Explaining Social Behaviors Via Cognitive Map

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ABSTRACT

Human thinking and behaviors vary under many circumstances such as social interactions and stress. A major psychological view that forms the foundation of this phenomenon was schema, which refers to a hierarchical representation of explicit knowledge and suggests that this allows us to reason and make inferences to a novel situation. In addition, script, which is involved in explaining multiple procedural behaviors, may play an important role in determining how we behave given by the prior knowledge. Recent studies in neuroscience may explain these proposed psychological theories. Especially cognitive map, an idea proposed by Tolman, which was initially used to explain spatial cognition but later found to be explained the encoding of more abstract variables, may explain human thinking and behaviors. Moreover, the geometric properties of the activity of the neuronal population, via neural manifold modeling, provides more insights to the mapping of cognitive variables.

Keywords: Social behaviors, Cognitive map, Psychological, Neuroscience.

1. INTRODUCTION

Social behaviours were performed in a contextdependent manner, which also underlies human thinking in that context. Frederic Bartlett proposed that any knowledge acquired is organized and categorized into a structural form, allowing humans to make inferences and guiding human behaviours through navigating and integrating the information this mental structure [6, 15]. In particular, script, which derived from schema, consists of a series of behaviours under a specific social context, inspired by the information stored within schema [62]. Moreover, these behaviors also vary depending upon social identity within different groups, such as family, workplace. Some individuals identify themselves as one of the member of the group (in-group), while identifying themselves as not a member of another group(outgroup)[56, 57]. The neural basis for supporting such psychological phenomena may be explained by cognitive map based on spatial navigation system, which was recently found to possess the ability to, not only encode spatial information, but also encode abstract knowledge, form abstract knowledge space and allow us to make inferences using previous stored knowledge [12, 19, 20, 30, 38].

2. SCHEMA EXPLAINS HOW WE ORGANISE ACQUIRED KNOWLEDGE AND INSTRUCT BEHAVIOURS

As one of the earlier discovered, well-established psychological concepts, schema, introduced by Frederic Bartlett in his major work, is being widely adopted to explain myriad cognitive, perceptual, and behavioural patterns, phenomena, and tendencies in people's cognition [6]. Namely, as suggested by Bartlett as well as the contemporary field of psychology, schema is a mental structure that organizes and categorizes abstract and explicit knowledge learned by an individual through observation, explicit learning, and social norms, which then facilitates the individual's cognitions of objects, events, the world, etc [6]. By integrating past knowledge and information, which attributes are extracted to form a network that allows individuals to make inferences of and classify novel things or situations, schemas are the key to perceiving and understanding the world [15]. Notably, a process of abstracting knowledge is involved in the sequences of the formation of schemas. Hence, the brain's cognition is plastic and is capable of being more widely applying in identifying and making sense of various situations that do not necessarily embody the exact, but similar, attributes as the knowledge that is formerly possessed do. The abstraction of attributes from

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various subjects will allow for the processing of more abstract interpretations and information.

3. SCRIPT PROVIDES A SET OF BEHAVIORS UNDER A CERTAIN CIRCUMSTANCE

Based on schemas, multiple deriving concepts have gradually been proposed and associated with the theory, such as stereotypes and heuristics. Scripts and schemas are both involved with constructing a framework for the categorization of abstract and concrete knowledge learned through observation of social norms and from the social environment[49,62]. Nonetheless, each theory is applied differently. While a schema can be referred to as the mental structure that facilitates one in understanding the world, a script is a narrower concept that is contextbased. As Tomkins suggested, a script is when a person predicts, interprets, responds to, and controls a set of scenes [62]. Scripts can also be explained as a series/sequence of actions to perform, or expected to happen, under certain situations (note that it is always context-dependent). For instance, when an individual enters a restaurant, a sequential activity occur: they will get seated, order food, dine, pay, then leave. Actions that are uncommon or novel in the script of a restaurant such as not eating the food is not part of the script, thus they will not be expected to happen. In short, scripts aid individuals in performing, expecting and perceiving a sequence of actions in different familiar contexts.

In-group and out-group theories provide an explanation of varying behaviors in humans under different social context

In-group and out-groups refer to the groups that an individual identifies with and does not identify with. That is, the groups that one is in and the groups that they are not, which is based on social identity theory and become a major view in psychology [57]. Tajfel had also proved that an inter-group discrimination exists, meaning that individuals within a group compose a body with common interests while discriminating against their out-group[56]. Groups such as families, co-workers, communities, and nations could bond individuals together if they identify themselves as members of these groups. In addition, human behaviors were also affected by this sense of recognition.

