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Cities have a negative impact on navigation ability: evidence from 38 countries

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This Data Blitz talk will briefly summarise the key information in a recent preprint from our lab with some new data analysis:

<https://www.biorxiv.org/content/biorxiv/early/2020/02/04/2020.01.23.917211.full.pdf>

Cultural and geographical properties of the environment have been shown to deeply influence cognition and mental health. While living near green spaces has been found to be strongly beneficial, urban residence has been associated with a higher risk of some psychiatric disorders. However, how the environment experienced during early life impacts later cognitive abilities remains poorly understood. Here, we used a cognitive task embedded in a video game to measure non-verbal spatial navigation ability in 397,316 people from 38 countries across the world. We found that on average, people who reported having grown up in cities have worse navigation skills than those who grew-up outside cities, even when controlling for age, gender, and level of education. The negative association between cities and spatial ability was stronger in countries with low average Street Network Entropy, i.e. whose cities have a regular layout. The association was weaker in countries with more complex, organic cities. This evidences the impact of the environment on human cognition on a global scale, and highlights the importance of urban design on human cognition and brain function

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Modulation of spatial cue processing across the lifespan: a geometric polarization of space restores allocentric navigation strategies in children and older adults

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The impact of development and healthy aging on spatial cognition has been traditionally attributed to a difficulty in using allocentric strategies and a preference for egocentric ones. An alternative possibility, suggested by our previous works, is that this preference is actually conditioned by the spatial cues (e.g., geometric or landmark cues) present in the environment rather than a strategic choice per se. We tested this prediction by having 79 subjects (children, young and older adults) navigating a Y-maze composed either of landmarks or geometric cues, with an immersive head-mounted display that allows us to record both head and eye movements. Our results show that when the performance is based on landmarks solely, children and older adults exhibit a deficit in using allocentric strategies when compared to young adults. Hence, an inverted U-profile of allocentric strategies was observed across the lifespan. This was not due to a default of attention to the landmarks, as evidenced by analysis of gaze dynamics. When geometric were provided, however, older adults and children used allocentric strategies in the same proportion as young adults. They were, in addition, as efficient and quick to implement the strategy. We thus propose a reinterpretation of the previous data in the literature, whereby reference to geometric cues is the default mode for spatial representations, which is immune to age, whereas spatial representations fail to be anchored on landmarks early in development and later in aging.

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The role of working memory capacity in spatial learning depends on spatial information integration difficulty in the environment

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A substantial amount of research has been conducted to uncover factors underlying the pronounced individual differences in spatial navigation. Spatial working memory capacity (SWM) is shown to be one important factor. In other domains such as reading comprehension, the role of working memory capacity in task performance differences depends on the difficulty of other task demands. In the current study, we investigated whether, similarly, the relationship between SWM and spatial performance was dependent on the difficulty of spatial information integration in the environment. Based on our prior work, spatial information integration difficulty depends on 1) difficulty in observing spatial relationships between locations of interest in the environment, and 2) the individual's ability to integrate such relationships. Leveraging virtual reality, we manipulated the difficulty in observing the spatial relationships during learning by changing the visibility of the buildings, and measured individual's self-report sense of direction (SOD) which modulates the ability to integrate such relationships under different degrees of visibility. We consistently found that in the "easy" spatial integration condition (high SOD with high visibility), high SWM did not significantly improve spatial learning. The same pattern was observed in the difficult condition (low SOD with low visibility). On the other hand, high SWM improved spatial learning for medium difficulty (high SOD with low visibility, or vice versa). Together, our results reveal that the role of SWM in spatial learning differences depends on spatial integration difficulty. Our results also have significant applied implications for using virtual reality to target and facilitate spatial learning.

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Navigation Using Odor Landmarks And Path Integration

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The convergence of internal path integration and external sensory landmarks generates a cognitive spatial map in the hippocampus. We studied the recognition of spatially localized odor cues as landmarks to guide navigation by recording the activity of neurons in the hippocampus of mice performing a virtual navigation task. We found that odor cues greatly enriched neural representations of place and dramatically improved navigation. Presentation of the same odor at different locations generated distinct place cell representations in the hippocampus. An odor cue at a proximal location enhanced the local place cell density and led to the formation of place cells beyond that cue. This led to the recognition of a second, more distal odor cue as a distinct landmark, suggesting an iterative mechanism for extending spatial representations into unknown territory. Our results establish that odors can serve as landmarks to guide navigation and motivate a model in which path integration and odor landmarks interact in a sequential, iterative process to generate cognitive spatial maps over long distances.

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Navigating word maps using multiple spatial codes in the human brain

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Recent theoretical and empirical work suggests that brain regions and neural codes typically recruited for spatial navigation also support navigation in abstract representational spaces. Here we investigate one of the most abstract forms of mental navigation: the one involved in comparing the meaning of words, conceived as assessing their relative positions in the conceptual semantic space. Human participants learnt the meaning of novel words as arbitrary labels for a set of audiovisual objects defined as points in a 2D space of varying sizes and sounds. While they performed a semantic comparison task over the words, we recorded the activity of their brain using functional magnetic resonance imaging (fMRI). By applying a combination of representational similarity and fMRI-adaptation analyses, we found evidence of three different 2D spatial codes: i) a grid-like code in the right postero-medial entorhinal cortex, representing the general layout of the semantic space; ii) a head-direction-like code in parietal cortex and striatum, representing the direction of transition between words; and iii) a place-like code in medial prefrontal, orbitofrontal, and mid-cingulate cortices, representing the Euclidean distance between words. Finally, we found evidence that the brain also represents the single dimensions of the words in the semantic space: their implied size was encoded in visual areas, and their implied sound in Heschl's gyrus/Insula. These results reveal that mentally processing words defined in a 2D semantic space is supported by a network of brain regions hosting unidimensional codes and a variety of bidimensional codes that largely overlap with those recruited in navigating physical space.

