Abstract:

The hippocampal-entorhinal (HPC-ERC) system may serve a general mechanism for navigating non-spatial cognitive maps. Here, we investigate whether this system uses the same principles to represent entities along abstract and discrete dimensions, and how the brain integrates separately learned relational structures. Participants learned ranks of individuals in two groups on two separate dimensions independently. Their knowledge about between-group relationships was limited to selected individuals called hubs, who created a unique associative path between groups. In fMRI, participants made inferences about the relative ranks of novel pairs between groups. During inferences, the ERC and ventromedial prefrontal cortex (vmPFC) encode Euclidean distances from the hub on the 2-D social space. Trial-by-trial fMRI suppression analysis revealed that HPC activity was suppressed when the novel face pair was followed by their relevant hub compared to other matched hubs, suggesting a neural reinstatement of the hub. Finally, we found a robust linear relationship between the pairwise Euclidean distance between individuals in the social network and the dissimilarity in activity patterns in the HPC, ERC, and orbitofrontal cortex (OFC). These results shed light on how abstract and discrete structures are represented, navigated, and combined in the human brain, suggesting that general mechanisms in the HPC-ERC system are leveraged to navigate discrete and abstract social networks.

Keywords: Cognitive map; Euclidean distance; Combining structures; Entorhinal cortex; Orbitofrontal cortex

Recent findings suggest the hippocampal-entorhinal (HPC-ERC) system may serve a general mechanism for navigating cognitive maps of non-spatial tasks (Behrens et al., 2018; Bellmund, Gärdenfors, Moser, & Doeller, 2018; Schiller et al., 2015). These demonstrations have used continuous task dimensions with continual sensory feedback (visual, vestibular, or auditory) (Aronov, Nevers, & Tank, 2017; Constantinescu, O’Reilly, & Behrens, 2016; Epstein, Patai, Julian, & Spiers, 2017; Kaplan & Friston, 2019; Nau, Navarro Schröder, Bellmund, & Doeller, 2018), whereas many everyday tasks involve decisions between abstract and discrete entities. Here, we test whether the human brain uses the same principles when making binary decisions about the rank of individuals in a social hierarchy, which required one to combine two pre-learned knowledge structures.

We designed a novel task that required subjects (n=27) to integrate two previously learned social hierarchies (groups 1 and 2). These were learned from binary decisions comparing people in a group who differed by one level only on one of two dimensions (competence or popularity) at a time (Fig. 1A). Crucially, subjects were never shown the 1- or 2-D structures but could construct them through transitive inferences (Fig. 1B). In each trial of the fMRI experiment, subjects made inferences about the relative rank of two individuals, one from group 1 (F1) and one from group 2 (F2), on a given dimension who had never been directly compared. To facilitate these decisions subjects could leverage previous comparisons between “hubs” and people from the other group (Fig. 1A and B). These hubs effectively created a unique associative path between groups, enabling inferences to be made about the relative position of novel pairs (Fig. 1C). We tested for behavioral and neural evidence that people retrieved these hubs and effectively navigated through them to guide their decisions.

Behaviorally, multiple linear regression indicated that choice reaction times were faster when both the 1-D distance (D) between F1 and F2 (DF1F2) was larger as well as when D and the 2-D Euclidian distance (E) to the relevant hub (DHF1 and EHF1) were larger (pFWE<0.01, Fig. 1D), demonstrating that significant additional variance in RT was captured by D and E to
These effects of \( E \) are noteworthy because there is no incentive to combine dimensions in our task; each decision should be based on either popularity or competence alone.

