iNAV 2022 - Poster abstracts

1. Neighborhoods, Directions and Distances: Segmentation Effects in a Real-World City

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People often segment spaces into hierarchically structured subspaces. Judgments about inter-point distance and direction are more accurate within segments than between segments. However, segmentation may be necessary for flexible navigation, especially in complex spaces at an environmental scale. In this study, we looked at spatial segmentation in a real-life city to understand how residents of a real-world city represent its spatial structure with physical and conceptual boundaries, and how segmentation of the environment into subspaces affects spatial judgments. We asked citizens of Istanbul, a transcontinental city spread over Europe and Asia with salient spatial boundaries that are natural waterways that divide it into multiple neighborhoods, to indicate how they segment their city and to perform distance and direction estimations between well-known landmarks. We examined segmentation effects for divisions they endorsed, and for those others use but do not report using. In addition, we examined the impact of gender, age, time spent in the city, and frequency of using connecting routes and bridges between segments. We replicated basic segmentation effects for the primary division, used by all, between the European and Asian sides. For the European side, which has a geographic boundary (The Golden Horn Waterway), segmentation impaired the accuracy of spatial representation of participants. For the Asian side, where there is a potential division that is more notional, we found different effects. Individual's age, sex, time spent in the city, and frequency of using connecting routes also influenced spatial judgments. These results suggest that spatial segmentation effects exist in the real-world and segmentation in a city-scale environment is differently affected by physical and conceptual boundaries. Further, sex, age, and navigation experiences are associated with the cognitive representation of a city.

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2. Tracking navigation and spatial memory in small-scale spaces using mobile eye tracking

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The contributions of vision and body-based cues to active navigation and memory have long been researched yet their exact contributions to human spatial navigation remains unclear. In addition, navigation and memory are often studied under controlled conditions that do not capture more naturalistic, ecological navigation. The current research aimed to investigate the degree to which body-based cues can enhance memory in small real- world spaces by pairing mobile eye tracking with a navigation and memory task in which participants encoded and retrieved objects in 3D space when they were free to move. Thirty participants donned a mobile eye tracker and stood stationary for 30s to encode the layout of 8 items affixed to the walls of a 6m x 6m room. Then they were asked to either remain still while the research removed the items (stationary condition) or were guided around the room blindfolded and removed the items (walking condition). Then participants placed the items back in their original positions from either the same location as encoding (same viewpoint) or on the opposite side of the room (different viewpoint). Walking around the room to collect the items did not increase object location accuracy compared to beginning replacement in the same location as encoding, suggesting that initial viewpoint did not have a beneficial effect on encoding. Items next to immovable wall features (e.g., door handle, fire alarm) were remembered more accurately than items that were not next to the local "wall landmarks". Finally, we found a small but significant negative

correlation between placement error and total duration of fixations during encoding, showing better placement accuracy for longer total fixation duration, but there was no correlation between placement error and number of fixations during encoding. These results suggest that for small spaces, vision may be sufficient for learning the locations of a small set of items.

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3. Spatial features in human social interaction: emerging spatial patterns in academic gatherings on proximity chat platforms

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Human social interaction with peers naturally has spatial elements. We can approach people of interest or move away from others, we can turn to talk to specific people, we expect talking volume to be modulated by direction and distance and more. All of these aspects were unfortunately limited during covid lockdowns and limitations, and the video based platforms such as Zoom which became the main mode of communication do not include these features. Thus, we wanted to test the effect of spatial features in social interaction.

To do so, we compare large multi-person interactions via video based platforms which lack these features (e.g. Zoom), with platforms which offer spatial features (e.g. Gather). Specifically, we focus on the use case of poster sessions. Poster sessions, like the one you are in now, are an important part of academic conferences. They are an opportunity to present early work in a manor tailored to the individual visitor, but also serve as an opportunity to receive personal feedback, to strengthen social and collaboration networks and get a wider view of the status of the field. We organized several poster sessions of medium sized crowds (N=200-300 per session), and test: (1) users subjective preference and comparison to zoom based poster sessions (2) spatial behavior emerging during the use of these platforms. We find that users were highly enthusiastic about the platforms which included spatial features, and we show the emergence of a series of spatial behavioral patterns which exist in real world poster sessions but are missing in video-conferencing based platforms.

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4. GPS Usages and Their Relations to Spatial Ability and Scenario Familiarity

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Reliable GPS technology is a newer advancement in society – however, when it comes to studying the impact using GPS has on spatial cognition, the research is relatively limited. The present study aimed to delve into the specific ways GPS can be used in various navigational scenarios and their relations to spatial ability. Additionally, we assessed whether people modulate their use of GPS with the familiarity level of a navigation scenario. Generally, we found that using GPS more often for turn-by-turn directions was most strongly associated with lower perceived sense of direction, higher spatial anxiety, and greater overall GPS dependence. However, people use GPS most frequently for time and traffic estimation, which is assumed to augment navigation. Finally, it was generally found that as people become more familiar with an environment, the less they use GPS (regardless of perceived sense of direction levels). This provides preliminary evidence of overall intelligent GPS use in the general population, and gives direct insight as to what aspects of GPS are associated with detriments in spatial ability (i.e., functionalities that provide turn-by-turn directions).

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5. Spatial memory distortions for the shapes of walked paths occur in violation of physically experienced geometry

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An important question regards the nature of our spatial memories for the paths that we have walked and in particular how our memories for the shapes of paths might be distorted. A second question regards whether such distortions arise from competition between idiothetic (self-motion) and visual cues or some other possible mechanism. We tested humans in situations in which idiothetic and visual cues either matched or mismatched and when one cue dominated over another. Participants walked four- segment paths with 90° turns in immersive virtual reality and pointed to their start location when they arrived at the end of the path. In paths with a crossing, when the intersection was not presented, participants pointed to a novel start location suggesting a memory distortion involving non-crossed paths. In paths without a crossing, when a false intersection was presented, participants pointed to a novel start location suggesting a memory distortion involving crossed paths. In paths without crossings and without false intersections, participants showed reduced pointing error that more closely followed the physically experienced geometry. Errors were also significantly reduced for walked paths involving path integration with limited visual cues; conversely, errors were significantly increased when idiothetic cues were diminished and navigation relied primarily visual cues.

Our findings suggest that our spatial memories for walked paths sometimes involve distortions that violate the properties of the geometry of the physical world, particularly when there is competition between idiothetic and visual cues.

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6. VNT: A toolkit for virtual navigation experiments

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The advent of virtual reality (VR) technology has opened up a wide range of new possibilities in human navigation research, offering an unprecedented degree of control over the design and presentation of experimental tasks and greatly increasing the ease of data collection for experimenters.

Thanks to the availability of powerful 3D graphics engines, researchers in recent years have been able to create complex virtual worlds without the aid of external programmers and designers. Nevertheless, implementing custom virtual experiments still comes with a significant cost in development time.

Happily, several software packages have been published recently to aid in this process, utilising the free-to-use Unity3D engine. These packages, however, leave a large implementation gap when it comes to concrete requirements of navigation tasks, like managing participant interaction and creation of visual scenes.

We want to fill this gap, by creating a modular toolkit that is compatible with existing frameworks. Therefore, we designed the virtual navigation toolbox (VNT), which provides a set of independently usable components to speed up the implementation of navigation experiments using the Unity3D engine. The toolbox is under active development and has already been used successfully to run several virtual homing tasks deployed on participants' desktop computers to collect data during the pandemic.

These experiments explored the impact of path configuration and translational speed in virtual homing, as well as the effect of different degrees of visual clutter in virtual environments (Mu ller & Scherer, in prep.), and showcase the use of VNT features.

This includes our custom tools to provide 3D pointing functionality in visual scenes, dynamically create 3D environments, place landmark objects and interactive waypoints and to manage the flow of experimental trials. We thus show, how the VNT can aid in designing and running VR navigation experiments.

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7. 1/f power spectral density as a neurocognitive marker of age-related spatial memory decline

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Past research has suggested that a decrease in 1/f power spectral density (PSD) may be a useful neural signature of aging, but its significance as a functional marker of spatial cognition has not yet been investigated in detail. In this study, 43 subjects (20 to 65 years of age, mean age 38) performed a task in which they were passively driven through a virtual environment and then given a spatial memory test; their neural activity was recorded using a 32-channel EEG system. The environments and paths were varied across trials, with some environments containing local landmarks (e.g. buildings along the path), others environments containing distal (e.g. mountain) landmarks, and a control condition with only a few indistinguishable buildings and/or natural objects (e.g. trees).

Overall, the aging group (age 40-65) showed significantly lower accuracy compared to the younger (age<40) group in the local landmark condition (but not in the control condition), demonstrating that landmarks were not effectively utilized for spatial mapping in older adults. We found neural correlates of this age-related memory decline in the frontal-midline channels: Consistent with previous studies, a flatter 1/f PSD (i.e., decreased low frequency power and increased high frequency broadband power) was observed in the aging group widely across the scalp. More importantly, a flatter 1/f PSD in the frontal-midline channels was associated with worse spatial memory in the local landmark condition, even after accounting for general effects of age, implicating that a flattened frontal 1/f PSD may be an informative marker of navigation-specific decline in cognitive function. This effect was not observed in younger subjects (<40 years).

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8. Changes in Spatial Exploration Patterns in Early Aging are Associated with Declines in Spatial Memory

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Studies investigating how spatial navigation changes with healthy aging have in large part only studied how individuals use their spatial memory to navigate a learned environment, but have not investigated the navigation patterns individuals exhibit as they explore and learn novel environments. Hence the extent to which spatial exploration patterns may be altered in healthy aging is at present poorly understood. The aim of this study is to investigate how spatial exploration behavior is altered in healthy midlife adults, and to what extent these alterations may mediate age-related declines in their spatial memory. 51 healthy young adults (ages 18-28) and 109 healthy midlife adults (ages 43-61) underwent a maze learning task using desktop virtual reality. In the exploration phase, participants freely explored the maze using button presses on a keyboard and learned the locations of 9 target objects. Here, we measured the number of button press moves, total distance traveled, number of object visits, evenness of exploration, and pause duration. In the test phase, participants were placed at a target object and instructed to navigate to other target objects within a given timeframe. Here, navigation accuracy (i.e., % of correct trials) was measured. We found that midlife adults made less button press moves ($p = 0.03$), travelled less distance ($p = 0.01$), visited target objects more often ($p < 0.001$), had less even exploration ($p < 0.001$), had longer pause durations ($p < 0.001$), and had less navigation accuracy ($p < 0.001$) when compared to the young. We also found that the number of target object visits during exploration mediated the age-related differences in navigation accuracy. The results of this study will enhance our understanding of how spatial navigation declines in healthy aging, as well as provide a platform for future studies to investigate whether altered spatial exploration behavior could be a cognitive marker for AD.

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9. Age-related navigation impairments are moderated by testing modality

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Spatial navigation declines during healthy aging and is exacerbated by age- related neurodegenerative disorders, such as Alzheimer’s disease. The few studies in humans that have looked at age-related changes in spatial navigation have often relied on experimental paradigms that restrict locomotion, such as in desktop virtual reality, limiting ecological validity. Moreover, desktop-based navigation tasks that require keyboard/joystick responses to navigate are confounded by cross-sectional differences in prior gaming experience. In the present study, cognitively healthy young (N=20) and older (N=18) adults navigated a virtual variant of the Morris water maze task to learn the location of hidden targets in each of two conditions: a desktop-based condition requiring a keyboard/mouse to navigate and a fully immersive virtual reality (VR) condition that permitted free ambulation. Following a learning phase, participants were tested on their immediate and delayed recall of the hidden target locations. Memory was operationalized as the Euclidean distance between the remembered and actual target locations (i.e., distance error). Immediate and delayed recall for spatial locations were significantly impaired in older adults relative to younger individuals. Moreover, a significant age x condition interaction indicated that the effect of age on spatial memory was exaggerated when navigating a desktop-based virtual environment compared to the unrestricted immersive VR condition. These results are consistent with the hypothesis that the effect of age on spatial navigation is modified by availability and integration of visual and self-motion cues. Reconciling how older navigators integrate multisensory cues is critical for understanding the biological significance of findings from navigation paradigms that restrict self-motion and body-based feedback.