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Flexible modulation of navigational processing in association cortices as a function of task context

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Animals engage in a variety of navigational behaviors that require different regimes of behavioral control and different temporal scales of predictive coding. In the wild, rats readily switch between foraging and more complex behaviors such as chase, wherein they pursue other rats or small prey (Calhoun, 1963). These behaviors require vastly different tracking of multiple behaviorally-significant variables including self-motion state. It is unknown whether changes in behavioral context flexibly modulate the encoding of these variables. To explore this possibility, we compared self-motion processing in multisensory association cortices while rats performed alternating blocks of free foraging and visual target pursuit. Rats learned the pursuit task and demonstrated predictive processing by anticipating target trajectories and intercepting them. Relative to free exploration, pursuit sessions yielded greater proportions of parietal and retrosplenial cortex neurons with reliable sensitivity to self-motion. Pursuit self-motion correlates possessed enhanced signal-to-noise ratios, as a consequence of multiplicative gain modulation, which led to greater decoding accuracy of self-motion state over extended temporal windows of behavior. Finally, many self-motion sensitive neurons conjunctively tracked the position of the visual target relative to the animal in egocentric coordinates providing a potential mechanism for the observed gain changes to self-motion signals. We conclude that association cortex ensembles multiplex navigation-relevant variables in a dynamic manner to enhance behaviorally-relevant computations as a consequence of task demands.

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Representations for real world space during virtual reality navigation in the rat hippocampus

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During unconstrained real world (RW) exploration, rodent hippocampal activity shows robust spatial selectivity, which is hypothesized to be governed by distal visual locomotion cues, along with contributions from other sensory-motor cues. To dissect the contributions of these different variables on hippocampal spatial selectivity, we have recently developed a virtual reality apparatus. Here, the rat runs on a spherical treadmill that floated freely on an acoustically quiet air cushion, to receive liquid rewards through a tube in front of the rat. Our VR system employs a hinged harness that gently body-fixes the rats but allows for head movements around body. The harness, reward tube and VR chassis constitute a novel, constrained real world (c-RW) where the rat's legs and head can move freely but his body does not. Movement of his legs cause a rotation of the spherical treadmill that induces a change in the virtual scene, i.e. virtual movement, without any significant change in the rat's position in the c-RW position. In previous studies we found that during random foraging in VR, spatial selectivity is markedly reduced while directional modulation was comparable to RW [1, 2]. Here, we investigated the selectivity in c-RW while the rat performed two dimensional navigational tasks in the VR space. We find that a substantial number of neurons showed selectivity to the rat's head angle in the c-RW environment, in the absence of task demands in the c-RW frame and in the absence of active navigation driven changes in c-RW position (owing to body restriction). Our results suggest that hippocampal neurons can simultaneously maintain representations of real and virtual environments and have important implications for the growing use of virtual reality for scientific, and commercial uses.

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Learning cognitive maps as structured graphs for vicarious navigation

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Cognitive maps are mental representations of spatial and conceptual relationships in an environment. These maps are critical for flexible behavior as they permit us to navigate vicariously, but their underlying representation learning mechanisms are still unknown. To form these abstract maps, hippocampus has to learn to separate or merge aliased observations appropriately in different contexts in a manner that enables generalization, efficient planning, and handling of uncertainty. Here we introduce a specific higher-order graph structure – clone-structured cognitive graph (CSCG) – which forms different clones of an observation for different contexts as a representation that addresses these problems. CSCGs can be learned efficiently using a novel probabilistic sequence model that is inherently robust to uncertainty. We show that CSCGs can explain a variety of cognitive map phenomena such as discovering spatial relations from an aliased sensory stream, transitive inference between disjoint episodes of experiences, formation of transferable structural knowledge, and shortcut-finding in novel environments. By learning different clones for different contexts, CSCGs explain the emergence of splitter cells and route-specific encoding of place cells observed in maze navigation, and event-specific graded representations observed in lap-running experiments. Moreover, learning and inference dynamics of CSCGs offer a coherent explanation for a variety of place cell remapping phenomena. By lifting the aliased observations into a hidden space, CSCGs reveal latent modularity that is then used for hierarchical abstraction and planning. Altogether, learning and inference using a CSCG provides a simple unifying framework for understanding hippocampal function, and could be a pathway for forming relational abstractions in artificial intelligence.

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Looking, liking and locating: an experimental aesthetics of orienting

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Perceiving an object in the world is an experience defined in space and time and stored in memory with this contextual information. Memory for object-location associations has been extensively studied in the spatial cognition literature, but little is known about the interplay between subjective aspects of experience and spatial representation. We here investigated how aesthetic experience of an object could incidentally affect the representation of that object's spatial location. 96 participants (86 tested at science festivals, 10 at the laboratory) visited an onscreen virtual museum, with the sole instruction of evaluating the paintings they saw. Afterwards, participants were represented with the paintings, reported their liking for them and recalled their location on the museum map. Participants remembered better the location of paintings that created strong aesthetic experiences, whether positive or negative, suggesting an arousal effect. In turn, more positive aesthetic experience increased the ability to recall on which wall the painting was hung. Since recalling the wall requires recalling heading direction, this finding suggests that positive aesthetic experience enhances first-person spatial representations. These results were independent from looking time. Overall, this suggests that the affect-space association, which has an obvious ecological importance in the case of highly emotional threatening events, might also extend to aesthetic stimuli, that generate distinctive human experiences without evident link to basic survival behaviors. Aesthetic experience of stimuli can thus shape the cognitive map. These results may have implications for museum design.

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Place to place: comparing place learning across immersive and desktop VR platforms

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Place learning is a key component of navigation and describes the use of internal and external informational cues to encode and recall a location in the world around us. Empirical examinations of this behaviour typically employ tasks in which participants learn a hidden location using allocentric and egocentric navigational cues, the availability or reliability of which can be manipulated to identify their respective contributions to performance. These tasks commonly use desktop PC-based virtual environments that require participants to be seated at a computer, thus limiting the full motility that characterises (and informs) real world navigation. This presentation details a direct comparison between immersive VR and desktop versions of the same place learning task. Participants learned the location of a target object relative to either allocentric or egocentric cues (i.e. landmarks, or their starting position, respectively), or in conjunction, across three conditions. We observed similar patterns of results across both platforms, although there was no correlation in individual performance across the two versions of the task when participants employed either egocentric or allocentric cues in isolation. Whilst the absence of correlations may correspond to differences resulting from translating the task across experimental platforms (e.g. environmental scale), they may also highlight the contribution of self-movement information when completing assays of navigational ability.

