



The Structural Logic of the Brain’s Representation of Space

How studies in rodents can inform architectural design for humans

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Fig. 1. Neurobiological studies in rodents have much to tell us about architecture. Photo courtesy of Roddy Grieves

Architects design buildings for humans to use, and as such, it is relevant to consider how it is that we internally represent space, because this highlights factors that should be prioritised in design. Recent discoveries in neuroscience, made by studying the neural activity patterns in rodents, have uncovered a spatial mapping system that is recruited when physically moving around in a space. This system evidently exists in humans too. The core of the system is formed by sets of neurons that seem to be sensitive to, or “encode”, fundamental aspects of space including the location of the agent within it and its facing direction, how far it is away from the borders and the identity and overall structural symmetry of the space itself. Study of how these neurons adjust their activity when these aspects of the space, or of the subject within it, are changed has yielded insights about how space is mapped. One of the oddest findings has been that – all other things being equal – the fundamental metric structure of this “cognitive map” is hexagonal. In this paper I outline the basics of the cognitive mapping system, describe the properties that have emerged from studying it in rats and mice, and then consider how these might influence architectural design for humans.

1. THE COGNITIVE MAP

The cognitive map was proposed as a theoretical entity by Edward Tolman in the early part of last century. By studying how rats solved mazes to find food he wrote “We believe that in the course of learning something like a field map of the environment gets established in the rat’s brain” [Tolman, 1948]. By this view, navigation is not a set of perception-action associations, but is mediated by an internal representation of some sort, which he called a “cognitive map.”

In 1971 a neuroscientist at University College London, John O’Keefe, claimed to have found this map. He had been studying the activity of neurons in rats: specifically, in an ancient part of the cerebral cortex (archicortex) called the hippocampus, which emerging evidence suggested is important for episodic memory (i.e., memory of personally experienced events). O’Keefe developed a method for capturing the electrical impulses from single neurons in freely exploring rats, using tiny microwires, becoming one of the first people to study neural activity in awake, behaving, thinking animals. He found that individual hippocampal neurons would become active when the rat was in particular

places in the environment (Fig. 2), with different neurons preferring different places, leading to the proposal that these neurons, which he called place cells, are the substrate for Tolman’s cognitive map [O’Keefe and Nadel, 1978]. The place in which each cell would be most active (fire) he called the cell’s place field.

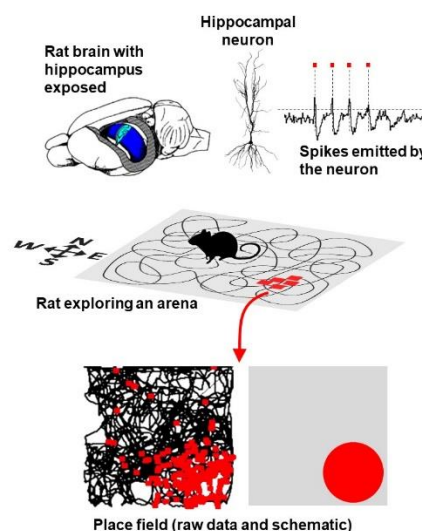
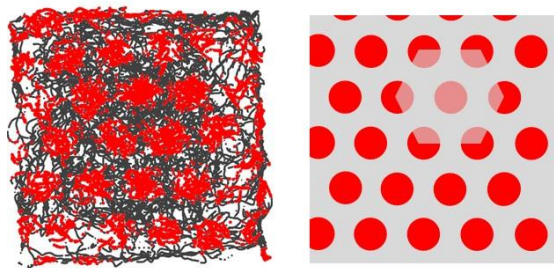


Fig. 2 Place cell recording. A rat, implanted with microelectrodes in the hippocampus, explores an arena (path shown by the squiggly black line) while the electrical nerve impulses (spikes) of single neurons are collected by recording equipment. Small red squares show the location of the rat when each spike was emitted: in this example they congregate in the South-West corner of the arena, shown here as individual spikes (left plot) or as a schematic (right plot). This region is called the cell’s place field.