Furthermore, there are several factors that could potentially affect a person's connection with an in-group and an out-group, for instance, their beliefs and sense of belonging. In short, the general determinants of the connectivity of an individual to their in-group can be classified as: 1) power and 2) affiliation.

3.1. Episodic memory lays a foundation in social understandings

Scripts, social schema, self-schema or any other kind of schema require the storage of the information for organizing purposes, as well as a way that allows fast retrieval given a stimulus. This information often relates to personal experience, person's past events, which is stored as episodic memory. Attractor theory proposed a neural mechanism for storing such information: a recurrent neural network tends to evolve to certain states or firing patterns, known as attractors (Fig.1). Researchers [33,36, 37, 50] showed that CA3, a region in the hippocampus, shows a recurrent structure [3, 4, 26] that encodes episodic memory, which allows the initiation of the whole representation of that memory by presenting stimuli that activate a small part of that representation in CA3. Moreover, other regions of the hippocampus connected to CA3 play an important role in the association and storage of social memory[44].

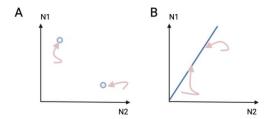


Figure 1 Attractor network of two neurons.

Two axis corresponds to the firing frequency of neurone 1 (N1) and neurone 2(N2), respectively. A) discrete attractor (shown in blue). B) Linear continuous attractor shown in blue. The red curves in both graphs show the trajectory of two neurons over time.

Episodic memory has several components, including spatiotemporal context, objects and social context(who) [2, 24]. This allows the context reinstatement of that episodic memory when a stimulus (e.g., object) is presented [51], which might inform its downstream network for social relationship and therefore instructing behaviours (e.g. handshaking) in social interactions. However, these findings do not explain how these memories are organized and the fast retrieval of associated memories encountering different situations. In the mid 20th century and followed by H.M, studies regarding spatial navigation shed light on this question [53].

4. COGNITIVE MAP IN SPATIAL NAVIGATION

In 1948, Tolman proposed an idea known as a cognitive map, suggested that both humans and animals form a mental map for spatial navigation. About three decades later, place cells, which fire at a specific region



known as place field in an environment (Fig.2A), were discovered and thought to be the neural basis for forming a cognitive map for that environment [43]. These cells were found in every vertebrate including humans [14] and their place fields were found in both two-dimensional space and three-dimensional space [21]. In addition, the firing of place cells persists over many times and multiple trials [41], indicating that the memory regarding the environment was stored via a cognitive map. Moreover, their firing patterns differ from one environment to another, which means they form a different map when the subjects encounter a novel environment [8, 66]. This phenomenon is called 'remapping' and interestingly, tends to be all-or-nothing, showing attractor dynamics [65].



Figure 2 Spatial Cells.

A) An example place cells with its place field shown in red. 2) An example grid cell with hexagonal firing fields in space (shown in red). Black lines indicate the trajectory of mouse movement and the red dots indicate the firing of place cells/grid cells. C) An example HD cell with preferred direction of the west. Adapted from Grieves & Jeffery, 2017.

From these fascinating findings of place cells, a natural question was raised: how do place cells know the place of the subject in an environment and know which map for navigation? In 1990, Taube et al. discovered head direction cells (HD) that fire at preferred heading directions (Fig.2C) [58]. Since then, HD cells were found in numerous brain regions, including medial entorhinal cortex that projects into multiple areas in hippocampus [59], which suggests that HD cells might be the source of direction information for place cells [30]. Two important characterizations of HD further supported the idea that HD cells might inform place cells: 1) self-motion information is generated from multiple sources [59]. This is consistent with the finding that the orientation of place field is controlled by the internal sense of direction of the rat [27], suggesting both place cells and HD cells can track dynamic movement. 2) HD cells respond to visual landmarks as well as odour landmarks by shifting their preferred heading directions [19, 68]. This 'resetting' was also found in place cells: place fields change when visual landmarks altered in an environment [40],

possibly via the resetting from HD cells. In addition, the activity of HD cell ensembles was modelled by a continuous attractor network, suggesting HD cells encode heading direction by using angular displacement as a result of the integration of angular velocity and angular acceleration [47, 48, 52, 67].

