Lindy Roy
with Leah Kelly

Navigating a Nervous Ecology

Architecture borrowed the idea of the cognitive map from neuroscience and got it wrong. Urban planner Kevin Lynch introduced cognitive mapping to architecture in 1960 in his book *The Image of the City*, in which he discussed the habitual "mind's eye" maps made by city residents and aimed to improve urban policy through direct public engagement and the consideration of diverse experiences. Two decades later, however, according to Lynch, the book had had the diametrically opposite effect.[1] Broadly embraced by design professionals as a new formula, it had been used as a superficial prescription for generating predictable and marketable urban form. Today, as cognitive, biology-based technologies infiltrate life and reshape architectural thought and production, the expanding view of cognitive maps now emerging in neuroscience could provide insight to designers negotiating the sociopolitical, ecological, cultural, economic, and technological into melded assemblies of matter and data in which artificial intelligence and human experience commingle.

Experimental psychologist Edward C. Tolman invented the term *cognitive map* in the 1940s to describe the internal representations that a nervous system in motion forms of its external world.[2] Observing how rats seemed to link together different laboratory mazes encountered only on separate runs over several days, it was apparent to Tolman that the animals had assembled some type of spatial representation, which he called a cognitive map. I first encountered Tolman's ideas in the late 1990s while researching models of coordination for an extreme wildlife project in the Okavango Delta, a wetland in the northern Kalahari Desert of Botswana.[3] From the altitude of a light aircraft approaching the site, I could see hundreds of sand-gray termite ventilation towers poking through the ground plane, evenly spaced in a barely discernible offset grid. Solid ground in the delta, built up over millennia, is assembled by colonies of subterranean, fungus-farming Macrotermitinae that produce a cementitious mix of desert sand and a termite pheromone that emits signals into the air evoking a swarm's nest-building behaviors. During this same period, I observed a different kind of silica-based swarm some

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[1] See Kevin Lynch's rebuke of design professionals in "Reconsidering *The Image of the City*," in *Cities of the Mind: Images and Themes of the City in the Social Sciences*, ed. Lloyd Rodwin and Robert M. Hollister (Boston: Springer US, 1984), 151–61. Here, Lynch reevaluates *The Image of the City* (Cambridge: MIT Press, 1960), in which he derived five classifications – node, landmark, district, edge, and path – that he believed contributed to the spatial salience of cities, and acknowledges economist Kenneth E. Boulding's *The Image: Knowledge in Life and Society* (Ann Arbor: University of Michigan Press, 1956) as the theoretical underpinning for his book. For Boulding, a cybernetician, human behavior is a product of individuals' holistic mental images of the world that circulate and are shared in the noosphere.

[2] See Edward C. Tolman, "Cognitive Maps in Rats and Men," *Psychological Review* 55, no. 4 (1948): 189–208.

[3] See Lindy Roy, "Coordination: African Delta Spa," *Assemblage* 36 (August 1998): 42–63.

14,000 kilometers away, in the Southwest United States at the Santa Fe Institute in New Mexico, where interdisciplinary research on complex adaptive systems was breaking new ground. Here, Swarm, an open-source multiagent simulation platform that had been initiated to predict the proliferation of the nascent World Wide Web through landline telecommunication networks, was also being used to investigate the behavior of emergent systems, from viruses to stock markets. The idea of a swarm as a holographic model of a collective, distributed brain that is mixed in with its environment and inseparable from it is among the speculations of early 20th-century biologists and scientists about the stimulus world where sentient behavior takes shape, and it is not new.[4] The interplay of these two completely different swarm representations, one gridded and apparently fixed at the scale of the landscape, and the other time-based and emergent at the scale of the swarm itself, stuck with me.