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Age-related differences in brain regions linked to visuo-spatial processing during landmark-based navigation

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Healthy older adults are impaired in their capacity to navigate efficiently which significantly reduces their autonomy and mobility. Behavioral studies have revealed age-related changes in multiple visuospatial abilities including the capacity to perceive and integrate visual landmarks for spatial navigation (e.g., a lamppost). However, the functional and neurobiological factors underlying the decline of landmark processing in healthy ageing remain insufficiently characterized. To address this caveat, we used functional magnetic resonance imaging to investigate the brain activity associated with landmark-based navigation in young and older participants. 25 young and 17 older adults took part in an active virtual navigation task in which they had to orient in a Y-maze using landmarks. Whole-brain as well as region-of-interest (ROI) analyses were conducted with a focus on high-level visual regions linked to navigational functions: the parahippocampal place area (PPA), the occipital place area (OPA) and the retrosplenial cortex (RSC). Results showed that older adults made more errors and that they relied on different navigational strategies to solve the task. Direct comparisons between groups revealed greater anterior temporal activity in young participants. In addition, only young adults showed activity in occipital areas dedicated to processing information from the central visual field. ROI analyses unveiled age-related differences exclusively in the OPA, with significantly higher OPA activity in older subjects. Overall, our results suggest that brain regions involved in the representation of fine-grained visual information may be disrupted in ageing which could in turn diminish the ability to use landmarks for navigation. This work helps towards a better comprehension of the neural dynamics subtending landmark-based navigation and it provides new insights on the impact of age-related visuospatial processing differences on navigation capabilities.

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Influence of sensory conditions on the hippocampal code for space

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Hippocampal place cells show both stable representation of the environment as well as flexibility to changes of the features of the environment, behavioral and task context. Balance between stability and flexibility of spatial representations relies on the concurrent update of internal spatial representation by external sensory inputs and self-motion cues, however, it is still not known how exactly these inputs interact to build a stable representation of a certain location ("place field") or how their mismatch results in changes of the representation. Here we use the novel CAVE Virtual Reality system for freely-moving rodents (Del Grosso et al., 2017) that allows to investigate the effect of visual- and positional- (vestibular) manipulation on the hippocampal space code while keeping natural behaving conditions.

Specifically, we investigate the effects of a conflict between visual-cue-defined and physical-boundary-defined reference frames on the hippocampal representation of space. Despite previous suggestions that place cells responsive to visual and self-motion cues are anatomically separated (Fattahi et al., 2018), we provide experimental evidence that the same place cell can be involved in representing both reference frames. We confirm the dominance of one reference frame on the other on the level of place fields, when the information about one reference frame is absent (Gothard et al., 2001). We show that the hippocampal cells form distinct categories by their input preference - surprisingly, not only that they are being driven either by visual / allocentric information or by self-motion / distance to the physical boundaries, but also by a specific combination of both. We found a large category of units integrating inputs from both allocentric and idiothetic pathways that are able to represent an intermediate position between two reference frames, when they are in conflict and controlled by a non-visual reference frame in darkness.

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Cognitive underpinnings of individual difference in spatial navigation

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There is great variability in spatial navigational abilities across the general population, and impairments can adversely affect quality of life. Previous research has sought to identify the cognitive underpinnings of variance, implicating factors that include spatial working memory and mental imagery manipulation. Assays of concomitant navigational difference have, however, tended to focus on a relatively restricted range of navigational processes. Here, we present findings from a large-scale project that seeks to examine differences across a wide range of behaviours in typical and impaired adults. Participants completed a comprehensive battery of measures that included real-world navigation (e.g. route learning, computing shortcuts), laboratory tasks (e.g. place learning, path integration), and standardised cognitive assessments (e.g. attention to detail, executive function). Analyses of typical adult data revealed several links between navigational behaviours and cognitive performance. In the real world, route learning from a map was associated with working memory, whilst combining two learned routes was related to mental rotation ability. In the laboratory, allocentric place learning shared variance with spatial working memory, path integration, and spatial anxiety. Ongoing testing will further enable us to characterise navigational impairment with inclusion of neuropsychological data from people with hydrocephalus, a common neurological condition associated with everyday wayfinding difficulty. Clusters of abilities that characterise strengths and weaknesses in performance, across participants, will be confirmed with machine learning techniques.

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Moving in the environment and finding the shortest way to places: the role of familiarity and individual visuo-spatial factors

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Individual familiarity with an environment and visuospatial factors (abilities, preferences and strategies) influence how well people form elaborate mental representations of environments. These representations are usually assessed with tasks that involve managing spatial information, such as pointing and landmark locating tasks. No studies published to date have used a “field” task, such as finding the shortest way to a destination in a familiar environment, to assess people’s mental representations.

The present study aims to examine: (i) the role of familiarity with an environment by assessing people’s performance in terms of their actual movements to find the shortest way to a destination, and in tasks that involve managing spatial information; and (ii) how their performance relates to individual visuospatial factors.

Undergraduates either highly or scarcely familiar with their university campus (45 in each group) were administered a shortest path finding task, and several visuospatial measures, as well as pointing and landmark-locating (spatial information managing) tasks. The results showed that the high-familiarity group performed better in finding the shortest ways to places on campus, and the effect an individual’s sense of direction. Familiarity had no effect on the spatial information managing tasks. An effect of individual visuospatial factors only emerged for pointing task performance.

This study contributes to what we know about how individual factors, in terms of familiarity and visuospatial abilities, preferences and strategies, jointly support our knowledge of an environment, also offering insight on the differences between various methods used to assess spatial knowledge.

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Cerebellum stabilizes and coordinates a unitary mental representation of direction

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A key element in navigation, direction, is encoded by the activity of head direction (HD) cells, where an HD cell fires when the animal's head points in a specific direction. HD cells anchor to external sensory (allothetic) cues, but maintain a coherent firing upon complete external cue removal, potentially driven by self-motion (idiothetic) cues. Although it is clear that HD cells have access to both types of information, it is unclear how and wherein the brain such information is processed and fed to the HD cells' circuitry. Since the cerebellum is involved in processing sensory signals, we hypothesized that an alteration in the cerebellar cortical function may impact HD cells' activity pattern and their network organization. We used two Purkinje cell-specific transgenic mouse models, one with a deficiency in protein kinase C (PKC)- mediated long-term depression (L7-PKC) and the other with a deficiency in protein phosphatase 2B (PP2B)-mediated potentiation (L7-PP2B).

