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Navigating Social Space

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Abstract

Cognitive maps are encoded in the hippocampal formation and related regions, and range from the spatial to the purely conceptual. Neural mechanisms that encode information into relational structures, up to an arbitrary level of abstraction, may explain these disparate functions. Research now indicates that social life can also be mapped by these mechanisms: others' spatial locations, social memory and even a two-dimensional social space framed by social power and affiliation. The systematic mapping of social life onto a relational social space facilitates adaptive social decision-making, akin to social navigation. This emerging line of research has implications for cognitive mapping research, clinical disorders that feature hippocampal dysfunction, and the field of social cognitive neuroscience.

The hippocampal formation performs functions that include spatial representation and episodic memory. These functions may reflect a multi-dimensional "cognitive map" that organizes previous experience to support flexible navigation (Tolman, 1948). The discovery of spatially modulated cells in the hippocampus and entorhinal cortex led to the view that these regions encode cognitive maps (O'Keefe and Nadel, 1978; Eichenbaum and Cohen, 2014). Subsequent research has shown that these regions are also sensitive to a variety of non-spatial and even abstract features, such as sound, time, reward and concepts (Schiller et al., 2015). The hippocampal formation maps and stores this information relationally, enabling inference and decision-making by utilizing stored memory elements (Eichenbaum and Cohen, 2014). Emerging research suggests the hippocampus also represents social stimuli within physical space, information about specific individuals, and abstract social dimensions, such as power and affiliation (Montagrin et al., 2017). The hippocampus and related regions may thus perform social functions and encode "social space" in the form of a cognitive map.

This perspective argues that social cognitive mapping occurs, and is supported by mechanisms that map physical space. The argument presents evidence for spatial mapping, followed by evidence that these same mechanisms also map non-spatial and even abstract information and enable the use of cognitive maps in decision-making. To support the idea

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that the hippocampus is involved in social cognitive mapping, we highlight research showing that spatially sensitive cells in the hippocampus encode social information, and discuss how this may relate to the role of the hippocampus in social memory. Finally, the "social space" is presented: abstract dimensions of social power and affiliation may be mapped by the same regions that map physical space and thus facilitate social navigation (figure 1). We end with a discussion of how social mapping research advances social cognitive neuroscience.

Mapping spatial dimensions

Tolman formed the cognitive map hypothesis when he observed that animals infer relationships between locations that had never been directly experienced together, a phenomenon that stimulus-response learning could not easily explain (1948). In one illustrative study, rats were trained to travel down a path to a food reward. After training, the rats were placed in a similar environment where the learned path to the food reward was now blocked. Now there were new, alternative routes, one of which led to the reward location. In a single trial test, the rats chose the correct path that angled towards the reward, despite never having been trained to take that specific path. The animals may have retained a representation of the reward's location and used it to flexibly navigate towards the reward despite obstacles, perhaps by searching an internal "cognitive map" of the relationships within the environment to predict decision outcomes.

The discovery of hippocampus pyramidal cells that encode the animal's current location ("place cells") led to the speculation that cognitive maps are encoded in the hippocampal formation (O'Keefe and Nadel, 1978), defined as entorhinal cortex, dentate gyrus, hippocampus CA subfields and subicular complex. Subsequent research has clarified many of the properties of place cells, and they are consistent with the basic idea of a cognitive map. The formation of these neurons' preferred spatial locations ("place fields") requires environmental experience but, once stabilized, spiking continues to be spatially specific absent external cues for a period of time (McNaughton et al., 2006), suggesting these representations are learned and at least in part internally maintained. This activity is stable and location specific within spatial contexts, but highly variable across contexts, indicating context dependence ("remapping"; Colgin et al., 2008). Place fields also get continuously larger from the dorsal to ventral hippocampal poles (corresponding to posterior to anterior in humans, respectively), suggesting a functional gradient that may allow for both precise and continuous spatial representations (Strange et al., 2014). This ability to learn and (in part) internally maintain location specific activity within spatial contexts provides some of the machinery necessary to encode the physical environment into a cognitive map.

Regions connected with the hippocampus also contain spatially modulated cell types. In superficial layers of medial entorhinal cortex, the main cortical input to the hippocampus, there are "grid cells" which fire at multiple, regular positions within the environment and are clustered in modules, with distinct scales and orientations (e.g., Hafting et al., 2005; Stensola et al., 2012). Like place cells, grid cells require some experience with the environment and their spiking remaps in new spatial contexts. Other medial entorhinal cortex cells also provide spatial information, including head direction (Sargolini et al., 2006), environmental borders (Solstad, 2008), speed (Kropff et al., 2015), and vectors

(distance and direction information) connecting the current location to objects (Høydal et al., 2018). Retrosplenial cortex, an area that is densely interconnected with the hippocampal formation, also contains place and head direction cells (Miller et al., 2014), as well as other spatial cell types. For example, some retrosplenial cells encode sub-routes within a larger environment, at multiple spatial scales, and others map the distance between current location and every other environmental position, giving relational information about complex paths (Alexander and Nitz, 2017). These neuronal subpopulations, among others, may cooperate within a spatially distributed network to support cognitive mapping.

Beyond spatial mapping: Increasing abstraction

Place cells encode more than the animal's current location: decoded place cell network activity reveals that place cells can represent prospective locations as well as locations the animal just left (Ferbinteanu and Shapiro, 2003). These cells bind recently experienced and to-be-experienced locations together into an orderly trajectory. Place cell sequences can also represent spatial locations that were visited further in the past. During rest or sleep, place cell ensembles often reactivate in patterns that correlate with sequences that were active during environmental experience, in both reverse and forward order (Pfeiffer, 2018). These "replay" sequences may reflect a variety of network level phenomena related to cognitive mapping, such as memory consolidation and memory-based planning (Pfeiffer, 2018). Grid cell replay-like activity has recently been observed as well, suggesting replay might be common across the cognitive map network (O'Neill et al., 2017).

Consistent with the encoding of trajectories that span the past, present and future, the hippocampus can track time (Eichenbaum, 2014). In addition to place cells, the hippocampus contains "time cells" and dual-functions cells that encode both time and place (Eichenbaum, 2014). Independent of spatial information or behavioral factors, time cells fire when an animal is at a particular point in time in a temporally structured experience. For example, when location is held constant, hippocampus CA1 neuronal activity is explained by delay duration, as individual cells fire at different time points to cover the entire delay period (e.g., MacDonald et al., 2011), similar to how place cells fire to cover a linear track. Like place cell remapping, this activity is context dependent: firing patterns change in new contexts such as when a delay period is increased. Therefore this activity does not reflect generic time tracking and instead likely reflects temporal context.

That space and time can be encoded similarly and simultaneously within the same or neighboring cells suggests they may be integrated into a unified spatiotemporal representation. Neural signal at the resolution of functional magnetic resonance imaging (fMRI) supports this interpretation. In a virtual navigation task, hippocampal multivoxel pattern similarity reflected events on both spatial and temporal dimensions, with spatial and temporal similarity having an additive effect on neural similarity (Deuker et al., 2016). Spatial grid cells can also track temporal features (Kraus et al., 2015), bolstering the view that the cognitive map incorporates an abstract temporal dimension.

The representation of space and time likely underpins the role of the hippocampus and related regions in spatial and episodic memory (i.e., memory for events in a specific place

and time). Hippocampal neural reinstatement of an item's spatial or temporal context is key to successful memory retrieval (Flegal et al., 2014), as is differentiating competing spatial or temporal context representations between memories (Copara et al., 2014). Other connected regions have similar memory encoding properties as the hippocampus. Retrosplenial cortex is important to both spatial and episodic memory and contains ensembles that can encode context-specific engrams (Milczarek et al., 2018). It also connects the hippocampus to posterior cingulate cortex (PCC), an area involved in autobiographical memory (Maddock et al., 2001). The interconnections and functional similarities of these regions suggest that the hippocampus, retrosplenial cortex and PCC are nodes within a memory system that builds and stores relational models of the contextual elements of an experience (Ranganath and Ritchey, 2012).