With hindsight it would be nice to say that this discovery took the neuroscience world by storm but in fact it was mostly disregarded for a long time because it ran counter to the then-prevailing behaviourist view in psychology, which is that knowledge is just a set of stimulus-response associations, as opposed to internal black-box representations. However, supportive evidence slowly accumulated over the ensuing decades, including the fact that humans have place cells too [Ekstrom *et al.*, 2003], until O’Keefe’s discovery was finally recognised with a half share of the 2014 Nobel Prize in Physiology or Medicine.

The suggestion that the hippocampus is the core of the brain’s spatial mapping system eventually attracted other neuroscientists, who began to ask the question: how does a place cell “know” where the rat is? In the 1990s, James Ranck and his research team, most notably his postdoc at the time, Jeffrey Taube, began to study neurons in a nearby region of more recently evolved cortex (neocortex) and found that neurons here would increase their activity markedly when the rat faced in a particular direction – a different direction for every cell [Taube, Muller and Ranck, 1990]. They named these neurons head direction cells and suggested that they are a compass signal for the place cells, albeit one that is local (specific to the room the rat is in) rather than global. Head direction cells have now been found in multiple brain regions: curiously, these regions conform closely to a circuit long known to be involved in episodic memory. The link between space and memory is thus pervasive: for some reason, nature has bound these two things together tightly in the brain: a point we will come back to later.

The third major discovery, and one that landed in the spatial neuroscience community like a bombshell, was made by Edvard and May-Britt Moser and their research team, particularly PhD students Marianne Fyhn and Torkel Hafting. The team were exploring a region of neocortex known as entorhinal cortex, which is the last major way-station for information coming in through the senses before it reaches the hippocampus. It seemed that logically, the source of the spatial signal in hippocampus ought to be here, but this region is very difficult to reach with microelectrodes and it took some time to get clear signals that could be understood. In the first half of the 2000s, the team published a paper showing that many entorhinal neurons have place fields, very much resembling those of hippocampal place cells except that there were more of them. Whereas hippocampal place cells typically have one, or sometimes two and only occasionally more place fields, entorhinal spatial neurons showed several, even in a small recording arena (1 m or so square) of the kind typically used in the laboratory. A year later the team published their bombshell paper [Hafting *et al.*, 2005]. Following a suggestion by the theoretical neuroscientist Bill Skaggs [Moser and Moser, 2008], they enlarged the span of their recording environment from 1 m to 2 m to see if these multiple place fields formed a pattern, and discovered to their enormous surprise that they did: a very regular, close-packed hexagonal array that spreads across the surface of the enclosure (Fig. 3). The regularity of this pattern, in which the firing fields form neat rows, led to their being called grid cells, and their discovery caused the Mosers to be awarded, as a team, the other half of the 2014 Nobel prize.



Grid cell firing pattern (raw data and schematic)

Fig. 3 The canonical pattern of a grid cell, depicted in the same way as for the place cell in Fig. 2. Note that this one neuron has many places in which it fires action potentials (firing fields), and these collectively form a close-packed hexagonal array (shown by the transparent overlay). The lining up of the firing fields in rows forms a grid-like organisation suggestive of a map grid.

Most neuroscientists in the field remember where they were when they first encountered grid cells. Their pattern is so surprising, given the generally random-seeming and noisy nature of brain signals, and it led to a great deal of speculation about how the pattern arises and what it might be for. In the next section, properties of these spatial coding neurons are discussed that seem to be relevant for architecture.

2. PRINCIPLES OF COGNITIVE MAPPING

In the 50 years since place cells were first discovered an enormous amount has been discovered about them: far too much to describe in detail here. What follows is, therefore, a vastly simplified view of this now well-characterised circuit, but a few highlights are examined because of the insights offered for understanding the human conceptualisation of space.

The first insight is that the place cells are not a simple pixel map of space: they are a combinatorial code. Thus, it is not a simple matter of one place cell per place in space, or even hundreds of cells per place: it is the *pattern* of activity across the population of place cells that is important. Thus, if the environment is changed radically, such as by altering its colour or odour [Anderson and Jeffery, 2003], then the place cells collectively alter their firing patterns completely [Muller and Kubie, 1987], a phenomenon known as remapping because they seem to be making a new map. This collective activity has led to suggestions that the place cells are organised in a mutually interconnected “attractor” network with collective dynamics that enable a coherent representation of location [Samsonovich and McNaughton, 1997], and a resulting confidence on the part of the animal about which environment it is in. However, if changes are subtle then sometimes only some place cells remap, and so the attractor notion has had to be modified somewhat [Jeffery, 2011]. It is now generally thought that one role of the hippocampus and its attractor dynamics is to decide whether one’s present location is a familiar one, a familiar one that has changed slightly (e.g., a repainted room), a different one that resembles one already known, or a completely unfamiliar one. Interestingly, unfamiliarity triggers exploration in both rats and humans, and it may be that one source of wandering behaviour by Alzheimer’s disease patients, who have hippocampal degeneration, is that no place looks familiar to them anymore.