As discussed above, HD cells convey internal and external cues to inform direction, while the discovery of grid cells had led to the idea that grid cells might help place cells to encode distance [20, 38]. Grid cells showed regular spacings between firing fields and they are arranged in a hexagonal manner (Fig.2B), and therefore these cells are thought to provide a metric for place cells to encode distance. Moreover, their grid-like firing patterns rotate with landmarks and remap if there is a dramatic change in context [39].

Furthermore, cells in entorhinal cortex that represent position, direction and velocity conjunctively were found. An increasing number of types of conjunctive cells (e.g. grid×direction, border×direction) were then found in other brain regions such as pre-and parasubiculum (reviewed in [22]). What's more, object cells encoding their trace and object itself were also found in medial entorhinal cortex [25, 63]. These findings might imply that conjunctive cells serve as an intermediate between primary sensory neurons and the spatial cells discussed above[25, 63].

5. COGNITIVE MAP OF ABSTRACT KNOWLEDGE AND SOCIAL RELATIONSHIP, AND ITS HIERARCHICAL ORGANISATION

Despite its functional role in spatial navigation, Constantinescu and her colleagues (2016) discovered cognitive map might be used for the organization of conceptual knowledge [12]. They designed a task asking the human subjects to learn the associations between birds with specific ratios of neck and length and Christmas symbols. They recorded the brain activity of subjects using fMRI and found that human navigates in a two-dimensional conceptual map (Fig.3) with a hexagonal signal similar to the signal when humans navigating in physical space, which they hypothesized the signal might be originated from grid cells. Furthermore, they suggested that humans might use preexisting spatial maps for mapping conceptual dimensions to encode learned associations between ratios and Christmas symbols and solve conceptual tasks using grid-like signal [13, 54].



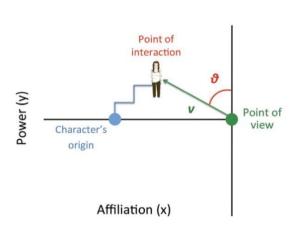
Figure 3 Cognitive map of abstract learned knowledge.

A) association between birds and Christmas symbols learned by the subjects. B) Cognitive map of abstract knowledge spanned by two dimensions. The θ indicate the direction of the trajectory of navigation in two-dimensional cognitive space. (Constantinescu et al. 2016)

Moreover, a social map was discovered by Tavares et al. (2015). They designed a role-playing game in which participants interacted with virtual characters for finding a job and a new home. Meanwhile, they recorded the activity of multiple regions in the brain using fMRI and found that the participants' hippocampal activities are highly correlated with 'movement' in social maps span by two social dimensions: power and affiliation (Fig.4 left) [60]. In a more recent study, a group of researchers also identified a social map spanned by popularity and

dimensions in entorhinal cortex, which demonstrated a grid-like code plays a role in sampling abstract spaces and making inferences when the subjects was asked to choose a partner for a starting business [45].

Taken with the findings of 'remapping' of spatial cells in spatial navigation, it is thus reasonable to hypothesize that the hippocampus may utilize this phenomenon to adapt to different social contexts and instruct behaviors.



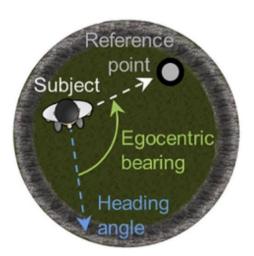


Figure 4 Social map and Egocentric Bearings.

Left: show a cognitive map of social interaction. The blue line and green line show the trajectory during the course of interaction from an egocentric view. Right: definition of egocentric bearing. Adapted from Tavares et al. 2015, Kunz et al., 2021

Furthermore, this social map is constructed from a self-centered point of view or egocentric view. Recent studies had begun to unravel the neural basis and mechanisms for such egocentric map in non-humans during spatial navigation, including the discovery of cells activated at preferred egocentric directions from the boundaries and objects [1, 18, 23, 64]. More recently, the cellular basis of egocentric spatial map in humans was identified: egocentric bearing cells (EBCs) that encodes

egocentric bearing towards a reference point (Fig.4, right), conjunctive object cell by EBCs that encodes both egocentric bearing and object [32]. Combining with the fact that the social map spanned by power and affiliation is from an egocentric view [60], these cells may track the trajectory of humans navigating social space during social interactions, and the location of reference points might underlie the position of reference the subjects were used to compare with its target in a social map.