These elements include more than the spatiotemporal context (the "where" and the "when") of an event, however. The hippocampus can also encode information about specific elements within a spatiotemporal context (the "what" of an episode), such as object identity (Manns and Eichenbaum, 2009). For example, some hippocampus neurons respond optimally to the combination of a specific object and a specific location, and in some cases do not fire at all to the object or location alone (e.g., Komorowski et al., 2009), Conjunctive signaling of this sort may encode what happened where and is a possible consequence of the "what" and "where" visual pathways converging in the hippocampus (Komorowski et al., 2009).

The same mapping mechanisms that encode spatiotemporal contexts and their specific elements might function to organize relationships between environmental elements into a stable, relational framework for visual perception. When individuals visually explored a virtual environment, there was a grid-like BOLD signal in entorhinal cortex, suggesting the presence of visual grid cells with similar properties to spatial grid cells (Julian et al., 2018), a finding supported by single-cell recordings in monkeys (Killian et al., 2012). Additionally, single entorhinal and hippocampal neurons can respond preferentially to the visual perception of spatial layouts (Kreiman et al., 2000). Visual exploration and physical exploration may therefore use some of the same mechanisms to map the physical environment.

Other sensory modalities, such as auditory environments, are similarly encoded by the hippocampal formation, with specific place cells and grid cells responding to specific sound frequencies in a manner akin to spatial mapping (Aronov et al., 2017). Sound frequency exists on a single dimension, like a linear track, and navigation in these two domains yields very similar neural representations, suggesting the same mechanism underlies both spatial and non-spatial dimensional mapping. Additionally, professional piano tuners, who navigate a complex auditory landscape, were found to have larger than normal hippocampal volumes, an effect that was experience-dependent as it was larger in tuners who had more years of practice (Teki et al., 2012). This finding mirrors the larger posterior hippocampal volumes found in longtime taxi drivers (Maguire et al., 2000) and suggests that hippocampal structure changes in response to non-spatial navigation similarly to how it changes in response to spatial navigation.

Hippocampal dimensional encoding extends beyond information encoded by the senses to include abstract information - with abstract defined as latent information that is not directly reducible to immediate sensory perception. This can include abstract information embedded within spatial environments, such as reward location. Indeed, place cell activity is altered by the presence of reward: individual place cells increase their firing around rewards (Poucet and Hok, 2017) and place fields cluster around reward sites (Hok et al., 2007). There is also a dedicated sub-population of hippocampus ventral CA1 and subicular “reward cells” that encode reward location across environments (Gauthier and Tank, 2018). Their activity was not explained by reward related behaviors, suggesting they represent reward location itself.

That the hippocampus encodes behaviorally relevant information like reward location is unsurprising: energy resources are limited and information about the environment is not equally important and thus is not attended to with equal probability. Attentional processes may directly engage the hippocampus to support behaviorally relevant encoding: attention to task goals modulates hippocampal fMRI signal and relates to subsequent task-relevant recall (Aly and Turk-Browne, 2016a, 2016b). Additionally, while task relevant variables, such as spatial context and item identity, can be encoded in the activity of hippocampus CA1 and CA3 ensembles, task irrelevant regularities do not seem to be tracked (McKenzie et al., 2014). Attention guided encoding may thus preferentially map information relevant to the current task, including information outside of the immediate sensory experience of the animal, such as temporal context, object identity and reward - in other words, non-spatial and abstract information.

The relational information between such behaviorally relevant elements is extracted to generate relational models. For example, the hippocampus is important in learning spatial relationships between visual cues (Lavenex et al., 2006), statistical relationships between task items across modalities (Covington et al., 2018), and hierarchical relationships between stimuli via transitive inferences but not discrimination between individual stimuli (Dusek and Eichenbaum, 1997). Similarly, hippocampal damage impairs scene perception that relies upon relationships between features but not perception that relies on individual features (Aly et al., 2013), consistent with a role for the hippocampus in constructing orderly relations between information. The hippocampus therefore helps encode behaviorally relevant statistical patterns into a relational framework, which allows generalizations and inferences about relationships.

This relational mapping likely reflects a general circuit mechanism that may allow for any arbitrary dimension to be encoded, accounting for the wide range of information the hippocampal formation can represent. Purely conceptual information, abstract and not spatially embedded, may be mapped by the hippocampal formation in this same way. Across different images and even the names of the same individual, object or landmark, a subset of hippocampal formation neurons responded to the concept of the item rather than its sensory details (Quiroga et al., 2005). Entorhinal cortex, home of grid cells and an input to the hippocampus, can also map conceptual dimensions. This region contains grid cells that in the spatial domain are conjunctive for location and direction, and fire with a particular spatial periodicity. In fMRI virtual navigation, when participants moved along the orientation of a spatial grid, blood oxygenation level dependent (BOLD) signal in entorhinal

cortex oscillated in a manner consistent with grid cell activation (Doeller et al., 2010). Conceptual knowledge can be organized in a similar manner. When participants had to associate birds of varying leg and neck length with specific objects, creating a two-dimensional conceptual space, BOLD activity within entorhinal cortex and other regions (e.g., medial prefrontal cortex) was modulated in a spatial grid-like fashion (Constantinescu et al., 2016). More grid-like representations correlated with better task performance, suggesting representational quality related to memory. These findings were strikingly similar to Doeller and colleagues (2010), again suggesting that abstract space is mapped by the same regions and computations as physical space, with resulting representations being similar when the underlying statistical relationships (e.g., same dimensional space) are similar.

Relational frameworks may also encode the relationships between individual episodic memories. Temporal organization is crucial in recollection and may help explain how the hippocampus organizes memories for specific events across time (Eichenbaum, 2013). The hippocampus is associated with memory for the correct order of sequences (Davachi and DuBrow, 2015), with damage resulting in deficits, even when memory for individual items is spared (Mayes et al., 2001). Furthermore, memories that have overlapping elements, such as in where events occurred and the features within events, may be stored within relational structures, encoded by correlated ensemble firing patterns within CA1 and CA3 (McKenzie et al., 2014). Thus, memory “space” may be mapped by the same mechanisms that map physical space. Within the hippocampus and related structures elements of experience are represented, bound and stored within relational models, including the relationships between events such as their relative order, the locations where they occurred and the features within them.

Using the map: Prediction and navigation

Forming a map and navigating through the environment are two very different operations, however. If the cognitive map is ultimately about navigation there should be mechanisms that use map elements to simulate novel routes and predict decision outcomes, in order to facilitate flexible goal-related navigation across spatial, non-spatial and abstract domains. Several lines of evidence are consistent with this view.

As reviewed above, place and grid cells are sensitive to information about direction, time and speed, and can track progression through space. They may also contribute to path integration, a navigational strategy that does not use landmarks and instead depends upon updating current position and orientation using internal signals (Collett and Graham, 2004). The hippocampus, parahippocampal cortex and retrosplenial cortex contain cells that encode a homing signal that tracks the movement of an animal relative to home (Chrastil et al., 2015). Hippocampal replay sequences can represent all environmental trajectories, whether they have been experienced or not, suggesting active map maintenance that goes beyond simple memory processes (Gupta et al., 2010). These sequences are functionally important for spatial decision-making: disrupting replay sequences during sleep impairs subsequent performance in hippocampus-dependent memory tasks (Jadhav et al., 2012) while pairing reward related stimulation with replay sequences caused rodents to prefer areas represented

by those place cells (De Lavilléon et al., 2015). Additionally, grid cells compute vectors that connect locations and therefore represent distances and directions, a key function for goal directed navigation (Høydal et al., 2018; Bush et al., 2015).