In the pristine Okavango Delta landscape, humans, just one among many sentient species in circulation, can leave an outsize footprint. For the project's site design, to facilitate the movement of people through the ecosystem's circuits of hydrology, geology, vegetation, and predators and prey, I looked to neuroscience for an explanation of spatial navigation and how sentient beings become coordinate with their environment and integrated into it. In the 1970s, neuroscientists began to develop techniques to record electrical activity in the brain cells of animals in motion and identified networks of specialized neurons generating those internal representations of physical space that Tolman could only speculate about. Cognitive maps laid the foundation for understanding how space is represented in the brain, but Tolman wasn't only referring to physical space. He considered cognitive maps as *general* knowledge structures that organize information from across a diversity of life experiences, according to its relevance in an ever-changing environment. It turns out that we may use our brain's cognitive mapmaking networks to navigate not only physical space but abstract space too. Conceptual thinking, sound, and even social affiliations and power hierarchies – all fundamental aspects of human experience and cognition – are now understood to be spatially underpinned and navigated using the same ensembles of spatially tuned neurons that guide our movement through the physical world. Why is that?

There is a fit between a nervous system and its life-sustaining environment. Consider the sea squirt, for example,

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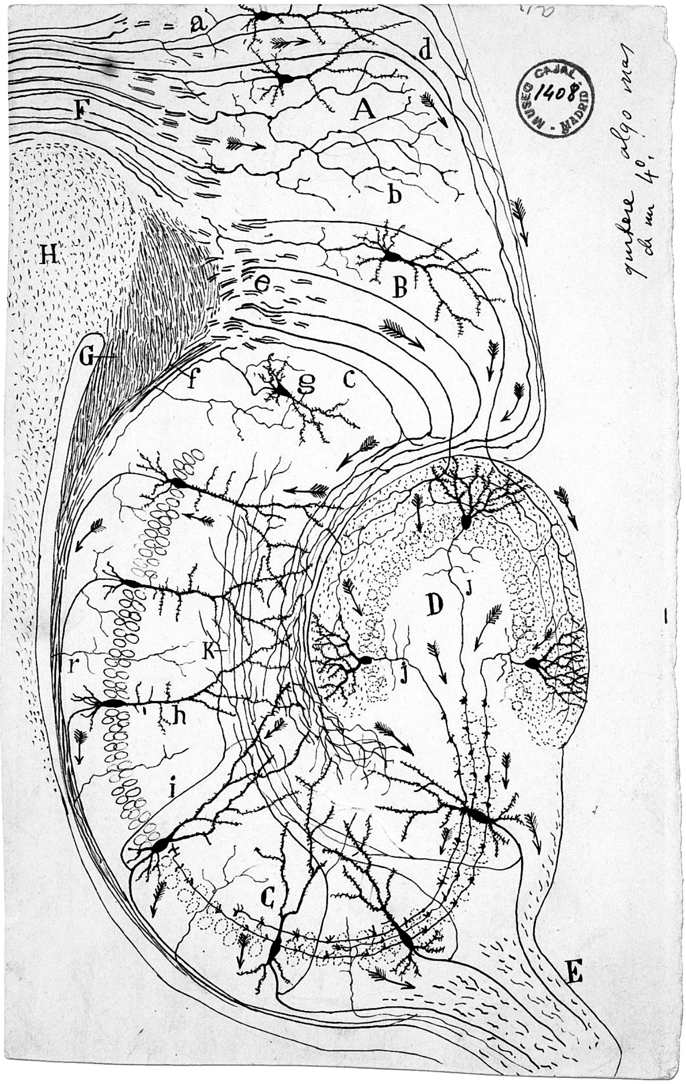
[4] See Lindy Roy, "Geometry as a Nervous System," *ANY* 17: Forget Fuller?: Everything You Always Wanted to Know About Fuller But Were Afraid to Ask (January 1997): 24–27.

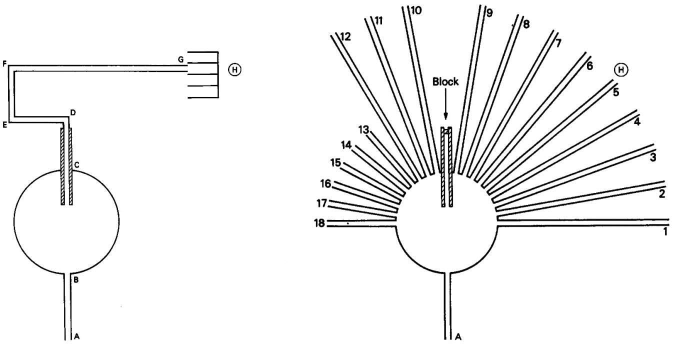
[5] Considered "motor chauvinism" in some neuroscience circles, using the example of the sea squirt to explain why we have a brain ignores movement in organisms without a nervous system.