A second insight has been that self-localisation arises as a cooperative interaction between the detection of static spatial features in the environment, particularly boundaries, and the self-motion signals that come from moving through that environment [Samsonovich and McNaughton, 1997]. Positional computation arising from processing of self-motion information is known in biology as path integration (an alternative older term, borrowed from sailing, is dead reckoning). Thus, the reason you know where you are is a combination of knowing where you just were, knowing what movement you just made, and recognising the features in the place you are in now. If you pass from one familiar city street to another then you instantly recognise the features in the new street because you were expecting them. If you made a navigational mistake and found yourself somewhere instead, then even if that place were also familiar, you would probably have to pause for a long moment to reorient because those features are not what you were expecting, and so seem strangely unfamiliar even though you know them well. This type of cue combination, where cues in one’s stimulus domain (e.g., landmarks) are used to help disambiguate those in another (e.g., path integration) is a canonical property of cognitive systems in the brain.

A third insight is that the spatial reference frame against which place and grid cells conduct their spatial computations is created by the environment boundaries, at least in rodents in laboratory arenas. Of course, not all spaces are bounded in the real world, and not all species live in spaces where boundaries are a prominent feature, but the principle by which static environmental features create the backdrop against which movements are measured seems general. The effect of boundaries on place cells is shown by stretching the environment and seeing that place cells stretch their place fields too [O’Keefe and Burgess, 1996], although by a lesser amount, due to the counteracting effect of path integration. A similar effect occurs with grid cells [Barry *et al.*, 2007]. Boundaries have such a strong effect that the entire enclosure a rat is in can be moved and the place cells just moved their activity along with it, until such time as the system catches on that the enclosure can be in two places and the cells start to distinguish them [Hayman *et al.*, 2003].

The final insight to be highlighted here is the fundamental importance of the head direction signal to spatial orientation. When head direction cells were first discovered, it was puzzling that there is not a strong direct connection between these neurons and place cells, even though the activity of the two systems seems to be tightly coupled [Yoganarasimha and Knierim, 2005]. Also, place cells seem to be somewhat resistant to damage to head direction cells [Sharp and Koester, 2008], although they do show a reduction in stability [Calton *et al.*, 2003] and an insensitivity to directional cues [Harland *et al.*, 2017]. This may be because the main function of place cells is to localise the self within a bounded space, and multiple other cues (landmarks, local olfactory markers etc.) can substitute for a compass signal. The head direction system may be more needed when linking spaces together. This brings us to the main topic for this article, which is the role of the spatial system in understanding more complex, structured space.

3. STRUCTURED SPACE

Traditional laboratory spaces are simple small enclosures, usually symmetrical in shape and uniformly decorated except for a polarising cue, such as a landmark card on a wall, so that the animal knows which way is which. By contrast, real space is multi-compartmented and the sub-compartments can be complex in shape, variably sized and decorated, and may be distributed throughout 3D space. The unnatural nature of laboratory settings seems so far away from the real world that architects, understandably, may have not felt that these experiments in rats have much to offer them in the way of insights for real-world design for humans. However, it is the nature of the scientific method to break a complex problem down into its component parts, understand those, and then understand how those parts are related. In the case of space, now that we have a reasonable understanding of simple space, it is time to understand how these simple units are related: the results of these experiments bring us closer to architecture and real-world spatial experience.

The step up from a simple enclosure is two or more simple connected enclosures, and the question arises as to how place and grid cells deal with these. *A priori* we might predict that because the different enclosures are in different places and one can walk between them, they should be represented differently, using the path integration signal generated by walking as the clue that informs the place cells. Surprisingly, however, this does not seem to be the case. Studies of connected identical compartments in place cells have found that the cells tend to treat these compartments as essentially the same [Spiers *et al.*, 2015], producing the same pattern in each sub-compartment even if the rat can walk between them. Place cells can, however, distinguish compartments if there is a strong signal that distinguishes them, such as a different colour in one of the rooms [Spiers *et al.*, 2015] or if the rooms are oriented differently and thus associate with a different set of active head direction cells [Grieves *et al.*, 2016; Jacob *et al.*, 2017].