Route planning and navigating recruits the hippocampus as well: during virtual spatial navigation in fMRI, hippocampus signal relates to the number of available routes (Javadi et al., 2017), the planning of new routes at choice points (Spiers and Maguire, 2006), the use of novel routes and shortcuts (Marchette et al., 2011), the proximity of the participant to a known goal (Patai et al., 2017), and success in navigation (Suthana et al., 2009). Subpopulations of CA1 place cells signal vectors towards spatial goals, some even when the goals are hidden, indicating a role for memory (Sarel et al., 2017). Different regions within the hippocampal formation may encode complementary information about spatial goals. For example, entorhinal cortex BOLD signal relates to the Euclidean distance to a goal whereas hippocampus BOLD signal relates to distance along a path to the same goal (Howard et al., 2014). Unsurprisingly, individuals with damage to the hippocampal formation have trouble navigating physical locations (Maguire et al., 2006).

To support spatial decision-making the hippocampus may simulate future behavioral possibilities. Rodents often stop at decision points in mazes and perform hesitating behaviors called vicarious trial and error, likely reflecting active planning. When this occurs, place cell trajectories “sweep” ahead of the animal, sequentially sampling the available behavioral options (Redish, 2016). Similarly, place cell trajectories can predict where a rat will travel to next in a decision-making task within an open arena, even when the start and goal locations are novel (Pfeiffer and Foster, 2013). Given that this activity occurs within environments where decision points are cued, it may be stimulus bound with only the most immediate future being simulated.

Other hippocampal ensemble patterns may reflect simulations for future behavior on longer time scales. Prior to an animal’s journey on a given trial and in the absence of an overt stimulus, sequences of place cells can evolve in forward order, consistent with simulating an upcoming journey. These “preplay” events may be constructed from stored place cell sequences (Dragoi and Tonegawa, 2013) and depend upon having some experience with the particular environment (Silva et al., 2015), suggesting that, given knowledge of the environment’s topology, spatial memory can be reconfigured to simulate possible future trajectories. Reward location also influences which trajectories are simulated. Preplay for unexplored regions occurs after seeing reward deposited there, suggesting these ensemble events can be goal-directed (Freyja Ólafsdóttir et al., 2015), while reward specific cells in CA1 and the subiculum fire in prediction of an upcoming reward, and strongly relate to slowing behavior upon reaching the reward location (Gauthier and Tank, 2018). Memory readouts from a spatial cognitive map may simulate paths to future reward, in the service of adaptive behavior.

Consistent with a role for hippocampal memory in decision-making, the hippocampus is important in using relational memory in sequential decision-making tasks (Yee et al., 2014), and is a key region in reconfiguring memory to predict consequences of future scenarios (Barron et al., 2013). Episodic simulation (i.e., imagining future episodes) might depend on

these same mechanisms: it shares extensive behavioral and neural similarities with episodic memory, such as temporal and experiential properties, as well as a common neural circuitry that includes the hippocampus (Schacter et al., 2012). Patients with hippocampal damage often cannot describe coherent scenes for imagined future events and will resort to describing each individual component of a scene separately (Hassabis et al., 2007), and they report almost no scene or visual imagery-based mind wandering (McCormick et al., 2018).

An open question is where and how a map's code is read out to guide action selection. One candidate region is the orbitofrontal cortex (OFC), which is anatomically connected to the hippocampus and has value and decision-making functions, as well as grid-like properties during conceptual mapping (Constantinescu et al., 2016). The OFC may map a "task space," the set of possible states associated with a given task, by segmenting the world into discrete states and tracking information related to these states, allowing values to be assigned to them (Schuck et al., 2016). This mapping is in some ways analogous to hippocampal cognitive mapping, and these regions may interact to facilitate decision-making. For example, during vicarious trial and error behavior at decision points OFC neurons that are responsive to reward receipt are active around the same time place cell ensembles would be expected to sample the available options (Steiner and Redish, 2012). The close timing suggests that behavioral options simulated by the hippocampus may be subsequently evaluated for reward value in OFC (Wikenheiser and Schoenbaum, 2016). Other work supports this view: suppressing ventral hippocampus output in the ventral subiculum disrupts the formation of OFC representations of task structure and expected outcomes (Wikenheiser et al., 2017), further evincing an interaction between these regions in decision-making related processes.

Nearby medial prefrontal cortex (mPFC) may serve a similar role in cognitive map-based decision-making. Traditionally studied for its role in value representation during decision-making, mPFC may structure a "decision space" via grid-like computations (Constantinescu et al., 2016) that decompose large goals into smaller goals, similar to how grid cells section up physical and conceptual space, and then use hippocampal dependent memory to meet task demands via hippocampal connections (Kaplan et al., 2017). Evidence is consistent with this account: both regions represent goal proximity (Balaguer et al., 2016), and bidirectional covariation between the hippocampus and mPFC during a context memory-guided decision task has been observed (Place et al., 2016). Additionally, increased BOLD covariation between hippocampus and ventromedial PFC accompanies episodic simulation, suggesting ventromedial PFC has a role in reconfiguring memories into a novel episode (Campbell et al., 2018). Hippocampal memories may serve as templates to guide mPFC-based decision-making. Though much work remains to fully elucidate how cognitive maps are used to guide decision-making, this research suggests an intriguing possibility. Relational models, encoded in the hippocampal formation, may allow the simulation of behavioral possibilities, which are subsequently evaluated by OFC and used to guide task relevant behavior by mPFC. This also hints at how greater computational efficiency may be achieved in decision-making even in novel scenarios in which the animal has no experience. The world's statistical regularity (i.e., reality's non-randomness) allows memory elements to be generalized and constrain representations of possible behaviors and decision outcomes. This reduces the number of computations needed to generate a decision, greatly increasing the efficiency of decision-making (Kaplan et al., 2017). These processes may support spatial

navigation as well as more abstract goal-oriented behavior. This research has slowly been piecing together how Tolman's map leads to flexible navigation.

Navigating into the social domain

So far, it has been argued that the hippocampal formation and related regions treat spatial and non-spatial information similarly, up to levels of full abstraction. The unique structure of the hippocampus may underlie its functional flexibility: a highly recurrent structure processing all sources of incoming information through its intrinsic circuitry in the same relational manner (Lisman et al., 2017). Internal representations of the statistical structure of information in the world (i.e., 'cognitive maps') are generated, which can be generalized to new situations. Thus, non-spatial and abstract information is mapped much like spatial information: this was demonstrated with evidence for non-spatial mapping that requires sensory experience, such as auditory mapping, and evidence for abstract mapping, from time to reward location to purely conceptual spaces.

This same hippocampal centered network likely maps social life. Social information exists in an orderly, dimensional fashion in a manner akin to spatial information. Social dimensions rooted in social memory and relationally bound together frame social interaction, making social space an ideal candidate for cognitive mapping. This kind of social topography may represent individuals as coordinates within social space, from which social vectors can be computed and social inferences and decisions can be generated. Some of the same mechanisms that facilitate adaptive spatial navigation may underlie adaptive social navigation.

Research into social memory supports a role for the hippocampus in organizing social information. For example, faces associated with biographical information or behaviors recruit greater left hippocampus BOLD signal relative to novel faces (Todorov et al., 2007). Other fMRI work corroborates and extends this finding: bilateral hippocampus activity relates to correct recollection for individuals and tracks pre-experiment familiarity of a famous or personally known face, independent of presentation recency (Trinkler et al., 2009). This activity may be specific to social or biological stimuli, as another study showed that landmark familiarity did not relate to hippocampal activity (Viskontas et al., 2009). Social memory also likely underpins social networks: in healthy adults, social network size can be predicted by performance on hippocampal dependent tasks (Stiller and Dunbar, 2007), whereas individuals with hippocampal damage have difficulty retrieving information about individuals (Sanders and Warrington, 1971) and difficulty maintaining relationships, leading to more restricted social networks than healthy individuals (Davidson et al., 2012). These studies, among others, suggest social memory may in part be organizational, systematically managing social information to guide behavior.