Simultaneous monitoring of thalamic and retrosplenial HD cells' activity in freely behaving mice revealed an intact generation of HD activity patterns in these mice. However, while the HD activity pattern in L7- PKCI mice exhibited significantly lower stability during navigation by self-motion cues, in L7-PP2B mice it exhibited an impaired anchoring to the external cues. Furthermore, while the HD cell pairs in control mice exhibited a preserved temporal coordination under different sensory conditions, thalamic and retrosplenial HD cell pairs in L7-PKCI mice exhibited weakened coordination during navigation by self-motion cues. This suggests that the thalamus and the retrosplenial cortex might be part of two independent attractor networks under the influence of cerebellar computations. Overall, our results suggest that the cerebellum drives the stabilization and the coordination of a unitary mental representation of direction by playing a pivotal role in processing multimodal sensory signals.

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The effects of acquired vestibular pathology on the organization of exploratory behavior in mice

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A growing body of literature involving genetic mouse models (e.g., tilted, Usher) has demonstrated a crucial role for the vestibular system in the organization of exploratory behavior. Movement during exploration consists of highly organized sequences of stops and progressions centered around a home base under dark and light conditions. Whether disruptions in the organization of exploratory behavior observed in genetic models reflect developmental effects associated with vestibular pathology, or are a direct result of vestibular dysfunction, remains to be determined. The current study investigated the effects of acquired vestibular pathology on the organization of exploratory behavior under dark and light conditions in adult mice. Mice that received bilateral chemical labyrinthectomies and non-operated control mice explored a circular table three weeks after surgery under completely dark conditions, followed by another exploratory session one week later under light conditions. Average peak speed and total stop time were included as measures of general locomotor function. Average change in heading and average peak error were included as measures specific to movement organization. Changes in heading occur between stops and are typically small in control rodents. Peak error measures the variability in the location of the peak speed during a progression and is typically seen at the midpoint of a progression in control rodents. Vestibular lesions spared measures of general locomotion, while measures specific to exploratory organization were disrupted in mice with vestibular pathology. This pattern of results depended on the environmental condition, with deficits in peak error mediated by access to visual cues. The results of this study add to a growing body of literature demonstrating a role for the vestibular system in supporting spatial orientation.

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Subiculum neurons respond to multiple orientations to encode a direction-based map of the environment

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Hippocampal and cortical neurons exhibit a diversity of forms by which neurons map an animal's location and orientation within a well-defined set of boundaries. Yet, natural settings have complex borders such that humans orient to a variety of reference cues including landmarks and major pathways.

We recorded spiking activity from subiculum (SUB) and CA1 in rats as they foraged in an open arena and as they navigated within a path network of three repeatedly intersecting axes. For the latter, rats were cued on each trial to start at a given perimeter position and ran triangle-shaped routes of large or small scale as dictated by the local maze structure. Nearly all rats proved capable of solving this problem, yet they relied upon location in the experimental room to guide their choices.

CA1 neurons exhibited typical place-specific firing, but SUB neurons did not. Instead, multiple activity fields dispersed across the path network were best described as directional tuning fields. In contrast to what are known as 'head direction cells', SUB directional tuning fields were more complex, often having multiple orientation tuning peaks with different peak firing rates. Thus, the tuning of SUB neurons is distinct from that of 'place' and 'head direction' cells when animals locomote known routes within a path network. Multi-orientation tuning for individual neurons varied according to task demands (open-field foraging versus route-running), suggesting that such tuning is learned and/or context-dependent.

The present findings extend those of earlier work demonstrating 'axis tuning' of SUB neurons to show that SUB neurons exhibit a wide range of offsets in directional tuning peaks. In the context of a path network, this means that unique sub-populations will encode not just the animal's current heading, but the combination and sequencing of headings it takes before and after turns.

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The benefit of multisensory integration in spatial navigation

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During navigation, information about external objects used as landmarks usually comes from different sensory modalities, such as vision and audition. Past research has shown that integration between visual landmarks and self-motion information based on vestibular and proprioceptive cues can improve navigation. However, it is still unclear the advantage of combining multisensory external cues on navigation. Here we investigate how humans exploit multisensory landmarks to improve their performance in a navigation task. In a dark room, subjects had to return a bright object to its original location by using landmarks after an exploration phase. The three provided landmarks could be only visual, only auditory, or both visual and auditory. Participants could see only the bright object and visual landmarks, but did not have other spatial references of any sort. Return and exploration phases were interleaved by a disorientation phase, which prevented the use of self-motion information. Root mean square error (RMSE) and variable error of responses were measured. Results showed that, when both visual and auditory information were available, RMSE decreased, if compared with only auditory landmarks condition. Moreover, variable error slightly decreased if compared with only visual or only auditory landmarks conditions, thus indicating increased precision when multisensory cues are available. In addition, modeling analysis revealed that variable error in multisensory landmarks condition was consistent with Bayes optimal integration model. These findings suggest that landmark-based spatial navigation might benefit from the integration of audio-visual cues.

The present study shows that multisensory processing of landmarks can improve the ability to orient and spatially navigate through space. This finding provides the basis for the development of novel rehabilitation tools and procedures to enhance orientation and mobility based on the integration of different sensory modalities.