More interestingly, the scales describing the responses of grid cells and place cells change along the dorsal-ventral axis of rodent's hippocampus, which is equivalent to the anterior-posterior axis of humans', [5, 10, 28, 29, 38]: width of place fields increased from dorsal to the ventral region of the hippocampus [29] and increasing spacing between firing fields of grid cells was also observed from dorsal to the ventral region [5, 9, 38, 54]. These multiple scales in neural codes may indicate a hierarchical organization of information [7, 35].1) finetuned scaling of place cells and grid cells in dorsal/posterior region may discriminate objects or events, or element separation within the same context, which were both demonstrated in rodents and humans. 2) larger scale may allow for the generalization across events within the same context, as also demonstrated in the ventral/anterior region of the hippocampus in both rodents and humans [31, 35, 46]. This hierarchical organization might also be applied to conceptual knowledge as well as social relationships represented in the form of the cognitive map. It is, therefore, possible that this allows us to make inferences and apply knowledge to a novel situation, where bias might form in social context during this process. Moreover, multiple scales of encoding might be the neural basis for schemas, as it might encode from details (e.g. individuals, events, relationships, associations) to the general context (e.g. workplace).

6. MANIFOLD – GEOMETRIC PROPERTIES OF NEURAL ACTIVITY MAY FUNDAMENTALLY EXPLAIN DECLARATIVE MEMORY AND COGNITIVE MAP

As discussed above, hippocampal neurons not only encode space [22], but also encode abstract learned knowledge [12] as well as social structures [60] via cognitive maps which can be described by geometric distances or adjacency [7], suggesting that neural activity corresponding to these maps might also have an intrinsic geometric structure. Starting from this point, they hypothesized that a point in a high-dimensional space can be used to describe the neural activity of a population of neurons at a particular state. The trajectories in this high-dimensional space describe the population dynamics over time, which were found to be constrained in a subset of this high-dimensional space — a low-dimensional manifold (Figure 5A) [34].

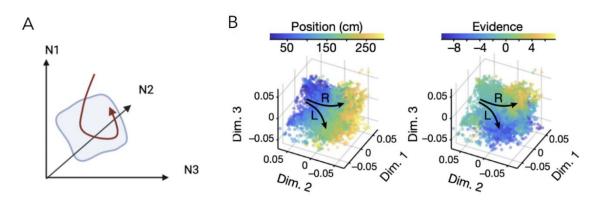


Figure 5 illustration of neural manifolds.

A) An example manifold: a curved surface (shown in blue) lying on a three-dimensional neural state space. B) task variables are orderly organized in a neural manifold. Adapted from Nieh et al. 2021

Recently, Nieh et al. (2021) investigated whether a low-dimensional manifold underlies representations of abstract learned knowledge as well as space [42]. By implementing two-photon calcium imaging to record the dorsal CA1 region of the hippocampus in mice performing accumulating tower test, they found that the manifold structure indeed showed a conjoint representation of important task variables, including positions and evidence (i.e. the number of towers). In addition, these task variables are also highly organized on a low-dimensional manifold, indicating that the firing fields are highly tiled in the manifold (Figure 5B). Furthermore, the manifold approach is also useful for extracting latent variables that are omitted by

conventional nonlinear dimensionality reduction methods. The data decoded from the manifold predicted over 80% of doublets, suggesting that the manifold encodes sequential activity. Followed by the identification of choice-predictive doublets, they concluded that behaviours of mice can be predicted from neural manifold [42].

The study of Nieh et al. suggested geometry of the neural activity jointly encode physical variables, abstract knowledge, and intrinsic behaviors. Meanwhile, another neural manifold approach was implemented to investigate HD system, reporting that an intrinsic ringshape attractor was automatically generated [11,16,]. These results provide evidence that the analysis of



topological representation of neural activity, described by manifold, can elucidate states of abstract variables encoded and therefore enables memory-guided behaviors.

Overall, the topological representation of neural activity, a manifold spanned by important task variables or neural modes, explains two important functions of the hippocampus: forming cognitive maps for the organization of information as well as storage for declarative memory. Meanwhile, neural manifolds are also observed in other regions of the brain [17], suggesting that this might be a general mechanism for neural computation. Therefore, the trajectories of neural activity when subjects navigate in social space may also be confined in a neural manifold, where the variables are represented by the intrinsic dimensions of the manifold and the social position of individuals are represented accordingly to these dimensions. Interestingly, given the finding of grid-like code system may have a role in inference construction for social relationship [45], gridlike code may guide the construction of manifold by organizing these variables and help the mapping of highdimensional neural data to a low-dimensional manifold.