Social information in physical spaces

Knowing other animals' locations is a particularly important piece of social information, as it is key to communication, mating and survival. Given their biological relevance and the role of the hippocampus in representing abstract features of spatial environments, the

hippocampus may encode the spatial location of conspecifics. Such “social place cells” were detected in the hippocampus dorsal CA1 when bats had to observe and then perform the same flying behavior as another bat in order to receive a reward (Omer et al., 2018). To investigate the effects of observational learning on place cell activity, separate firing-rate correlation maps were computed for the locations of the observer and the demonstrator. Some cells’ spiking correlated with the observer animal’s current location, in classic place cell fashion. A subset of these cells’ activation patterns also correlated with the location of the demonstrator bat. This conspecific related activity was unlikely to be simple sensory stimulus tracking: inanimate moving objects also elicited place cell activity, but with different representational properties. Rather than sensory details, these cells seem to encode abstract information about the social or behavioral relevance of the conspecific. One possibility was not ruled out in this design, however; this activity could have reflected the simulation of a future self-trajectory.

Another study in rat dorsal CA1 included an experimental condition where future self and current conspecific trajectories could be fully disentangled (Danjo et al., 2018). Rats had to observe a conspecific’s trajectory in a T-maze and, depending on the trial, perform the same or opposite turn as the conspecific. If dorsal CA1 contains social place cells, then their activity during observation should correlate with the conspecific’s location even on trials when the observer had to make the opposite decision. This pattern was observed, which ruled out the hypothesis that this activity was simply future-self- or goal-related and strongly suggested that dorsal CA1 place cells encode the spatial location of other animals.

Dorsal CA2 place cell activity also alters in response to social stimuli. These neurons globally remap in the presence of other rats as well as novel objects, without changes in overall firing rates, perhaps binding social and novelty information to spatial representations (Alexander et al., 2016). Dorsal CA1 neurons did not show this same change in activity, raising a question of what precisely dorsal CA1 and dorsal CA2 are doing in these social processes. Alexander and colleagues did not use an observational learning task as did Danio et al (2018) and Omer et al (2018), thus dorsal CA1 may reflect active spatial tracking of functionally important conspecifics, especially in the service of learning, and dorsal CA2 may reflect passive binding of social information to spatial representation.

Regardless of what explains the differences between these data, these studies show that both CA1 and CA2 have place cells that are sensitive to social context, mirroring previous work showing that place cells are modulated by abstract information. These subfields are also important for social memory. Under normal conditions mice tend to spend more time interacting with unfamiliar mice, a phenomena employed to study social recognition. Optogenetic inhibition of mouse dorsal CA2 neurons prevented the normal decrease in time interacting with a familiar mouse (Hitti and Siegelbaum, 2014), indicating a lack of social recognition for the previously experienced mouse. This effect was not explained by general function loss, such as motor behaviors or spatial or contextual memory. Additionally, optogenetic excitation of mouse dorsal CA2 neurons during memory acquisition increased memory for specific mice, an effect that was dependent on vasopressin receptor function (Smith et al., 2016). In both of these studies, interest in new mice was unaffected, suggesting the effects were specific to social memory rather than social interest. Optogenetic inhibition

work showed that ventral CA1 neurons and their projections to nucleus accumbens shell are necessary for social recognition behavior as well. Reactivation of this circuit was sufficient to induce social recognition behavior, suggesting this circuit stores social memory engrams (Okuyama et al., 2016). A subpopulation of neurons within ventral CA1 has been shown to reliably encode reward location across environments. It is possible that a dedicated subpopulation of social cells also exists, or that conspecifics are in part represented by hippocampal reward circuitry.

This research demonstrates that cell populations within the CA1 and CA2 hippocampal subfields are important for processing both the current location of conspecifics and for a specifically social form of recognition. These functions may be related: social place cell activity may underlie social recognition. Although Alexander and colleagues (2016) found that firing rates in dorsal CA2 place cells did not differ between the presence of novel and familiar rats, when the animals were placed back into the original environment without the conspecific, the original place fields did not return, suggesting a memory trace in environments in which social interaction previously occurred. This mirrors evidence that cells in lateral entorhinal cortex continue to code for an object even after the object has been removed from an environment (Tsao et al., 2013).

In seeming contradiction to the evidence of hippocampal involvement in social recognition, hippocampal damage in humans can spare facial recognition while impairing other memory functions (Aly et al., 2010; Bird et al., 2007). This seems to argue against the points just made: if the hippocampus is essential to social recognition, then hippocampal damage should profoundly affect this function. There are several possible explanations for this data. First, there may be other circuits that can support face recognition and thus compensate for hippocampal damage. Another possibility is that different regions subserve facial and social recognition: the hippocampus may not contribute to memory for faces devoid of social relevance. Those studies testing patients' recognition of previously unknown faces did not pair the faces with any behavioral or social information (Aly et al., 2010; Bird et al., 2007). In other domains, hippocampal damage can impair relational memory while sparing memory for individual items (e.g., Dusek and Eichenbaum, 1997; Mayes et al., 2001), suggesting hippocampal social memory functions may be specific to relational mapping, rather than individual social items like faces. An unusual property of CA2 may also explain this: sources of tissue damage to the hippocampus, from diverse causes such as epilepsy, ischemia, hypoxia and trauma, spare CA2 relative to other subfields (Dudek et al., 2016). Research on patients with hippocampal damage does not always account for subfield damage differences, leaving open the possibility that spared facial recognition reflects a relatively spared CA2.

In addition to resilience to damage, a variety of other factors differentiate CA2 from the other hippocampal subfields and may be relevant to understanding subfield contributions to cognitive mapping. These include gene expression, molecular profile, long-term potentiation, dendritic branching, density of inhibitory interneurons and connectivity (Dudek et al., 2016). CA2 pyramidal neurons have a larger excitatory response to entorhinal input than CA1 neurons, likely because of greater innervation and more efficient signal propagation (Srinivas et al., 2017). Entorhinal projections to the hippocampus are also

topographically mapped and CA2 largely receives lateral entorhinal cortex inputs that convey non-spatial information (Hargreaves et al., 2005). Consistent with this, CA2 is less essential to spatial representation than the other subfields, as CA2 place fields change more over time than place fields in CA1 and CA3 (Mankin et al., 2015), and CA2 inactivation does not impair spatial performance (Hitti and Siegelbaum, 2014). As such, projections directly from CA3 to CA1 might adequately support spatial functions, while CA2 to CA1 circuitry might be non-spatial and maybe even have a specifically social function. CA2 pyramidal neurons are rich in vasopressin and oxytocin receptors, neuropeptides important in many social behaviors (Young et al., 2006), and plasticity induced by concurrent stimulation of entorhinal inputs and CA3 affects CA1 and CA2 differently: it improves contextual memory in CA1, and improves social recognition in CA2 (Leroy et al., 2017).

The interconnection of the CA2 and CA1 subfields (the deep layer of CA1 receives inputs from CA2) (Kohara et al., 2014), and the relative specificity of their social functions suggests they may contain circuitry specialized for social cognition. During the encoding of social information vasopressin and oxytocin may regulate CA2 activity, which in turn can modulate CA1 excitation (Piskorowski and Chevaleyre, 2018). Through this pathway, social information could have a modulatory role in hippocampal function generally.

Mapping abstract social dimensions

Mirroring the mapping of abstract dimensions, the hippocampal formation may represent abstract social information dimensionally. One such dimension is dominance hierarchy. Understanding the relative social power of individuals is vitally important to social animals, as status affects resource allocation, mating opportunities and physical safety. Accurately representing hierarchy likely requires repeated interactions with conspecifics where status representations get formed and updated. As the hippocampal formation is critical to representing others in space, social memory, and in learning, storing and inferring hierarchical relationships, it is likely also central in social hierarchy.