The picture seems slightly different for head direction cells. The reason head direction cells can adopt different orientations in identical rooms that are oriented differently is because they *can* use path integration to disambiguate them [Taube and Burton, 1995]. Thus, to reduce people's confusion in a multi-roomed space, it helps to make rooms different in appearance, or orientation, or ideally both. Grid cells, interestingly, seem unable to distinguish identical compartments initially [Carpenter *et al.*, 2015], but were found to do so after the rat had walked back and forth between them a few times: now they formed a single grid that spanned both sub-compartments (and hence was slightly different in each of them). Thus, grid cells seem able to use path integration to distinguish compartments, but only with practice. This reflects the propensity of the spatial system to show plasticity: that is, to adapt with experience, which is another core capability of cognitive systems.

Being able to distinguish compartments does not, however, mean that the *relative* positioning of the rooms is encoded: that is, knowing in your mental map which room is adjacent to the one you are in, and in which direction. The question of the mental map beyond immediately perceived space has been a harder question to address, because we can't ask rats about their imagination. A recent study of four connected rooms in which doors between the rooms could be open or closed looked for evidence that place cells encoded the changing connectivity [Duvellé *et al.*, 2021],

which is a kind of relatedness. In essence, the graph structure of the environment has changed. However, there was no evidence that place cells were sensitive to the door state of open vs. closed. Head direction cells, because they can associate their directional firing with different sub-compartments based on the orientation of those compartments, may provide a mechanism for linking different compartments in the cognitive map. This notion is supported by the recent finding that in one neocortical brain region, retrosplenial cortex, a sub-population of head-direction-like cells anchor their activity strongly to the local sub-compartment orientation, whereas the ordinary "classic" head direction cells remain oriented by global direction [Jacob *et al.*, 2017; Zhang, Grieves and Jeffery, 2021]. The result of this organisation is that when the rat stepped through the doorway from one compartment to another, some of its cells re-oriented their firing to align with the rotated room structure, while others maintained stable orientation consistent with the global layout.

This experiment revealed an unexpected extra finding that may shed light on how global spatial structure can be encoded in local neural patterns of activity. Strangely, within sub-compartments in the multi-compartment array, some cells developed multi-directional firing that matched the overall symmetry of the global space – even though the local sub-compartments are simple spaces. For example, a cell that looked like it should be a head direction cell (with one direction in which it preferred to fire) would start to fire in two directions if the rat had just experienced a two-compartment space, or four directions if a four-compartment space: the cells seem to have picked up the global symmetry and then re-expressed it locally. We think that head direction cells might be the mediators of this learning [Page and Jeffery, 2018], and one could speculate that the function of this symmetry encoding may be to allow local expression of global space for navigational planning purposes.

4. THREE-DIMENSIONAL SPACE

Most laboratory experiments on the spatial neurons have been conducted in simple, two-dimensional environments, but the real world is 3D, and so the question arises as to whether the spatial neurons encode the full 3D volume, to make a volumetric map, or whether they only care about the horizontal plane. Grid cells open up the possibility to examine this question because of their metric properties: acting like the grid reference in a map (or so we believe), they provide clues as to the metric structure of the cognitive map.

One difficulty with studying grid cells in 3D is that the cells are usually recorded in rats (although they have also been studied in bats, as we will see) and rats don't swim or fly. However, they can be persuaded to climb – they are quite good climbers in fact – and so we have conducted a number of experiments to see what would happen to grid cells when rats got off the floor and began to explore vertical space. We have found that the pattern of place and grid cell firing depends strongly on the nature of the environment the animals are in (see summary in [Jeffery, 2021]).