Santiago Ramón y Cajal's canonical map of the hippocampus, 1901. Drawing courtesy Legado Cajal, Instituto Cajal (CSIC), Madrid.

a one-millimeter-long, tadpole-like larva that begins life equipped with a rudimentary 177-neuron brain used to navigate its ocean *umwelt* by integrating sensory inputs from a single eye, feedback from a crude balance organ, and propulsion from a pulsing tail. This motile existence is only temporary. To assume adult form, a larval sea squirt attaches its head to a rock and, once permanently affixed, consumes its own brain. Sedentary life is jump-started by metabolizing a redundant nervous system for energy, because once the creature stops moving, it doesn't need a brain.[5]

The human nervous system, too, is fundamentally bound up with motion. We can't take in our whole environment all at once, so we assemble mental representations as we move



Edward C. Tolman's spatial orientation experiments in the 1940s showed that rats develop broad spatial maps of their environment. In the preliminary training apparatus (left), a rat crosses a circular table and moves along passageway C directly to a food reward in location G. After four days, that training apparatus is replaced by the so-called sunburst maze (right) in which passageway C is blocked. After exploring a few inches of other radial pathway options, a substantial number of rats ran directly down passageway 6, the route terminating closest to the previous food reward at location G. Drawing from E.C. Tolman, B.F. Ritchie, and D. Kalish, "Studies in spatial learning. I. Orientation and the short-cut," *Journal of Experimental Psychology* 36, no. 1 (February 1946).

around. We also move through problems, explore options, and arrive at decisions; spatial metaphors are used unconsciously to engage abstract concepts all the time. As the dimensions of our physical world multiply into ever more complex social, cultural, and technical realms, is it possible that spatially modulated networks in the evolving human brain expand to navigate those abstract spaces as well? And if maps represent relations between things, could cognitive maps allow relationships between things to be *inferred* without ever being directly experienced? The answers to these questions may have to do with how the brain's energy economy is managed. It's important for a nervous system to conserve energy, and surprise is expensive. Anticipating uses far less energy than reacting. We may assume sensory stimuli are just passively received, but what if, to avoid surprise, a nervous system actively seeks out information from its surroundings to compare how similar something new is to something already known? A theory of the brain based on Bayesian probability,[6] which has been instrumental in the development of certain types of artificial intelligence, proposes exactly that. It sees the brain as a statistical model of the world it inhabits and perception as a type of hypothesis testing. From the tiniest calibrations of the retina to an unconscious assessment of surface stability, the Bayesian brain uses the body to actively sense its world, continuously sampling sensory fluxes, looking for evidence to update earlier predictions already neurally encoded.[7] This is where Tolman's cognitive map, plotted in electrical signals in the brain, is thought to come in. Setting incoming new information in relation to corresponding known information in a spatiotemporal matrix, a cognitive map's coordinating frame of reference organizes bits of information with spatially prescribed proximity and relational hierarchies, making it available to other parts of the brain to reconfigure through acts of imagination, planning,

[6] Bayes's theorem describes the probability of an event based on prior knowledge that may be related to that event. See Dirk De Ridder, Sven Vanneste, and Walter Freeman, "The Bayesian brain: Phantom percepts resolve sensory uncertainty," *Neuroscience & Biobehavioral Reviews* 44 (July 2014): 4–15.

[7] See Karl Friston, "The free-energy principle: a unified brain theory?," *Nature Reviews Neuroscience* 11, no. 2 (February 2010): 127–38. According to Friston, to be alive is to act in ways that reduce the gulf between sensory inputs and expectations, and all life – from a single cell to the human brain with billions of neurons – is driven by that same imperative to minimize free energy.