Indeed, lesions in the hippocampus disrupt hierarchy formation in rodents (Gray and McNaughton, 1983), while hierarchy disruption decreases hippocampal neurogenesis and induces social behavioral changes, such as a preference for familiar over novel animals (Opendak et al., 2016). Dominance hierarchies affect the hippocampus to the level of gene expression, with subordinate mice showing higher expression of serotonin receptor subtypes (Horii et al., 2017). The hippocampus also represents and updates information about hierarchies: hippocampal BOLD activity relates to reading about status hierarchies relative to reading about objects (Muscatell et al., 2012), tracks the emergence of social hierarchies, correlates with confidence in hierarchical rankings (Kumaran et al., 2012), and increases during rank updating (Kumaran et al., 2016).

Work in social psychology suggests another important social dimension in addition to social power: affiliation (e.g., kinship, bonding) is central in social interaction. These two dimensions are important for social relationships in rodents (Insel and Fernald, 2004), nonhuman primates (Brent et al., 2013) and humans (Fiske, 2012). Although there is evidence for the hippocampus processing social hierarchy, evidence is scant for the role of

the hippocampus in processing affiliation information. There is some evidence for hippocampal processing in affiliation broadly, as rhesus monkeys with hippocampal lesions respond less to affiliation signals and behaviors (Machado and Bachevalier, 2006). Social psychology theories suggest that dimensions of power and affiliation are computed jointly (Fiske, 2012; Todorov et al., 2008; Wiggins et al., 1989), creating a two-dimensional cognitive map that locates others relative to ourselves in social space (Tavares et al., 2015). Social coordinates of power by affiliation thus may be mapped in a manner akin to two-dimensional egocentric mapping of physical space, providing the scaffold for navigating social relationships (figure 1).

Social navigation and decision-making

Adaptive social behavior requires many similar processes as adaptive navigation: we have to use memory to draw upon experiences, simulate future social situations and infer the mental states of others. These processes (episodic memory, episodic simulation and mentalizing) all activate a common network circuitry, including the hippocampus, retrosplenial cortex, precuneus, PCC and mPFC, roughly the same network that is active during spatial navigation (Spreng et al., 2009). Social space mapping and navigation might engage some of the same mechanisms as cognitive mapping and navigation generally (figure 2).

Tavares and colleagues (2015) examined this possibility using a role-playing game during fMRI. In the game, participants had just moved to a new town and had to find a job and a place to live. To do this, they interacted with fictional characters and made decisions that altered the relative power and affiliation of the characters. For power interactions, participants could submit to a demand, or refuse or make demands of the characters themselves, increasing or decreasing the relative power of the character. For affiliation interactions, participants could engage in physical touch or personal conversation, or not, increasing or decreasing their affiliation with the character. The choices accumulated into a power by affiliation social coordinate for each character at each decision point throughout the game, from which vector angle and length were calculated using the vector between the participant's theoretical point of view and the character's coordinates. Importantly, both of these metrics included information about both the power and affiliation of the character at each decision. The normalized vector angle and length were used as parametric predictors in the fMRI analysis of the decision trials.

As participants made power and affiliation decisions, several different regions had BOLD activity that uniquely correlated with the vector angle to the characters' locations within the two-dimensional social space. Only one of these regions had activity that correlated with self-reported social skills: the left hippocampus. The relationship between hippocampal activity and the movement of the characters through social space, as measured by the vector angle, was stronger in participants with less self-reported social avoidance and neuroticism. This correlation demonstrates that hippocampus social tracking relates to social skills among healthy individuals, suggesting social cognitive maps are important to real world social behavior.

Hippocampal damage leads to more dramatic and unstable character judgments, perhaps because of an inability to contextualize a person's current behavior in light of their past behavior, causing an overweighting of current behavioral information (Croft et al., 2010). Taken together with the centrality of the hippocampus in dimensional mapping and the correlation between hippocampus BOLD activity and vector angle in this task, the hippocampus is likely a crucial player in accurately representing the relative social standing of the characters. Under this account, information about an individual, including their identity and previous behavior, facilitates relational mapping of individuals in a power by affiliation social space, reflecting the role of the hippocampus in relational structures more generally.

The well described cell types and circuitry in the hippocampus allows for some speculation on cellular mechanisms. One possibility is that social place cells spiking rate or number of cells recruited is modulated by social information. Research indicates individual hippocampal cells can be sensitive to specific people, responding more to the faces of known people (Kreiman et al., 2000) and invariantly representing the same individual across sensory modalities (Quian Quiroga et al., 2009). It is possible that individual cells, or cell ensembles, can also represent factors such as an individual's relative power and affiliation. There may even be specialized circuitry (e.g., CA2-CA1) dedicated to representing social dimensions. Another possibility is that reward cells have a more general role that includes social reward: interacting with individuals higher in the social hierarchy might be more rewarding and recruit greater activation.

Two other regions had unique correlations with the vector angle: left inferior parietal lobule and left dorsolateral PFC. The possible roles of these regions are less clear. Inferior parietal lobule, an output for CA1 neurons, was previously implicated in representing distance from oneself in a variety of domains, including spatial, temporal and social familiarity (Parkinson et al., 2014). Additionally, it has been involved in representing spatial locations numerically (Krause et al., 2014) and uncertain decisions (Vickery and Jiang, 2009). One possibility is that the inferior parietal lobule may assist in transforming abstract coordinates into a more concrete form, facilitating distance representation and guiding social decisions under the uncertainty of the social environment.

Dorsolateral PFC can control attention to spatial location (Hagler and Sereno, 2006), influence hippocampal memory expression (Anderson et al., 2004), and may be central in goal-directed and norm-guided behavior, particularly in associating social norms with the value of outcomes (Buckholtz, 2015). What is normative social behavior in any particular situation will depend in large part on social context and might be especially sensitive to the relative power and affiliation of the individuals involved. Dorsolateral PFC, which is connected to the hippocampus, might direct attention to the locations of individuals within the social cognitive map to evaluate social rule-outcome associations given their social standing, ultimately to facilitate social decision-making.

While vector angle is necessary information for locating others in space, the map is incomplete without the distance between the characters and the participant within the space. Only one region related to vector length: posterior cingulate cortex (PCC; extending into

precuneus), a region connected with both inferior parietal lobule and the hippocampus (via the retrosplenial cortex). Previous literature has found that PCC contributes to a variety of social cognitive processes: it has been linked to self-referential processes, such as self-judgment (Ochsner et al., 2005) as well as other-referential processes, such as forming and updating first impressions (Schiller et al., 2009; Mende-Siedlecki et al., 2013). Additionally, PCC is anatomically and functionally related to the precuneus, retrosplenial cortex and hippocampal regions: all contribute to the default mode network, a network of areas whose activity is highly correlated with one another and is active when individuals are involved in processes such as remembering and imagining events, thinking about themselves and others, navigating (Spreng et al., 2009)and goal-directed cognition (Spreng et al., 2010).

Mapping properties have been specifically observed in PCC: fMRI research has uncovered a grid-like signal in PCC during the mapping of abstract conceptual dimensions (Constantinescu et al., 2016). Given that grid cells can represent distance (Bush et al., 2015), grid-like representations within PCC might help represent the distance between self and other within social space, with greater PCC signal magnitude reflecting a larger social distance. Calculating social distance might underlie the social functions that have been ascribed to this region, such as mentalizing (i.e., the ability to understand the mental states of others). Consistent with this, an individual's own social status impacts mentalizing network activity, with lower status individuals showing a greater engagement of this area while encoding social information (Muscatell et al., 2012).

Mentalizing shares similarities with episodic simulation: both require the reconfiguration of mental elements to simulate an experience, and both rely on a similar neural architecture based in the default mode network. Mentalizing operates independently of hippocampus-mediated episodic memory (Rosenbaum et al., 2007), but PCC engagement is seen during the retrieval of autobiographical memories (Maddock et al., 2001) and PCC based memory of one's own past mental states might inform mental state inferences about others. Social distance might be an important moderating factor in this process. Consistent with this possibility, mentalizing about close others and recalling autobiographical memories recruits many of the same brain areas, including the hippocampus, retrosplenial cortex, PCC and precuneus whereas mentalizing about unfamiliar others does not, suggesting different neural systems subserve these processes (Rabin and Rosenbaum, 2012). While the direction of PCC activation in this study seems to differ from Tavares and colleagues (2015), it may be that mentalizing about known individuals involves social distance representation from one self, whereas mentalizing about unknown individuals may be supported by different mechanisms altogether.