One finding emerging from these experiments has been that the processing of vertical space is, in some situations, more limited than that of horizontal space, perhaps because spatial coding is so tied to movement, and movements are more difficult in the vertical dimension. If rats climb a climbing wall by standing on horizontal pegs then grid cells seem not to track the vertical distance moved [Hayman *et al.*, 2011]. This may explain the documented confusion that people experience in multi-level buildings [Hölscher *et al.*, 2006], in which vertical travel is more laborious and interrupted. If rats can instead roam freely over a vertical surface, by climbing on chicken wire, then the grid pattern is now back again, but expanded and irregular. This expansion seems to be a consequence of impaired speed processing on the unusual surface [Casali, Bush and Jeffery, 2019]. And finally, if rats can climb through a volumetric lattice then the grid pattern is blobby throughout all three dimensions, and irregular rather than neatly patterned [Grieves *et al.*, 2021]. The grid cell pattern is thus very environment-dependent, raising the possibility that our mental map of space is as well.

In general, it seems that the canonical hexagonal close-packed grid cell pattern really only appears if animals can move in an unconstrained way in all directions in a symmetric environment. If the environment is asymmetric [Krupic *et al.*, 2015], or if the animal's path is impeded [Derdikman *et al.*, 2006], or if it otherwise isn't getting normal self-

motion signals (for example in virtual reality [Aronov and Tank, 2014]) then the pattern is repetitive, expanded or irregular. Two things are constant, however: one is that grid cells are always active, even if their activity isn't always grid-like; the second is that the pattern is always blobby, even if the blobs don't always have a fixed size or regular arrangement. This leads us to think that either rats have very poor conception of space when the environment is even the slightest bit complex (which seems unlikely) or, alternatively, that regularity isn't the important thing about the cells. The important thing may be that they separate space into discrete chunks, which may be important for memory.

5. SPACE AND MEMORY

Things brings us to space and memory, which we touched on briefly earlier. One of the most important findings to emerge from study of the cognitive neuroscience of space is that it is almost indistinguishable from the cognitive neuroscience of episodic memory. Episodic memory is memory for personally experienced events, and is dependent on having an intact hippocampus: indeed, this has been known since 1957 and the famous neurosurgical case of Henry Molaison (long known as H.M. until his name was revealed after his death in 2008). He was an epileptic young man who underwent surgical removal of the temporal lobes, which house the hippocampus. One-sided removal is usually without effect (except on the epilepsy) but it transpired that removal of both sides causes instant, profound and irreversible amnesia [Scoville and Milner, 1957]. As the neural circuitry of space has been uncovered it seems to conform almost perfectly to the circuitry for memory, and it seems that the same system does both things.

This will not be a new idea for architects: the links between space and memory go back millennia in the humanities, and the method of loci in classical Greece and Rome, and the memory palace of Matteo Ricci, are long-familiar concepts in art and architecture. One can imagine why it makes sense for space and memory to have co-evolved in the brain, because events happen in a place, and being able to associate and recall both the events and where they occurred is useful (indeed essential) for survival. Discovery of how the mental map is structured may therefore tell us something about memory. For example, the pre-eminence of boundaries for the spatial neurons has led to investigations of memory when people cross boundaries, with the discovery that memory for events in a room is modulated by their going through the doorway (the doorway effect: [Radvansky and Copeland, 2006; Horner *et al.*, 2016]). It may be that this compartmentalisation provides a mechanism to stop memories from interfering with each other, and also to bring to the fore the memories that are most relevant in the here-and-now.

The finding that grid cell activity is always clustered in space ("blobby") raises another memory-related possibility, which is that the use of boundaries to keep memories in their place, as it were, and stop them interfering with each other, may extend to the regions *within* a bounded space too. It may be that the gaps between grid cell firing fields act as a kind of self-imposed boundary, to stop memories from, as it were, leaking into each other between adjacent spaces: so that, for example, you can remember that the tea is made at one end of the kitchen counter and the toast in another, even though they are in nearby locations. One can only speculate, at this early stage, but there is no doubt that grid cells have given us much to speculate about.

6. HUMAN SPATIAL CODING: IMPLICATIONS FOR ARCHITECTURE

The properties of neural spatial mapping seem to have some universalities, at least across mammals, which mean we can learn things about the human experience of space by looking inside the heads of rats. A more detailed discussion of how these discoveries might impact on architecture can be found in [Jeffery, 2019], but a few additional thoughts are offered here on how these findings relate to humans.