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10. Characterising sources of path integration errors in healthy older adults and those with subjective cognitive decline

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Path integration deficits are apparent in healthy older adults and Alzheimer’s disease (AD) patients. Yet, it remains unclear which specific aspects of the path integration process are most affected and whether these processes are differentially affected in older adults and those with AD. Here, we used immersive virtual reality to characterise path integration deficits in healthy older adults and those with subjective cognitive decline (SCD). During the task participants had access to multisensory self-motion cues (visual, vestibular and proprioceptive) as they were immersed in an open- field virtual environment and guided along short, curved paths. At certain points participants were asked to stop and indicate their initial heading orientation and start location. Preliminary analysis shows that path integration errors increase over the course of the walked trajectories. Interestingly, this increase was larger in the SCD group compared to healthy older controls. Similarly, errors for initial heading orientation estimates increased over the course of the walked trajectories, with a trend for a larger increase in errors in the SCD group. To characterise the sources of the observed errors we used a computational model that allows us to decompose different parameters that contribute to the observed path and angular integration errors. For SCD group, distal velocity estimates predicted path integration error, whilst for older controls, distal velocity estimates, memory leak and accumulating random noise were all predictive of path integration error. For orientation errors, accumulating angular noise was a single predictor for healthy older adults, whilst for SCD group angular velocity estimates, memory leak and accumulating angular noise predicted angular integration errors. The results are discussed with reference to different mechanisms contributing to path integration deficits in healthy older adults and in older adults with SCD.

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11. Multicentric tracking in human cingulate cortex and frontopolar cortex during navigation towards a dynamic goal

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The ability to navigate efficiently allows one to explore the world in a way underappreciated unless this ability is suddenly lost, such as in the onset of Alzheimer’s Dementia. This ability requires integration across several brain areas, yet can be reduced to a relatively simple process one typically does numerous times on an average day (Goodroe et al., 2018). Despite the presence of robust evidence towards map-like behavior, work is limited where realistic navigational flexibility is concerned. Specifically, the neural mechanisms supporting shortcutting behavior and flexible adaptation to detours within one’s environment. Lastly, some recent evidence from work with primates suggests a role for anterior cingulate in multicentric tracking (Goodroe & Spiers, 2022; Yoo et al., 2021). To observe flexible navigation behavior in a similar framework with humans, we tested 22 participants in a virtual environment made up of 16 interconnecting rooms with either impassable or passable connections. The goal on each trial was to ‘catch’ a reward object that moves probabilistically within the environment. In addition, participants were aided in this task by a virtual companion in order to compare tracking of this agent against tracking of the goal. We find evidence consistent with the proposed role of cingulate cortex and frontopolar prefrontal cortex in reward based decision making as well as multicentric tracking in spatial navigation. Additionally, we find tracking of trial path distance in dorsolateral prefrontal cortex as well as frontopolar prefrontal cortex, middle cingulate cortex, and caudate / nucleus accumbens with an increase in activation correlated with longer distances, suggesting moderation of planning complexity. Additionally, we find new evidence for multicentric tracking [egocentric] in the human [middle] cingulate cortex and dorsomedial prefrontal cortex with activity in these regions tracking Euclidean distance to a non-goal agent (the companion).

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12. One-shot learning and goal representations during flexible navigation

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Mammals are capable of solving challenging navigation tasks using remarkable behavioural flexibility (Gahnstrom & Spiers, 2020); however, the mechanisms by which they are able to efficiently solve such tasks are unclear. We investigate human trajectory behaviour and fMRI BOLD responses during navigation to hidden goal locations in a constantly changing maze environment. We hypothesise that humans learn and update goal-related information, including path distance to goal for efficient navigation. Our task is based on a rodent experiment with a similar paradigm (Pfeiffer & Foster, 2013) and implemented in a virtual desktop environment. In contrast to the original task, we added impassable barriers in order to maximally separate goal parameters including euclidean and optimal path distances to goal. Each trial alternated between random exploration and goal-directed navigation. Participants quickly converged their navigation trajectories toward optimal path trajectories and were able to rapidly learn and relearn new hidden goal locations after a single trial. We identified a network of brain regions involved in updating these hidden goal locations including bilateral hippocampus, lateral orbitofrontal cortex (OFC), bilateral caudate nucleus, dorsal cingulate cortex, and dorsomedial prefrontal cortex. Recent work suggests the caudate nucleus is involved in representing the transition structure, or the action-outcome associations, of a task (Sharpe et al., 2019; Javadi, Patai et al., 2019). We report evidence consistent with this theory as the caudate nucleus BOLD responses were parametrically modulated by Euclidean distance to goal during active navigation in our task. Before onset of navigation, optimal path distance to goal was positively correlated with bilateral hippocampal activation, a finding consistent with BOLD response during navigation of a previously learned London street network using real-world video stimuli (Howard et al., 2014).

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13. Neural correlates of strategy shifts in navigation behavior

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Deficits in spatial navigation can negatively affect quality of life. For example, people who tend to make more navigation errors also report higher levels of spatial anxiety (Hund & Minarik, 2006). Spatial navigation shifts have largely been linked to hippocampal activation. While much of the research on navigation strategies has focused on the hippocampus, it has neglected other neural mechanisms that could account for deficits in flexible navigation. Here, we take a closer look at the caudate nucleus – an area of the brain that remains relatively intact during aging – to disentangle navigation success from changes in navigation strategy. To test the neural mechanisms involved in flexible navigation strategies, participants first viewed videos of navigation through a maze containing various objects while lying in an MRI scanner. Outside of the scanner, they were placed in the location of one object and were asked to navigate to another object in a virtual environment (DSP; Marchette et al., 2011). We will present results from this study examining the relationships between individual differences in navigation strategy and hippocampal and caudate activation during a navigation task. Findings from this study will provide a better understanding of behavioral shifts in navigation strategy and their associated neural mechanisms. They will also provide new insights for intervention and training.

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14. The Temple Tour: Neural coding of episodic and spatial representations in young adults

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Navigation and episodic memory are two fundamental cognitive processes that guide mature decision-making. Conceptually, they are linked by reliance on accurate retrieval of spatial and temporal context and accurate integration of different types of information. However, the extent and nature of interdependence at behavioral and neural levels is unclear, with some recent evidence suggesting they are mechanistically distinct. In this study, we investigate how spatial navigation and episodic memory relate to each other behaviorally and how they are represented in the medial temporal lobe in young adults. We developed a real-world tour task in which adults (18-30 years) took a guided walk through a novel environment and encoded sixteen distinct events. Next, they experienced a second encoding event in a testing room that was episodically rich but devoid of a spatial component. We assessed knowledge of the environment (only tour encoding) and episodic recollection of the events (both tour and room). On the second day, participants received an fMRI scan while viewing images of the tour and room objects, along with brand new objects. In ongoing analyses, we will isolate areas of BOLD activation and contrast neural representations of the tour, room, and new objects, evaluating differences in neural representation of the spatialized components (tour v room) and episodic components (room v new). We will present neural data from a full adult sample (N=40). These data will elucidate the neural coding underlying the spatial and episodic memory systems and tease apart how they are similar and different.

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15. Virtual visual navigation during context-dependent learning in the human hippocampus using intracranial recordings (SEEG)

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The hippocampal cognitive map can reflect spatial and nonspatial task conditions by binding relevant aspects of experiences within a context. Sharp Wave Ripples (SWRs) are known as the most synchronous neural pattern during memory consolidation. Using a visual context associative learning paradigm, we look for the temporal relationship between the incidence of hippocampal SWRs and collected targets across trials. This study investigates how activity in the human hippocampus changes according to different contextual conditions in the same space. We anticipate that learning the task will increase the likelihood of detecting these task-related activities.

Participants were implanted with depth intracranial electrodes using StereoElectroEncephaloGraphy (SEEG) for preoperative evaluation. Participants navigated the circular maze's boundaries while collecting treasure boxes and earning points. Contextual information was displayed on the maze walls and then coloured targets were displayed in the decision zone after leaving the navigation zone. We developed our algorithm for detecting SWRs and synchronized it with a behavioural state-space model.

The initial learning trial is defined as when 0.99% of the performance was correct. We determined that the rate of SWRs is significantly higher compared to the baseline activity after that. The SWR rate increased during learning across four implanted electrodes in the right and left hippocampus. When the player reached 30% of the task's total duration, the rate of ripples was at its highest. The rate of normalized events was about 10 times greater for the significant change in incorrect vs correct trials.

Preliminary findings from one patient recording indicate that the rate of SWRs increases as learning occurs. Two specific increases in SWRs were detected in both successful and unsuccessful trials.

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16. Navigation and mental replay involve different frequencies of theta oscillations

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Theta oscillations, semi-periodic fluctuations in the local field potential of the hippocampus, play an important role in supporting spatial learning in humans. Both theta power and frequency increase with increasing movement speed although the functional significance of this effect remains unclear. A separate line of research has shown that hippocampal theta oscillations also contribute to episodic memory and relate to successful encoding of memories. Yet, these two areas of research remain poorly connected and how imagination as part of episodic memory relates to navigation remains unclear. To address this issue, patients with implanted intracranial electrodes navigated specific routes and then imagined the route that they had just navigated in vivid detail. Consistent with past work, we found a significant correlation between navigation and replay duration, suggesting that the route replay related to the route just navigated, although replay occurred at faster rate than navigation. Electrophysiologically, we found significant increases in theta power in the range of 8 – 14 Hz during replay compared to both movement and standing still during navigation. We used the extended Better OSCillation detection toolbox (eBOSC) to compare the frequency specific amplitude and duration profiles during navigation and replay. The prevalence of oscillatory events in the low theta frequencies (2-4Hz) was significantly greater during navigation than during replay while the prevalence of oscillatory events in the high theta frequencies (8-11Hz) was significantly higher during replay than during navigation. Given previously demonstrated correlations between speed and theta power/frequency, our findings suggest that replay likely involves recapitulation of learned routes but at a faster rate neurally than during navigation. Our findings also imply that part of episodic memory may involve replay of memories but at a compressed rate to which they were originally experienced.

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17. Successful memory retrieval modulates spatial maps in the medial temporal lobe of freely ambulating humans

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Experimental studies across species have highlighted the important role that medial temporal lobe (MTL) structures play in encoding and retrieving memories and supporting spatial navigation. However, until

recently, memory and spatial navigation studies in humans have been constrained by immobile neuroimaging methods. Here, we investigate how the MTL supports memory and spatial navigation in freely ambulating humans. Our lab has developed a platform to wirelessly record intracranial electroencephalography (iEEG) from the MTL of individuals chronically implanted with depth electrodes, while they complete mobile navigational memory tasks presented in virtual reality (VR) on a head-mounted display, a critical advance that allows for probing human cognition during behavioral constructs with high ecological validity. In this study, participants learned to retrieve the locations of multiple distinctly positioned- and colored- visual cues (cylindrical translucent halos) over the course of repetitive encoding and retrieval trials.

We found that theta power (6-9Hz) was elevated as participants approached a previously learned halo position, but only on correctly remembered trials. MTL theta spatial maps of the environment reflected previously learned halo locations during task phases when halos were not visible. The spatial map was modulated by successful vs. unsuccessful memory retrieval. Furthermore, theta power was elevated in the 500ms preceding successful memory retrieval relative to unsuccessful memory retrieval across participants. In addition, theta-gamma phase amplitude coupling was present during memory retrieval, when halos were not visible and the frequency of gamma to which theta was coupled shifted higher during successful retrieval.

Together, our results present one of the first examples of how theta and gamma oscillations in the MTL support correct memory recall in freely navigating humans.

