

Navigation: Whence Our Sense of Direction?

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Behavioral data have long implied our sense of direction derives from global environmental shape; electrophysiological evidence, however, has seemed to imply it derives from salient non-geometric landmarks. Experiments on the re-establishment of place fields in disoriented mice now align the electrophysiological data with the behavioral data.

From insects to humans, animals construct metric spatial and temporal maps of their experienced environments. These spatio-temporal maps serve as the foundation for their behavior [1–5]. A metric spatial map represents the shape of the navigable environment — the distances and directions between the surfaces and/or drop-offs that bound it. This remembered geometry provides a frame of reference within which location and direction vectors are defined. In its absence, an animal has no sense of where it is nor which way is which. Direction, however, is an abstract property of the animal's experienced environment, definable only by reference to the map itself, so a question of fundamental importance is: what on the map forms the basis for the brain's sense of direction? Definitive new electrophysiological experiments on place cell firing in disoriented mice as they reorient, reported in this issue of *Current Biology* [6], now aligns with long-standing and extensive behavioral evidence in strongly suggesting that the sense of direction depends on the computation of global shape parameters.

Tolman [7] posited a cognitive map to explain the shortcuts he observed in rats. His hypothesis remained controversial while the anti-representational stance of the behaviorists dominated psychological and neuroscientific thinking. It began to win broader acceptance with the discovery of place cells, head-direction cells, boundary-vector cells and grid cells in the hippocampus and associated brain structures [4, 8–10]. Place cells are neurons that fire when the animal is in a small cell-specific region of a familiar environment (see heat map in Figure 1). They fire in their given locations even

when there are no sensory inputs unique to those locations. Head-direction cells fire when the head points in a cell-specific direction, even though the sensory input from that direction varies from location to location and even in the open in the dark, when direction-specific input is absent altogether.

The ability of neurons to signal place and direction in the absence of distinctive sensory input unique to a given place or a given direction depends on dead reckoning, also known as path integration: The brain integrates multimodal linear and angular velocity signals to maintain an estimate of heading direction and location as the animal moves through its environment. The values of these angular and linear integrals depend, of course, on the animal's having an initial sense of place and direction, the sense it obtains when it gets its bearings after becoming disoriented or badly oriented. A question of fundamental importance is whether an animal's initial sense of place and direction — the sense acquired when a disoriented animal becomes re-oriented — arises from the overall geometry of the framework or from the perception of distinctive landmarks within that framework.

Cheng [11] discovered that, when disoriented rats reorient themselves in a familiar rectangular environment, they rely on the environment's overall shape, ignoring salient non-geometric landmarks, such as wall markings or textures, that unambiguously indicate which way is which within the rectangle but do not affect the shape of the rectangle (Figure 1). A rectangle is congruent with itself when rotated by 180°, so when Cheng's disoriented rats re-established

their sense of direction, they were misoriented by 180° on half the trials. On those trials, instead of digging for buried food where they knew it was, they dug at the rotationally equivalent location (Figure 1). Many subway riders experience similar misorientations when re-emerging into the above-ground world.

Keinath *et al.* [6] have now shown that the same indifference to salient non-geometric landmarks in favor of a reliance on the ambiguous global shape of the enclosure is seen in hippocampal place cells in mice. On half the trials on which a disoriented mouse reorients within a rectangle, a given place cell does not fire when the mouse is at the place where that cell should fire, but rather when the mouse is at the rotationally equivalent location (faded heat map in Figure 1). This rotational misorientation happens despite the fact that one end wall is painted with white and black stripes, unambiguously marking which end is which. Moreover, the rotationally misplaced firing of the place cells predicts the animal's subsequent rotationally misplaced digging. And finally, the mislocation of place fields in the re-oriented mouse is seen only in environments that have this rotational symmetry; it is not seen in an environment with the shape of an isosceles triangle.