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Improving Human Spatial Orientation Using A Virtual Training Program

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Learning to form a mental representation of the surrounding is a critical skill for human spatial navigation since, once formed, they allow individuals to reach any place from anywhere within the environment. Such a mental representation is commonly referred to as a “cognitive map” and exist to provide detailed information about environmental landmarks and, importantly, their spatial relationships. Although evidence suggests that spatial orientation skills are malleable in humans, it remains unknown whether cognitive map formation as a skill can be adequately improved with a training program. In this study, we present a newly developed, 12-day computerized training program situated in a virtual environment that was designed explicitly to improve the ability to form cognitive maps. We asked 15 healthy volunteers to complete the training program and a comprehensive spatial behavioral assessment before and after the training. Throughout the training program, participants were asked to navigate back and forth between environmental landmarks until they developed an understanding of the spatial relationship between those landmarks. They started first in a small area of the virtual environment and slowly progressed to larger and larger areas. Participants continued this process until they had learned the spatial relationships of each landmark to one another. Participants’ performance at the pre and post-training tests provide evidence that the training program was sufficient to improve participants’ ability to form mental representations of environmental-scale surroundings, suggesting that the ability to form cognitive maps for human navigation and orientation can be trained. We discuss the potential impact of the training program to improve the lives of those affected by topographical disorientation resulting from an acquired brain damage or affected by Developmental Topographical Disorientation.

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A systematic view of the interactions between Theta and Gamma generators in CA1

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Can we obtain a detailed picture of the theta-gamma interactions in CA1? We exploit silicon probe recordings perpendicular to the hippocampal layers to address this issue.

To get rid of volume conductance effects we first applied Current-Source Density analysis to contact points spanning the entire interval between CA1 pyramidal layer and the Dentate Gyrus. For each CSD time-series we computed the phase-amplitude relationship between the theta oscillation and the power of oscillations at higher frequencies. Each CSD signal is then associated to a 2D matrix describing the coupling of specific "Gamma" frequencies to certain phases of the theta period. Significant components of this coupling can be defined by circumscribing contiguous regions of above-mean correlation. To follow the presence of certain coupling components across different depths we tiled the 14 2D matrices from each contact as slices of a global 3D matrix. Significant coupling values found at different depths are then concatenated along the vertical axis. We consider an extended notion of interaction components as continuous regions in the 3D phase-amplitude-depth space, or basins.

We identify 3 of these basins consistently present in all animals (n=6), coinciding with 3 separate ranges of gamma frequencies, already familiar in the hippocampal literature: Low (20-45 Hz), Medium (60-90 Hz), and Fast (100-180 Hz) Gamma. Each of them has a distinctive profile: Medium and Fast Gamma are the most localized, with a prominent maximum in the SLM and pyramidal layer respectively. Slow gamma shows a slight dominance in the s.pyramidale and s.radiatum. We show that the relative strength of the basins components varies according to task demands. A more accurate description (and visualization) of the interaction between the Theta and Gamma generators in CA1 can help disentangle the contributions of such computational entities to spike-time-dependent phenomena, like phase precession and theta sequences.

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Phase precession selectively appears in a sub-population of CA1 place cells in association with dominant medium Gamma power

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The phenomenon of phase precession is considered as the potential foundation for the emergence of temporal coding in the hippocampal region, especially in the CA1 network. Nevertheless, the underlying mechanisms remain largely unknown, also in terms of the contribution of the different input sources converging on this area.

Here we investigate the association of oscillatory events at distinct gamma frequency ranges with the emergence of phase precession in CA1 pyramidal cells. We take advantage of a combination of silicon probe recordings spanning the entirety of the CA1 layers, and of tetrode recordings in the pyramidal layer to study phase precession during linear track exploration in mice. We removed volume-conductance effects from the LFPs with the use of Current-Source Density analysis.

First, we observe a clear-cut separation of otherwise homogeneous place cell population in two classes, depending on the cell's spikes relationship with the theta oscillation. The two classes present complementary properties emerging from an unsupervised clustering procedure: cells in one class present neat phase precession profiles, and low phase locking scores; conversely, the other class is characterized by high mean vector lengths scores, and poor phase precession scores.

Furthermore, we identify a strong correspondence between the relative strength of gamma oscillations in the slow (20-45Hz) and medium (60-90Hz) range, and the appearance of the phase precession slope. By inferring spike occurrence probabilities from a GLM fitted to the combination of instantaneous location in the place field, theta phase and gamma power extracted from different layers, we are able to show how phase precession only becomes predominant in the presence of a strong medium gamma, and conversely almost completely disappears when slow gamma dominates. These results point to a major role of Entorhinal Cortex input interacting with local circuits in regulating and sustaining the phenomenon.

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Passive paradigm grid-cell-like representations at 7 tesla fMRI

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Individuals at genetic risk of Alzheimer's disease (AD) show altered grid-cell-like fMRI activation in entorhinal cortex (EC), where pathological tau protein initially accumulates. Identifying quantifiable markers of EC dysfunction in preclinical AD would aid early detection of disease and application of therapeutics aimed at delaying or preventing the onset of dementia. This pilot study explored two new methods for assessing fMRI grid-cell-like representations (GLRs). First, we used ultra-high-resolution 7 tesla (7T) MRI to segment anterolateral and posteromedial EC subdivisions to determine the anatomical origin of EC GLR. Second, we employed a passive path integration paradigm that does not require a joystick or buttons for participant self-motion.

10 healthy volunteers (age range 23-56 years) completed this video-based path integration task during 7T BOLD fMRI. We demonstrate significant hexadirectional GLRs in the right but not left posteromedial EC subdivision – independent of age, gender, temporal signal-to-noise ratio and volume. GLRs were reduced in anterolateral EC and other control comparators. Age moderated the effect, with older adults showing increased left, but decreased right, posteromedial EC GLRs.

This shows GLRs can be reliably achieved using 7T during a passive navigation paradigm. The maximal signal in right posteromedial EC subdivision is concordant with previous fMRI studies and the regional specificity of grid cells in the homologous rodent medial EC. This may deliver a clinically appropriate fMRI measure for detecting and tracking the earliest EC dysfunction at the onset of AD.

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Cognitive mechanisms of Developmental Topographical Disorientation

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Navigating and orienting in the environment is a complex and demanding process that occasionally results in getting lost. However, for certain people without brain damage or other cognitive or neurological complaints, getting lost is a daily challenge they have experienced their entire adult life. These individuals are affected by Developmental Topographical Disorientation (DTD). Individuals with DTD get lost even in the most familiar surroundings including their neighbourhood or the building where they have worked for many years, and in the most extreme cases, their own homes. Here, we report the findings of a decade-long study aiming at describing the behavioural and cognitive mechanisms of DTD in a large sample of over 1200 cases. We describe the demographics, heritability pattern, self-reported and objective spatial ability, and some personality traits of individuals with DTD as compared to a sample of over 1600 healthy controls. We found that individuals with DTD reported relatively greater levels of neuroticism and negative affect, and rated themselves more poorly on self-report measures of object, face, and place memory and imagery. On interactive assessments of cognition, the individuals with DTD struggled on a scene-based perspective-taking task and on tasks that demand the generation and use of a cognitive map, but not on a face memory task. These novel findings help to phenotypically describe DTD, and provide a foundation for future investigations into the neurological and genetic mechanisms of this developmental condition.

