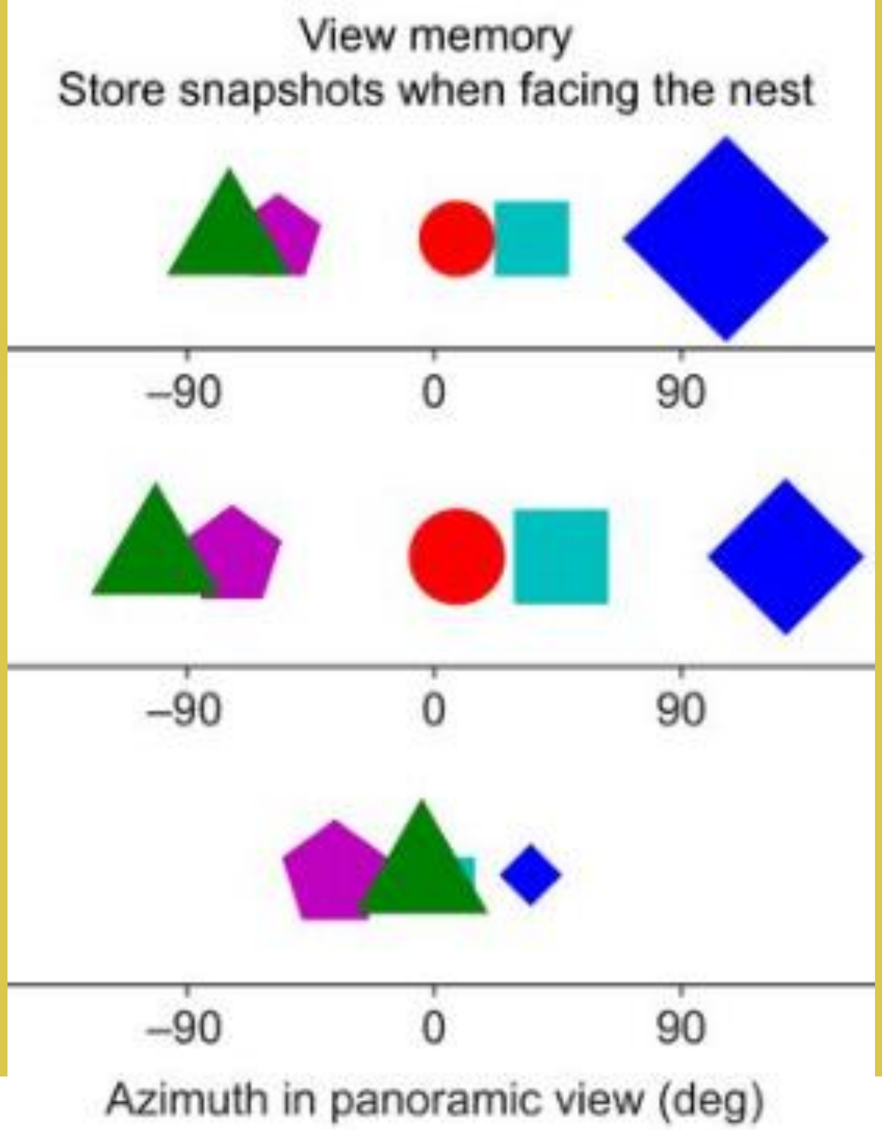
Julie Carcaud, Marianne Otte, Bernd Grünewald, Albrecht Haase, Jean-Christophe Sandoz, Martin Beye

Published: January 31, 2023 • https://doi.org/10.1371/journal.pbio.3001984

“However, genetic methods are particularly difficult to apply in eusocial insects, since genetic transformation rates are low, endogenous promoters for neuronal expressions are unknown and the genetically manipulated, reproductive individuals (the queens) have to be maintained in larger colonies with workers in containments.”

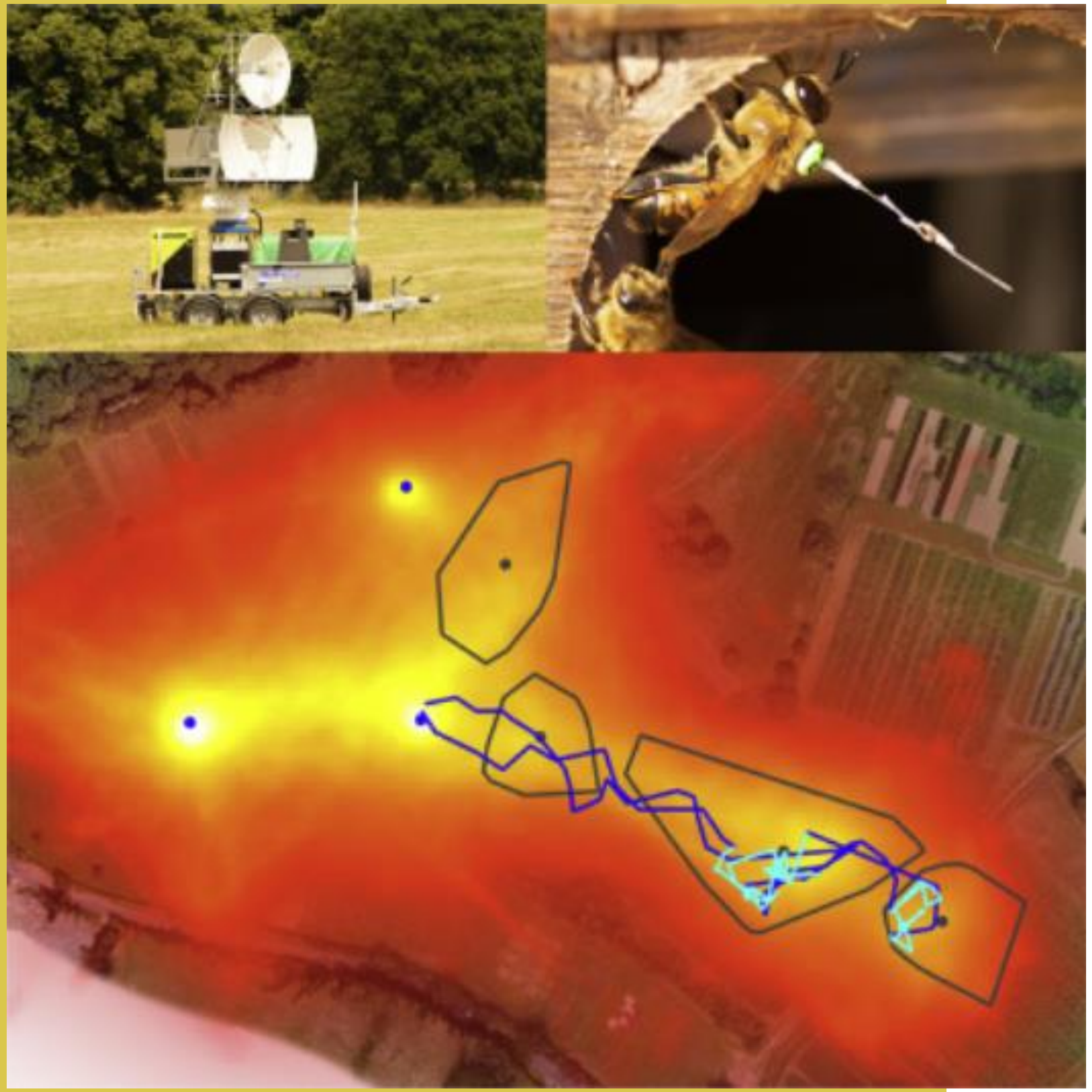
Evidence against base model (= for cognitive maps)





Testing difficulties with bees

- Earlier: estimate initial head direction and/or note whether and when arrived home
- Recently: radar tracking
- Alternatively: bees can be trained to fly through smaller controlled space/tunnels (-> only distance component of PI state considered)