There are currently three theories of how a disoriented animal reorients: no-map theories [12]; mapped-landmarks theories [13]; and shape-parameter theories [14]. No-map theories, also known as beacon theories, assume that the animal has no representation of the shape of its navigable environment; it locates its goals solely by their proximity to salient and unique sensory cues in the currently perceived scene, much as a

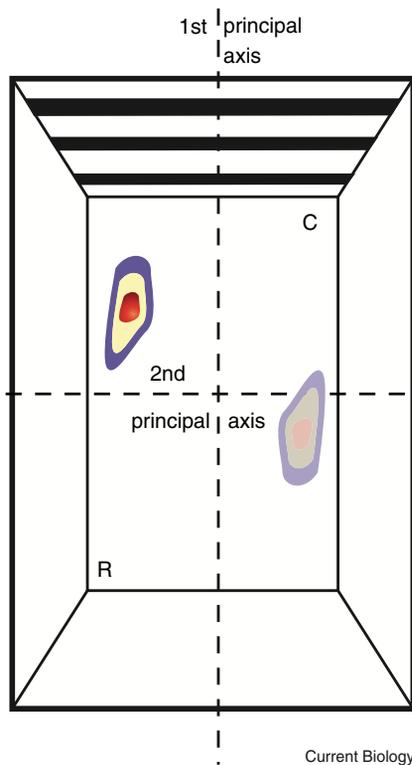


Figure 1. Schematic rendering of rotational misorientation in animal and neuron behavior.

Rectangular box seen from above. Mouse is shown location of hidden food at C, then disoriented and reintroduced to the box. It digs at C on about half the trials, but on the other half, it digs at R, the rotationally equivalent location. Strongly colored blob is heat map of the firing seen in a typical hippocampal place cell. On half the trials, the cell fires here when the disoriented mouse is returned to the box to search for the food, but on the other half it fires in the rotationally equivalent location, which is indicated by the faded heat map. On those trials, the mouse digs at R rather than at C. Dashed lines indicate the 1st and 2nd principal axes. Black stripes on one end wall are a salient non-geometric orientation cue, but they are ignored.

hopelessly lost sailor might home on the only blinking red light she can see (blinking red lights mark harbor entrances at night).

Mapped-landmark theories ([13] for example) assume that there is a map that has fiduciary points. A fiduciary point is a mapped location that can be unambiguously recognized by a distinctive feature or constellation of features unique to it, such as a distinctive surface reflectance or height or smell or sound or feel. The smoke stacks of power stations often play this role in near-shore marine navigation. Fiduciary point is

computer-science terminology for what navigators call landmarks.

Shape-parameter theories [14] share with mapped-landmark theories the assumption that the map encodes non-geometric features of the environment, as well as its geometry. Like mapped-landmark theories, they assume that the animal uses those features as both signs and beacons under ordinary navigational circumstances, when it is oriented (compare [15]). When, however, the animal is disoriented, the re-alignment of its current perception of environmental shape with the remembered environmental shape is mediated by a computation that relies on parameters computationally abstracted from global shape, such as principal axes or medial axes. Shape parameters are determined solely by the global shape of the environment.

The computational problem that must be solved by the brain of a disoriented animal reorienting to a familiar space is the same as the image-alignment problem in computerized image processing. When one has, for example, an autoradiographic image and a stained image of the same tissue slice, one often wants the computer to superimpose the stained image on the autoradiographic image. In this analogy, one image is the map in memory, while the other is the current percept of the shape of the environment into which the disoriented animal has emerged or been introduced. There are two approaches to this problem: the fiduciary-points approach; and the shape-parameters approach. The first approach requires the computer to recognize distinctive and corresponding points in both images (corresponding landmarks) and to then minimize the mean squared deviations between the two sets of corresponding fiduciary points. The second approach requires the computer to compute the centroids and principal axes of both images and superimpose these global shape parameters. I can testify from extensive experience that, when it comes to superimposing autoradiographic and stained images of the same tissue sections, the second approach is more accurate and reliable. The behavioral and electrophysiological results suggest that the same is true for the brain when it comes to aligning the currently perceived

shape of its environs to the remembered shape of that same environment.