[8] See John O'Keefe and Lynn Nadel, "Remembrance of places past: a history of theories of space," in *The Hippocampus as a Cognitive Map* (New York: Oxford University Press, 1978). The authors note that the hippocampus should be called a cognitive mapping system and the term *cognitive map* should be reserved for the products of that system, but they use the term to refer to both the neural structure and the representation it produces.

social interaction, and even dreaming. How such divergent information forms a coherent model of the world is not understood, but a substantial amount is known to be spatially encoded by the hippocampus and a neighboring brain region called the entorhinal cortex.

In their 1978 book *The Hippocampus as a Cognitive Map*, neuroscientists John O'Keefe and Lynn Nadel begin with an analysis of ideas about space from philosophy, mathematics, and physics that reads like a history of the theory of architecture in a parallel universe and locates O'Keefe's groundbreaking research within that intellectual tradition.[8] A few years earlier, O'Keefe identified the first neural representation of space when he found a direct correlation between a single cell in the hippocampus of a rat and a particular spot in the animal's environment in his lab.[9] This so-called place cell was active in a way not seen in a neuron before. It turned on and off as the rat crossed in and out of an area along its path of travel. Firing from a location inside the animal's brain, the place cell demarcated a corresponding circular zone of space – a place field – out in the world.[10] Combinations of individual place cells appeared to form the mental map that Tolman had intuited decades before. When those same cells were found to remap, creating an entirely new representation as the rat explored a different environment, and *that* representation remained intact over several days, the first inkling of the neural underpinning for another of Tolman's consequential theories emerged: Could cognitive maps be the substrate for certain types of memory?[11] For Tolman, spatial navigation was a form of learning in and of itself; rather than relying on the association of individual movements to recall a route through space, a nervous system constructs maps to represent spatial relationships between the things it experiences. The idea was so controversial in the 1950s that it triggered a sea change in psychology and reverberated through the social sciences. In a clear dismissal of the behaviorist's stimulus-response paradigm, in which behavior was believed to be reflexively conditioned by external stimuli alone, Tolman's was a goal-directed, information-processing cognitive model of behavior. We carry the environment around with us as an engram, an alteration in our neural tissue. In a cognitive map's selective spatial array, related salient features about the world are tapped for inference, and in energy-efficient simulations of possible futures, a course of action – a decision – emerges.[12] But what that coordinating construct was exactly remained a mystery.

The Bayesian brain hypothesis argues that the brain conserves energy by not re-creating the world anew with each encounter. In this model, the brain continually makes predictions about the world and updates those predictions based on what it senses. The environment is tapped for thermodynamic free energy and scanned for information that reduces uncertainty. The creation of perception increases certainty and decreases free energy and the cycle restarts. Drawing adapted from Dirk De Ridder, Sven Vanneste, and Walter Freeman, "The Bayesian brain: Phantom percepts resolve sensory uncertainty," *Neuroscience & Biobehavioral Reviews* 44 (July 2014).

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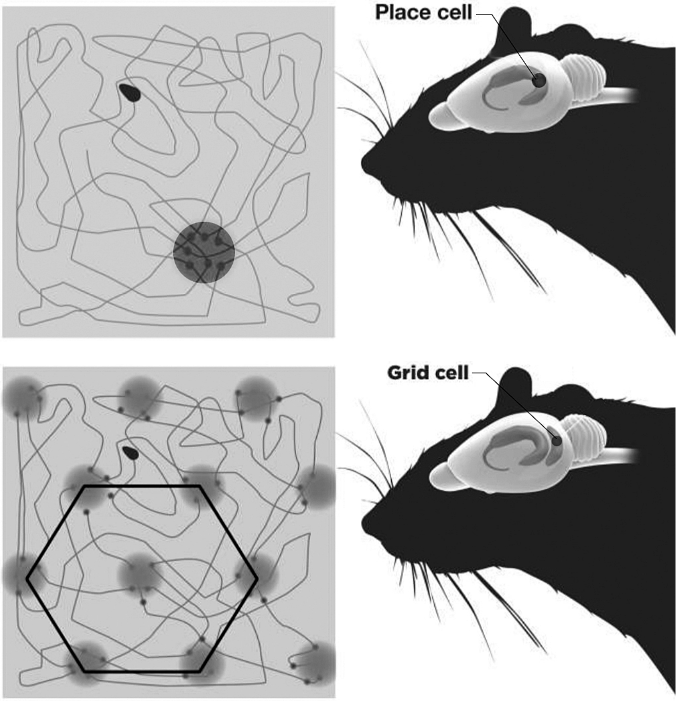
9. See J. O'Keefe and J. Dostrovsky, "The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat," *Brain Research* 34, no. 1 (November 12, 1971): 171–75.