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Sex Differences and Age-Related Changes in Spatial Navigation

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Spatial navigation is supported by a set of cognitive processes that are essential to everyday life. Sex differences in spatial ability are evident across mammalian species, and distinct aspects of successful human navigation—including wayfinding, path integration, and navigation strategies—change with advanced age. However, it is unknown whether navigational deficits emerge early in the aging process or whether age-related changes vary by sex. This represents a critical gap in our understanding of the aging brain, especially given an increasing awareness that navigation deficits are an early behavioral fingerprint of dementia. Here, we tested the hypothesis that age-related deficits in navigation are evident by midlife and vary by sex. In a series of studies, we tested healthy young (ages 18-28, n = 85) and midlife (ages 43- 61, n = 66) adults on three aspects of navigation using immersive virtual environments: 1) path integration, which relies on proprioceptive and vestibular self-motion cues; 2) spatial knowledge, the process of forming and using a cognitive map to navigate in a new environment; and 3) navigational strategy, which refers to the nature of the path (learned route or shortcut) individuals select to navigate to a goal location in a known environment. Results reveal three major findings. First, path integration ability is preserved through midlife and does not differ by sex. Second, robust sex differences in spatial knowledge acquisition are observed in young adulthood, which persist but are diminished with age. Third, by midlife men and women show decreased ability to acquire spatial knowledge and an increased reliance on taking habitual paths. Together, our findings indicate that age-related changes in navigation ability and strategy are evident by midlife. Although path integration is typically used as an early marker for dementia, spatial knowledge acquisition and strategy use may be more sensitive to the earliest stages of the aging process.

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AutoPI: a new behavioral paradigm to study path integration in mice

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When external landmarks are absent or unreliable, animals rely on self-motion cues such as proprioceptive and vestibular information to keep track of their position. This form of navigation, called path integration, has been observed in many animals, ranging from insects to humans. Progress in our understanding of the neural basis of path integration has been slowed down by the lack of standardized tasks suitable for simultaneous electrophysiological recordings in rodents.

Here we present a new automated task to study path integration in mice. The mouse first learns to press a lever to obtain a food reward in a home base. During training, the lever is moved out of the home base and onto a circular arena. On each trial, the mouse has to leave the home base and search for the lever on the arena. Pressing the lever triggers the delivery of a food reward in the home base. The mouse has to return to the home base to receive the food reward. Half of the trials are performed in total darkness, and the position and orientation of the lever vary across trials. The ability of a mouse to return to its home base in darkness relies on path integration.

We found that mice can perform more than 100 trials per day and that simultaneous recordings of spatially selective neurons during the task is possible. In a pilot study, we assessed homing accuracy in a mouse model of tauopathy (TauP301S). Homing accuracy in mutant mice was impaired when performance depended on path integration.

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Effects of visual inputs on neural dynamics for coding of location and running speed in medial entorhinal cortex

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Neuronal representations of spatial location and movement speed in the medial entorhinal cortex (MEC) during the “active” theta state of the brain are important for memory-guided navigation and rely on visual inputs. The spatially periodic firing of grid cells in the MEC is widely recognized as a neuronal correlate of spatial location and two potential speed signals, a speed signal by firing rate and a speed signal by local field potential theta frequency, have been hypothesized to estimate changes in location and update grid cell firing. However, little is known about how visual inputs change the neural dynamics underlying the coding of location and running speed as a function of time. By manipulating visual inputs in mice, we demonstrate that changes in spatial stability of grid cell firing as a function of time correlate with changes in the proposed speed signal by local field potential theta frequency. In contrast, visual inputs do not affect the speed modulation of firing rates. Moreover, we provide evidence that sensory inputs other than visual inputs can support grid cell firing, though less accurately, in complete darkness. In summary, changes in spatial accuracy of grid cell firing on a 10-s time scale suggest that grid cell firing is a function of velocity signals integrated over past time.

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Ripple Band Phase Precession of Place Cell Firing During Replay

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Phase coding offers several theoretical advantages for information transmission compared to an equivalent rate code. Phase coding is shown by place and grid cells in the rodent hippocampal formation, which exhibit theta phase precession, firing at progressively earlier phases of the movement related 6- 12Hz theta rhythm as their spatial receptive fields are traversed. Importantly, however, the opportunity for phase coding does not depend on a specific carrier frequency. We therefore asked whether hippocampal place cells also exhibit phase coding during 150-250Hz ripple band activity, when they are thought to replay information to neocortex. We found that place cells show robust ripple band phase precession during replay events. Specifically, we demonstrate that place cells which fire multiple spikes during candidate replay events do so at progressively earlier phases of the ripple band cycle; and that spikes fired by each place cell across all replay events exhibit a consistently negative relationship between decoded location within the firing field and ripple band firing phase. These results provide insights into the mechanisms underlying both phase coding and place cell replay, as well as the neural code propagated to downstream neurons.