Mentalizing may in part function to improve social decision-making via social predictions. PCC tracked the social vector length at each decision point, when social decisions could affect the mental states and behaviors of others and therefore impact ones own social trajectory. Both passively watching social interactions (Iacoboni et al., 2004) and engaging in social interactions (Rilling et al., 2004) recruit PCC and precuneus, suggesting mentalizing processes may be engaged in support of social decision-making. Speculating from this evidence, PCC grid-like representations might compute social distance, which in turn informs autobiographical memory-mediated mental state inferences.

The correlations between hippocampal social tracking and self-reported social skills suggest that social mapping is important to real world functioning. Social avoidance behaviors, which have been linked to hippocampal function (Lagace et al., 2010), might in part reflect dysfunctional social cognitive mapping, at least among healthy individuals. This opens another possibility: hippocampal dysfunction might cause inaccurate or unstable social maps and lead to psychosocial psychiatric impairments.

Clinical disorders often implicate both hippocampal and social dysfunction, suggesting a link between the two. Schizophrenia patients show dysfunctional social behavior (Fett et al., 2011), as well as reduced hippocampal volume relative to healthy individuals (Adriano et al., 2012). Additionally, they have been found to have reductions in non-pyramidal neurons in CA2 (Benes et al., 1998) including in parvalbumin expressing interneurons (Knable et al., 2004), interesting findings given the significance of CA2 in social memory and behavior. Major depressive disorder is also linked with both hippocampal and social dysfunction. Smaller hippocampal volume in depressed versus healthy individuals is a consistent finding (MacQueen and Frodl, 2011) and ventral hippocampus connections with the nucleus accumbens might be especially important in depressive-like behaviors in rodents (Bagot et al., 2015). Individuals with major depressive disorder also show impaired social functioning (Segrin, 2000). Autism spectrum disorder (ASD) features profound social dysfunction, characterized by an inability to regulate social interactions (Leekam, 2016) as well as hippocampal abnormalities (Amaral et al., 2008).

This review underscores this point: if the social map is instantiated in these circuits social dysfunction should accompany circuit dysfunction. Impaired tracking of dimensions such as power and affiliation might explain some of the social behavior problems observed in these disorders. There are three broad ways in which this could occur. First, map inputs could be dysfunctional. This may include information from structures like the amygdala, which shares bilateral connections with the hippocampus, is an important input region to the hippocampus in social behaviors (Felix-Ortiz and Tye, 2014) and may help drive map properties, such as saliency representation. Second, mapping processes themselves could be dysfunctional, as a result of dysfunction within the hippocampus and related structures. Social stress could induce plasticity within the CA2 to CA1 circuit and via CA1 modulation, for example, affecting both social and non-social hippocampal functions. Third, the map could be misread. Even in cases of normal mapping, downstream regions (e.g., PFC) could be impaired, leading to aberrant social decision-making. For instance, vmPFC volume predicts mentalizing capabilities and social network size (Lewis et al., 2011). Given other work showing spatial overlap between cognitive mapping and mentalizing related regions (Spreng et al., 2009), and that hippocampal measures predict social network size (Stiller and Dunbar, 2007), the interaction between these regions may be important in both healthy and unhealthy social cognition. This framework offers a basic path forward but much more work is needed to precisely delineate the ways in which neural social mapping may relate to social behavior deficits.

Conclusions

We have argued that a common set of computations underlies different types of cognitive maps and their respective forms of “navigation.” Additionally, we have claimed there is a common neurobiology that implements these computations, in regions including the hippocampal formation, retrosplenial cortex, PCC, precuneus and PFC (figure 3). These functions may reflect a multi-dimensional map of the statistical relations between environmental elements, the so-called “cognitive map”. According to this view, contextual information, from spatial to conceptual, is represented, learned and integrated into a relational memory framework, which can be searched to simulate and generate predictions about trajectories. In particular, we explored the social variant of this idea, the social cognitive map. Evidence shows that the hippocampus and related regions encode social information, such as the physical location of conspecifics, information about specific individuals, and power and affiliation in an abstract two-dimensional social space. We argued that social information is relationally mapped to generate an internal model of the social environment - the social space. This mapping may engage the same mechanisms as spatial mapping but there may be additional social computations recruited as well, within specific hippocampal cell populations (e.g., social place cells), subfields (e.g., CA2) and circuitry (e.g., CA2 to CA1). Different pieces of information (e.g., episodic memories, behavioral information) about an individual may relate to specific social coordinates within this social space. Therefore, cue-independent (i.e., across cues and cue types) activation related to an individual may reflect the concept of that individual and their mapping within the social space. Adaptively navigating social interactions might depend on this map.

Thinking about social interaction in this way allows the field to advances in several ways. For one, applying the cognitive mapping framework to social interaction gives researchers a large literature (place cells, episodic memory, etc.) from which to generate hypotheses and gather methods. The merger of social cognition with cognitive mapping is likely to generate many new testable predictions (Box 1). Relatedly, this point of view offers specific candidate neural mechanisms which may underlie social processes (e.g., social place cells), which can be explored in depth in model organisms. For human work, Tavares and colleagues (2015) generated a naturalistic, role-playing task that more closely models real-world behavior than traditional social cognitive experiments. This task captures movement through social space as social trajectories, allowing a rich exploration of dynamic social relationships. Ecologically valid experiments will be crucial to exploring complex social behaviors. The social cognitive map also provides a novel route forward for examining social deficits in clinical disorders: links may exist between dysfunctional social cognitive mapping and social behavior. Many other questions remain to be explored and while social cognitive mapping research is in its early stages, its growth is sure to provide a valuable new perspective for social cognitive neuroscience.

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This review highlights emerging work that suggests the hippocampal formation encodes relational maps in spatial, non-spatial and abstract domains. Additionally, this review argues that these functions extend to the social domain – and may include specialized social computations.

Box 1: Outstanding Issues

How do maps in different domains, such as place, time, reward and social, interact to form a “life space” and guide episodic memory encoding and behavior? On a cellular level, one possible mechanism is conjunctive encoding - cells that fire optimally to the combination of different factors and may integrate these factors into a single representation.

What are the properties of hippocampal social cells and social space mapping? Clarifying these properties can probe mechanisms of representation, integration and the domain specificity of the network’s computations. Questions include whether cell populations overlap between spatial, social and other types of cells; whether they exhibit replay and preplay; and whether they remap (an individual’s coordinates might depend upon social context, e.g., work versus an after work happy hour).

How do reference frames (i.e., mapping from the observer’s point of view, or egocentric; object to object mapping, or allocentric) play out across domains? In spatial mapping these frames can be hard to separate: for example, place and grid fields are often not simply allocentric, as they can be modulated by variables like head direction and running speed - egocentric information. It is also possible that there are separate systems for reference frames, or that the brain does not respect this reference frame distinction, and we need new ways to conceptualize reference framing in cognitive mapping.

Does system consolidation (i.e., hippocampal memories become independent of the hippocampus over time) apply to other domains? For example, it is possible that long-term information regarding an individual’s power and affiliation eventually becomes hippocampus independent.

How is within-individual social information mapped and stored? A single social coordinate could index a wide variety of information related to that specific individual. A related question concerns the neural representation of individuals within the space – how are individuals with adjacent social space coordinates discriminated despite similar locations?

How does the structure and shape of cognitive maps affect behavior and decision-making? As Tolman predicted, could “narrow” or distorted maps impair behavioral functioning and lead to aberrant decision-making? The study of psychosocial and cognitive symptoms may benefit from testing within such an explicit computational and relational framework.