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18. Saccadic modulation of human medial temporal lobe oscillatory activity during real-world spatial navigation

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Humans perform saccadic eye movements to explore their environment. Previous studies have shown that theta (~5-8 Hz) oscillatory activity in the medial temporal lobe (MTL) supports spatial navigation and memory in computer-based laboratory studies. However, the relationship between human MTL theta activity, spatial navigation, memory, and visual exploration in the real-world is unclear. In this study, we recorded intracranial electroencephalography (iEEG) data from five participants while they physically explored a real-world environment. During a self- navigation task, participants walked to and learned a hidden target location in the room. In a stationary observation task, participants sat in a corner of

the room and observed another person navigate, and pressed a button

whenever the other person crossed one of the previously-learned hidden target locations. MTL theta activity (5-8Hz) was significantly higher during saccadic eye movements versus fixations during both self-navigation and observation tasks. Prevalence of MTL theta oscillatory bouts also occurred slightly more frequently during saccades versus fixations. During self- navigation, participants alternated between two different cognitive states:

19. Mechanisms of spatial navigation in the Hippocampus of the common marmoset

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The hippocampus is a specialization of the mammalian brain that plays an important role in spatial navigation. Most of our knowledge of the hippocampus physiology comes from studies in freely navigating nocturnal surface dwellers such as mice and rats. Studies in freely 3D navigating primates with sensory adaptations to a diurnal lifestyle are scarce. Here we test the hypothesis that a diurnal primate with high resolution foveal stereo- color vision, the common marmoset, uses visual navigation to explore the environment, and that such strategy has shaped the mechanisms enabling spatial navigation in the hippocampus. We show that during foraging marmosets navigate the environment through alternations of full body displacements and stops. During stops, marmosets navigate the environment visually, through rapid head-gaze shifts, which allows exploiting their far sensing capabilities (e.g., vision) to build cognitive maps of the environment without visiting locations and landmarks. On the other hand, during foraging rats predominantly use body displacements to visit locations and landmarks, which allows exploiting their near sensing capabilities (e.g., whiskers). In the marmoset hippocampus CA3 and CA1 regions, neurons were predominantly selective for head-view orientation, rather than spatial location or place as commonly found in the rat. Moreover, most of narrow spiking interneurons in marmosets were tuned to head angular speed rather than to body speed as in rats. Finally, theta oscillations were considerably less frequent during locomotion in marmosets than in rats, and were rather coupled to rapid head-gaze shifts (head phase resetting). Our results demonstrate that the mechanism of spatial navigation in the common marmoset hippocampus have evolved relative to those documented in rodents such as rats and mice, likely reflecting evolutionary adaptations to diurnal life styles.

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20. A place with a view: parietal and hippocampal neuronal activities during virtual navigation in the macaque

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Can place be inferred from visual input? In the posterior parietal cortex (PPC), regions from the lateral and ventral intraparietal sulcus play a role in visuo-motor processing by controlling eye movements to salient cues and inferring motion perception of the self or objects. Here we asked whether neural activity in the PPC encodes self-position in a virtual reality environment, and how this activity ties to saccades and fixations of salient cues of this environment during navigation. We further compare PPC activity to that of hippocampus recorded in the rhesus macaque to understand computations performed in the two regions, that are separated by two synapses. Via unsupervised clustering analysis, we showed that position-related activity grouped parietal neurons into clusters that partition the maze into task-specific segments more strongly than hippocampal neurons. We showed that clustering in the parietal cortex was not directly explained by saccade-induced response per se, but rather by the actual visual context in the maze. When expressing neurons firing rates as a function of monkeys' eye position in the panoramic scene, PPC appeared to be more strongly modulated when landmarks were at a precise position on the retina, while hippocampus was rather sensitive to their presence in the field of view, independently of fine eye positions. Cells could thus be classified as "landmark" or as "periphery" cells, depending on if they responded to the direct gazing of landmarks or to their position at the periphery of the field of view. Those two populations displayed different temporal dynamics, taking part respectively in the acquisition of stimuli, and in their anticipation. Overall, the results identify the nature of sensory context driving the recruitment of parietal cortex during active navigation, and how this translate in codes for position, through a task-based processing of the visual cues, hence shedding light on the neural processes linking place and view.

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21. A brainstem integrator for self-location memory and positional homeostasis

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To track and control self-location, animals integrate their movements through space. While self-location is represented in the hippocampal formation, it is unknown how such representations arise from integrated self-motion, whether they exist in more ancient brain regions, and by what pathways they control locomotion. Fish can be carried by water currents to potentially dangerous areas; here we report that larval zebrafish track their displacements to later return to previous locations. Whole-brain functional imaging revealed the circuit enabling this 'positional homeostasis'. A newly identified brainstem positional integrator stores a memory of past displacements and induces an error signal in the inferior olive, which controls future corrective swimming. Optogenetically manipulating functionally-identified integrator cells evokes displacement-memory behavior; ablating them, or downstream olivary cells, abolishes positional homeostasis. These results reveal a multiregional hindbrain circuit in vertebrates for integration of self-motion, memory of self-location, and control of locomotor behavior.

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22. How the insect central complex could coordinate multimodal navigation Xuelong Sun(1,2); Shigang Yue(2); Michael Mangan(3);

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The central complex of the insect midbrain is thought to coordinate insect guidance strategies. Computational models can account for specific behaviours but their applicability across sensory and task domains remains untested. Here we assess the capacity of our unified insect navigation model to generalise to olfactory navigation and its coordination with other guidance in flies and ants. We show that fundamental to this capacity is the use of a biologically-plausible neural copy-and-shift mechanism that ensures sensory information is presented in a format compatible with the insect steering circuit regardless of its source. Moreover, the same mechanism is shown to allow the transfer cues from unstable/egocentric to stable/geocentric frames of reference providing a first account of the mechanism by which foraging insects robustly recover from environmental disturbances. We propose that these circuits can be flexibly repurposed by different insect navigators to address their unique ecological needs.

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23. A recurrent neural network model of travel direction in humans

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Maintaining a representation of travel direction is crucial to the formation of travel trajectory. However, how travel direction is represented in the human brain is still unknown. Recently we reported motion aftereffects of the travel direction in a series of psychophysics studies, suggesting a behavioral signature of travel direction signals in humans that is independent of head direction (Cheng, Ling, Stern, Huang, & Chrastil (submitted)). The discovered travel aftereffects were in the opposite direction of traditional motion aftereffects reported in low-level vision, which raises a question: how does the travel direction system work in the human brain such that it demonstrates this unique adaptation property? We suggest that the representation of global travel direction in the human brain may be supported by a recurrent neural network. We developed an echo state network model to test this hypothesis. The model was able to successfully simulate experimental findings by showing separate trajectories for the experimental adaptation condition and the control condition. The model was also able to qualitatively reproduce travel aftereffects that were modulated by remote cues and scaled with adaptation duration, as observed in the behavioral study. Perturbations demonstrate that the key features of the model are driving the findings, rather than artifacts from other components of the model. Moreover, model comparison suggests that understanding the relationship between initial adaptation and top-up adaptation trials might be essential in predicting travel aftereffects. This is the first computational model of travel direction in humans and it suggests a biologically plausible mechanism for how tracking this information could be implemented in the human brain.

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24. Servomechanisms working with oscillators: ubiquitous in navigation and orientation

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In navigation, ants oscillate as they walk. Not only do their six legs work as teams of coupled oscillators, but the insects also zigzag left-right in transverse oscillations. Navigational servomechanisms adjust oscillators according to sensory input, adjusting their amplitude and frequency. This theme of servomechanisms working with oscillators is found ubiquitously in animals, such as the roundworm Caenorhabditis elegans and Drosophila larvae. In both these well-studied animals, transverse oscillations provide crucial material for servomechanistic course control. This theme of servomechanisms working with oscillators even applies to single-celled organisms, both eukaryotes and prokaryotes, if the notion of oscillators is defined broadly. In these tiny lifeforms, however, servomechanisms work primarily to interrupt the forward movement driven by oscillating systems, with the rate of interruption responsive to sensory input, a form of orientation called kinesis. When the going is good, the rate of interruptions is lowered; when the going is not getting better, the rate of interruptions is increased. Oscillations are also found in other domains of cognition. Oscillators provide effective ways of organising an organism's own behaviour, while servomechanisms help an organism to adjust to the environment, including the environment within its body. These points may explain their ubiquity in life.

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25. Place-grid cells dynamic coupling enables error minimization for path integration

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Navigation is one of the most fundamental animal skills. Grid cells (GCs) in the medial entorhinal cortex (MEC) use speed and direction to map the environment during spatial navigation. In turn, hippocampal place cells (PCs) encode place and seem to minimize the accumulated error of GCs for path integration. Despite PCs and GCs being part of a generalized path integration system, the dynamic relationship between both cell types and the involved mechanism for error minimization is yet to be understood. Recent theoretical studies have suggested the possibility of a network of loops between the Hippocampus and MEC. We hypothesized that the dynamical coupling between these cell types could coordinate the integration of velocity input to the GCs network and update the network's estimated position using PC network signals. A realistic toroidal topology model of GCs was implemented based on path integration to address this issue. The grid network received velocity information of a simulated animal and PCs' information through their place fields (PFs). Place cell-like neurons were modeled by defining their PFs through visual flow detection and proximity information during the animal's exploration of a squared arena. PCs were activated by the information from GCs with a similar spatial phase but a diverse spacing and orientation. PFs appeared mostly during early exploration, helping to decrease the path integration error of GCs. PFs closer to the animal's current location contributed more to minimizing the error accumulation than distal PFs. Relatively slow-emergent PCs enabled anchoring signals for a precise GCs path integration. Consistent with our experimental observations that place cells can retrieve spatial information from grid-like cells to create a more accurate spatial representation, the dynamic coupling between PCs and GCs may be one of the key components of the brain's navigational system.

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26. Graph properties influence route selection for equidistant paths

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The idea of cognitive maps – accurate mental representations of space that transcend stimulus-response behaviors – has existed for 70+ years. Although often thought to be metrically precise replications of physical Euclidean space, studies demonstrating cognition and behavior that violates Euclidean rules have received renewed attention. Some researchers now advocate that spatial knowledge may be better described by labelled graphs, in which landmarks (nodes) are connected by paths (edges) and loosely constrained through the inclusion of some local metric detail. However, direct tests for the existence of cognitive graphs have mostly relied on virtual environments that simulate violations of Euclidean space. Here, we developed a 2- alternative force choice navigational decision-making task to test the influence of graph-like spatial properties (total turns) on route preference in physically plausible virtual environments with equal metric properties. We hypothesized that routes with fewer turns would be favored, suggesting a graph-based preference. Participants learned rectangular environments with three main paths: one on the right side, one on the left, and one in the middle. During test, the middle hallway was blocked, and participants had to use either the right or the left path to reach a goal on the other side. Several environments were learned, each with the number of turns differing between left and right paths. Crucially, the length of the two paths was equivalent in each environment. Logistic regression revealed that participants displayed a tendency toward selecting routes with fewer turns, but this was attenuated by individuals who chose randomly or were biased to choosing either left or right. We explored some of the sources of these individual differences. These findings elucidate the role of non-metric spatial properties in navigation and decision-making; results may be extended to other fields such as civil engineering.

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27. The Intersection of Space and Time in Navigation and Episodic Memory

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The ability to successfully navigate through an environment is an instrumental skill needed for our everyday experiences. An integral component of successful navigation includes the ability to integrate both spatial and temporal information in order to form memories of our spatial environments. How space, time, and episodic memory relate, however, remains unclear; additionally, how the presence of immersive body-based cues impacts the encoding of these variables remains unresolved. To address these issues, participants navigated a large-scale virtual environment containing roads and rich visual cues. Subjects were randomly assigned to one of two conditions, an immersive condition in which they navigated by walking on an omnidirectional treadmill and a stationary condition in which they navigated with a joystick. Following navigation, subjects completed a temporal reproduction task, a judgment of relative direction task, and verbal episodic memory recall. These verbal responses were recorded and scored using a method that allowed us to determine the richness of episodic memories. Our preliminary findings suggest that participants optimized their paths more rapidly in the immersive compared to the stationary condition. In contrast, temporal

reproduction error was numerically higher in the immersive compared to the stationary condition. These findings suggest a dissociation between spatial and temporal judgments based on the availability of body-based cues in the environment. Future analyses will consider how verbal episodic memories relate to space and time.

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28. Effect of optic flow on spatial updating: insight from an immersive virtual reality study

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Self-motion information is required to keep track of where we are with respect to our immediate surroundings (spatial updating). Visual information, such as the optic flow, is essential to provide information about self-motion, especially in the absence of vestibular and/or proprioceptive cues generated by physical movement. However, the role of optic flow on spatial updating is still debated. A Virtual Reality system based on a Head Mounted Display (HMD) was used to allow participants to experience a realistic sensation of self-motion within a naturalistic environment in the absence of proprioceptive and vestibular information. We asked participants to keep track of the spatial position of a target during simulated self-motion. Crucially, we manipulated the availability of optic flow coming from the lower part of the environment (ground plane), which is known to provide information about self-motion. In each trial, the ground could be a green lawn (optic flow ON) or covered in snow (optic flow OFF). We observed that the ability to update spatial locations is particularly impaired in the OFF condition as compared to ON condition, indicating that the lack of optic flow on the ground plane had a detrimental effect on spatial updating. The interaction between the optic flow availability and different characteristics of self-motion, such as speed (10, 20, 30 Km/h), direction (leftward, forward, rightward), and path (translational and curvilinear) was also considered. We observed that the velocity of self-motion (but not the direction and the path) affected the spatial updating performance, especially in the absence of optic flow. Overall, these results demonstrated that, in the absence of other idiothetic cues, the optic flow information provided by the ground plane has a dominant role for the estimation of self-motion and, hence, for the ability to update the spatial relationships between one's position and the position of the surrounding objects.