7. CONCLUSION

The semantic coherence between the concept of cognitive map and the concept of schema indicates the knowledge associated in social contexts and their associated bahaviours is encoded in a structural way. Spatial navigation system discovered in animals and its roles on abstract knowledge provide potential mechanisms underpinning varied human behaviors. This spatial positioning system is not only responsible for encoding physical space but also for abstract concepts including social cognitions, while the grid-like code system further involved in retrieval of information and allow for reasoning for novel solutions in social interactions.

REFERENCES

- [1] Alexander, A. S., Carstensen, L. C., Hinman, J. R., Raudies, F., Chapman, G. W., & Hasselmo, M. E. (2020). Egocentric boundary vector tuning of the retrosplenial cortex. Science Advances, 6(8), eaaz2322.10.1126/sciadv.aaz2322
- [2] Allen, T. A., & Fortin, N. J. (2013). The evolution of episodic memory.Proceedings of the National Academy of Sciences - PNAS, 110(Supplement 2), 10379-10386. 10.1073/pnas.1301199110
- [3] AMARAL, D. G., ISHIZUKA, N., & CLAIBORNE, B. (1990). Neurons, numbers and the hippocampal network. Progress in Brain Research, 83, 1-11. https://www.ncbi.nlm.nih.gov/pubmed/2203093

- [4] Amaral, D. G., & Witter, M. P. (1989). The three-dimensional organization of the hippocampal formation: A review of anatomical data. Neuroscience, 31(3), 571-591. 10.1016/0306-4522(89)90424-7
- [5] Barry, C., Hayman, R., Burgess, N., & Jeffery, K. J. (2007). Experience-dependent rescaling of entorhinal grids. Nature Neuroscience, 10(6), 682-684. 10.1038/nn1905
- [6] Bartlett, F. C. (1995). Remembering: A study in experimental and social psychology (reissued ed.). Cambridge Univ. Press.
- [7] Bellmund, J. L. S., Gärdenfors, P., Moser, E. I., & Doeller, C. F. (2018). Navigating cognition: Spatial codes for human thinking. Science (American Association for the Advancement of Science), 362(6415), 654. 10.1126/science.aat6766
- [8] Bostock, E., Muller, R. U., & Kubie, J. L. (1991). Experience-dependent modifications of hippocampal place cell firing. Hippocampus, 1(2), 193-205. 10.1002/hipo.450010207
- [9] Brun, V. H., Solstad, T., Kjelstrup, K. B., Fyhn, M., Witter, M. P., Moser, E. I., & Moser, M. (2008). Progressive increase in grid scale from dorsal to ventral medial entorhinal cortex. Hippocampus, 18(12), 1200-1212. 10.1002/hipo.20504
- [10] Brunec, I. K., Bellana, B., Ozubko, J. D., Man, V., Robin, J., Liu, Z., Grady, C., Rosenbaum, R. S., Winocur, G., Barense, M. D., & Moscovitch, M. (2018). Multiple scales of representation along the hippocampal anteroposterior axis in humans. Current Biology, 28(13), 2129-2135.e6. 10.1016/j.cub.2018.05.016
- [11] Chaudhuri, R., Gerçek, B., Pandey, B., Peyrache, A., & Fiete, I. (2019). The intrinsic attractor manifold and population dynamics of a canonical cognitive circuit across waking and sleep. Nature Neuroscience, 22(9), 1512-1520. 10.1038/s41593-019-0460-x
- [12] Constantinescu, A. O., O'Reilly, J. X., & Behrens, T. E. J. (2016). Organizing conceptual knowledge in humans with a gridlike code. Science (American Association for the Advancement of Science), 352(6292), 1464-1468. 10.1126/science.aaf0941
- [13] Dordek, Y., Soudry, D., Meir, R., & Derdikman, D. (2016). Extracting grid cell characteristics from place cell inputs using non-negative principal component analysis. eLife, 5, e10094. 10.7554/eLife.10094
- [14] Ekstrom, A. D., Newman, E. L., Caplan, J. B., Fried, I., Fields, T. A., Isham, E. A., & Kahana, M. J.