Evolution has led the brain to rely on the shape-parameters even in those presumably rare situations where reliance on non-geometric fiduciary-points would be better.

This cognitive neuroscience insight into the origin of our sense of direction may shed light on developmental topographic disorientation [16,17], which could better be named developmental topographic misorientation. In this transient malfunction, sufferers perceive their environment as misoriented by 90° so that no matter how they turn everything is 90° away from the direction in which it should be. In other words, they appear to have interchanged the first and second principal axes, thereby making it impossible to align their current percept with their cognitive map.

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Evolution: Flight of the Ratites

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The flightless ratite birds are scattered all across the Southern hemisphere, on landmasses that have long been separated from each other. But how did they get there? They flew in from the North.

Try to channel your inner David Attenborough voice for a moment and imagine him creeping through the shrubbery somewhere in Madagascar: “this is an elephant bird. Unable to fly, she is, if not the tallest, almost certainly the heaviest bird that ever lived on Earth, weighing nearly half a ton. And she is about to lay an equally impressive ten-kilogram egg.” Sadly, this is but a poor fictional rendering of an encounter that never happened. All that David Attenborough, or anyone alive today, ever got to see of the elephant bird was a bunch of bones and empty eggshells (<https://www.youtube.com/watch?v=VhIk3AW04Ck>).

Countless species go extinct every year, many of which remain entirely unknown. And while every species matters, sometimes the loss feels particularly tragic, when species with a truly peculiar appearance or life-style vanish. This is probably true for the enormous elephant birds — known locally as ‘vorompatras’ — or their cousins, the majestic moas of New Zealand, some of which stood over three-and-a-half meters tall. Both lineages disappeared not long after specimens of our own fine species set foot on these islands — *honi soit qui*

mal y pense. But imagine you could see these birds, which went extinct only a couple of centuries ago, in a zoo or in the wild (Figure 1). Imagine what formidable biology they could teach us. Moas and elephant birds are ratites, a group of bird that — paradoxically — found its evolutionary niche by abandoning the very essence of birdness, the ability to fly. With their extinction, two of the seven major ratite lineages were lost. But thanks to the ingenuity of science, moas and elephant birds, by way of DNA locked away in their bones, did give up some of their secrets and helped resolve the riddle of ratite evolution. A recent paper by Masami Hasegawa and colleagues [1] in *Current Biology* uses elephant bird DNA to erect the most detailed and informative family tree for the ratites yet and proposes an evolutionary scenario for how these birds lost the ability to fly, grew big and wound up on far-flung lands from Madagascar to South America. The paper nicely illustrates how current biology builds on molecular, morphological, fossil and biogeographic data combined under a phylogenetic framework to infer evolutionary scenarios that played out over tens of millions of years.

Rattling the Ratite Tree

All living ratites are unable to fly. Freed from the constraints of having to take to the air, some ratites could grow big. The largest birds living today, the African ostrich and the Australian emu, are ratites. There are ten more living ratite species: two species of South American rhea, five species of New Zealand kiwi and three cassowary species, found in Australia and adjacent islands. The peculiar distribution of the ratites has intrigued biologists for a long time. How could flightless birds get onto these remote lands? Continental drift seemed to provide a clue: until about 150 million years ago, Africa (including Madagascar), South America, Antarctica, India, Australia and New Zealand were part of the erstwhile supercontinent Gondwana. As Gondwana broke up, the resident ratites could just have rafted along and evolved into the different clades on the different continents. Such vicariance is by no means an uncommon biogeographical pattern; it explains the distribution of many groups of plants and animals, and in fact ratites became somewhat of a poster child for Gondwanan vicariance [2,3]. Unfortunately, however, this rafting story just does not seem hold for the ratites.