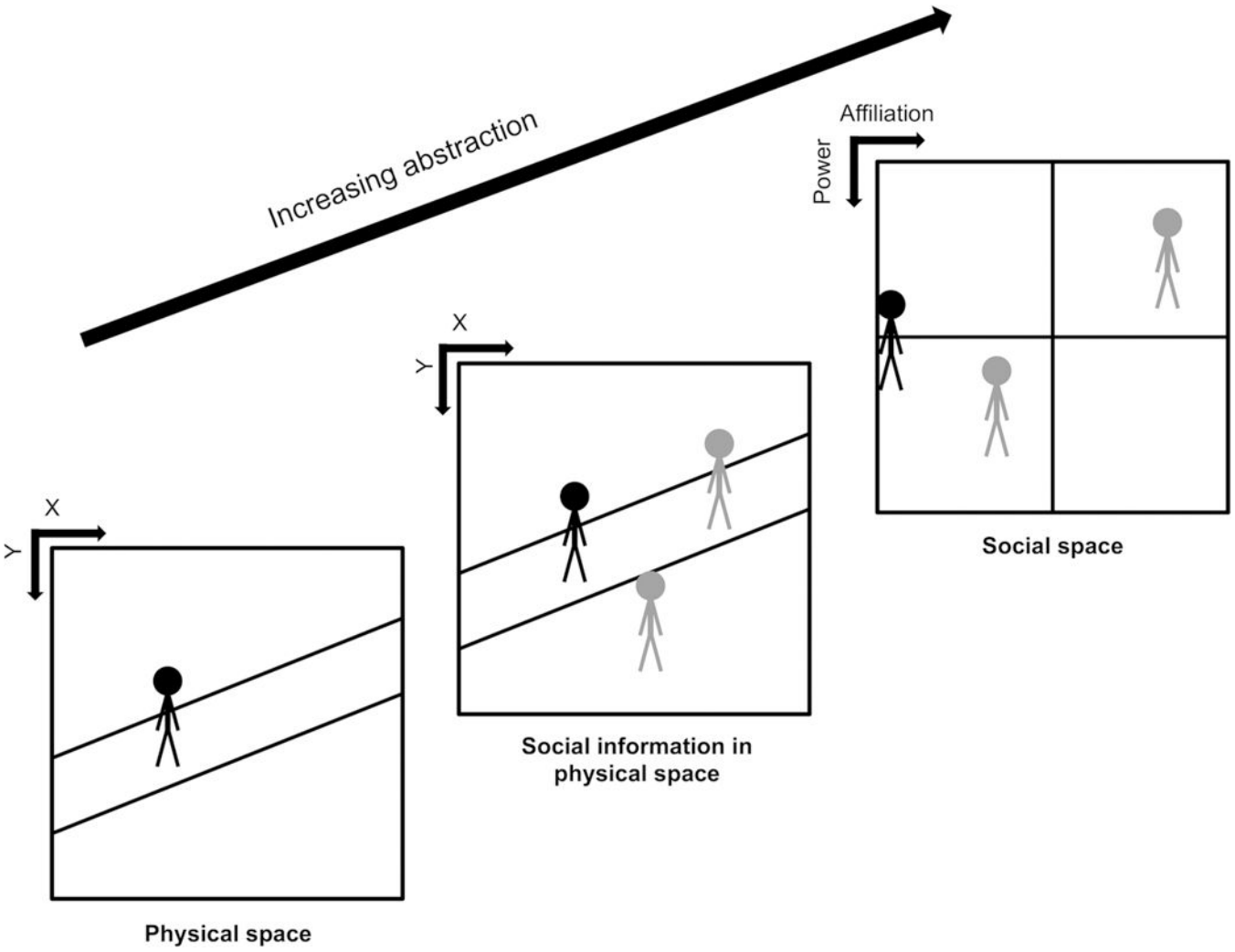


Figure 1: Increasing abstraction in cognitive mapping.

Cognitive mapping occurs at various levels of abstraction. **Physical space:** An individual's location (represented by the black stick figure) and the environmental context can be mapped. **Social information in physical space:** Abstract information within physical environments, such as the locations of conspecifics (represented in grey), can also be cognitively mapped. Other kinds of abstract information, such as reward, are also mapped in this manner. **Social space:** The social map is fully removed from the sensory details of the environment, and as such is purely abstract. The social space (relative power and affiliation of others, the grey stick figures) is referenced to the individual (black stick figure), in contrast to physical space mapping, which is referenced to the environment (see Box 1 for a brief discussion on reference frames). Evidence shows that other fully abstract spaces, such as reward and concepts are mapped as well.