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29. Why do you get lost?: A T-maze spatial navigation study in humans

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In this study, we assessed how people learn to navigate through a virtual T- Maze arena, and evaluate whether varying landmark distances to the goal location (a Wi-Fi hotspot) affects learning about global boundary information. Additionally, we considered other factors that may modulate competition in human spatial performance. Namely, starting-point locations and the amount of training trials. In Experiment 1, three groups experienced a landmark placed at varying distances from the goal (Proximal, Middle, Distal) and the Control group was trained in the absence of any landmarks. Importantly, all groups were released from a fixed start location during the training phase. The global representation of the arena was tested immediately

after and the results showed competition between boundary and landmark representations in the Proximal group, but not in the others. In Experiment 2, groups and conditions were similar, but participants' starting-point location was changed from trial to trial. Competition was not observed in any of the groups. In Experiment 3, we reproduced Experiment 1 but with shorter training (3 trials rather than 15), competition was no longer observed in the Proximal group.

Our results show that the global representation of the environment was acquired early in training (Experiment 3), but this memory was hindered by extended training in Experiment 1 only in the Proximal group. These results suggest that landmarks proximal to the goal location support the use of egocentric strategies which compete with the use of a global representation of the environment. Overall, these results reveal that humans flexibly use different spatial representations during navigation.

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30. The influence of environmental complexity on the mechanisms of multi- guidance in human navigation

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Humans navigate by combining multiple guidance systems, however, the mechanisms and factors influencing their combination are still poorly understood. Two important strategies used by humans to return to a previously visited location ("homing") are path integration and landmark guidance. For path integration, humans use body-based, idiothetic cues to track walked distances and angles. In landmark guidance, environment- based, allothetic cues are used for orientation and place recognition. This study aims at understanding the influence of environmental complexity on the combination of path integration and landmark guidance.

A classic experimental setup to test homing and path integration in humans is a triangle completion task, in which participants are guided away from a home location via two sides of a triangle, and asked to return straight home from the endpoint of this displacement. We used a triangle completion task in a virtual environment, remotely presented as a video game on participants' computers, in which environmental complexity was varied from bare to cluttered landscapes by the number of available landmarks. We find that homing precision and accuracy are highest with three landmarks and decrease when more or less landmarks are available. We also observe that inter-individual differences affect navigation performance considerably. Therefore, we quantify individual biases in triangle completion tasks. Our findings highlight the difficulty to home in bare environments and propose individual biases to be an important factor in human navigation. We emphasise the importance of considering individuality when interpreting results of similar former and future navigation studies.

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31. How curiosity guides spatial exploration in humans

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A large literature on hippocampus-dependent navigation has shown that active exploration of novel environments is key to building cognitive maps in non-human animals and humans. Early influential theories have highlighted curiosity as one of the primary drivers of exploratory behaviour across the animal kingdom, and therefore might be central to the formation of cognitive maps across both spatial and conceptual domains. Despite this, the relationship between curiosity (and particularly states of curiosity) and human spatial exploration is unknown. A better understanding of the relationship between curiosity and exploration has the potential to reveal new insights into how humans learn and navigate novel environments, as well as inform the design of better spaces attuned to human exploratory behaviour. To address how curiosity affects human spatial exploration, we designed a novel virtual reality (VR) paradigm in which participants rated their curiosity before exploring a range of novel rooms (i.e., pre-room curiosity). After exploring each room, participants rated how interesting they found the novel room (i.e., post-room interest). Informed by real-world studies of human exploration, as well as evidence in nonhuman species, we indexed the complexity of exploratory behaviour using roaming entropy for both spatial and head-direction movement. Our findings revealed a double dissociation, whereby pre-room curiosity was associated with the magnitude of path roaming entropy (i.e., spatial exploration), and post-room interest was associated with the magnitude of head-direction roaming entropy (i.e., visual exploration). The findings suggest that curiosity for novel information and the actual interestingness in the novel information is associated with different types of exploratory behaviour. Furthermore, our results in humans are in line with findings in rodents in how novelty affects the dynamics of explorative and rearing behaviour.

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32. Navigating to moving goals - do humans implicitly assume movement patterns?

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Finding our way to goals is a common task for humans. How do we plan routes and navigate to our targets? Most previous work on this topic focused on navigation to stationary targets, suggesting several potential models for how our brain represents targets and builds paths to them. Moving targets have a significantly harder level of complexity, but the differences in calculation and behavior are expected to become larger as well, potentially better revealing the differences between the different underlying neural systems. Here, we present a series of virtual environments in which participants and computational agents, trained with deep reinforcement learning methods, comparatively attempt to reach stationary and moving goals as a basis for testing such models. Specifically, we test how participants react to different types of target movements - Are they assuming that the target would keep moving the same way it did and how quickly can they adapt to a movement change? We present preliminary results (N=10) and compare them to the results acquired from different RL agents to demonstrate the participants tendency to implicitly assume set movement patterns.

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33. Evidence for flexible strategies during spatial learning involving path choices

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There is little debate that humans can learn to optimize their paths during spatial learning, but the conditions under which they spontaneously employ shortcuts remain unclear. In a classic study, Tolman et al. (1946) trained rodents to follow a path to a goal location. They found that the rodents chose the optimal path to the

goal location when the originally learned route to the goal was blocked and the remainder of the environment was replaced with a starburst maze. Subsequent studies found more mixed results , suggesting non-optimal response strategies. We addressed this issue across three different experiments by creating a virtual replica of Tolman's maze. We tested human participants under situations in which a light cue was either absent, consistently located from training to test, or moved a large or small distance between training and test. In Experiment 1, we replicated the finding that in the absence of a light cue, the majority of participants chose a hallway that was close to their originally learned route. In conditions in which the light moved, participants switched the hallway they searched based on the movement of the light. In Experiment 2, we tested whether distal visual cues (in the form of a boundary with differently colored walls) would result in a greater use of optimal shortcuts. In contrast to predictions, we replicated the same overall results from Experiment 1. In Experiment 3, we tested whether stronger idiothetic cues would result in greater use of optimal shortcuts by having participants navigate using an omnidirectional treadmill. In contrast to predictions, we again replicated the same results overall from Experiments 1 & 2. Our findings suggest participants' search strategies are flexible in that they vary depending on external cues and the previously learned path, even when these do not lead to the optimal route to the goal. Moreover, this pattern of strategy selection was robust even when distal or idiothetic cues.

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34. Sources of systematic errors in human path integration

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Triangle completion is a task widely used to study human path integration, an important navigation method relying on idiothetic cues. Systematic biases (compression patterns in the inbound responses) have been well documented in human triangle completion. However, the sources of systematic biases remain controversial. We used cross-validation modeling to compare three plausible theoretical models that assume that systematic errors occur in the encoding outbound path solely (encoding-error model), executing the inbound responses solely (execution-error model), and both (bi-component model), respectively. The modeling algorithm used one inbound response (i.e., response to the home) or multiple inbound responses (i.e., responses to two non-home locations and the home) for each outbound path. The algorithm of using multiple inbound responses demonstrated that the bi-component model outperformed the other models in accounting for the systematic errors. This finding suggests that both encoding the outbound path and executing the inbound responses contribute to the systematic biases in human path integration. In addition, the results showed that the algorithm using only the home response could not distinguish among these three models, suggesting that the typical triangle-completion task with only the home response for each outbound path cannot determine the sources of the systematic biases.

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35. Flexible Path Planning in a Spiking Model of Replay and Vicarious Trial and Error

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Flexible planning is necessary for reaching goals and adapting when conditions change. We introduce a biologically plausible path planning model that learns its environment, rapidly adapts to change, and plans efficient routes to goals. Our model addresses the decision-making process when faced with uncertainty. We tested the model in simulations of human and rodent navigation in mazes. Like the human and rat, the model was able to generate novel shortcuts, and take detours when familiar routes were blocked. Similar to rodent hippocampus recordings, the neural activity of the model resembles neural correlates of Vicarious Trial and Error (VTE) during early learning or during uncertain conditions and preplay predicting a future path after learning. We suggest that VTE, in addition to weighing possible outcomes, is a way in which an agent may gather information for future use.

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36. Spatial navigation impairment in post COVID-19 syndrome

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Post COVID-19 syndrome refers to new or persisting symptoms 12 weeks or more after SARS-CoV-2 infection. Fatigue, attention and memory deficits are among the most common symptoms. However, comprehensive neuropsychological assessments also revealed impairments in visuospatial abilities. In addition, MRI studies identified distinct brain damage patterns following COVID-19. This raises the question if spatial navigation is impaired after COVID-19 and whether such navigation deficits are associated with structural brain alterations.

Methods: We assessed 48 patients (38 female, age: M = 44.2 years (18 - 69)) from the post-COVID clinic at the Department of Neurology (time since confirmed infection: M = 37.4 weeks (14 - 84), hospitalized: n = 7 (15%), ICU: n = 3 (6%)) in comparison to 47 healthy age, sex and education matched controls. To assess online navigation, we applied the Virtual Environments Navigation Assessment for young and middle-aged adults (VIENNA Young), which does not rely on an episodic memory task. MRI data was obtained using a 3T Siemens PRISMA system (MPRAGE, 1x1x1mm3; diffusion-weighted: multiband EPI, 1.5x1.5x1.5mm3).

Results: We found lower navigation performance in post COVID-19 patients in comparison to healthy controls ($d = -0.68$, $t(93) = 3.29$, $p = .001$), which was robust to correction for divided attention performance ($p = .017$). Nine patients (19%) showed an impaired VIENNA Young performance ($z < -1.5$). In patients, worse navigation performance correlated with lower hippocampal volumes (left: $r = .49$, $p < .001$; right: $r = .38$, $p = .008$) and decreased integrity of hippocampal white matter tracts, including fornix (FA: $r = .37$, $p = .009$) and cingulum (MD: left: $r = -.42$, $p = .002$; right: $r = -.41$, $p = .003$). Conclusions: Persistent cognitive deficits following COVID-19 are not limited to attention or memory domains but also affect navigation performance. Follow-up assessments will be important to evaluate whether these cognitive deficits persist.

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37. Effects of acute stress on rigid learning, flexible learning and value- based decision-making in spatial navigation

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We often learn and make decisions in stressful situations. How acute stress affects learning and decision-making has been studied for decades, but few studies have investigated whether stress differentially affects rigid (i.e., repeating learned behaviors) and flexible learning (i.e., learning the structure of the task), and even fewer studies have investigated how stress affects flexible learning when it is contingent on the outcome of rigid learning. Furthermore, few studies have investigated how stress affects the way memory was utilized from such learning experience to inform value-based decision-making. In the current study, participants first learned to find locations of various objects in a virtual environment from a fixed starting location (rigid learning), and then learned to find the same objects from unpredictable starting locations (flexible learning) in the same environment. Participants then decided whether to reach goal objects from the fixed or unpredictable starting locations, with different penalties associated with each option. We find that 1) stress impairs rigid learning, but only in females, and 2) it does not impair flexible learning but even improves flexible learning when the performance with rigid learning is controlled for. When examining how earlier learning influences subsequent decision- making using a computational model, we find that 3) stress reduces memory integration in both genders, making participants focus more on recent episodic memory and less likely to integrate information from other related sources in decision-making. Collectively, our results show how acute stress impacts different memory systems and the communication between episodic memory and decision-making.

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38. L-DOPA enhances neural direction signals in younger and older adults

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Previous studies indicate a role of dopamine in spatial navigation. While it is well known that dopamine and spatial cognition both decline sharply in old age, how these factors affect neural representations of spatial specifically is not well understood.