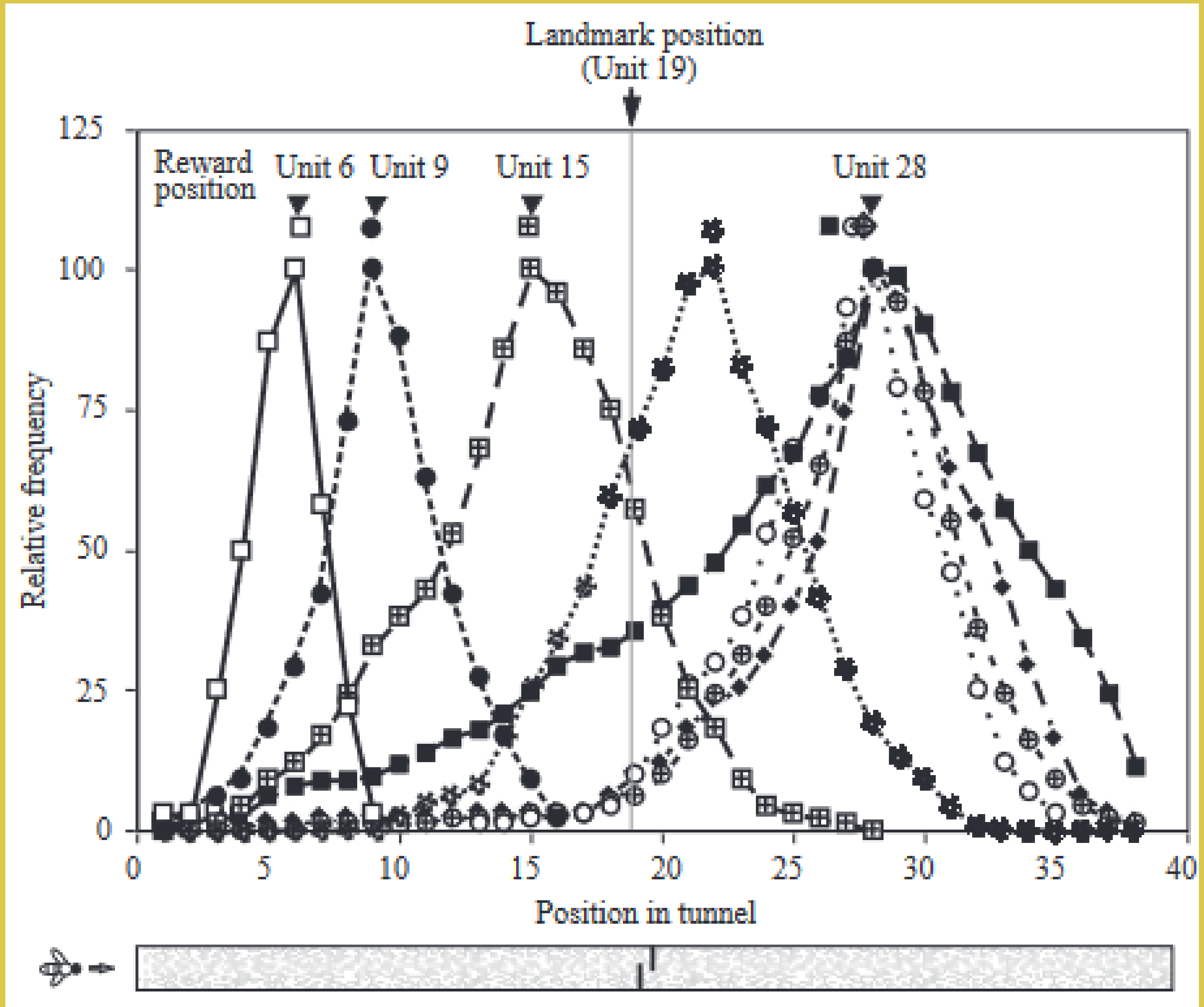


Insects might use view memory to correct path integration

- Especially for long distances, the error in PI can accumulate
- If bees encounter landmarks/other significant views stored in the view memory, they can reset PI (PI associated with landmark)

Evidence

Bees reduce odometrics errors during flights by resetting path integrator whenever landmark cues appear

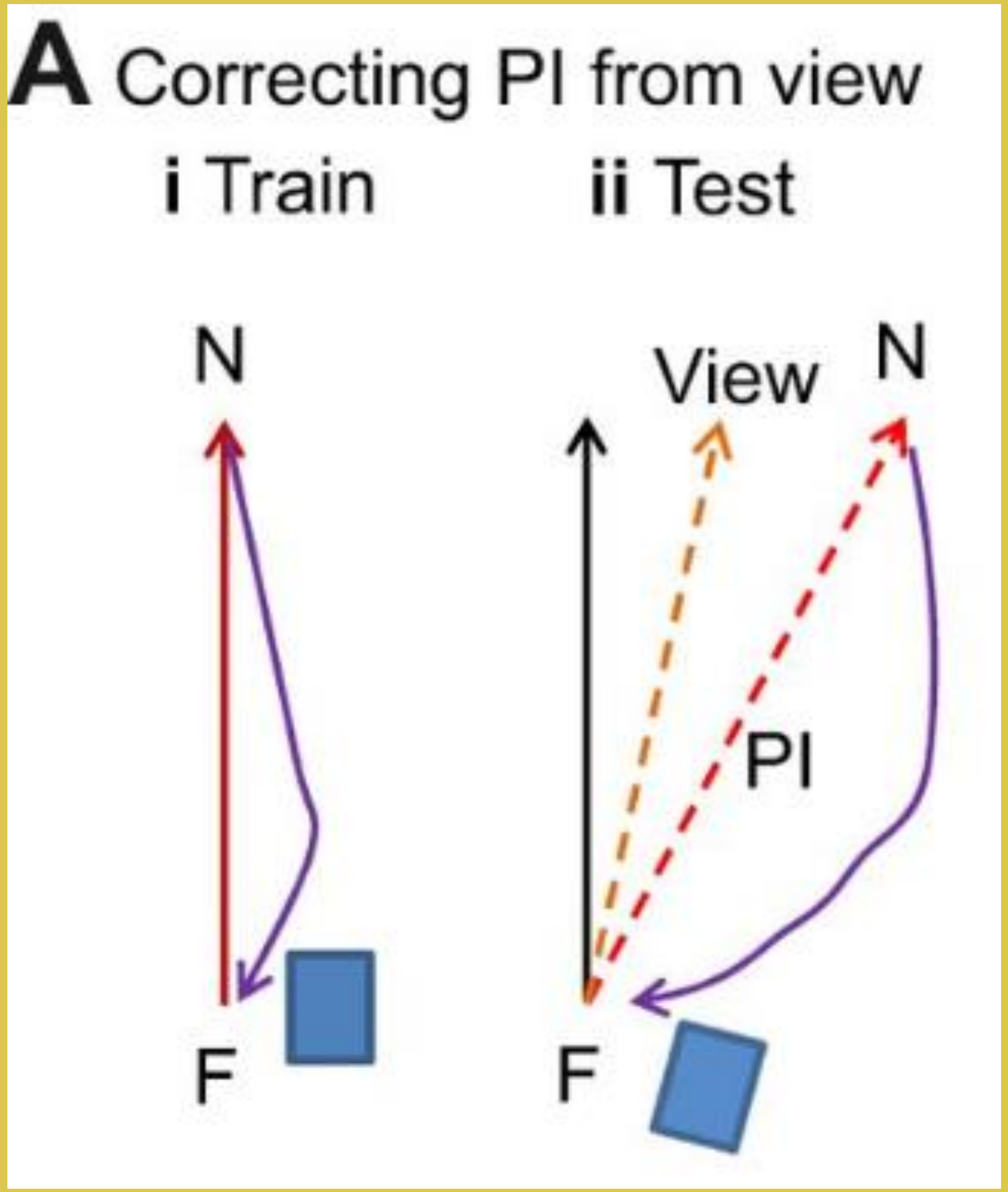


Srinisavan et al. (1997)

Width of distribution of search increases with distance, but reduced when landmark provided

Evidence

Bees reduce odometrics errors during flights by resetting path integrator whenever landmark cues appear



Chittka et al. (1995)

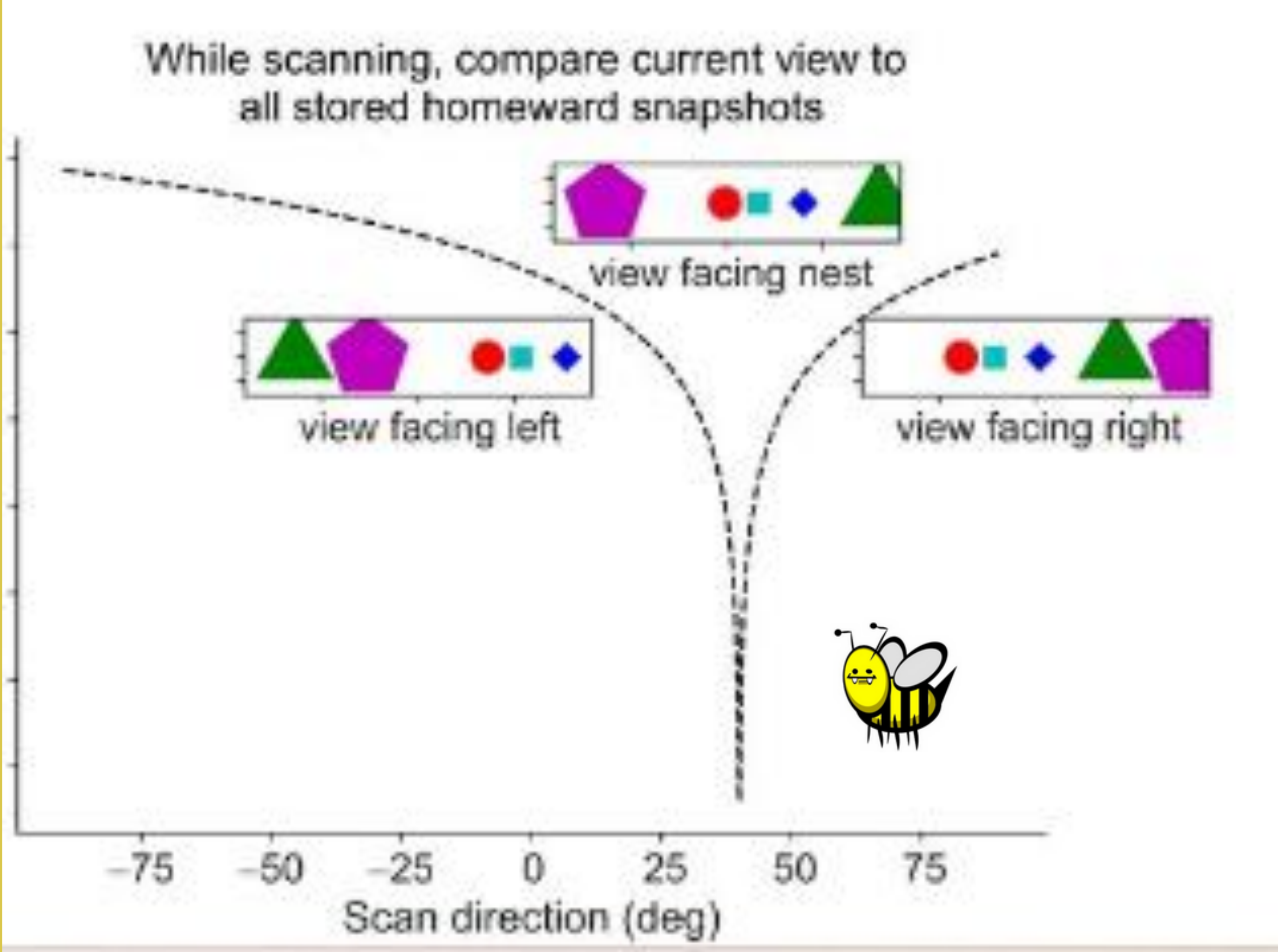
In contrast: Menzel et al. (1998) - bees no PI update