As mentioned earlier, place cells have been found in humans [Ekstrom *et al.*, 2003] as have grid cells [Jacobs *et al.*, 2013]: these findings have emerged from clinical studies in which patients like Henry Molaison are, these days, implanted prior to surgery with diagnostic microelectrodes. Also, with modern whole-brain imaging methods it has recently been possible to see hints of the hexagonal activity patterns of entorhinal neurons. Although single neurons can't be seen with whole brain imaging, the rise and fall of activity of a whole neuronal sub-

population in 60-degree cycles, occurring as a function of travel direction, has revealed itself during virtual exploration of space by human subjects in a brain scanner [Doeller, Barry and Burgess, 2010]. This sixfold-symmetric activity pattern is called hexadirectional coding, and it has now been seen in several brain regions (including entorhinal cortex) in several different experiments. This methodology has also revealed that people at genetic risk of Alzheimer's disease, which is a disease of the hippocampal system, seem to have less regular hexadirectional coding [Kunz *et al.*, 2015], long before they have begun to show any overt signs of navigation difficulty or memory loss. Interestingly, these types of imaging experiments have also shown that a hexadirectional pattern forms when people "navigate" through an abstract, non-spatial cognitive space [Constantinescu, O'Reilly and Behrens, 2016], raising speculation that this system is used in humans for processing location in non-spatial cognitive dimensions. Thus, our spatial map may be deployed to help us organise complex information of the type we manipulate mentally when thinking about multi-dimensional problems.

The hexagonal coding pattern of grid cells also raises questions about the nature of our conception of space itself. Do we have a predilection for hexagonal spaces arising from the symmetry of entorhinal grid cell patterns? It would seem not: in fact, despite the advantages afforded by hexagonal structuring in terms of packing efficiency, which also leads to route efficiency, we have almost no hexagonal city layouts, nor hexagonal buildings. It might be that, by contrast, we have an *aversion* to this type of structure because we prefer the discordance and contrast of 90-degree symmetries, which jar with our grid cell pattern: or perhaps we prefer them simply because our physical bodies have front/back-left/right symmetry, or because 90 degrees is easier for engineers to work with. Nevertheless, the question of spatial symmetries and how we engage with the psychologically is interesting to ponder in light of grid cells.

Moving on from grid cell symmetry, the cognitive neuroscience of spatial coding has other insights to offer. One is the pre-eminence of directional information for the linking of spatial maps. This linking becomes necessary when we move from one enclosed space to another that isn't visually connected: here the self-motion-sustained sense of direction is needed to allow coherent linking that places these sub-maps in their correct spatial relationships. Otherwise, you develop a fragmented maps in which you know all the sub-spaces but not their relationships. If the spaces are mutually visible (e.g., separated by glass or by large openings) then there is less need to rely on the internal sense of direction: something to think about when, for example, designing for people with early Alzheimer's disease. Conversely, if mutual visibility is impossible, then the sense of direction could be supported or even replaced with environmental information that enables the head direction system to align coherently. One example might be a landmark that can be seen from both spaces: another could be some type of common directional coding scheme, such as dark shading at the (say) North end of every room in a building. Before this is attempted, however, work needs to be done to determine what information the human head direction system *does* make use of when orienting. If it transpires that the sense of direction can be anchored with symbols or objects, then architects can consider providing these as a way of enabling building users to remain oriented in whatever space they are in, which might help prevent people from getting lost in complex buildings. However, it may be that the system is insensitive to these types of human-made, symbolic landmarks, and works better with more naturalistic structures.

A final area for consideration is the relationship of space and time in the brain. Place cells are also time cells [MacDonald *et al.*, 2011], and much research links the hippocampus to the sequential organisation of experiences in a timeline [Howard and Eichenbaum, 2015], to form – over and above the spatial coding – a "memory space." This interweaving of time and place is a notion familiar to architects, who have long considered space as, mentally, a temporal sequence of experiences (see for example [Build LLC, 2014]). It is also a familiar notion to those who study episodic memory, for which when an event occurred, and the sequence in which it components occurred, is critical to the memory [Tulving, 1983].

In summary, then, the hippocampus and its construction of a spatio-temporal framework for the mental organisation of lived experience is vital for our interaction with the built environment. Principles that emerge

from study of this critical brain network will become increasingly relevant to architecture as the discipline extends its reach towards a deeper understanding of human spatial experience.

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