10. See J. O'Keefe and D.H. Conway, "Hippocampal place units in the freely moving rat: Why they fire where they fire," *Experimental Brain Research* 31, no. 4 (April 1978): 573–90.

11. See Daniela Schiller et al., "Memory and Space: Towards an Understanding of the Cognitive Map," *Journal of Neuroscience* 35, no. 41 (October 2015): 13904–11.

12. See Howard Eichenbaum and Neal J. Cohen, "Can We Reconcile the Declarative Memory and Spatial Navigation Views on Hippocampal Function?," *Neuron* 83, no. 4 (August 20, 2014): 764–70.



A place cell in the hippocampus of a rat (right) and its corresponding firing location in the rat's environment (left). Bottom: A grid cell in the entorhinal cortex of a rat (right) and the locations where that grid cell fires in the rat's environment (left). Drawings: Mattias Karlen. © The Nobel Assembly, The Nobel Prize in Physiology or Medicine.

In 2005, after time as visiting scientists in O'Keefe's lab, neuroscientists Edvard Moser and May-Britt Moser focused their research on cells in the medial entorhinal cortex, a brain region relaying signals to place cells in the downstream hippocampus. They were looking for the origin of place cells' spatial signal. Recordings from these cells also revealed activity never seen in a neuron before. Unlike the single-location firing fields of place cells, these cells each fired in multiple locations as the animal moved around, creating a distributed pattern. To take in the overall schema, the researchers zoomed out and recorded the electrical activity of a single cell as the animal moved freely around a much larger space. Astonishingly, the imaging revealed a regular triangulated hexagonal grid tiling the entire floor of the animal's enclosure.[13] Those neurons, named grid cells, are organized in firing modules with the same spacing and orientation but different phasing, generating offset grids that cover every point in a space. Independent of context or landmarks, these endogenous grids appeared to act as a completely autonomous, two-dimensional coordinate system. As researchers probed the medial entorhinal cortex along a dorsal-ventral axis from top to bottom, the size, spacing, and resolution of the grid modules scaled up from a few centimeters to a few meters the deeper into the brain they went.[14]

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[13] Hexagonal grids occur frequently in nature, from the microscopic lattice of a superconductor to the camouflage spots on a predatory animal, and they can be explained as Turing patterns. In "The Chemical Basis of Morphogenesis," *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 237, no. 641 (August 14, 1952): 37–72, mathematician Alan M. Turing described how spatially periodic patterns like grids spontaneously emerge in solutions made up of chemicals with different diffusion rates. Could the ubiquitous architectural grid be an expression of our brain chemistry?

[14] See Torkel Hafting et al., "Microstructure of a spatial map in the entorhinal cortex," *Nature* 436, no. 7052 (August 11, 2005): 801–06.

Since the 1950s, when foundational neuroscientific research began to show how basic sensory processes – vision, touch, sound, taste, and smell – form maps in the brain's sensory cortices, it's been known that certain types of neurons respond to specific sensory features in an environment.[15] Millions of mechano-, chemo-, photo-, and thermoreceptors distributed throughout the body tune to energy in the environment with a distinctive spatial signature or temporal pattern. That energy is transduced by sensory receptors into electrical energy, establishing a common type of signal across the body's visual, auditory, tactile, olfactory, vestibular, and proprioceptive systems.[16] But place and grid cells showed for the first time that a higher-order cognitive function – navigating space – is mapped in the brain. O'Keefe and the Mosers shared the 2014 Nobel Prize in Physiology or Medicine for their place cell and grid cell discoveries, and by the following year, both neural correlates were confirmed to be active in humans too.[17]