If path integration state is zero, insects might use view memory to reload a previous path integration state

- Insects correct PI when they have followed their home vector with PI=0, but do not find themselves home
- If insects then see previously experienced surrounding (in certain PI state), it reloads that PI state and use it to find home
- Menzel et al. (1998): bees transported from nest to one of two feeders would take appropriate PI direction home from each

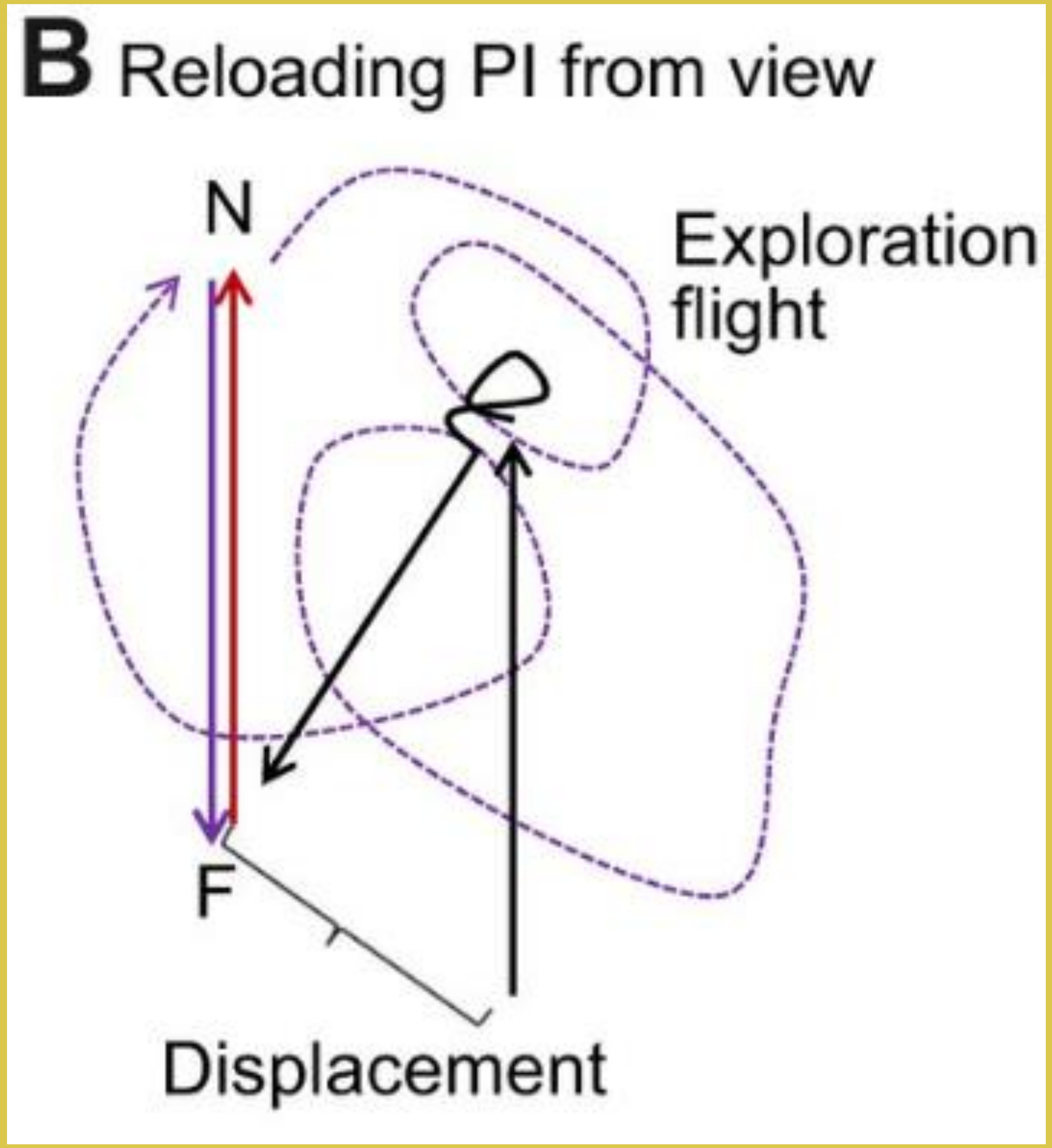
Need for good studies

- Homewards direction taken by zero-vector insect from familiar location not enough evidence it has reloaded PI state
  - direction could be explained by alignment to homeward view stored at this location
- Need studies where bees move in direction
  - consistent with having reloaded PI state
  - inconsistent with view alignment



Evidence: Menzel et al. (2005)

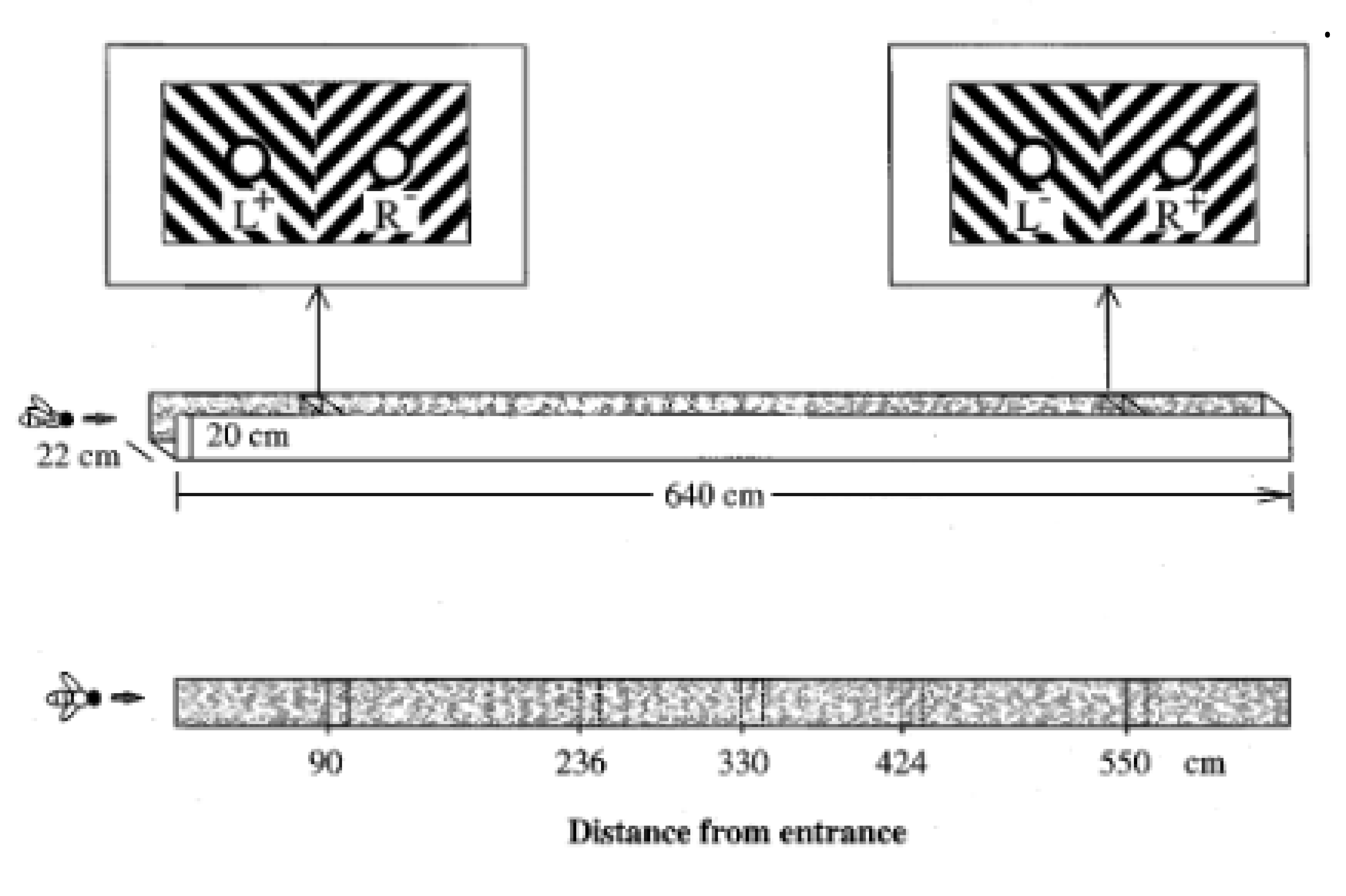
- Bees caught when either leaving nest or leaving feeder
  - passively transported to location well out of view of either nest or feeder
  - but within previous learning flight experience
- Bees first fly according to home vector (PI should be near zero) -> then perform search -> At some point take directed path home or to feeder
- No reason bees ever learned visual route from random location to feeder