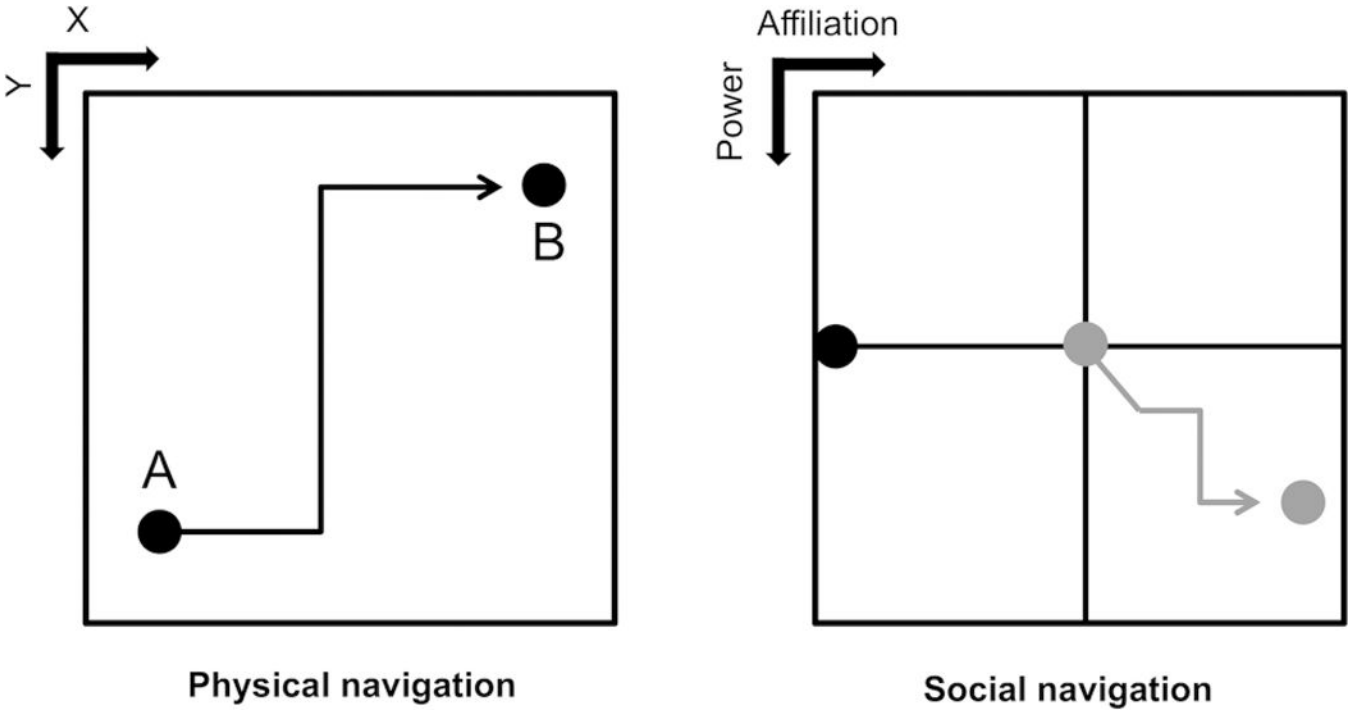
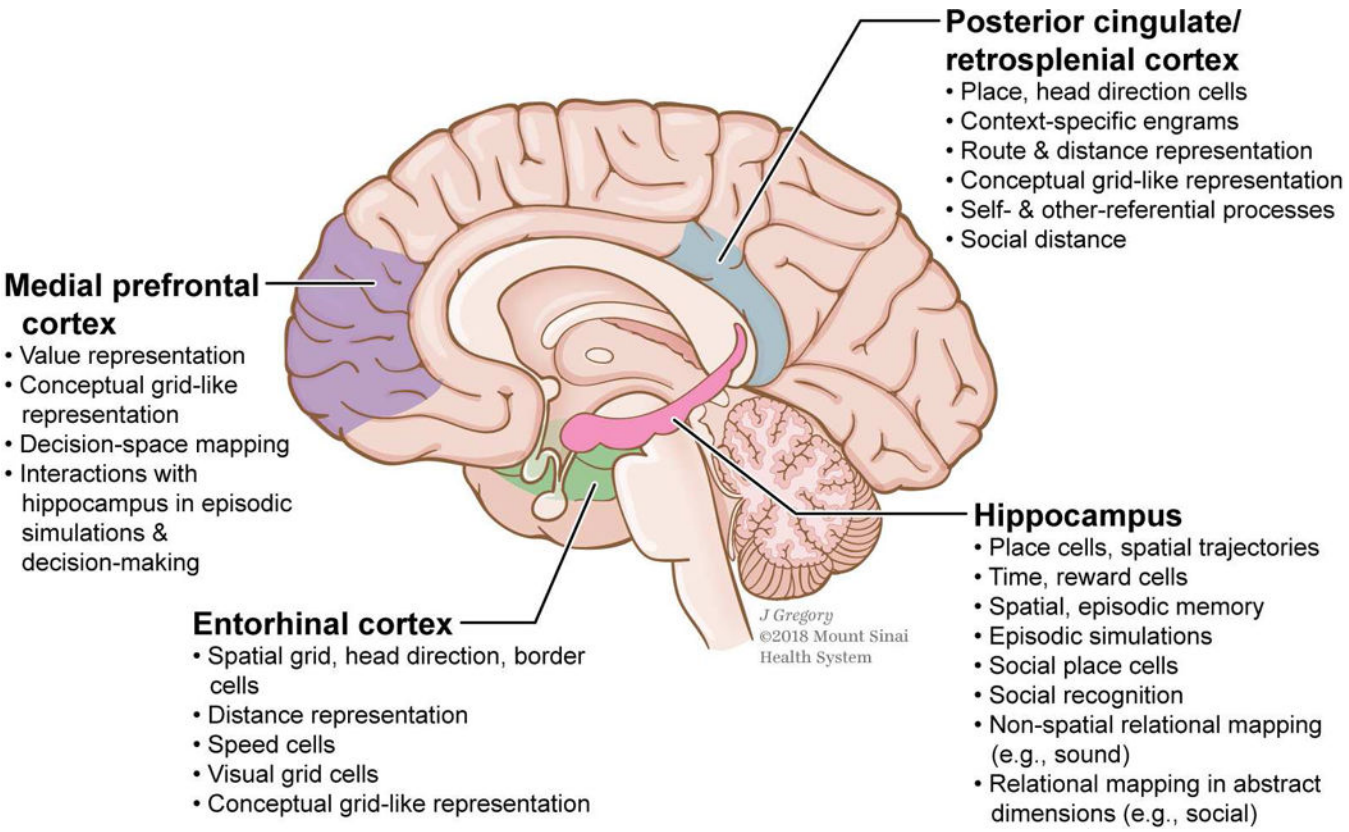


Figure 2: Navigating through space.

Facilitating navigation through physical space (left panel) is a key function of the spatial cognitive map. Information within the map can be used to simulate trajectories and their consequences, leading to an individual animal (represented by the black dot) navigating adaptively (black trajectory from A to B). Social navigation (right panel) may occur by the same mechanisms, albeit in a more abstract manner. As interactions occur, an individual (grey dot) within the social context will change in power and affiliation (grey trajectory) relative to the observer (black dot). An accurate social map facilitates adaptive social decision making as the interactions accumulate.



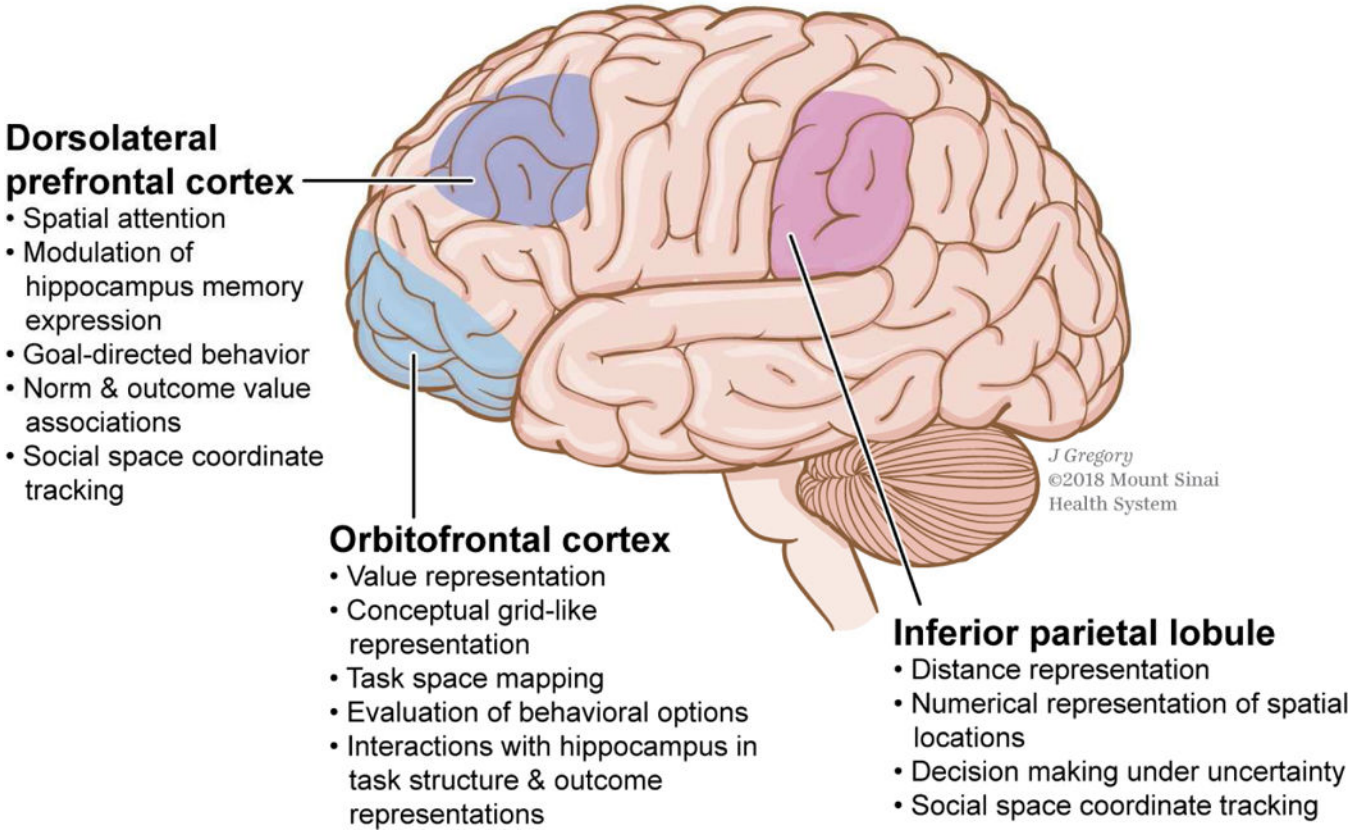


Figure 3: Visual summary of the current evidence on the neural systems mediating navigational computations in spatial, non-spatial and abstract domains.

Key regions in cognitive mapping and some of their relevant functions are highlighted. Colors indicate approximate functional distinctions.