- (2003). Cellular networks underlying human spatial navigation. Nature, 425(6954), 184-188. 10.1038/nature01964
- [15] Elio, R., & Anderson, J. R. (1981). The effects of category generalizations and instance similarity on schema abstraction. Journal of Experimental Psychology. Human Learning and Memory, 7(6), 397-417. 10.1037/0278-7393.7.6.397
- [16] Gallego, J. A., Perich, M. G., Miller, L. E., & Solla, S. A. (2017). Neural manifolds for the control of movement. Neuron (Cambridge, Mass.), 94(5), 978-984. 10.1016/j.neuron.2017.05.025
- [17] Gallego, J. A., Perich, M. G., Naufel, S. N., Ethier, C., Solla, S. A., & Miller, L. E. (2018). Cortical population activity within a preserved neural manifold underlies multiple motor behaviors. Nature Communications, 9(1), 4233-13. 10.1038/s41467-018-06560-z
- [18] Gofman, X., Tocker, G., Weiss, S., Boccara, C. N., Lu, L., Moser, M., Moser, E. I., Morris, G., & Derdikman, D. (2019). Dissociation between postrhinal cortex and downstream parahippocampal regions in the representation of egocentric boundaries. Current Biology, 29(16), 2751-2757.e4. 10.1016/j.cub.2019.07.007
- [19] Goodridge, J. P., Dudchenko, P. A., Worboys, K. A., Golob, E. J., & Taube, J. S. (1998). Cue control and head direction cells. Behavioral Neuroscience, 112(4), 749-761. 10.1037/07357044.112.4.749
- [20] Gothard, K. M., Skaggs, W. E., & McNaughton, B. L. (1996). Dynamics of mismatch correction in the hippocampal ensemble code for space: Interaction between path integration and environmental cues. The Journal of Neuroscience, 16(24), 8027-8040. 10.1523/JNEUROSCI.16 24-08027.1996
- [21] Grieves, R. M., Jedidi-Ayoub, S., Mishchanchuk, K., Liu, A., Renaudineau, S., & Jeffery, K. J. (2020). The place-cell representation of volumetric space in rats. Nature Communications, 11(1), 789. 10.1038/s41467-020-14611-7
- [22] Grieves, R. M., & Jeffery, K. J. (2017). The representation of space in the brain. Behavioural Processes, 135, 113-131. 10.1016/j.beproc.2016.12.012
- [23] Hinman, J. R., Chapman, G. W., & Hasselmo, M. E. (2019). Neuronal representation of environmental boundaries in egocentric coordinates. Nature Communications, 10(1), 2772-8. 10.1038/s41467-019-10722-y
- [24] Hitti, F. L., & Siegelbaum, S. A. (2014). The hippocampal CA2 region is essential for social

- memory. Nature (London), 508(7494), 88-92. 10.1038/nature13028
- [25] Høydal, Ø A., Skytøen, E. R., Andersson, S. O., Moser, M., & Moser, E. I. (2019). Object-vector coding in the medial entorhinal cortex. Nature (London), 568(7752), 400-404. 10.1038/s41586-019-1077-7
- [26] Ishizuka, N., Weber, J., & Amaral, D. G. (1990). Organization of intrahippocampal projections originating from CA3 pyramidal cells in the rat. Journal of Comparative Neurology (1911), 295(4), 580-623. 10.1002/cne.902950407
- [27] Jeffery, K. J., Donnett, J. G., Burgess, N., & O'Keefe, J. M. (1997). Directional control of hippocampal place fields. Experimental Brain Research, 117(1), 131-142. 10.1007/s002210050206
- [28] Jung, M. W., Wiener, S. I., & McNaughton, B. L. (1994). Comparison of spatial firing characteristics of units in dorsal and ventral hippocampus of the rat. The Journal of Neuroscience, 14(12), 7347-7356. 10.1523/JNEUROSCI.14-12-07347.1994
- [29] Kjelstrup, K. B., Solstad, T., Brun, V. H., Hafting, T., Leutgeb, S., Witter, M. P., Moser, E. I., & Moser, M. (2008). Finite scale of spatial representation in the hippocampus. Science (American Association for the Advancement of Science), 321(5885), 140-143. 10.1126/science.1157086
- [30] Knierim, J. J., Kudrimoti, H. S., & McNaughton, B. L. (1995). Place cells, head direction cells, and the learning of landmark stability. The Journal of Neuroscience, 15(3), 1648-1659. 10.1523/JNEUROSCI.15-03-01648.1995
- [31] Komorowski, R. W., Garcia, C. G., Wilson, A., Hattori, S., Howard, M. W., & Eichenbaum, H. (2013). Ventral hippocampal neurons are shaped by experience to represent behaviorally relevant contexts. The Journal of Neuroscience, 33(18), 8079-8087. 10.1523/JNEUROSCI.5458-12.2013
- [32] Kunz, L., Brandt, A., Reinacher, P. C., Staresina, B. P., Reifenstein, E. T., Weidemann, C. T., Herweg, N. A., Patel, A., Tsitsiklis, M., Kempter, R., Kahana, M. J., Schulze-Bonhage, A., & Jacobs, J. (2021). A neural code for egocentric spatial maps in the human medial temporal lobe. Neuron, https://doi.org/10.1016/j.neuron.2021.06.019
- [33] Levy, W. B. (1989). A computational approach to hippocampal function. Psychology of learning and motivation (pp. 243-305). Elsevier Science & Technology. 10.1016/S0079-7421(08)60113-9