The state of the home vector may prime the recall of specific views

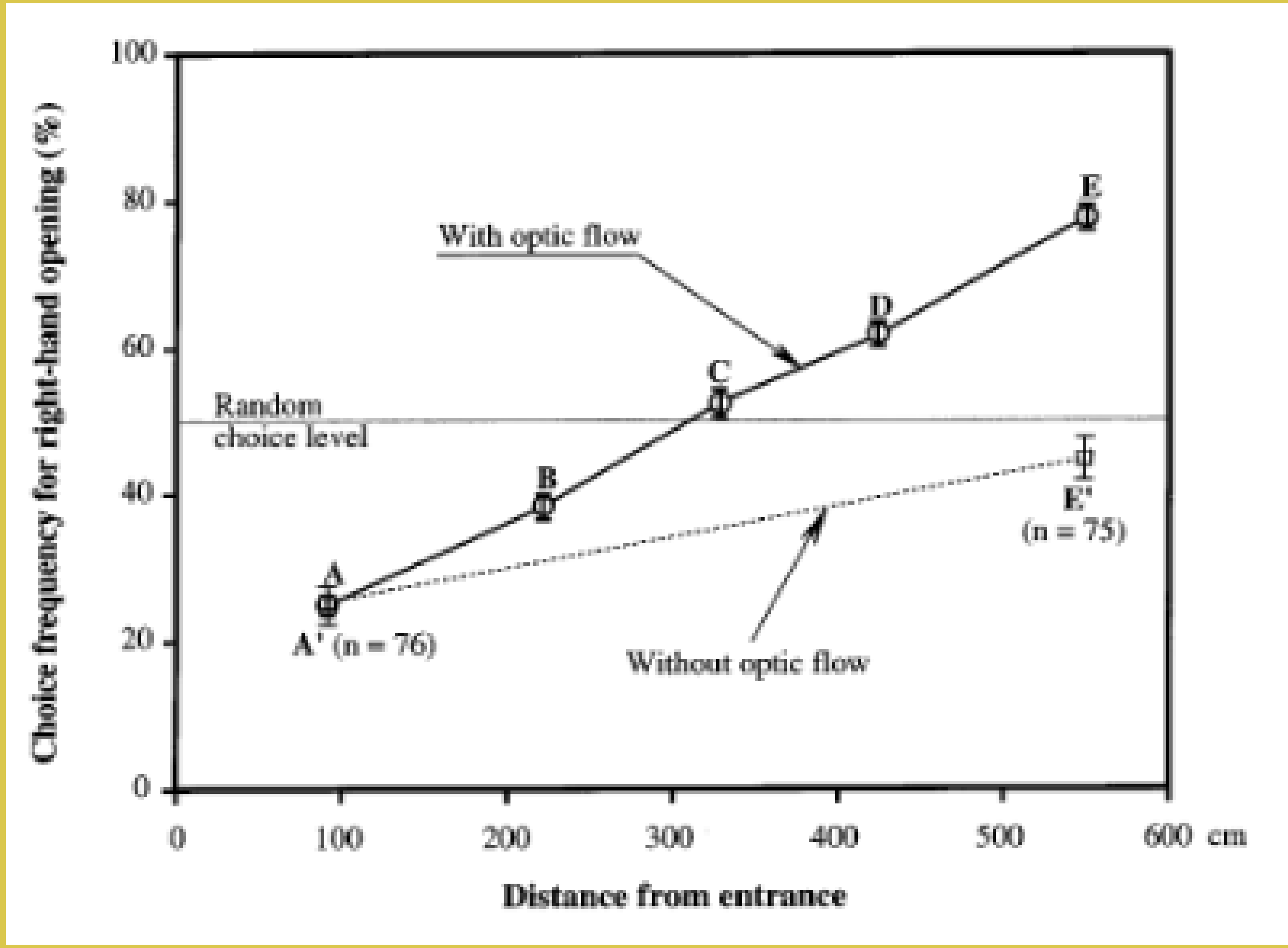
- Can PI state prime recovery of the memory of a corresponding view + thus alter likelihood that the animal will be influenced by it?

Evidence No. 1 - Srinivasan et al. (1999)



- Bees can be trained to make visual choices depending on PI
- choice frequency linearly related to distance

Evidence No. 1 - Srinivasan et al. (1999)



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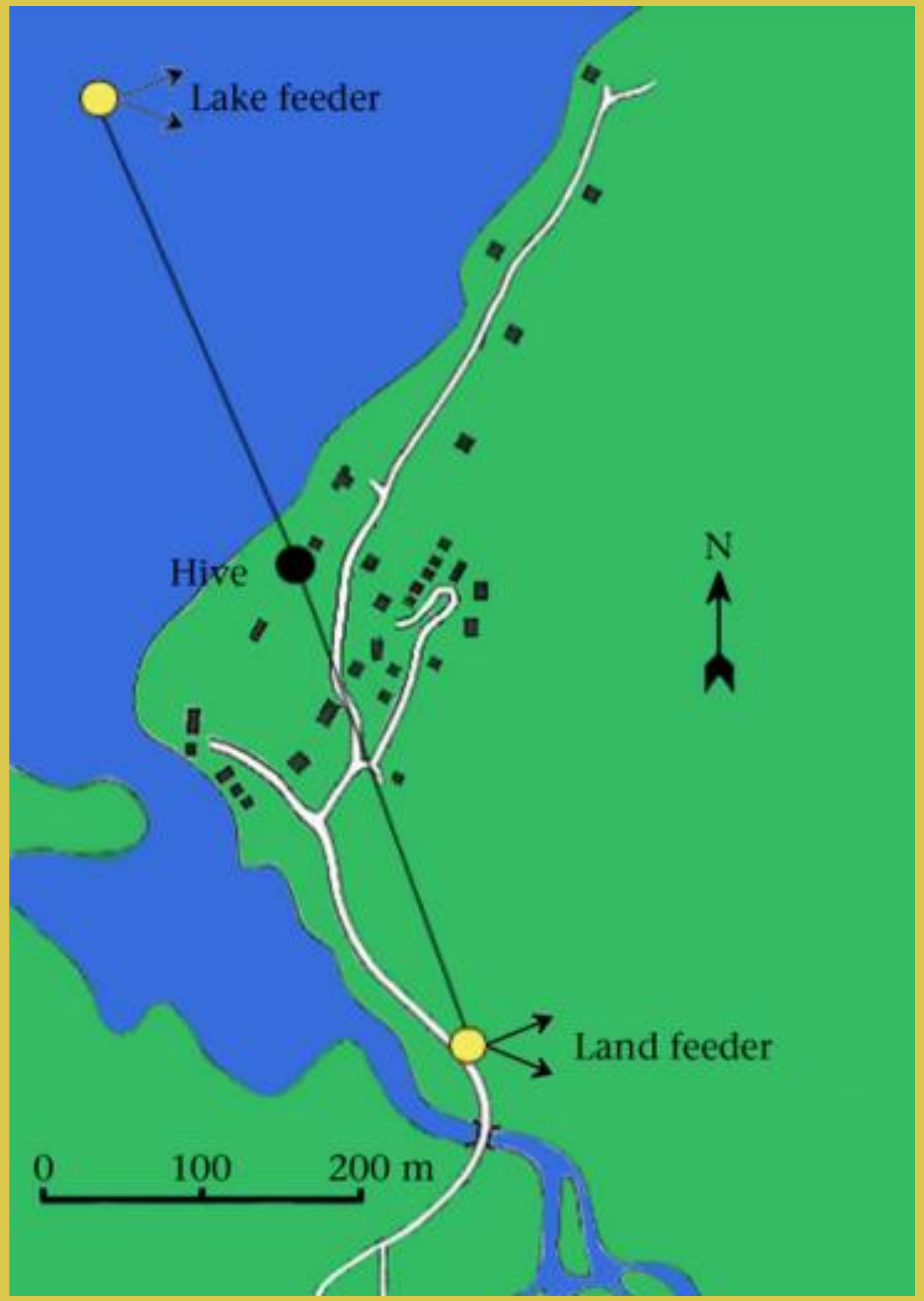
- Without optic flow = distance cues, (random texture on walls and floor replaced by pattern of axial stipes): discrimination performance worsened