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Cellular determinants of locomotion-dependent CA1 pyramidal cells activation (or silencing) during virtual navigation

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Spontaneous locomotion strongly influences the state of the hippocampal network and is critically important for spatial information coding. However, the intracellular determinants of CA1 pyramidal cells activation (or silencing) during locomotion are poorly understood. Here we recorded the membrane potential of CA1 pyramidal cells (PCs) while non-overtrained mice spontaneously alternated between periods of movement and immobility during a virtual spatial navigation task. We found opposite membrane potential (Vm) polarization between two populations of CA1 PCs during movement. While the Vm of regular firing CA1 PCs was depolarized during movement leading to higher firing rates (LocomON cells), the Vm of intrinsically bursting CA1 PCs was hyperpolarized in a speed dependent manner (locomOFF cells). Furthermore, LocomON cells were depolarized during sharp wave-ripples (SWRs) while LocomOFF cells were hyperpolarized in line with recent report of functional heterogeneity among CA1 pyramidal cells during these network events (Valero et al., 2015). At the population level, 2-photon calcium imaging experiments revealed an absence of recruitment of LocomOFF CA1 pyramidal cells during synchronous calcium events and cell assemblies during immobility unlike LocomON cells. Altogether these results reveal the locomotion and speed dependent hyperpolarization of the Vm of a specific population of intrinsically bursting CA1 pyramidal cells likely embedded in a specific subnetwork. This mechanism could enhance signal to noise ratio for efficient spatial coding at high speed in familiar environments.

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The fear to move in a crowded environment. A poor spatial memory related to agoraphobia disorder

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Individuals with agoraphobia, who have fear of moving in large or crowded open spaces, exhibit an impaired exploratory activity when navigating in an unfamiliar environment, focusing primarily on escape routes. However, no studies investigated their ability to acquire and process spatial information, considering the use of egocentric and allocentric frames of reference, or taking into account environments with or without people. 106 individuals (53 with agoraphobia and 53 control compared by age, sex and education) navigated in a virtual public square for 12 minutes, in order to acquire spatial information which included recognition of landmarks, the relationship between landmarks and themselves (egocentric coordinates) and regardless themselves (allocentric coordinates). Half of participants of both groups navigated in a square without people and the others in a crowded one. Successively, they completed a visuo-spatial working memory test and spatial tasks measuring landmark recognition as well as egocentric and allocentric judgments concerning the explored square. Results showed that individuals with agoraphobia recognized a lower number of landmarks only in the crowded condition ($p < .05$), had a worse performance in egocentric and allocentric tasks in both conditions ($ps < .001$), and a reduced working memory only when active processing of spatial elements is required ($p < .001$), than the control group. Summarising people with agoraphobia were able to recognize landmarks, except when they were in a stressful condition, whereas they were unable to provide egocentric and allocentric judgments in both conditions. Worse performance in the active process of the visuo-spatial working memory suggests that these individuals exhibit spatial difficulties particularly when performing complex spatial tasks requiring them to process and transform information simultaneously.

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What's in a task? Support for the construct validity and the ecological validity of several spatial cognition tasks.

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In our daily lives, we learn information about spatial environments across different timescales. When we visit a new town for the afternoon, we have only hours to learn its structure. When we move to a new town (e.g., to go to college), we have weeks or months to learn the environment. When we have lived in the same town for many years (e.g., our hometown), we have had extensive experience to accumulate spatial knowledge. The first goal of our project was to test spatial knowledge across these timescales.

We suggest that one critical aspect of the construct validity of spatial memory tasks is that there should be a similar pattern of errors between tasks (Huffman and Ekstrom, 2019 *Spatial Cognition & Computation*). Thus, the second goal of our project was to seek converging evidence of how participants distort their spatial memories across many tasks and timescales.

In three experiments, we studied the structure of spatial representations across tasks and varying levels of exposure. In Experiments 1 and 2, we compared the relationship between new spatial learning and spatial memory for a local university campus with which participants had moderate levels of recent exposure. In Experiment 3, we compared the relationship between new spatial learning and spatial memory for the participants' hometowns (i.e., very long-term experience). We observed a similar pattern of errors across tasks and this relationship held for both recently learned environments and for real-world environments with which participants had varying levels of experience navigating in their daily lives. Moreover, extending other studies using virtual environments, our results provide support for the notion that participants employ non-Euclidean spatial representations, even for their hometown environments with many years of experience. Altogether, our results provide converging evidence to support the construct validity and the ecological validity of several commonly used tasks in spatial cognition.

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A sampling model of multimodal spatial orientation

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Building accurate spatial representations requires us to combine beliefs about continuous movements in space (path integration) and reorientation cues (sensory inputs). Previous work has identified two broad strategies for such “cue combination”: Averaging strategies, in which each cue contributes to the final estimate, and Sampling strategies, in which one cue overrides the other. To distinguish between these accounts, we designed an experiment in which participants had to estimate their heading direction by combining continuous vestibular cues with punctate, and sometimes erroneous, visual input. By measuring the extent to which their estimated heading changed as a function of the mismatch between the visual cue and the true heading direction, we found that people either reoriented entirely to the visual cue, or else ignored it completely, sticking with the predictions of their internal model. Such behavior is the hallmark of sampling. Moreover, the probability with which sensory cues were ignored was well described by a computational model in which the estimate is sampled from a posterior distribution over heading direction given the path integration and sensory input cues. Taken together our findings suggest that heading direction is computed using a sampling approximation to the optimal Bayesian strategy.

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The role of visual, auditory, and tactile cues in the perception of illusory self-motion (vection)

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Virtual reality (VR) is being increasingly used in a variety of domains, such as training, research, and entertainment. One of the most critical components to an immersive experience in VR is vection, defined as the illusion of self-motion. The objective of the present study was to investigate the influence of different sensory cues on the sensation of vection in a virtual environment. To achieve this, a sample of 24 younger adults was recruited to participate in a study at the Toronto Rehabilitation Institute's VR laboratory. Participants were seated on a rotatable chair and exposed to a revolving stimulus aimed to induce the illusion of self-rotation (i.e., circular vection). The rotating stimulus contained visual (photorealistic virtual office scene), auditory (three stationary sound sources placed within the same virtual office scene), and/or tactile (a circular handrail within reach that rotates around the participants) cues. All participants were exposed to trials that either included a single sensory input, a combination of two, and all three sensory cues presented together. Following each trial, data on vection intensity and duration was collected verbally using scales ranging from 0-10, and 0-100%, respectively. Results indicated that all three sensory cues successfully induced vection when presented independently, with visual cues eliciting the most compelling sensation followed by auditory and tactile to a smaller degree. A prominent multisensory effect was also found wherein vection intensity and duration were both notably higher in conditions that contained multiple sensory cues compared to just one. These findings confirm that vection is not just a visual phenomenon but rather a multisensory experience that can be bolstered with the addition of sensory cues. These findings will contribute towards understanding how multisensory stimulation influences vection, and furthermore inform strategies to improve levels of immersion for an optimal VR experience.