To address this questions, we studied the effect of L-DOPA, a dopamine precursor, on neural signals related to walking direction in older and younger adults. Specifically, we used a double-blind cross-over L-DOPA/Placebo intervention design in which 43 younger and 37 older adults navigated in a virtual spatial environment while undergoing fMRI.

We trained logistic regression classifiers in a set of predefined regions of interest, including the early visual cortex, retrosplenial cortex, and hippocampus. Classification of brain activation patterns associated with different walking directions was improved following L-DOPA administration, with the clearest effects emerging in the hippocampus and the retrosplenial cortex. In the hippocampus these results were found in both age groups, while in the RSC they were only observed in younger adults.

Taken together, our study provides evidence for a mechanistic link between dopamine and the specificity of neural responses during spatial navigation.

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39. Multisensory input modulates memory-guided spatial navigation

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Successful memory-guided spatial navigation depends on the integration of multisensory input with spatial memory representations. Multisensory information can be acquired both from the environment, supporting a hippocampus-dependent allocentric framework, and from body movements, contributing to an egocentric framework that relies primarily on extrahippocampal brain regions. Despite the complexity of spatial navigation, human studies frequently use stationary experimental designs that neglect multisensory input from body motion. Here, we investigated the effects of multisensory input on memory-guided spatial navigation in patients with hippocampal lesions and hypothesized that patients' spatial navigation performance may be modulated by the availability of body-based information.

Ten patients with hippocampal lesions and 20 matched control participants performed a virtual water maze task, once in a stationary desktop setup displayed on a screen and once in a mobile virtual reality setup in which participants could move freely. In both setups, participants learned six target locations and navigated back to those locations from alternating starting positions.

While we found greater spatial navigation efficiency in both groups when multisensory input was available, we observed a group difference in the use of reference frames. Patients more frequently repeated previously learned path sequences, indicating the use of an egocentric reference frame. In contrast, control subjects rotated their heads more often, indicating the use of distal cues for an allocentric reference frame. Remarkably, the patients' spatial memory performance benefited more from the multisensory information than that of the control group, as evidenced by a greater reduction in the distance between the remembered and the actual target location.

In conclusion, multisensory input modulates navigational behavior and compensates for deficits in spatial navigation due to hippocampal lesions.

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40. Spatial Performance Assessment for Cognitive Evaluation (SPACE): A novel tablet-based tool to detect cognitive impairment.

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The diagnosis of cognitive impairment (including dementia) requires expensive or intrusive methods such as Positron Emission Tomography (PET) and Cerebrospinal fluid (CSF) analysis. Alternative paper and pencil tests like the Montreal Cognitive Assessment (MoCA) and the Mini Mental State Examination (MMSE) have also been developed as screening tools for cognitive impairment, but these tests can only be administered by qualified personnel. While the MoCA and the MMSE have been successful in discriminating healthy patients from dementia patients, these tests lack the necessary sensitivity to identify individuals with early signs of cognitive impairment. Recently, deficits in navigation have been found to be promising markers for detecting early stages of cognitive impairment. Indeed, navigation is known to recruit subcortical regions (e.g., hippocampus and entorhinal cortex) that are among the first to be compromised by early stages of cognitive impairment. In this poster, we showcase a novel and easy-to-administer tool for iPads designed to detect early signs of cognitive impairment. The Spatial Performance Assessment for Cognitive Evaluation (SPACE) consists of a series of gamified navigation tasks specifically developed to tap into different aspects of navigation ability known to be compromised during early cognitive impairment. SPACE will be deployed as part of two large cohort studies with elderly individuals in Singapore and evaluated in relation to a full neuropsychological assessment and blood and saliva biomarkers. Here, we present preliminary data on the usability and performance in the different navigation tasks in SPACE.

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41. L-Dopa suppresses grid-like activity and impairs spatial learning in novel environments in a young adult sample

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Dopamine is implicated in the spatial learning of goal locations [1], which is a process thought to be supported by the activity of place cells, grid cells, and head direction cells. Whereas effects of neuromodulation on place cell firing have been established in animal studies, it remains unclear whether dopaminergic modulation impacts spatial representations and spatial memory processes in humans.

In Parkinson’s disease, we previously observed that the influence of intra- maze cues on object-location memory was more pronounced under the dopamine precursor L-Dopa [2]. To test for an effect of L-Dopa on spatial memory in a non-clinical population, we performed a within-subject, double-blinded, placebo-controlled intervention study combined with fMRI. Healthy young adults (N=55, 21 females, aged 25-35 years) underwent a virtual spatial navigation task [3] for which previous studies reported grid- like activity in the entorhinal cortex [4]. Participants received L-Dopa (225 mg in two doses) in one of the two fMRI sessions and Placebo in the other session, with the order counterbalanced. In both intervention sessions, we analysed grid-like activity in the right entorhinal cortex during virtual navigation. We found that L-Dopa administered during the first session impaired grid-like activity, accompanied by reduced spatial memory performance. We observed no impairment when L-Dopa was administered in the second session, after prior experience with the task. These results support a role of dopamine in the encoding of novel spatial experiences. We interpret the negative impact of L-Dopa on grid-like activity and spatial learning in young adults in terms of the inverted-U function of dopamine regulation.

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42. Modulation by movement speed as a predictor of grid-code integrity and behavioral performance in linear path integration

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There is evidence that grid cells play a key role in path integration, our ability to continuously update the position based on sensory and body-based self-motion cues. Compromised grid-like representations, measured by functional magnetic resonance imaging, have been reported in older adults and in individuals at increased genetic risk for Alzheimer's disease, but the underlying causes of such perturbations are poorly understood. One candidate mechanism is movement speed, because it is assumed to be a key input for the formation of grid patterns and concurrent impairments in grid- cell activity and velocity coding in MEC have been shown in a mouse- model of tauopathy. Based on these findings, we hypothesized that the degree of modulation by movement speed may predict the integrity of grid- like BOLD signals. To test this prediction, participants perform two virtual navigation tasks while undergoing fMRI scanning. First, an established grid-localizer task is used to identify voxels with grid-like signal and to measure the integrity of their activity. During the second task, participants traverse distances at different speed levels on a linear track before having to estimate the travelled distance at the end of each trial. We will test if the extent of modulation by movement speed can predict the integrity of the grid code and behavioral performance on the distance estimation task. We will also analyze whether distance can be extracted from the collective activity of voxels with grid-like signal. Preliminary analyses of a behavioral pilot study revealed that both speed and distance can affect estimation error significantly, but significant variability was observed between subjects.

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43. Entorhinal grid-like signals reflect temporal context for human timing behavior

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The entorhinal cortex (EC) supports the encoding of task regularities. A critical function may be the encoding of temporal context (i.e., forming integrated relational representations of co-occurring events and stimuli). A key neural component in the EC are grid cells, whose activity likely exhibits a six-fold rotational symmetry as a function of gaze direction as measured by functional magnetic resonance imaging (fMRI). Here, we combined fMRI and a time-to-contact estimation task to test whether temporal context modulates this grid-like fMRI activity in the human EC. In addition, we characterized in detail the relationship between trial-wise entorhinal activity and participants' task performance. We found that activity in the EC reflected biases in timing behavior, and that the cross-validated amplitude of grid-like signals indeed depended on the timing errors consistent with temporal-context encoding. These findings suggest that the human EC contributes to adapting internal timing mechanisms to the temporal statistics of the environment in accordance with the predictions from Bayesian models of time perception.

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44. Partially overlapping spatial environments trigger reinstatement in hippocampus and schema representations in prefrontal cortex

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When we remember a city that we have visited, we retrieve places related to finding our goal but also non-target locations within this environment. Yet, understanding how the human brain implements the neural computations underlying holistic retrieval remains unsolved, particularly for shared aspects of environments. Here, human participants learned and retrieved details from three partially overlapping environments while undergoing high-resolution functional magnetic resonance imaging (fMRI). Our findings show reinstatement of stores even when they are not related to a specific trial probe, providing evidence for holistic environmental retrieval. For stores shared between cities, we find evidence for pattern separation (representational orthogonalization) in hippocampal subfield CA2/3/DG and repulsion in CA1 (differentiation beyond orthogonalization). Additionally, our findings demonstrate that medial prefrontal cortex (mPFC) stores representations of the common spatial structure, termed schema, across environments. Together, our findings suggest how unique and common elements of multiple spatial environments are accessed computationally and neurally.

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45. MEG frequency-tagging reveals the emergence of a grid-like code during covert attentional movements

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Grid-cells in the entorhinal cortex represent space with a 60° periodicity, providing a reference system for spatial navigation. Recent evidence in monkeys demonstrates grid-cells recruitment independently of eye-movements, suggesting the contribution of attention to the generation of the grid-code. We investigated whether movements of covert attention can elicit grid-like coding in humans by concurrently recording MEG and eye-tracker. To obtain a measure of grid-like signal non-invasively with high SNR, we developed a new paradigm based on frequency-tagging. While keeping central fixation, participants were presented visually with sequences of linearly-spaced trajectories (15° or 30° in different conditions) formed by static lines or moving dots in separate sessions. Trajectories appeared sequentially on the screen at a fixed rate (6 Hz), allowing different spatial periodicities (e.g. 45°, 60°, 90°) to have corresponding temporal periodicities (e.g. 1, 1.5, 2 Hz), thus resulting in distinct spectral responses in the recorded brain signal.

Analyses of inter-trial coherence evidenced a higher response for the 60° periodicity than the control periodicities. This effect was localised in medial temporal sources and not in control regions. Moreover, in a control experiment using a recurrent sequence of letters featuring the same temporal periodicity but lacking spatial structure, the six-fold effect did not emerge, suggesting its dependency on the spatial periodicity of grid-like firing fields. We report the first evidence, in humans, that grid-like signal in the medial temporal lobe can be elicited by covert attentional movements. Moreover, we propose a new neuroimaging paradigm based on frequency-tagging to study grid-like activity non-invasively.

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46. An Examination of the Behavioural & Neural Correlates of Spatial Navigation

Conor Thornberry (Presenter) Prof. Sean Commins (PhD Supervisor)

Learning how to navigate our environment and recall important locations is an essential cognitive task we perform every day. Navigation, along with the required learning and memory, has been examined extensively in animals using the Morris water maze (Morris, 1981). In this task animals are required to find a platform, hidden somewhere in a large circular pool of water (below surface level). As animals cannot see the goal directly, they must use various cues in the environment to locate it and escape. With advancements in virtual reality technologies, navigation can now be directly examined in humans using a virtual version of the task. For this project, we have used our open-source virtual water maze software NavWell (Commins et al., 2020) to record real-time navigation learning and recall in human participants. We have also simultaneously recorded neural activity using 32- channel Electroencephalography (EEG). Participants were randomly assigned to either an Experimental group (who were required to learn the location of a hidden target across 12 trials), or a Control group (who were required to move around the same arena for 12 trials, but without the presence of a goal; each trial was timed-matched to the experimental group). There were 25 participants in our Experimental Group (mean age = 22.5, 9M, 16F) & 25 participants in our Control Group (mean age = 21.2, 7M, 18F). All participants in the Experimental group exhibited good learning. During goal-approach behaviour, we demonstrated significant increases in Theta (4-8Hz) and Alpha band (8-12Hz) power across Parietal, Central & Frontal sites on Trial 12 compared to Trial 1. Similar increases across the two bands were demonstrated in the Experimental group when compared to the non-learning Control group. Results are discussed in terms of the interaction between the two bands and their possible role in human place learning. We aim to further examine changes during phases of navigation, such as planning & traveling.

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47. Novel virtual reality-enabled path integration task for freely moving rats.

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Spatial navigation of rodents is supported by a flexible combination of multisensory-based allothetic representation of space and self-referenced path integration. How the two navigational strategies relate to neural representation of space remains poorly understood, in part due to a difficulty in dissociating which strategy is used by the freely-moving behaving animal. In this study we designed a path integration task that relies on a 3D virtual reality beacon to mark an arbitrary homing location in the arena. Rearing behavior serves as a readout of both initiation of outbound foraging and path integration-dependent completion of the inbound trajectory in the darkness. Randomized computer-controlled variation over blocks of trials of the homing location makes the task majorly reliant on path integration. We combine the task with perturbation of the idiothetic sensory inputs via vestibular and optic flow manipulations to understand their respective roles in path integration. We quantify animal performance on the task and effect of perturbation with measures characterizing their trajectories and rearing patterns. In order to understand how spatial representation is related to behavioral strategy of navigation we use wireless silicon probe recordings in the rats performing the task and numerous controls. We quantify the effect of the task and perturbations on spatial coding of the populations of hippocampal place cells.