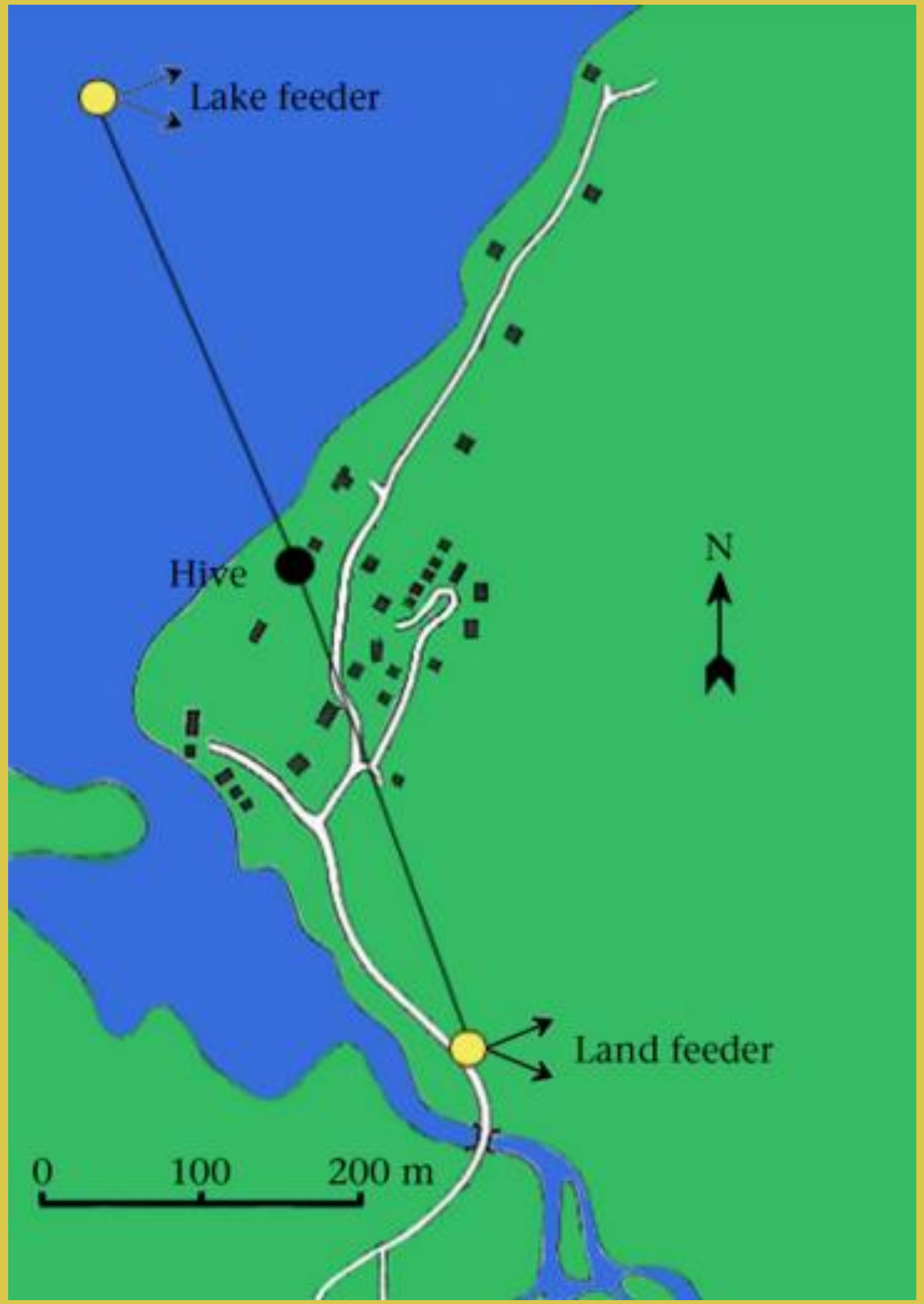
Evidence No. 2? - "Lake Experiment" (Gould & Gould, 1982)

- Priming convincing if: bees use dance information (which is in form of a vector) to index their view memories
- Bees were trained to visit a feeder on a boat in the middle of a lake
    - When the trained foragers performed dances for this location, no recruits arrived at the lake feeder during 5 of 6 days of training
    - Dances for an equidistant feeder on land elicited heavy recruitment



Evidence No. 2? - "Lake Experiment" (Gould & Gould, 1982)

- Bees used the direction and distance information to index an associated view memory and
  - "picture" the lake (implausibly located) and refuse to respond
  - "picture" the location on the land (more believable) and act on the information
- <u>BUT:</u> replication -> bees follow dance and leave nest in search of food (Wray et al. 2008)

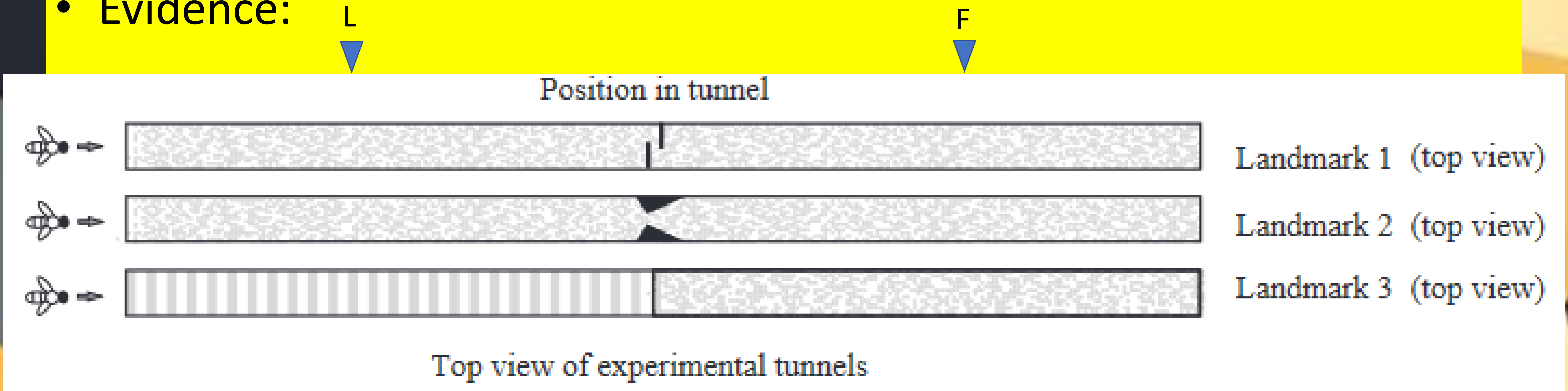


Overview

- More experimental evidence
  - → Local Vectors?
  - → Topological sequencing
- Do bees have a cognitive map or not?
- Why are we even interested in bees?
  - → Implications for (human) cognition
  - → Applications for robotics

Do bees associate view memories with a local vector?

- Idea: If a certain vector is activated at a certain location (other than the nest), it is indicative of topological processing
- Evidence:



Srinivasan, M. V., Zhang, S., & Bidwell, N. (1997). Visually mediated odometry in honeybees. *The Journal of Experimental Biology*, *200*(19), 2513-2522.

Do bees associate view memories with a local vector?

- But…
- This only considers 1 dimension. Evidence wrt. naturalistic settings is limited.
- Possibly because of global, distant views