Generating data to explore how movement on a two-dimensional surface translates in three-dimensional space was beyond the technical capacities of researchers until scientists at the Weizmann Institute of Science outfitted Egyptian fruit bats with tiny, ultralightweight wireless electrophysiology equipment and recorded the animals expertly traversing their vast Negev Desert habitat.[18] Three navigational modes were identified, each generating a distinct neural model of space: planar navigation limited to movement along horizontal, vertical, or inclined surfaces; multilayered navigation incorporating movement across several interconnected planes (for people, that would involve stacked floors, stairs, and ramps); and volumetric navigation allowing unconstrained movement through space, including swimming, gliding, jumping, and flying. Like bats, humans flexibly switch between all three modes. How all this is integrated into a continuously updating model of the world is not understood, but it is thought that fragments of two- and more recently identified three-dimensional grid and place cell representations are stitched together by compass-like signals emitted by neurons called head direction cells that reference orientation in space.[19] Ensembles of other specialized neurons further refine and enhance the model: speed cells act like a speedometer tracking a body's velocity, border cells mark the boundaries of enclosed space, firing rates of goal cells accelerate as a targeted area comes in range, and the elastic firing durations of time cells encode the variable temporal context of experience.[20] Both place and grid cells appear to respond to specific sound frequencies and are

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[15] See D.H. Hubel and T.N. Wiesel, "Receptive Fields of Single Neurones in the Cat's Striate Cortex," *Journal of Physiology* 148 (1959): 574–91.

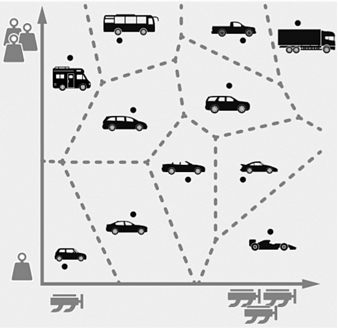
[16] The intensity of a stimulus was described in the early 20th century as an analog signal transformed by the body's sensory receptors into a digital pulse code. The now outdated idea of this analog-to-digital transformation came from the all-or-nothing properties of the action potential in sensory neurons discovered by Edgar Adrian and Yngve Zotterman in 1925. Later Zotterman wrote: "We were discovering a great secret of life, how the sensory nerves transmit their information to the brain. . . . We had found that the transmission in the nerve fiber occurred according to an impulse frequency modulation [FM], twenty years before FM was introduced in teletechnique." Yngve Zotterman, "How It Started: A Personal Review," in *Sensory Functions of the Skin of Humans*, ed. Dan R. Kenshalo (New York: Plenum Press, 1979), 6–7.

[17] Christian Doeller and Neil Burgess showed that entorhinal grid-like representations were formed in the human brain when a virtual maze was navigated using virtual reality.

[18] See Arseny Finkelstein, Liora Las, and Nachum Ulanovsky, "3-D Maps and Compasses in the Brain," *Annual Review of Neuroscience* 39 (July 2016): 171–96.

[19] Data presented by Nachum Ulanovsky at the 2021 Inaugural Weizmann-Columbia Brain Symposium suggest that grid cells are not active when bats navigate large distances. Given the amount of information a grid cell mapping of that scale would involve, this can be thought of as a "neural bandwidth" issue, but it also raises questions about what exactly grid cells are actually for.

[20] See Howard Eichenbaum, "Time cells in the hippocampus: a new dimension for mapping memories," *Nature Reviews Neuroscience* 15, no. 11 (November 2014): 732–44.