- [34] Low, R. J., Lewallen, S., Aronov, D., Nevers, R., & Tank, D. W. (2018). Probing variability in a cognitive map using manifold inference from neural dynamics. bioRxiv, 418939. 10.1101/418939
- [35] McKenzie, S., Frank, A., Kinsky, N., Porter, B., Rivière, P., & Eichenbaum, H. (2014). Hippocampal representation of related and opposing memories develop within distinct, hierarchically organized neural schemas. Neuron (Cambridge, Mass.), 83(1), 202-215. 10.1016/j.neuron.2014.05.019
- [36] McNaughton, B. L. (1991). Associative pattern completion in hippocampal circuits: New evidence and new questions. Brain Reviews, 16, 193-220.
- [37] McNaughton, B. L., & Morris, R. G. M. (1987). Hippocampal synaptic enhancement and information storage within a distributed memory system. Elsevier Ltd. 10.1016/0166-2236(87)90011-7
- [38] Molden, S., Moser, M., Fyhn, M., Hafting, T., & Moser, E. I. (2005). Microstructure of a spatial map in the entorhinal cortex. Nature, 436(7052), 801-806. 10.1038/nature03721
- [39] Moser, M., Fyhn, M., Hafting, T., Moser, E. I., & Treves, A. (2007). Hippocampal remapping and grid realignment in entorhinal cortex. Nature (London), 446(7132), 190-194. 10.1038/nature05601
- [40] Muller, R. U., & Kubie, J. L. (1987). The effects of changes in the environment on the spatial firing of hippocampal complex-spike cells. The Journal of Neuroscience, 7(7), 1951-1968. 10.1523/JNEUROSCI.07-07-01951.1987
- [41] Muller, R. U., Kubie, J. L., & Ranck, J., Jr. (1987). Spatial firing patterns of hippocampal complex-spike cells in a fixed environment. The Journal of Neuroscience, 7(7), 1935-1950. 10.1523/JNEUROSCI.07-07-01935.1987
- [42] Nieh, E. H., Schottdorf, M., Freeman, N. W., Low, R. J., Lewallen, S., Koay, S. A., Pinto, L., Gauthier, J. L., Brody, C. D., & Tank, D. W. (2021). Geometry of abstract learned knowledge in the hippocampus. Nature (London), 595(7865), 80-84. 10.1038/s41586-021-03652-7
- [43] O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map. preliminary evidence from unit activity in the freely-moving rat. Brain Research, 34(1), 171-175. 10.1016/0006-8993(71)90358-1