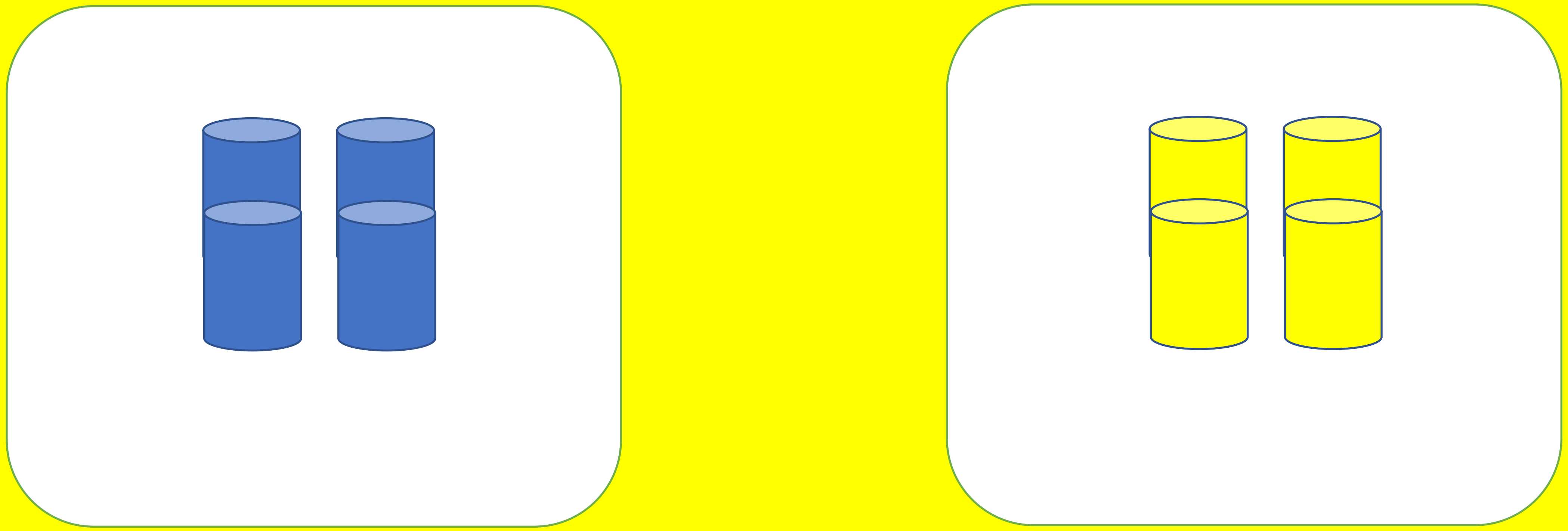
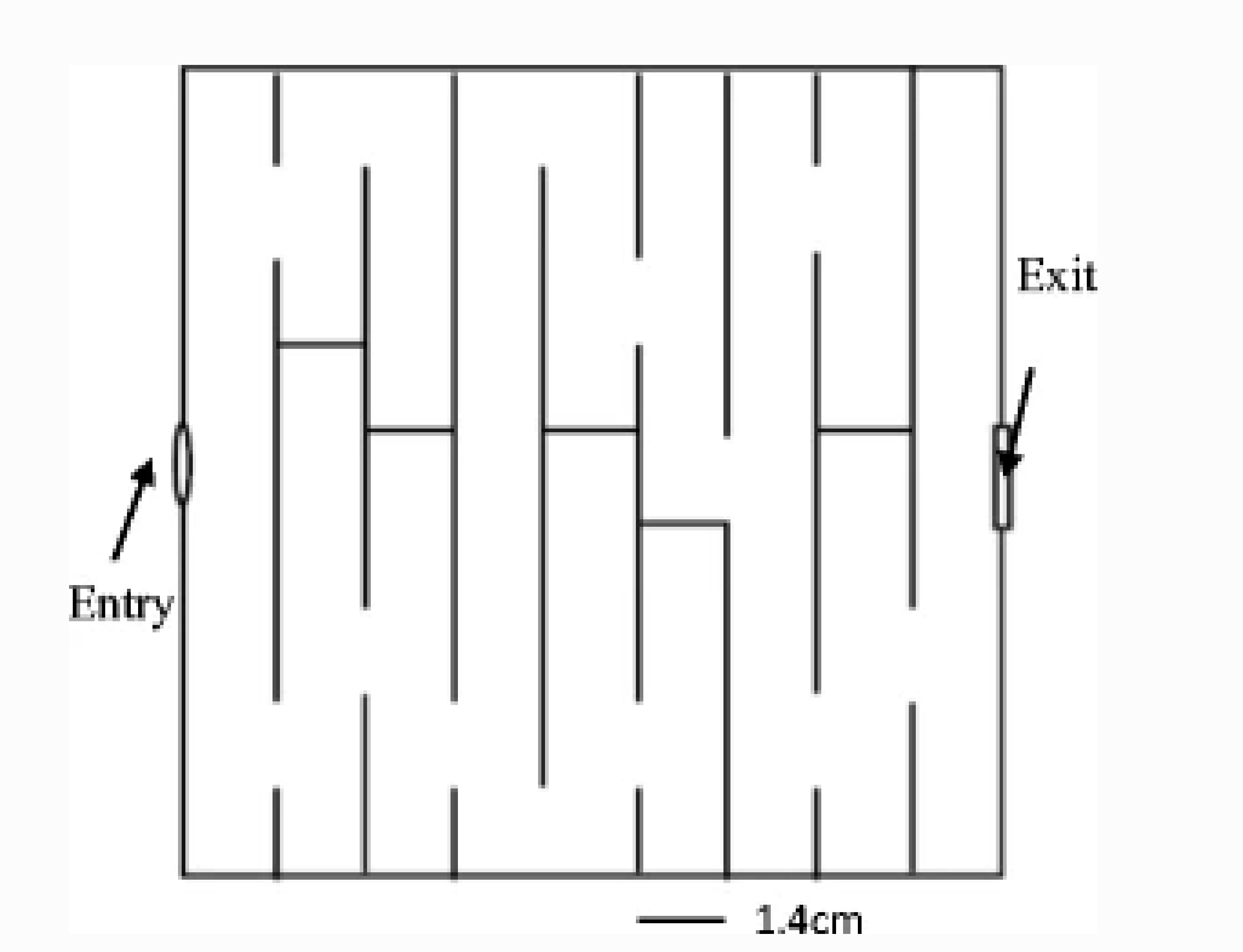


Illustration of experiment in Collett, T. S., & Kelber, A. (1988). The retrieval of visuo-spatial memories by honeybees. *Journal of Comparative Physiology A*, *163*, 145-150.

Do bees store topological sequences?

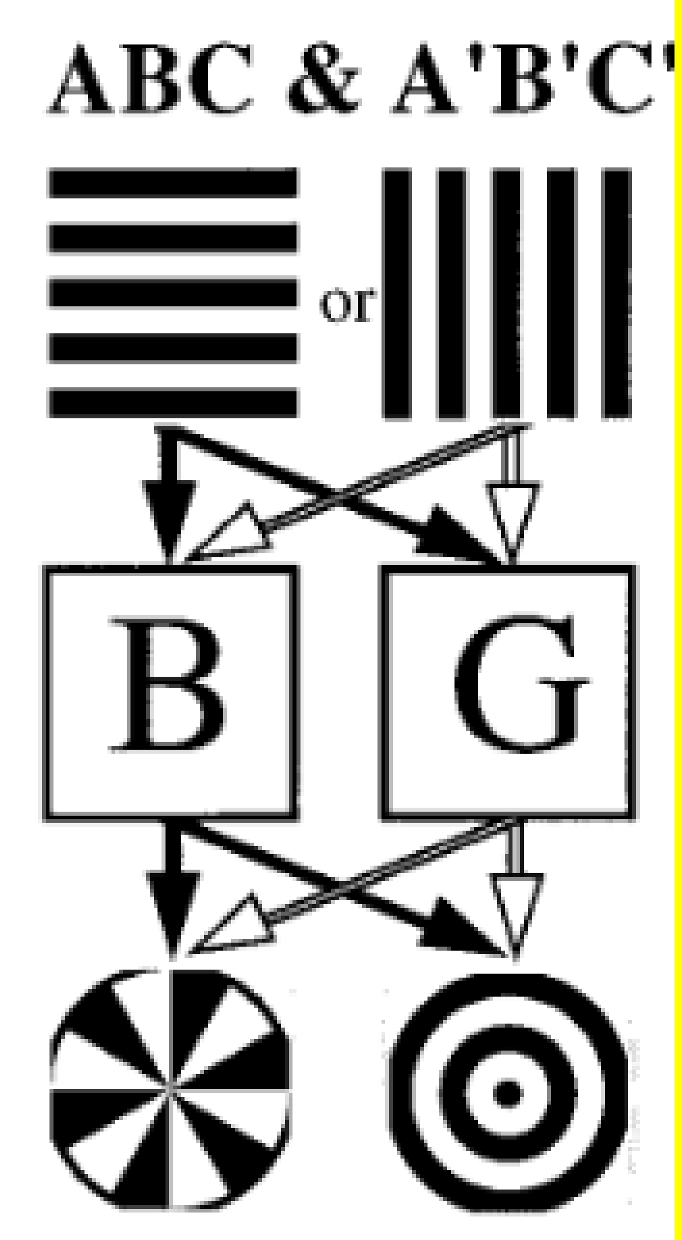
- Bees can do mazes!
- In unknown of 4 mazes, also may build evidence for a context
- May show expectation of visual scenes

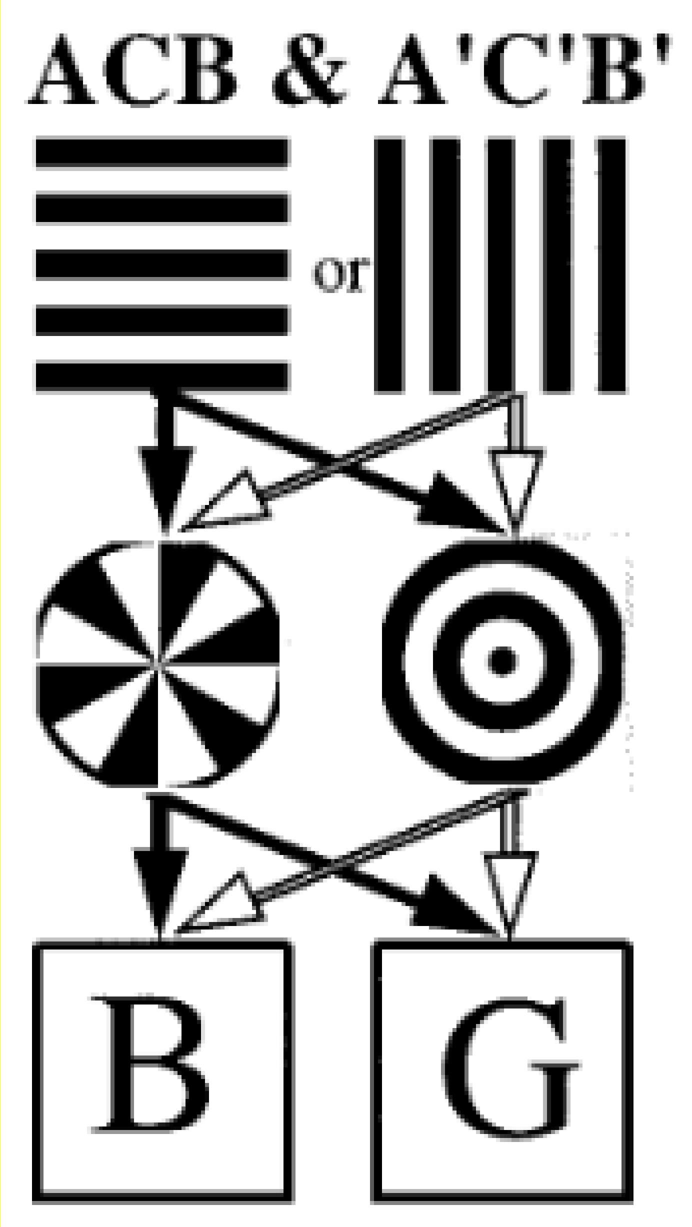


Mirwan, H. B., & Kevan, P. G. (2015). Maze navigation and route memorization by worker bumblebees (Bombus impatiens (Cresson)(Hymenoptera: Apidae). *Journal of Insect Behavior*, *28*, 345-357.