A representation of two-dimensional conceptual space shown as a Voronoi tessellation in which vehicles are arranged according to their weight and engine power. Positions in space are activated along a trajectory allowing different car types to be evaluated and compared. Drawing from Jacob L.S. Bellmund et al., "Navigating cognition: Spatial codes for human thinking," *Science* 362, no. 6415 (November 9, 2018). Reprinted with permission from AAAS.

active in assembling complex soundscapes.[21] In an experiment in which an observer bat watched a navigating bat negotiate a maze, social place cells in the brain of the observer fired at locations corresponding to the navigator's transient positions; the observer was apparently learning the maze by simply watching.[22] Social stimuli, conveyors of information about our relationship to people we encounter or know, may also be data points encoded by grid and place cell networks. Details of social affiliation, status in a power hierarchy, or place in a family structure are organized spatially according to closeness to or distance from an individual in reconfigurable representations of relative power, intimacy, and equity.[23]

While architects engage with an energy economy usually confined to the thermodynamics of materials and bodies in space, cognitive maps – that is, electrochemical encryptions of the external world inside our brain – encompass the broader reality that every encounter with the environment, every thought, action, or decision, is a constant transformation of one form of energy into another. We are in fact continuous with our world. My problem with the grid cell is its name. Because neurons fire out (x, y, z) coordinates over time, it doesn't mean space is those numbers. I think about the two silica-based swarms I observed almost 30 years ago computing the environment in exchanges of signal and cross talk. The offset spacing of termite cooling towers in the desert landscape does not result from a Cartesian impulse to order. Instead, it emerges out of myriad activities and interactions across many scales that organize resources and relationships in an ecology. Circular zones of space, not unlike grid cell firing fields, mitigate competition between subterranean colonies and enhance the productivity of the ecosystem as a whole by evenly distributing resources at finer and finer scales.[24] Working in pristine and contaminated fluvial environments made me realize that no site is fixed, not historically, ecologically, geographically, or in terms of its jurisdiction.[25] Ideas may in fact be inscribed in space, only not in the ways architects imagine. Cognitive maps situate thought and ideas along a gradient of abstraction, from physical to purely conceptual.[26] As a discipline that operates at the confluence of space and thought, what new relationships could architecture activate? What new behaviors? The cognitive map was used as a metaphor decades ago, but it's not a metaphor. It is a model for dealing with unpredictability, risk, and change. Today, when new models for architectural thought and action are urgently needed, it is a useful one.

[21] See Dmitriy Aronov, Rhino Nevers, and David W. Tank, "Mapping of a non-spatial dimension by the hippocampal-entorhinal circuit," *Nature* 543, no. 7647 (March 30, 2017): 719–22.

[22] See David B. Omer et al., "Social place-cells in the bat hippocampus," *Science* 359, no. 6372 (January 12, 2018): 218–24.

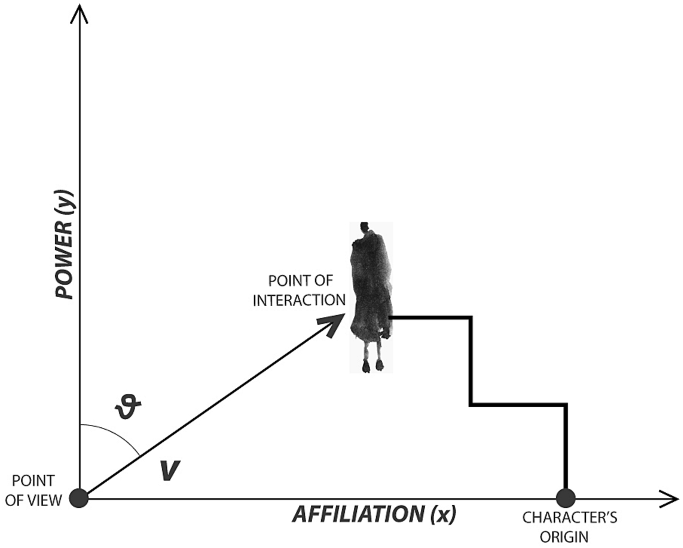
[23] See Matthew Schafer and Daniela Schiller, "Navigating Social Space," *Neuron* 100 (October 24, 2018): 476–89.

[24] See Robert M. Pringle et al., "Spatial Pattern Enhances Ecosystem Functioning in an African Savanna," *PLOS Biology* 8, no. 5 (May 2010), https://doi.org/10.1371/journal.pbio.1000377.