This behavioral evidence motivated us to search for neural evidence for each of the distance terms that drove subject decisions at the time of decisions (F2) in separate whole-brain parametric analyses (Fig. 2A). This revealed effects of each distance metric, with notable peaks in bilateral entorhinal cortex (ERC, \( p_{\text{FWE}} < 0.05 \) corrected in a small volume) and ventromedial prefrontal cortex (vmPFC, \( p_{\text{TFCE}} < 0.05 \)). To arbitrate between distance terms, we performed Bayesian Model Selection (BMS). This comparison revealed that \( E \) to the hub (\( \text{EHF}_1 \)) best accounted for variance in both ERC and vmPFC (Fig. 2B), providing evidence that these regions compute or use a Euclidean distance metric to a retrieved hub in abstract space in order to guide decisions.

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**Figure 1**

A. Participants made inferences about hierarchical relationships between a novel pair (\( F_1 \) and \( F_2 \)) in a given dimension (cue). A cover task (indicate gender) followed at the end of every trial. B. Participants learned the positions of members in each of two groups (brown and gray) separately in competence and popularity dimensions. During training, the relative rank between members of different groups was limited to highlighted people called ‘hubs’ in each dimension (e.g. red are hubs in the competence dimension), which creates a unique path per person in each dimension C. Possible trajectories for the inference of the relationship between novel pairs. The brain may encode the difference in the relevant dimension between \( F_1 \) and \( F_2 \) (\( D_{\text{F1F2}} \)) in the combined cognitive map (left); the distance in the relevant dimension from the hub that has a unique connection to \( F_2 \) (\( D_{\text{HF1}} \)) (right panel); or their Euclidean distance (\( E_{\text{HF1}} \)) within the combined cognitive map (right). D. Multiple linear regression results show that Euclidean distance from the hub (\( E_{\text{HF1}} \)) significantly explain the reaction time of inferences while competing with rank distance in the relevant dimension (D).

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**Figure 2**

A. DHF1, DF1F2, EHF1, EF1F2

B. ERC, vmPFC

C. HPC

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Having identified neural correlates of E to the hub, we next searched for evidence of a neural representation of the hub. For this aim, we capitalized on repetition suppression, but for a retrieved rather than explicitly presented representation. Specifically, directly after each decision (F2), we presented one of the 8 hubs randomly while subjects performed a cover task to indicate gender (Fig. 1A). We predicted suppressed activity when the relevant hub was presented, compared to carefully matched but irrelevant hubs (e.g. in terms of familiarity and win/loss history) in regions that reinstated the hub representation. This revealed significant suppression effects specifically in the right hippocampus (pFWE<0.05 small volume corrected over an anatomically defined HPC ROI, Fig. 2C).

Finally, we directly examined the architecture of neural representations of the combined 2-D social hierarchy. Using representational similarity analysis (RSA) (Nili et al., 2014), we examine the extent to which patterns of neural activity in the HPC-ERC system are predicted by the structure of the cognitive map representing social hierarchies. We found that, at the time of F1 and F2 presentation, people that are closer in the 2-D social space have more similar patterns of activity in anatomically defined a priori ROIs in the HPC and ERC (Fig. 3A). In addition to the HPC-ERC system, we found that the orbitofrontal cortex (OFC) showed a significant effect of E in a whole brain searchlight analysis (pTFCE<0.05). In particular, the 1-D rank distance, which is task-relevant, having partialled out the effect of E, is preferentially represented in the lateral OFC and the dorsomedial prefrontal cortex (dmPFC) (Fig. 3B). Importantly, even after partialling out the effects of D, the medial OFC, HPC, and ERC still show a neural representation that reflects distances between individuals embedded in a 2-D Euclidean space (Fig. 3C).

Taken together, these findings show that the HPC-ERC system combines two abstract dimensions, inferred from discrete choices, during decision making, even when there is no task incentive to combine the dimensions. These findings support the cognitive space theory that proposes that the HPC-ERC system provides a spatial representational format for abstract cognition such that each entity is located according to its feature values along the relevant dimensions, resulting in nearby positions for similar entities and larger distances between dissimilar stimuli. Finally, these representations may guide the vmPFC to make novel inference decisions using a cognitive map.

Figure 3

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