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48. Hippocampal representations of homing based on path integration

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Homing based on path integration (H/PI) is a form of navigation in which an animal processes self-motion cues to keep track of its location in order to return to a starting point. The neuronal representations supporting H/PI have remained largely unexplored because of a lack of H/PI tasks suitable for recordings of spatially selective neurons. Here we overcame this problem by developing an automated H/PI task for rodents. The task required a mouse to find for a variably placed lever on a circular arena, before heading back to their home base. H/PI was assessed in complete darkness, where performance depended on path integration. Recordings from CA1 pyramidal neurons in mice performing the H/PI task showed that several firing fields were anchored to the lever position. The spatial selectivity of these fields was reduced during trials with lower homing accuracy. In a subset of lever- anchored neurons, the field position around the lever predicted the homing direction of the mouse. These results demonstrate how object-anchored firing fields convey behaviourally relevant information for homing and navigation beyond the object vicinity.

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49. Sharper head-direction tuning in a rat model of autism

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Fragile X Syndrome is the most common monogenic cause of autism and intellectual disability. It is caused by mutations inactivating the Fmr1 gene. It is modeled using Fmr1 knockout (Fmr1-/y) rodents, which have been shown to have thalamocortical abnormalities. The head-direction (HD) system, the brain’s ‘compass’, includes a thalamocortical pathway. The HD system is wired up very early in development, and can be a useful model to study neurodevelopmental disorders. The population of HD neurons encodes a one-dimensional circular variable (current direction in allocentric space) and shows rigid co-activity patterns that are preserved even in absence of consciousness, therefore the HD signal can be probed without the need for the animal to be performing any tasks.

We hypothesised that loss of Fmr1 leads to deficits in thalamocortical processing and thus HD coding in the cortex. We recorded assemblies of HD cells in the postsubiculum (PoS) of 22-28 day old Fmr1-/y (n=6) and wild-type (WT; n=6) rats with silicon probes during open field exploration. Surprisingly, juvenile Fmr1-/y rats showed sharper and more stable HD tuning than WT. To exclude the possibility that differences in HD tuning are due to differences in sensory processing, we quantified the co-activity patterns of the same cells during rapid eye movement (REM) sleep - the sleep stage in which the dynamics of HD system are largely indistinguishable from wakefulness. During REM sleep, cell pairs from Fmr1-/y rats showed stronger temporal co-activity relationships indicating that improved HD tuning may be the result of more refined circuit connectivity.

We also performed ex vivo patch-clamp recordings from PoS cells in coronal slices from rats of the same age (n=7), to characterise their intrinsic properties and synaptic inputs. Putative pyramidal cells in Fmr1-/y brain slices showed unaltered intrinsic properties. However, PoS cells in Fmr1-/y rats seem to receive more excitatory inputs compared to WT.

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50. Ketamine Disrupts and Restructures Entorhinal-Hippocampal Spatial Coding

Francis Kei Masuda, Yanjun Sun, Emily Jones, Lisa M Giocomo

Ketamine is a commonly used rapid-acting dissociative anesthetic that has been used in clinics since the 1970s. Recently, ketamine has received significant clinical and scientific attention due to its ability to acutely treat depression a subanesthetic doses. Unfortunately, ketamine has a plethora of undesirable side effects—out-of-body experiences, dissociation, and cognitive spatial memory impairments. Yet despite the scientific and clinical attention, ketamine’s effect on neurological circuitry remains poorly understood. We used electrophysiology to examine ketamine’s impacts on the medial entorhinal cortex and hippocampus, which contain neurons that encode an animal’s spatial position relative to environmental features, as mice navigated virtual reality and real world environments. Ketamine induced an acute disruption and long-term reorganization of entorhinal spatial representations. This acute ketamine-induced disruption reflected increased excitatory neuron firing rates and a disruption of cell-pair temporal firing relationships. In the reciprocally connected hippocampus, a key region supporting spatial memory, neurons that encode the spatial position of the animal were suppressed after ketamine administration. Together, these findings point to disruption in the spatial coding properties of the entorhinal-hippocampal circuit as a potential neural substrate for ketamine-induced changes in spatial cognition.

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51. Converging lines on the horizon: The impact of linear perspective cues on spatial memory

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Grid cells in the entorhinal cortex provide spatial computations that allow humans and animals to navigate their surroundings. Recently, evidence has accumulated that grid cell firing patterns are more plastic than anticipated, and multiple environmental factors can affect both their firing behavior and spatial memory performance. In rodents, the regularity of grid cell firing patterns can be distorted by irregular enclosure shapes such as trapezoidal rooms. Similarly, a trapezoidal environment seems to result in altered grid- cell-like representations and a decline in spatial memory in humans. Beyond geometric shape, however, the role of other factors such as depth perception are less explored. For example, linear perspective is a monocular depth cue based on seeing parallel lines that converge towards the horizon, which provides information about the depth of an environment. To determine how linear perspective cues affect spatial memories, we investigated the association between spatial memory performance and linear perspective cues provided during navigation. We created three virtual environments with different depth illusions by employing linear perspective cues at various strengths - minimal, moderate, and maximal. In each environment, participants learned multiple object locations. We predicted to find relationships between the strength of the linear perspective cues and spatial memory distortions, and we explored if the narrow sides of the environments with prominent linear perspective cues resulted in increased spatial memory errors. Preliminary results of 24 participants showed that the environment with maximal linear perspective cues resulted in the most accurate spatial memory. Similarly, error rates were lower in the narrow sides of the environment. These preliminary results suggest that spatial memory can be affected by perceptual cues, which should be considered in theoretical models of spatial navigation and the underlying neural computations.

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52. The impact of task difficulty on wayfinding by the sequential response strategy and by the associative cue strategy

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The number of decision points has been proposed as an important determinant of wayfinding difficulty. The present study therefore quantifies the role of this determinant for two wayfinding strategies, the sequential response strategy and the associative cue strategy. All participants saw a sequence of four-way intersections. On a first trial, they were told in which direction to proceed across each intersection. On the five subsequent trials, they had to indicate the direction themselves. Participants from one group saw intersections which all looked alike, and had to recall the serial order of directions to take (group S, sequential response strategy). In contrast, participants from another group saw a different architectural or natural landmark at each intersection, and had to recall the direction associated with each landmark; the landmark order varied between trials, but the landmark- direction mapping was consistent (group A, associative cue strategy). Performance was quantified as the mean number of errors per intersection. We found that the error rate was better than chance (i.e., <0.66) already on the first self-guided trial, and that it continued to decrease across the subsequent trials. The error rate differed little between groups, but was larger if the task involved 18 rather than 12 intersections. From this we conclude that wayfinding performance depends on the memory load imposed by the number of intersections, and less so on the type of strategic processing.

Keywords: human, wayfinding, navigation, task difficulty, sequential response strategy, associative cue strategy.

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53. Spatial navigation and different domains of knowledge: The role of individual's visuospatial factors

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People vary for their navigation abilities. Learning from navigation provide the individual of different domains of knowledge, from the one about landmarks, to their locations (from egocentric and allocentric perspectives) and paths connecting them (in route and survey modes). The present study investigated whether individual's visuospatial abilities and self-reported wayfinding inclinations relate differently to the various domains of knowledge.

A sample of 270 people performed several individual visuospatial factors tasks and questionnaires. Then they learnt a virtual path, and their knowledge of the environment was assessed with a free recall of landmarks, egocentric and allocentric pointing (location knowledge), route direction and landmark locating tasks (path knowledge). The resulting models showed that visuospatial abilities and wayfinding inclinations compose two distinct factors, the former relating to all the domains of knowledge tasks except for route direction, and the latter relating to allocentric pointing task and landmark locating (path-survey knowledge). Overall, the relationship between individual visuospatial factors and environment learning from navigation depend on the domain of knowledge tested, with a stronger involvement of visuospatial factors in allocentric/survey knowledge.

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54. Euclidean maps for a non-Euclidean surface? Human spatial memory and path integration on the sphere

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Humans can build cognitive maps of the world. The nature of the cognitive map, relying on fundamental neural coding principles in the hippocampal formation, would be influenced by the environment, and most people live on a surface that can be best described with Euclidean geometry. Whether people can adapt and build a map for a novel environment in which they can no longer rely on Euclidean geometrical intuition is an intriguing question that can help us to understand the capacity and limitation of human cognition. To answer this question, we designed a study where participants explore the planar and spherical world on separate days using a virtual reality treadmill. They first learned a spatial layout of objects and were tested of their object-location memory, and then they completed a path integration task, known as the triangle completion test. Participants could recall the object location well above the chance on both planar and sphere environment, but the direction error was particularly large for the sphere condition when the target was farther away. This result suggests the participants used the locally planar maps rather than having a full volumetric 3D map. Participants also showed systematic overturn bias on the sphere, as a consequence of following the Euclidean geometrical rule on the non- Euclidean surface. This result implies a strong Euclidean geometrical prior in human mind despite the capacity of building a map for a non-flat surface, and can inform future neuroscientific investigations of the cognitive map.

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55. Spatial memory in 3d - flying a virtual water maze

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Spatial memory, recalling where things are, is essential for survival. While we live and navigate in a three-dimensional world, previous research into human spatial memory has mainly focused on the two-dimensional space. How do the results differ between 2D and 3D? Are there systematic biases between the axes defining the ground and the vertical axis? Prior studies offered conflicting answers. Several previous results suggest that humans are affected by a series of biases when encoding vertical vs. horizontal location, while others suggest that humans might use a 3D isometric representation of space. This paper utilizes the classic paradigm of spatial memory, the morris water maze, adapting it to 3d. Participants navigate on a 2d ground plane, 2d vertical plane and in full 3d and we compare their results. We find that while humans report greater difficulty with the vertical axis compared to horizontal axis, in practice there is no difference in accuracy between the axis. Our findings support the existence of a basically isometric representation of 3d space.

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56. This is not the way: A global directional cue does not improve spatial navigation in an immersive virtual environment

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Knowing where we want to go and how to get there is not always easy. Thus, one might need tools to support navigation behavior. A commonly used tool to help navigation is a compass, which provides a global reference direction and bearing. The present study investigated whether people learned a large-scale environment better with a compass in a fully immersive virtual environment. We found no evidence of a difference between those who had the compass available and those who did not (N = 54). Our results inform theories of improving spatial navigation support and are consistent with the importance of environmental reference frames. Future research will indicate whether this null result is specific to compass or is true for a variety of directional cues (e.g., salient landmarks, or geometry).

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57. The formation and consolidation of egocentric and allocentric spatial memories in children and adults

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Locations in space can be memorized in relation to the observer’s body coordinates (egocentric) or the environment (allocentric). Children develop egocentric before allocentric navigation. The corresponding spatial memories consolidate over time. This process is accelerated by pre-existing schemas, which become increasingly available with age. Here, we investigate the role of the developmental status of children for the consolidation of egocentric and allocentric spatial memories.

We compared memory-guided egocentric and allocentric navigation in a sample of thirty-three 6- to 7-year-old children, thirty-three 9- to 10-year-old children and thirty-two young adults. Participants searched and remembered goal locations in a virtual maze and were tested in egocentric and allocentric conditions. We assessed retrieval immediately after learning and after a consolidation period of two weeks. Our results show that younger participants were less likely to remember correct locations and navigated less directly and quickly in both conditions. After the two-week consolidation period, children of all ages forgot relatively more than adults. Unexpectedly, children did not perform substantially better in egocentric compared to allocentric navigation. Performance was particularly poor for egocentric trials requiring a sequence of multiple turns. Furthermore, children in both age groups had difficulties with identifying the geometric 2D layout of the virtual maze and integrating landmarks and goals into a 2D map although they identified landmarks as wells as adults. In conclusion, older participants showed a superior ability for egocentric and allocentric memory-guided navigation. This may be due to older participant’s advanced brain maturation and the availability of stronger pre- existing spatial schemas to build upon and consolidate faster. Egocentric and allocentric navigation were similarly affected, consistent with shared processes underlying both types of memories.

