Navigation and Spatial Representation 1:
Path integration in animals & humans

Animal Navigation
The Participants:
ants, bees, chicks, rodents, humans
Disciplines and Methods:
behavioral ecology: observation and field experiments
experimental psychology: laboratory experiments on spatial learning
Three Core Processes:
path integration ("dead reckoning")
scene recognition
reorientation

Path integration in desert ants

• The ant’s return journey can be as much as 40 meters long
• 1 ant body = 1cm long, so this means 4000 body lengths
• If an average human is 1.5 m tall, then for humans this means walking around randomly for an hour then turning and immediately walking 3.75 miles directly in a straight line towards home!
  i.e. (1.5m)4000 = 6000 meters
• How does an ant DO this?
Path integration in desert ants

1. By external cues or internal representation?
   possible cues: odor gradient?
   visible landmarks?

Ants navigate by internal representations: go straight to location
where nest would have been; then search

How accurate is an ant?
On a 500 m outward journey (or 47 mile-long journey in human
terms):
- direction ± 2°
- distance ± 10%

How do the ants know where the nest is? How do they represent
the distance and direction of home?

Nota Bene: Ant must represent home’s distance and direction at
each point in the journey, since they don’t know when or where
they will encounter food.

A model of path integration
At each step of a journey, the ant represents the distance and
direction of the nest:
As the ant moves, she represents the distance and direction of
her current displacement:
By subtracting her displacement vector from the original home
vector, she computes the new home vector

- If ants used perfect vector summation, they should show
  no error in returning home
- They do show error, and this error is not simply random error
- The pattern of error tells us which computations underlie
  ants’ performance
- And perhaps human performance as well (Data Section last week)
A model of path integration

Nest

Harbor

Ant Navigation

Direction: ?

Distance Traveled: ?

Marine Navigation

Magnetic Compass

Water Speed in Knots

Ephemeris Function

But There Is A Problem: the sun moves across the sky!

12:00 pm

Nest is at 120º, 40 meters

How does the ant represent its direction of travel?

experiments with mirrors: the sun

1:00 pm

Nest is at 110º, 40 meters

How does the ant represent its direction of travel?

experiments with mirrors: the sun

2:00 pm

Nest is at 100º, 40 meters

How does the ant represent its direction of travel?

experiments with mirrors: the sun
Ephemeris Function

But There Is A Problem: the sun moves across the sky!

How does the ant represent its direction of travel? experiments with mirrors: the sun

Ephemeris Function

But There Is A Problem: the sun moves across the sky!

•Ephemeris Function: keep track of time of day; correct angle for movement of the sun
•Evidence: studies of ants after delay; studies of jet-lagged bees.

Ephemeris Function

•A map is enduring, the relations between objects do not change with time
•An ephemeris function is ephemeral, the relations between objects change with time
•Eg. The Sun, and some Known Geographic Point

Distance Traveled

•How does the ant represent its distance of travel?
•Wehner’s hypothesis: the ant counts steps
•A test: Ants on stilts!!!

Let ant walk out on normal legs, at the food put them to sleep and either glue on stilts or cut legs shorter (stumps), displace them south (so they don’t walk over the nest) and measure how far they walk on their way back to the nest.

Results:
- Ants on stilts walk too far
- Ants with stumps walk too short
- But, on the very next journey with stilts or stumps, all ants walk just the right distance
- This shows that the step counter counts steps, no matter how big or small, no learning with stilts and stumps is required
How does the ant represent its distance of travel?

- Wehner’s hypothesis: the ant counts steps
- A test: navigating in a channel over hilly terrain

Ants are better than raw Step Counting—assess true distance
- Perhaps by using optic flow (texture as it goes by, can also give information about changes in height)

How do insects represent distance over changes in effort, time, # actions?

Hints from bees:
- Representing distance to food:
  --unchanged in wind (not effort, not # of actions)
  --DOES change with changes in texture on ground
- Bees assess distance traveled by optic flow
- BUT: ants can do dead reckoning in the dark: so optic flow is not the only cue to help correct the Step Counter. (perhaps proprioception: the way your body feels as you move)

As they move, ants represent the distance and direction they travel.

(A) To represent direction, the ant uses the sun as a compass, correcting for its changing position by keeping track of time of day.
(B) To represent distance, the ant counts its steps & corrects for its changing effort, probably in part by monitoring optic flow from the surrounding terrain.

At each step, the ant computes the new distance and direction of home by combining (A) and (B).
- To compute the new home vector, the ant uses an arithmetic approximation, not perfect vector summation.
path integration is subtly different in ships and ants

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Typical Ant Path

Typical Ship Path

How widespread is path integration?

NB: Ants have a tiny nervous system! If they can make these computations, in principle, other animals should be able to make them as well.
Laboratory experiments on gerbils in the dark (Mittelstaedt)
Mother gerbil leaves nestlings to eat; platform with food surreptitiously rotates. When finished, where does she go?

Red = Dead Reckoning    Blue = Scent, Sound etc.

Gerbil goes off in reckoned direction, oblivious to the cries of her nestlings.

Is path integration independent of experience?

Field experiments on goslings (N=7, never left home before)

von St. Paul, 1982
Is path integration independent of experience? 
Field experiments on goslings (N=7, never left home before)

Geese use path integration. Like ants and bees, they use visual information (optic flow) to monitor the distance and direction of their own travel.

von St. Paul, 1982

Path integration develops with no trial and error learning and little locomotor or visual experience, at least in some animals.

The cost of errors in navigation is high, perhaps leading to selection pressures for an innate path integration mechanism.

But if it is innate in ants, geese and gerbils, then is it also innate in humans?

Next Time: Scene Recognition and Path Integration in humans and other animals