Do bees store topological sequences?

- Can learn group associations



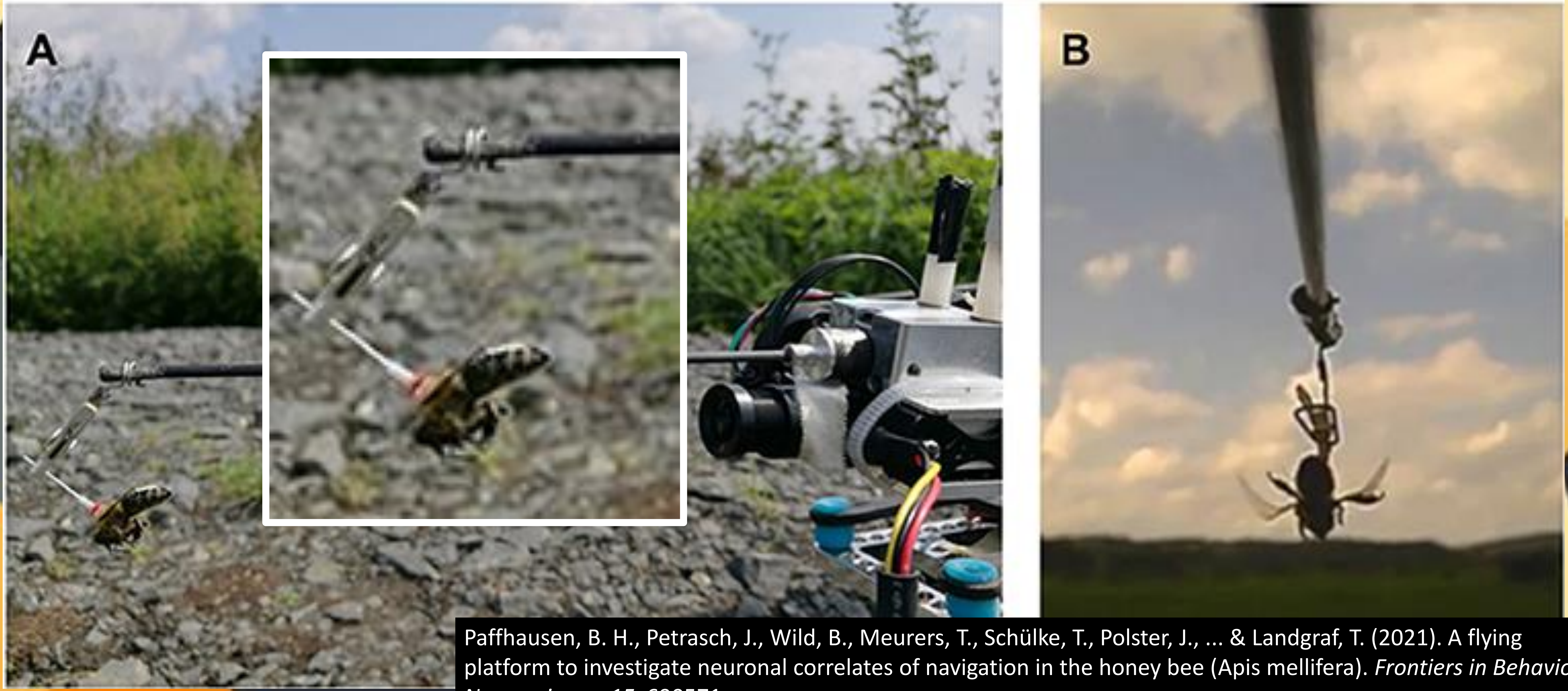


Zhang, S. W., Lehrer, M., & Srinivasan, M. V. (1999). Honeybee memory: navigation by associative grouping and recall of visual stimuli. *Neurobiology of learning and memory*, *72*(3), 180-201.

So, do bees have cognitive maps?

- Putting the question in the context of the seminar so far
- Tolman → Stimulus-Reward or Stimulus-Stimulus?
  → Latent Learning?
  → Spatial Orientation
- Reinforcement Learning
- Limitations of behavioural experiments…

The problem with bees…



Paffhausen, B. H., Petrasch, J., Wild, B., Meurers, T., Schülke, T., Polster, J., ... & Landgraf, T. (2021). A flying platform to investigate neuronal correlates of navigation in the honey bee (Apis mellifera). *Frontiers in Behavioral Neuroscience*, *15*, 690571.

So, do bees have cognitive maps?

- Putting the question in the context of the seminar so far
- Tolman → Stimulus-Reward or Stimulus-Stimulus?
  → Latent Learning?
  → Spatial Orientation
- Reinforcement Learning
- Limitations of behavioural experiments…
- Different to humans, product of environmental niche
- But both are flexible

So, do bees have cognitive maps?

… and if so why do we care?

- Comparative cognition
- Robotics

Stürzl, W., & Carey, N. (2012). A fisheye camera system for polarisation detection on UAVs. In *Computer Vision–ECCV 2012. Workshops and Demonstrations: Florence, Italy, October 7-13, 2012, Proceedings, Part II 12* (pp. 431-440). Springer Berlin Heidelberg.

Thank you for your attention!!

Created using Nightcafe

Created using DALL-E 2

Created using DALL-E 2

Please enjoy some AI generated art of bees & maps

Any Questions??

Discussion: Implicit or Metric Representation?

Knows where to go

Knows where it is on a map

Discussion Questions

Q. Horses are known to quite accurately find their way home (Stalltrieb) in many situations. How do you think their navigational systems differs from the insects?

A. Couldn't find any primary studies investigating navigation in horses. However, I did find a review about blindness in horses that suggests that horses use similar navigation strategies to humans. This review suggested that horses do have a cognitive map and use place cells/head direction cells/etc. It also mentioned that horses, especially blind ones because they are more reliant on idiothetic cues, could use dead reckoning (PI) and even echolocation!

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Discussion Questions

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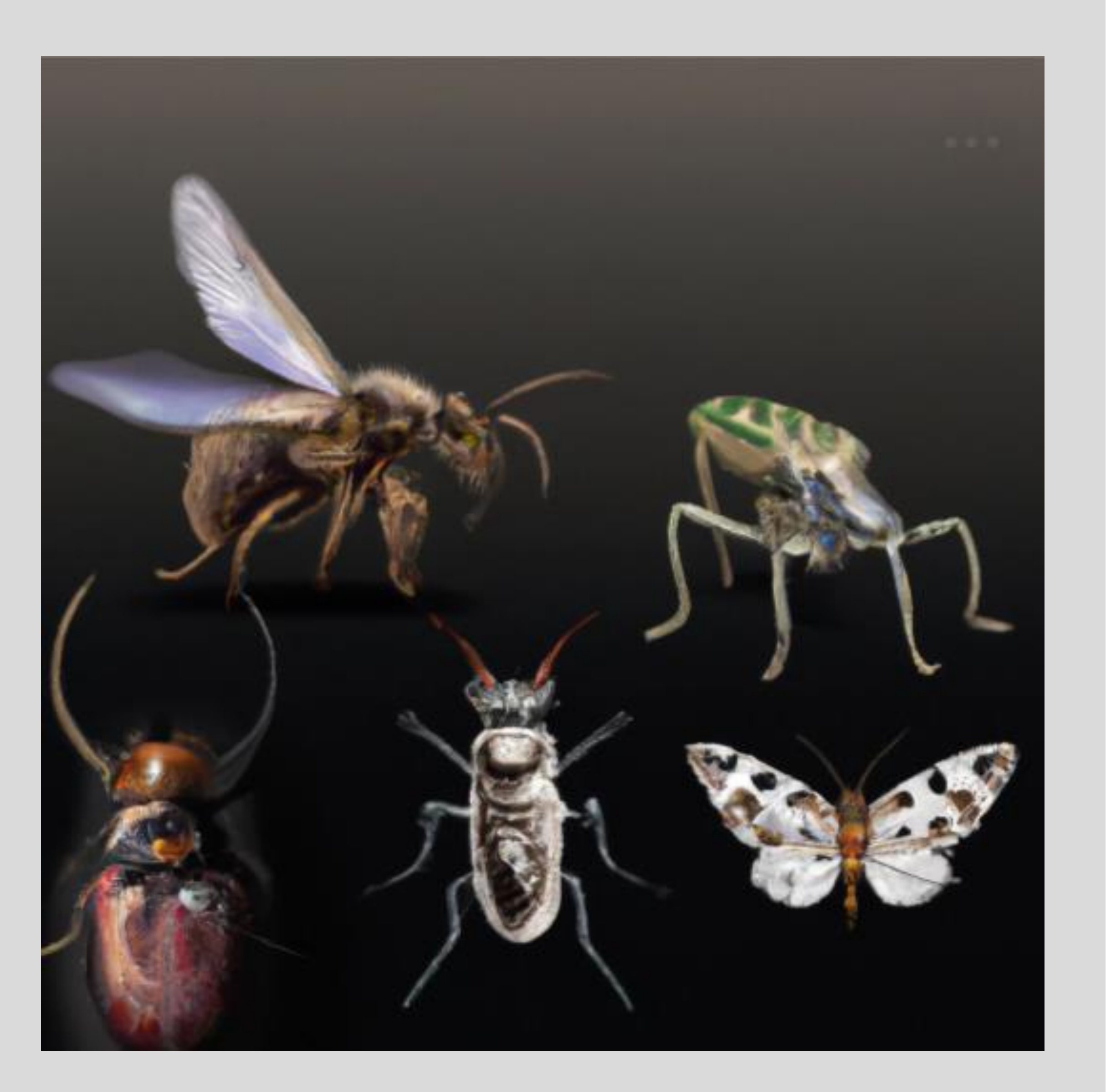
Q. Can you imagine any overlap of the mechanisms used for navigation in humans and insects?