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58. forming cognitive map of conceptual space through development

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How human make decision without prior experience? This requires inferential reasoning on a mental map of past experiences. Like physical space, conceptual space can be represented as a cognitive map and is supported by similar grid-like signal (like firing pattern of grid cell) in entorhinal cortex and medial prefrontal cortex. Very little is known, however, about the formation of cognitive map through development. This is important because the ability to reason and make novel inferences is a key feature of human intelligence, which develop rapidly from childhood to adolescence.

To study this question, we have designed a novel two-dimensional fighting game in a 5*5 grid, where 25 stimuli are organized base on two axes: attack and defence power. During training, subjects are given only pairwise relationship of adjacent stimuli, separately on each dimension. Only subjects who can memories at least 80% of all pairwise relationships are allowed to perform novel inference tasks. During two-dimensional (2D) inference task, subjects are asked to compare the attack power of object A to the defence power of object B. This task can be efficiently solved by placing all stimuli on a 2D map, and each inference is like mentally traversing this map.

We have so far collected fMRI data from 52 participants (8-30 years) performing this task. We found significant age effect on 2D inference, above and beyond transitive inference ability on single dimension ($p < 0.001$). Like previous studies, when focusing only on high performance subjects, we found significant grid-like signal in entorhinal cortex (EC), ventral medial prefrontal cortex (vmPFC) and posterior cingulate cortex (PCC). More interestingly, with age increase, we found significant increase of grid-like signal in the vmPFC, but decreases in the PCC, while grid-like signal in the EC covary with 2D inference performance. Our results chart the developmental profile of cognitive map, and its role for inferential reasoning.

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59. Does Vestibular Disease Affect the Sense of Direction?

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Our sense of direction (SOD) can be defined as our ability to find our way round and to know in which direction surrounding objects are. Given that vestibular input contributes to our SOD, the main aim of this study was to see how vestibular disorders affect SOD.

96 patients attending our neuro-otology service [30 PPPD, 13 BPPV, 12 Bilateral vestibular failure (BVF), 9 Downbeat nystagmus, 12 Meniere's disease and 20 Vestibular migraine], and 78 healthy control subjects, were assessed with validated questionnaires quantifying SOD; Santa Barbara SOD scale, spatial anxiety, dizziness handicap, motion sickness susceptibility and migraine screening questionnaires. 58 patients and 48 controls also completed an online Spatial Orientation test. The main findings were: 1) worse performance on both subjective an objective SOD measures in vestibular patients versus controls ($p<.001$), but no difference between patient groups. 2) A negative association between subjective SOD and spatial anxiety in all groups (R square = 0.41). 4) PPPD patients are highly symptomatic: a) they display similar prevalence of migraine symptoms to vestibular migraine patients; b) PPPD and Downbeat nystagmus patients report highest DHI scores with no significant difference between each other and c) both PPPD and Downbeat nystagmus patients show a negative association between objective spatial orientation ability and DHI score (R squares = 0.61, 0.65) - a trait not found in other organic vestibular patients or controls.

Conclusions: SOD and spatial orientation tasks are affected by vestibular disease and also show association with spatial anxiety. Functional vestibular patients experience migraineous symptoms and high disability, which impacts their spatial orientation. SOD does not seem to be dictated by individual susceptibility to motion sickness. Vestibular rehabilitation programs may benefit from adding strategies for improving patients' sense of direction and spatial anxiety.

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60. Navigation on virtual reality tasks is abnormal in patients with bilateral vestibular loss

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Objective: To compare spatial navigation ability in patients with bilateral vestibular loss (BVL) and normal control (NC) subjects within a virtual reality (VR) visual environment on stationary and dynamic navigation tasks.

Study Design: Cross-sectional study. Setting: Tertiary vestibular clinic. Patients: 18 BVL patients and 15 age-matched NC subjects.

Interventions: Subjects completed a VR spatial navigation “triangle completion task” in two conditions: 1) dynamic, in which subjects had access to visual, vestibular, proprioceptive, and efferent sensory signals and 2) stationary, in which subjects relied only on visual cues.

Main Outcome Measures: VR spatial navigation task performance measured by mean distance error (MDE), standard deviation of distance (SDD) and path length of the final segment of navigation.

Results: Male BVL subjects demonstrated decreased accuracy (greater MDE) and decreased precision (greater SDD) in a dynamic navigation task compared to male NC subjects ($U=65$, $p<0.05$ and $U=66$, $p<0.05$, respectively). While BVL males were less precise in the dynamic task compared to the stationary task ($V=55$, $p<0.01$), NC males were comparatively more precise in the dynamic task ($V=2$, $p<0.05$). Male BVL subjects demonstrated longer mean path lengths in the dynamic task compared to male NC subjects ($U=80$, $p<0.05$). Female BVL and NC subjects performed similarly on both dynamic and stationary tasks.

Conclusions: Patients with vestibular loss may perform more poorly on dynamic spatial navigation tasks compared to age-matched healthy subjects. Further research is needed to characterize the specific contributions of idiothetic cues on dynamic navigation tasks.

Key Words: Bilateral vestibular loss, spatial navigation, virtual reality, allothetic navigation, idiothetic navigation, path integration

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61. Recent advances in characterising the vestibular system in humans

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The vestibular system provides important sensory input for spatial navigation. In rodents, the head direction system loses its directional firing in the absence of vestibular input. Repeated exposure of rodents to high magnetic field strengths disrupts their spatial and locomotion behavior days to weeks after exposure. In humans, patients with vestibular sensory loss also suffer from spatial deficits, however understanding the relationship between the vestibular system and spatial cognition in humans has been difficult in part due to a lack of quantitative in-vivo measurements of the inner ear. Here we show our recent work towards characterizing the vestibular system in-vivo in humans. First, with high-resolution targeted MRI sequences we were able to create an atlas of the inner ear, based on previous anatomical subdivisions from micro-CT data. This atlas allows for the automatic segmentation and characterization of individual differences in inner ear structures. It recently allowed us to characterize the relationship between the orientation of individual semicircular canals and strength of magnetic vestibular stimulation. We are currently extending the atlas to nerve structures as well as non-brain tissues surrounding the inner ear with in-vivo histological MRI techniques. In addition to the peripheral vestibular organ, we have characterized the cortical structural and functional connectivity profiles of the human vestibular network, demonstrating a high level of stability and redundancy across the network of regions that process vestibular information. The stability may provide the framework for the robust compensatory mechanisms seen in humans. Our results show marked differences to other animals that may be important for understanding human spatial cognition.

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62. Largely Intact Memory for Spatial Locations During Navigation in an Individual with Dense Amnesia

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Spatial navigation and event memory are thought to be heavily intertwined, both in terms of their cognitive processes and underlying neural systems. Some theoretical models posit that both memory for places during navigation and episodic memory depend on highly overlapping brain systems. Here, we assessed this relationship by testing navigation in an individual with severe retrograde and anterograde amnesia; the amnesia stemmed from bilateral lesions in the medial temporal lobes from two separate strokes. The individual with amnesia and age-matched controls were tested on their memories for the locations of previously seen objects relative to distal mountain cues in a fully immersive virtual environment. All participants were tested from repeated and novel start locations and when a single distal mountain cue was unknowingly moved to determine if they relied on a single cue to a greater extent than the collection of all distal cues. Compared to age-matched controls, the individual with amnesia showed no significant deficits in navigation from either the repeated or novel start points, although both groups performed well above chance at placing objects near their correct locations. The individual with amnesia also relied on a combination of distal cues in a manner comparable to age- matched controls. Despite largely intact memory for locations using distal cues, the individual with amnesia walked longer paths, rotated more, and took longer to complete trials. Our findings suggest that memory for places during navigation and episodic memory may involve partially dissociable brain circuits and that other brain regions outside of the medial temporal lobe partially support some aspects of navigation. At the same time, the fact that the individual with amnesia walked more circuitous paths and had dense amnesia for autobiographic events supports the idea that the hippocampus may be important for binding information as part of a larger role in memory.

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63. Impact of Traumatic Brain Injury on different formats of topographical representation.

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Navigating in the environmental space requires processing and integrating different types of visuospatial information. It depends on activity of a large- scale brain network, which regions play different and complementary contributions. Thus, white matter damage may greatly impact on this complex skill. Here, we aimed to test whether and how diffused axonal damage, proper of traumatic brain injury (TBI), affects spatial navigation. We use the laboratory-based setting (LBS) we recently developed, which allows for testing route learning (RK; route learning task), landmark knowledge (LK; landmark recognition task), survey knowledge (SK; landmark positioning task) and landmark ordering (LO; ordering task). We compared the performance of patients with TBI (N = 18) with that of healthy controls (HC; N = 34) matched for age and gender. The inverse efficiency score index (IES), that balances and integrates accuracy and response time, was computed for each task of the LBS. Then we performed Mann-Whitney U tests to compare indexes of the two groups; in each group, Spearman's correlation coefficient was computed as well. The two groups differed significantly on the second attempt of the RK, but not on the third attempt, suggesting that although it took more time, patients with TBI learned the path similarly to the HC. However, performances differed

significantly in LK and SK task, suggesting a deficit in recollecting figurative memory of the landmarks and shifting from an egocentric to an allocentric representation. Performance did not differ significantly in the LO. Consistently with our previous results, performances on LO were associated with SK in HC; instead, they were associated with RK in patients with TBI. Results suggest that HC used SK to perform LO; instead, TBI used the route information they had correctly acquired, suggesting a different strategy in this sample of patients.

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64. The impact of landmark stability on the decoding of the head direction signal in the human brain

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Head direction (HD) cells have been shown to be important for navigating throughout our environment. These cells have been found in several brain regions such as the postsubiculum (PoS), retrosplenial cortex (RSC), entorhinal cortex (EC) and the thalamus in the rodent with converging evidence in the human brain. Their firing rate increases when the animal is facing a specific direction and decreases when the animal moves away from their preferred orientation. Thus, these cells have been thought to act as an internal compass. However, these HD cells have to remain stable in relation to their environment and landmarks are supposed to give such stable directional information. Indeed, results investigating the coding of landmark stability present that PoS and RSC would encode permanent landmarks. Since these two regions also code for the HD signal, it was hypothesized that the HD cells could be linked to the landmark stability. Therefore, the aim of this project is to decode the HD cell signal in the human brain by using an environment with both stable and unstable landmarks. Participants performed an immersive virtual reality task to learn the environment, using a head mounted display. Then, we used 3T magnetic resonance imaging and computational analysis to investigate if the HD signal can be decoded in RSC, PoS, EC and thalamus and whether or not the stability of landmarks have an impact. We collected data from 20 participants and the preliminary results suggest that the stable vs unstable landmarks can be detected in the human brain. Additionally, the different learning strategies observed between the participants are explaining the difference in the decoding results.

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65. Vectorial spatial coding in the human brain

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Various types of cells have been identified in the rodent studies to code spatial information relevant for navigation, such as the head direction cells in the Thalamus (Taube et al., 1990), place cells in the hippocampus (O'Keefe and Dostoevsky, 1971), and grid cells in the entorhinal cortex (Hafting et al., 2005). Recently, a vectorial coding scheme has also been observed in rodent (e.g., Deshmukh and Knierim, 2013; Hinman et al., 2019) as well as humans (Kunz et al., 2021), where activities of sub populations of cells are modulated by either non-extending landmark or boundaries at a certain distance and direction from the navigator. In this study, we examine such vectorial coding in healthy young adults with fMRI. Participants memorized four target locations in relation to a fixed landmark in a virtual environment, with the landmark providing both directional and distance information. Representational similarity analysis (RSA) reveals that

various regions within the navigational network (e.g, the hippocampus, the parahippocampus) as well as the visual-processing areas track participants' locations relative to the landmark. In addition, the Euclidean distance information among the targets themselves is represented in the parahippocampus and the lateral occipital area.

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66. Coexistence of Cue-specific and Cue-independent Spatial Representations for Landmarks and Self-motion Cues in Human Retrosplenial Cortex

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Landmark-based and self-motion-based navigation are two fundamental forms of spatial navigation, which involve distinct cognitive mechanisms. A critical question is whether these two distinct navigation modes invoke either common or distinct spatial representations for a given environment in the brain. While a number of electrophysiological studies in nonhuman animals have investigated this question but yielded inconsistent results, it still awaits rigorous investigation in humans. In the current study, we combined ultra-high field fMRI at 7T, desktop virtual reality, state-of-the-art fMRI data analysis techniques. Using a novel linear track navigation task, we dissociated the use of landmarks and self-motion cues, so that participants used different spatial cues to encode and retrieve the same set of spatial locations. Focusing on retrosplenial cortex (RSC) and the hippocampus, we observed that RSC contained both cue-specific and cue-independent spatial representations, which were driven by objective location (where the participant was actually located) and subjective location (where the participant reported he/she was located), respectively. The hippocampus showed strong functional coupling with RSC, and exhibited a similar spatial coding scheme, but with reduced effect sizes. Taken together, the current study demonstrated for the first time concurrent cue-specific and cue-independent spatial representations in RSC in the same spatial context, suggesting that this area might transfer cue- specific spatial inputs into a coherent cue-independent spatial representation to guide navigation behavior.