- [44] Okuyama, T. (2018). Social memory engram in the hippocampus. Neuroscience Research, 129, 17-23. 10.1016/j.neures.2017.05.007
- [45] Park, S. A., Miller, D. S., & Boorman, E. D. (2021). Inferences on a multidimensional social hierarchy use a grid-like code. Nature Neuroscience, 24(9), 1292-1301. 10.1038/s41593-021-00916-3
- [46] Preston, A. R., Shrager, Y., Dudukovic, N. M., & Gabrieli, J. D. E. (2004). Hippocampal contribution to the novel use of relational information in declarative memory. Hippocampus, 14(2), 148-152. 10.1002/hipo.20009
- [47] Redish, A. D., Elga, A. N., & Touretzky, D. S. (1996). A coupled attractor model of the rodent head direction system. Network (Bristol), 7(4), 671-685. 10.1088/0954-898X_7_4_004
- [48] ROBINSON, D. A. (1989). Integrating with neurons. Annual Review of Neuroscience, 12(1), 33-45. 10.1146/annurev.ne.12.030189.000341
- [49] Roger C. Schank, & Robert P. Abelson. (1975). Scripts, plans, and knowledge. Paper presented at the Tblisi USSR 151-157.
- [50] Rolls, E. T. (1987). Information representation, processing and storage in the brain: Analysis at the single neuron level. In M. Baudry, & J. Changeux (Eds.), The neural and molecular bases of learning (pp. 503–540). Wiley.
- [51] Rolls, E. T. (2007). An attractor network in the hippocampus: Theory and neurophysiology. Learning & Memory (Cold Spring Harbor, N.Y.), 14(11), 714-731. 10.1101/lm.631207
- [52] Skaggs, W. E., Knierim, J. J., Kudrimoti, H. S., & McNaughton, B. L. (1995). A model of the neural basis of the rat's sense of direction. Advances in Neural Information Processing Systems, 7, 173. https://www.ncbi.nlm.nih.gov/pubmed/11539168
- [53] Squire, L. R. (2009). The legacy of patient H.M. for neuroscience. Neuron (Cambridge, Mass.), 61(1), 6-9. 10.1016/j.neuron.2008.12.023
- [54] Stachenfeld, K. L., Botvinick, M. M., & Gershman, S. J. (2014). Design principles of the hippocampal cognitive map. NIPS Proceedings.
- [55] STENSOLA, H., STENSOLA, T., SOLSTAD, T., FRØLAND, K., MOSER, M., & MOSER, E. I. (2012). The entorhinal grid map is discretized.Nature (London), 492(7427), 72-78. 10.1038/nature11649
- [56] Tajfel, H. (1970). Experiments in intergroup discrimination. Scientific American, 223, 96-103.



- 10.1038/scientificamerican1170-96 https://www.jstor.org/stable/24927662
- [57] Tajfel, H. (1974). Social identity and intergroup behaviour. Social Science Information, 13(2), 65-93. 10.1177/053901847401300204
- [58] Taube, J. S., Muller, R. U., & Ranck, J., Jr. (1990). Head-direction cells recorded from the postsubiculum in freely moving rats. I. description and quantitative analysis. The Journal of Neuroscience, 10(2), 420-435. 10.1523/JNEUROSCI.10-02-00420.1990
- [59] TAUBE, J. S. (2007). The head direction signal: Origins and sensory-motor integration. Annual Review of Neuroscience, 30(1), 181-207. 10.1146/annurey.neuro.29.051605.112854
- [60] Tavares, R., Mendelsohn, A., Grossman, Y., Williams, C., Shapiro, M., Trope, Y., & Schiller, D. (2015). A map for social navigation in the human brain. Neuron (Cambridge, Mass.), 87(1), 231-243. 10.1016/j.neuron.2015.06.011
- [61] Tolman, E. C. (1948). Cognitive maps in rats and men. Psychological Review, 55(4), 189-208. 10.1037/h0061626
- [62] omkins, S. S. (1978). Script theory: Differential magnification of affects. Nebraska Symposium on Motivation, 26, 201-236. https://www.ncbi.nlm.nih.gov/pubmed/552608
- [63] Tsao, A., Moser, M., & Moser, E. (2013). Traces of experience in the lateral entorhinal cortex. Current Biology, 23(5), 399-405. 10.1016/j.cub.2013.01.036
- [64] Wang, C., Chen, X., Lee, H., Deshmukh, S. S., Yoganarasimha, D., Savelli, F., & Knierim, J. J. (2018). Egocentric coding of external items in the lateral entorhinal cortex. Science (American Association for the Advancement of Science), 362(6417), 945-949. 10.1126/science.aau4940
- [65] Wills, T. J., Lever, C., Cacucci, F., Burgess, N., & O'Keefe, J. (2005). Attractor dynamics in the hippocampal representation of the local environment. Science, 308(5723), 873-876. 10.1126/science.1108905
- [66] Wood, E. R., Dudchenko, P. A., Robitsek, R. J., & Eichenbaum, H. (2000). Hippocampal neurons encode information about different types of memory episodes occurring in the same location. Neuron (Cambridge, Mass.), 27(3), 623-633. 10.1016/S0896-6273(00)00071-4
- [67] Zhang, K. (1996). Representation of spatial orientation by the intrinsic dynamics of the head-

- direction cell ensemble: A theory. The Journal of Neuroscience, 16(6), 2112-2126. 10.1523/JNEUROSCI.16-06-02112.1996
- [68] Zugaro, M. B., Arleo, A., Berthoz, A., & Wiener, S. I. (2003). Rapid spatial reorientation and head direction cells. The Journal of Neuroscience, 23(8), 3478-3482. 10.1523/JNEUROSCI.23-08-03478.2003