A. Totally! We can also use dead reckoning (PI) and view memory! We are also capable of vector memory, but we would have to consciously monitor our self-motion cues.

Discussion Questions

Q. There is an incredible amount of insect species, do you think one model can really generalize insect navigation. Regarding the different demands for survival an the environment (alone/ swarm, flying/walking/ swimming/...), couldn't it be that the actual mechansims differ greatly, but the output may be similar for some species.

A. Yes and no. Different kinds of insects certainly use different mechanisms to achieve navigation. However, we see path integration in humans and bees and horses! I think if we look at the output of the model, it is decently generalizable for different insects (maybe even worms can use view memory based on different allothetic cues than vision). If we look more specifically at the mechanisms behind the three outputs, then we may see a lot more interspecies variation.



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Discussion Questions

Q. Insects use a celestial compass, they have visual receptors for polarised light (that changes with sun position) allowing them to use the sun as a compass accurately without "measuring" time. This is "accurate for short journey, but must be time compensated during longer journeys", does this imply there is a time perception and integration necessary for navigation? Would that account for a representation closer to a cognitive map?

A. It seems bees use primarily optic flow to judge distance moved. Over the course of the day though, the trajectory of polarised light through reaching the surface of the earth changes, but bees seem to be able to update their celestial compass accurately. It's not known how they do this - it might be they use a time-based model to predict the changing trajectory, but it might be more plausible that they use known vectors to update it.

Discussion Questions

Q. Honeybees have a rather short lifespan of only several weeks (during the work-intensive summer). Do you think a reason that so far (as far as I understood) no explicit map was found is that it might not be worth the effort, either energy- or maybe also place-wise (small brain)? Or do you think it is because a (maybe map-alike interaction of) the other mechanisms are already sufficient?

A. I think all of the above! I don't think there is convincing enough evidence to say for certain whether bees are capable of using cognitive maps or not. If we are under the assumption that they cannot, it is likely because the computational expenditure for cognitive maps is too high (because of their short lifespans, comparably small brains, and the fact that they already have viable navigational mechanisms in place).

Discussion Questions

Q. Would the described way of insect navigation not be very computationally demanding? Would a cognitive map not be a more efficient way of encoding the surroundings? How much of the insect brain is dedicated to navigation?

A. I would think the described way of insect navigation is inherently less computationally demanding than cognitive maps. Bees have one hundred thousand times fewer neurons as humans and appear capable of using this base model to navigate, but not necessarily cognitive maps… Current knowledge suggests only the central complex is explicitly used in navigation -> but we have to take into account how motion information and visual information influences these processes too.

Discussion Questions

Q. This model is built on the (usually fulfilled) assumption that the insects only possess one nest which they reference as their home location. What would happen if one were to experimentally induce an insect to have multiple nests? would the same model be applicable? or would the animal need to develop other strategies that do not rely on a fixed origin? or maybe would they always they get lost on the way to feeding and die from starvation?

A. Bees only have one nest and one queen. Inducing them to have more would amount to some thorough genetic tampering. For now at least this is not possible, and even if it was would likely cause too many changes to be imaginable.

Discussion Questions

Q. We as humans do not have that in-built compass as insects and thus cannot use vector memory. Do you think this is a bug or a feature?

A. We do seem to have the ability to form rough vector memories, they are however much worse than bees, because we do not have the ability to use a celestial compass as we cannot see polarized light. I would say it's not a bug or a feature, it's a just a manifestation of the different niches we occupy, and divergent evolution. Also, human vision is much better, so we can rely on it more.

Sources

Main:
Webb, B. (2019). The internal maps of insects. Journal of Experimental Biology, 222(Suppl_1), jeb188094.

Support:
Byrne, J. H. (2017). Learning and memory: a comprehensive reference. Academic Press.

Cheeseman, J. F., Millar, C. D., Greggers, U., Lehmann, K., Pawley, M. D., Gallistel, C. R., ... & Menzel, R. (2014). Way-finding in displaced clock-shifted bees proves bees use a cognitive map. Proceedings of the National Academy of Sciences, 111(24), 8949-8954.

Gould, J. L. & Gould, C. G. 1982. The insect mind: physics or meta?physics? In: Animal MindeHuman Mind (Ed. by D. R. Griffin), pp. 269e298. Berlin: Springer-Verlag.

Patel, R. N., & Cronin, T. W. (2020). Mantis shrimp navigate home using celestial and idiothetic path integration. Current Biology, 30(11), 1981-1987.

Sources

Support:

Srinivasan, M. V., Zhang, S. W., Berry, J., Cheng, K., & Zhu, H. (1999). Honeybee navigation: linear perception of short distances travelled. Journal of Comparative Physiology A, 185, 239-245.

Srinivasan, M. V., Zhang, S., & Bidwell, N. (1997). Visually mediated odometry in honeybees. The Journal of Experimental Biology, 200(19), 2513-2522.

Pictures:
https://www.istockphoto.com/de/grafiken/gl%C3%BChbirne
https://www.gran-turismo.com/sg/gtsport/user/profile/1761007/gallery/all/decal/1761007/5846248475522532864
https://www.sciencedirect.com/science/article/pii/S2589004221004673
https://soundcloud.com/greenstones/ich-bin-eine-biene

References

- Chittka, L., & Geiger, K. (1995). Honeybee long-distance orientation in a controlled environment. *Ethology*, *99*(1-2), 117-126.
- Collett, T. S., Fauria, K., Dale, K., & Baron, J. (1997). Places and patterns—a study of context learning in honeybees. *Journal of Comparative Physiology*, *181*(4), 343-353.
- Collett, T. S., Fry, S. N., & Wehner, R. (1993). Sequence learning by honeybees. *Journal of comparative Physiology A*, *172*, 693-706.
- Collett, M., Harland, D., & Collett, T. S. (2002). The use of landmarks and panoramic context in the performance of local vectors by navigating honeybees. *Journal of Experimental Biology*, *205*(6), 807-814.
- Collett, T. S., & Kelber, A. (1988). The retrieval of visuo-spatial memories by honeybees. *Journal of Comparative Physiology A*, *163*, 145-150.
- Mirwan, H. B., & Kevan, P. G. (2015). Maze navigation and route memorization by worker bumblebees (Bombus impatiens (Cresson)(Hymenoptera: Apidae). *Journal of Insect Behavior*, *28*, 345-357.
- Paffhausen, B. H., Petrasch, J., Wild, B., Meurers, T., Schülke, T., Polster, J., ... & Landgraf, T. (2021). A flying platform to investigate neuronal correlates of navigation in the honey bee (Apis mellifera). *Frontiers in Behavioral Neuroscience*, *15*, 690571.
- Srinivasan, M. V., Zhang, S., & Bidwell, N. (1997). Visually mediated odometry in honeybees. *The Journal of Experimental Biology*, *200*(19), 2513-2522.
- Stürzl, W., & Carey, N. (2012). A fisheye camera system for polarisation detection on UAVs. In *Computer Vision–ECCV 2012. Workshops and Demonstrations: Florence, Italy, October 7-13, 2012, Proceedings, Part II 12* (pp. 431-440). Springer Berlin Heidelberg.
- Webb, B. (2019). The internal maps of insects. *Journal of Experimental Biology*, *222*(Suppl_1), jeb188094.
- Wystrach, A., & Graham, P. (2012). What can we learn from studies of insect navigation?. *Animal Behaviour*, *84*(1), 13-20.
- Zhang, S. W., Lehrer, M., & Srinivasan, M. V. (1999). Honeybee memory: navigation by associative grouping and recall of visual stimuli. *Neurobiology of learning and memory*, *72*(3), 180-201.
- Zhang, S., Mizutani, A., & Srinivasan, M. V. (2000). Maze navigation by honeybees: learning path regularity. *Learning & Memory*, *7*(6), 363-374.