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67. The relationship between hippocampal subfield volumes and individual differences in navigation

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Despite the need for successful navigation, humans vary greatly in their abilities to navigate, and these individual differences may relate to differences in brain structure. Studies on navigation experts and older populations have shown a relationship between hippocampal volume and navigation ability, but this relationship in the healthy, young adult population has recently been called into question. Many of these studies analyzed total hippocampal gray-matter volumes despite there being anatomical differences in hippocampal subfields. This study tested the abilities of young adults to successfully navigate a virtual desktop maze environment, and the participants' high-resolution anatomical brain images were automatically segmented into four hippocampal subfields and three adjacent medial temporal lobe regions. We theorized that successful navigation correlates with the volumes of the Cornu Ammonis 3 (CA3) and dentate gyrus (DG) subfields since CA3 and DG volumes are related to pattern separation ability in humans. With the need to distinguish between similar-looking maze hallways and partially-overlapping routes, young adults who have stronger pattern separation ability may perform better in this task and have larger CA3 and DG

volumes. Rodent literature informs us that Cornu Ammonis 1 (CA1) and entorhinal cortex (ERC) are both associated with spatial memory, suggesting a possible relationship between their volumes and navigation performance. Our findings indicate that CA1 and DG volumes positively correlated with maze performance, consistent with a pattern separation hypothesis and findings from rodent research. This result is informative to our future understanding of the link between brain and navigation behavior for healthy, young adults.

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68. The neural correlates of spatial disorientation in head direction cells

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While the brain has evolved robust mechanisms to counter spatial disorientation, the neural underpinnings of these mechanisms remain unknown. To explore these underpinnings, we monitored the activity of 71 anterodorsal thalamic head-direction (HD) cells under different conditions associated with disorientation: 1) while rats underwent uni- or bi-directional rotations in the light, or 2) while blindfolded, and 3) during head-fixed passive restraint or while freely-moving. HD cells did not become quiescent, but continued to fire during disorienting rotations - their peak firing rates, burst frequency, and extent of direction-specific firing were all reduced, consistent with previous experiments where rats were inverted or climbing in zero-gravity. However, access to visual landmarks spared tuning stability, indicating that visual landmarks provide a stabilizing signal to the HD system while directional precision is maintained by vestibular inputs. Interestingly, at the beginning of head-fixed rotations, tuning curves shifted in the direction of rotation, suggesting that the HD system underestimated angular rotation. This finding could explain behavioral results in humans who often underestimate rotations. When passive rotations in the dark were terminated, HD cells fired in bursts, which matched the frequency of rotation. This phenomenon is reminiscent of post-rotational “nystagmus” in the vestibulo-ocular system and shares a number of striking similarities. Besides identifying the neural correlates underlying spatial disorientation, our findings provide the first evidence that the HD system receives input from a vestibular velocity storage mechanism that works to reduce spatial disorientation following rotation. Thus, the brain overcomes spatial disorientation through multisensory integration of different motor-sensory inputs.

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69. Coregistration of heading to visual cues in retrosplenial cortex

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Spatial cognition depends on an accurate representation of orientation within an environment. Head direction cells in distributed brain regions receive a range of sensory inputs, but visual input is particularly important for aligning their responses to environmental landmarks. To investigate how population-level heading responses are aligned to visual input, we recorded from retrosplenial cortex (RSC) of head-fixed mice in a moving environment using two-photon calcium imaging. We show that RSC neurons are tuned to the animal’s relative orientation in the environment, even in the absence of head movement. Next, we found that RSC receives functionally distinct projections from visual and thalamic areas, and contains several functional classes of neurons. While some functional classes mirror RSC inputs, a newly discovered class coregisters visual and thalamic signals. Finally, decoding analyses reveal unique contributions to heading from each class. Our results suggest an RSC circuit for anchoring heading representations to environmental visual landmarks.

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70. Laminar and projection-specific calcium imaging of spatial memory related retrosplenial cortex dynamics in freely moving rats

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Retrosplenial cortex (RSC) neurons encode a variety of spatial variables in allocentric, route-centric, and egocentric coordinate systems (Alexander et al., 2015; 2017; 2020). Lesions or inactivation of the area indicate that it is important for navigation and mnemonic processing. RSC activation supporting these processes in freely moving rats has primarily been characterized using in vivo electrophysiology. One-photon calcium imaging in behaving animals allows observation of larger populations of simultaneously recorded neurons. In retrosplenial cortex, imaging large populations affords the opportunity to examine interactions amongst neurons with activity anchored in distinct spatial coordinate systems which could reveal critical processing modes for the construction and use of internal maps for navigation and memory. In the current work, we utilized in vivo one-photon calcium imaging in Thy1-GCaMP6f transgenic rats to characterize population dynamics of hundreds of retrosplenial cortex neurons while animals learned and performed multiple tasks requiring spatial memory. We gained optical access to RSC ensembles by using microprism lenses which enabled a comparison of activation between deep and superficial layers of the region during behavior. Finally, retrograde- mediated transduction of GCaMP7 was used to investigate differences and similarities in task-related calcium signals between RSC neurons that project to the anterior thalamic nuclei or the extended hippocampal formation.

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71. Projections to the lateral mammillary and dorsal tegmental nuclei arise from a minimal but overlapping population of neurons in the supragenual nucleus.

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The Supragenual nucleus(SGN) is a brainstem nucleus critical to the head direction circuit that projects strongly to the contralateral DTN and ipsilateral LMN(reciprocally connected brainstem structures thought together to generate head direction selectivity in mammals). Lesions of SGN result in the ‘bursting’ effect also seen when lesioning the upstream vestibular nuclei indicative of a functional head direction circuit disconnected from a synchronizing or updating input. This suggests that SGN may be a primary, direct provider of vestibular input to the head direction system. While it is known that SGN projects to both structures in the putative ring attractor network, it is not known whether distinct or overlapping populations in SGN project to these structures which has implications for whether SGN plays a role in synchronizing both structures during head turns or communicating with these structures in a more complicated way. We performed an anatomical study to observe whether the DTN and LMN projection in SGN arise from the same or different population. The projection to DTN is markedly stronger than that to LMN, filling most cells within the central body of the SGN while cells projecting to LMN tended to be smaller, sparser and located on the periphery of the nucleus. Many cells projecting to LMN also projected to DTN(though not the reverse). However, caution must be taken in interpreting this result as evidence of collateralization as one injection that passed through the mammillary nucleus to the ventral pial surface resulted in a similar projection pattern as some brains with positive LMN hits. These results suggest that there is a large population of neurons in SGN with distinct location and morphology characteristics that project only to DTN. A smaller, more peripheral population projects to both DTN and LMN. Future studies will use discrete injections and antibodies to characterize this input in more detail.

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72. “This Is My Spot!”: Social Determinants Regulate Space Utilization in Macaques.

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Space can be a limited resource. Many species including humans evolved a compromise regulating space sharing and its occupancy based on social determinants. For example, students in a classroom tend to sit close to their friends, keeping the same spots across days, revealing the social structure in the classroom. This place preference suggests that factors such as social hierarchy and affiliation can shape space utilization; contrasting with classical random walk models of agents moving at random in any given direction. Here, we asked whether spatial occupancy of macaques (Macaca fascicularis and M. mulatta) within a unisex group, reveals a structured space utilization beyond simple spatial affordance of the finite space. To this end, in two groups of four animals, we analyzed the simultaneously recorded positions of each individual of the group while the group roamed in an enclosure. (1) The identity of each animal could be decoded from its individual pattern of spatial occupancy, revealing that each animal sustained its spatial footprint across multiple days. (2) Average distance between monkeys was a proxy of their social hierarchy, confirming that interpersonal distance is correlated to affiliation and dominance hierarchy. (3) Alternating the social context by removing one of the monkeys revealed that social context influences occupancy. (4) Finally, the distribution of distance between pairs of monkeys was bimodal and was modeled using random walk approach with an additional parameter reflecting propensity to stay in close proximity, which was again related to dominance hierarchy. These analyses reveal the hidden structured nature of space utilization as a function of social determinants in macaques and simple modeling approach to further study group organization in neuro-ethological settings.

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73. Systems neuroscience of navigation in the naturally behaving marmoset monkey

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The daily activities of primates involve foraging, exploration and other behaviors that require a rich postural repertoire. Some, like the common marmoset monkey (Callithrix jacchus), are strikingly capable climbers and move in a complex 3D arboreal setting. Even in species with modest locomotor abilities (such as humans), 3D orientation is a fundamental part of daily life, for instance when lying prone or to the side. How does the primate brain orient throughout natural behaviors? In the last few years, pioneers studies have demonstrated that head direction cells in rodents, bats and primates encode 3D head orientation. The next step is to study how the navigation system guides behavior in naturalistic environments. To this end, our laboratory has adopted the marmoset as a model organism. Here, we present our setup and methodology to study the neuroscience of marmosets’ behavior during natural activities. We designed and built a large enclosure (1.6 m side, 4 m^3) densely filled with assorted enrichments that reproduce the natural arboreal substrate. We use a retroreflective markers-based motion capture system (Optitrack) with 24 cameras to robustly track multiple animals’ head movement simultaneously, and we plan to use data- loggers (White Matter) to record up to 64 channels of neuronal data. We train pairs of marmosets (ordinarily housed together) to enter the setup at the same time. Marmosets spent several hours per session in the enclosure and exhibit a large range of natural behaviors (exploring, grooming, foraging, eating the environment). This methodology will pave the way for ethologically-relevant investigation of the navigation system.

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74. How does an inclined surface influence head posture and spatial orientation?

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Animals traveling on a horizontal surface stabilize their head in relation to the substrate in order to gather spatial information and orient. What, however, do they do when traveling on an inclined surface? We examined how three rodent species differing in motor abilities and habitats explore a platform tilted at 0°-90° degrees. We found that traveling up or down was mainly straight vertically and rarely diagonally, with the former but not the latter resulting in identical bilateral vestibular cues. This was also achieved when traveling horizontally through rotating the head to parallel the horizontal plane. These behavioral patterns were consistent in the three rodent species, attesting for their generality. Traveling diagonally up or down was avoided, perhaps due to different bilateral vestibular cues that could hinder orientation. Neurobiological studies demonstrate that the vestibular system input is required for the ongoing activity of place cells and head direction cells. Accordingly, we suggest that maintaining identical bilateral cues is an orientational necessity that overrides differences in motor abilities and habitats and that this necessity is a general characteristic of animals in motion.

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75. Cerebellar control of a unitary sense of direction

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The head-direction system, a key neural circuit in the animal’s navigation system, consists of several anatomical structures with neurons that fire selectively to the animal’s head direction. Population activity of these cells exhibits a ubiquitous temporal organization across different regions of the head-direction system, independent of the animal’s behavioral state or sensory inputs, creating a single, stable, and persistent head-direction signal. However, the mechanistic processes behind this temporal organization are unknown. Since the cerebellum is involved in processing sensory signals, we examined how suppressing two forms of cerebellar plasticity in Purkinje cells (PKC-dependent synaptic depression and PP2B-dependent potentiation) affects the head-direction system. We first show that head- direction cell pairs from the anterodorsal thalamus and retrosplenial cortex exhibit a robust and stable neuronal coordination in the presence of an external landmark in both controls and cerebellar alteration conditions. However, when the external landmark cue was removed, neuronal coordination between the thalamus and retrosplenial cortex was abolished following the suppression of cerebellar PKC-dependent plasticity. In addition, we identify distinct roles for cerebellar PP2B- and PKC-dependent mechanisms in maintaining a stable thalamocortical head-direction signal during navigation by external landmark and self-motion inputs, respectively. These results identify new roles for the cerebellum in mediating a unitary and stable head-direction signal across the head-direction system.

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