[25] See Kristine Synnes, "Cancer Alley," in *ROY: Architecture of Risk* (New York: Distributed Art Publishers, 2004): 42–57.

[26] See Alison Montagrin, Catarina Saiote, and Daniela Schiller, "The social hippocampus," *Hippocampus* 28, no. 9: Hippocampus and Memory Integration (September 2018): 672–79.

Diagram showing four encounters with a person in social space. Each interaction generates a change in power or affiliation. Drawing adapted from Rita Morais Tavares et al., "A Map for Social Navigation in the Human Brain," *Neuron* 87 (July 1, 2015).



Postscript

We translate sense into space. Even as sperm and egg, we move in response to the environment. Yes, there are the explicitly spatially tuned cells: the place, border, grid, and head direction cells. But these words, a siren outside, the coffee in your cup, your fingers on this page, the liquid sloshing in your inner ear, and the firing of your neurons responding to and representing these stimuli – are all data in and about space.

Architecture borrowed the cognitive map. Neuroscience provides experimental data to support it. And neuroscience is ripe for riffling. Collaborating with architect Lindy Roy in this speculative, interdisciplinary zone forces me to break down and remap how I think as a neuroscientist, lifting preconceived hierarchies, merging theory and data, just as separate grid cell patterns representing partitioned space merge into a uniform map when the partitions are removed.[27]

There is sound space, shape space, olfactory space, social space, face space, feature space, cognitive space. We navigate space by integrating egocentric and allocentric vectorial responses. These cognitive maneuvers are also proposed to be the way we navigate our own mind, forming the basis for semantic (allocentric) and autobiographical (egocentric) memory,[28] illustrating what has been understood since the time of Simonides: that time, space, and memory are coordinates of our being. If we continue to outsource our navigational skills to technology, will our cognitive skills shrink like the mapmaking hippocampi of retired taxi drivers?[29] Or will we think differently? Desert ants navigate huge distances and

[27] See Tanja Wernle et al., "Integration of grid maps in merged environments," *Nature Neuroscience* 21, no. 1 (January 2018): 92–101.

[28] See May-Britt Moser, David C. Rowland, and Edvard I. Moser, "Place Cells, Grid Cells, and Memory," *Cold Spring Harbor Perspectives in Biology* 7, no. 2 (February 2015); György Buzsáki and Edvard I. Moser, "Memory, navigation and theta rhythm in the hippocampal-entorhinal system," *Nature Neuroscience* 16, no. 2 (February 2013): 130–38.

[29] See Katherine Woollett, Hugo J. Spiers, and Eleanor A. Maguire, "Talent in the taxi: A model system for exploring expertise," *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 364 (2009): 1407–16.

path integrate without grid cells, they count steps.[30] The single-cell organism *S. roeseli* bends away from aversive stimuli without a single neuron.[31] Clearly there is more to space and computation than the grid.

As an experimentalist and an outsider, I see a divide in architecture between theory and practice. Search "grid cell movie" on the internet and witness a neuron-environment relationship in real time.[32] It will remap your cognitive coordinates such that your encoded vectors, both allocentric and egocentric, of brain and environment, will relate differently. Embody this knowledge. Design with this in mind. Realize that animate/inanimate and conscious/nonconscious, space traverses these constructed divides, that you are sculpting the medium of thought. – *LK*

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[30] See Matthias Wittlinger, Rüdiger Wehner, and Harald Wolf, "The Ant Odometer: Stepping on Stilts and Stumps," *Science* 312, no. 5782 (June 30, 2006): 1965–67.

[31] See Joseph P. Dexter, Sudhakaran Prabakaran, and Jeremy Gunawardena, "A Complex Hierarchy of Avoidance Behaviors in a Single-Cell Eukaryote," *Current Biology* 29 (December 16, 2019): 4323–29.

[32] See Dori Derdikman et al., "grid cell movie," 2010, available online as YouTube video, 0:49, December 30, 2014, https://www.youtube.com/watch?v=i9GiLBXWAHI.