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A river runs through it: Brain representations of segmented environments

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Spatial environments are often segmented into multiple regions or compartments. How is this spatial segmentation represented in the brain? Previous studies have suggested three possible mechanisms: grouping (boundaries warp the global map, making locations in different segments appear more distant than they actually are); schematization (locations are coded with respect to environmental boundaries, in a way that generalizes across segments); and remapping (each segment is represented independently, with no integration into a global map). To test these possibilities, we taught participants the locations of 16 objects within a segmented virtual environment and then used fMRI to assess location codes for these objects. The environment consisted of a virtual courtyard transected by a river that divided it into two geometrically identical segments. Visibility and spatial relations between objects were balanced to be identical within and between segments. After training, participants' distance estimations and free recall order were affected by the spatial segmentation, suggesting that their mental representations were affected by the presence of the river. Analysis of multivoxel fMRI activity patterns revealed that spatial relations between objects were coded in the hippocampus, occipital place area (OPA) and retrosplenial complex (RSC). Notably, OPA and hippocampus coded schematic representation of the individual segments, such that objects in geometrically equivalent locations within the two segments were represented as being spatially similar, while RSC coded a global map of the environment. We did not find evidence for grouping or remapping. Our findings suggest that spatial segmentation can be induced by topographic feature of the environment even when all parts of the environment are co-visible, and that segmented environments are encoded using a combination of schematic representations of the segments and a global map.

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Common and distinct roles of frontal midline theta and occipital alpha oscillations in coding temporal intervals and spatial distances

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Where and when are two critical elements essential to remembering daily events and navigating through space. The human medial temporal lobe play a significant role in supporting memory and navigation and also display low-frequency oscillations, a candidate mechanism underlying spatiotemporal processing. A previous study from our lab (Vass et al., 2018) showed that low-frequency oscillations code distance traveled in the absence of sensory input. It remains unclear, however, whether and how neocortical low- frequency oscillations recorded at the scalp might also be important for spatiotemporal coding. To address these issues, participants navigated a plus maze in virtual reality that contained teleporters while we simultaneously recorded wireless scalp EEG. Participants determined whether they were teleported a short or long distance/duration in order to find the appropriate navigational goal. Here, we show that spatial and temporal judgments manifested in partially independent oscillatory profiles: alpha power related to distance judgments while frontal theta power related to temporal judgments; beta decreases were related to both. Furthermore, we found changes in posterior alpha frequencies indexing both spatial and temporal judgments, suggesting a novel role of frequency coding in space and time. We also show that fine-grained time information could be decoded during teleportation by classifiers trained on 2-30Hz power at the level of hundreds of milliseconds. We also compared neural pattern similarity between trials with different perceptual histories, demonstrating an effect of past trials on temporal but not spatial judgments, suggesting an additional distinction between the neural codes for spatial and temporal judgments. Together, these findings support partially independent coding schemes for spatial and temporal information and suggest that low-frequency oscillations play important roles in coding both space and time.

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Effects of geographic scale and reference frame proclivity on spatial Learning

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Reference frames provide structure for spatial cognition across different scales. This study sheds light on the relationship between geographic scale, defined as the spatial extent visually accessible from a single viewpoint, and the preferential use of different reference frames for environmental learning. Participants learned target locations in a virtual maze. Leveraging the flexibility and potential of immersive technologies, we manipulated geographic scale using two perspectives, a ground-level view and a pseudo- aerial view, to examine how reference frame proclivity (egocentric vs. allocentric) affects spatial learning at each scale. Learning outcomes were measured using estimates of directions to landmarks. First, we found little effect of ground vs. pseudo-aerial perspective on spatial learning performance. Second, results of the pointing task showed that participants who preferred an allocentric reference frame benefited from the pseudo-aerial perspective, whereas participants who preferred an egocentric reference frame made more efficient use of the ground perspective. Our findings indicate that the preferential use of different reference frames affects how individuals use local spatial information during the process of spatial learning. Third, participants who preferred an allocentric reference frame spent more time exploring the environment and changed their locations more often in the learning phase compared to those who preferred an egocentric reference frame. These results suggest that the use of an allocentric reference frame demands greater effort to encode spatial information than does an egocentric reference frame. Finally, a fine-grained behavioral and cognitive analysis provided evidence for the existence of egocentric survey-based representations that preserved survey knowledge based on the primary engagement of an egocentric reference frame. The results are essential for understanding immersive technologies change spatial learning.

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Can spatial representations of the retrosplenial cortex emerge during free exploration of autonomous robots?

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Abstract: The retrosplenial cortex (RSC) interconnects multiple networks implicated in visual and spatial neural information processing, including the entorhinal cortex, the hippocampus, and the primary/secondary visual cortex, that contain grid cells, head-direction cells, and place cells. This rich pattern of representations converges onto the RSC which then provides a robust, egocentric spatial neural activity capable of supporting both navigation and reference frame (egocentric-allothetic) transformations in the mammalian brain. A recent study has demonstrated that this vector-based, self-location code is independent of self-motion and, more importantly, is context invariant; thus providing spatially stable activation patterns for egocentric and allothetic coordinate systems that can enable robust navigation behavior. In this project, we aim to incorporate the spatial neural code found in the RSC on a real robot so that they can acquire more flexible behaviors such as visual localization and navigation in real-world settings. Specifically, we propose to develop an explanatory, generalizable computational model capable of providing and integrating those spatial representations found in the RSC for enabling robust, goal-directed robot navigation capabilities and, at the same time, that can serve as a testbed for designing new biological experiments in a closed-loop manner between neuroscientists and roboticists. This research also aims to provide an experimental framework that can leverage state-of-the-art robotics systems, computational neuroscience/machine learning models, and neurophysiological experiments to motivate the development of next-generation, neuroscience-inspired autonomous robots.

Reference:

<https://advances.sciencemag.org/content/6/8/eaaz2322>

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Ability to Navigate by Novel Efficient Paths with Imprecise Spatial Knowledge

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Common measures of knowledge of spatial layout include pointing to unseen locations in the environment and taking shortcuts, but few studies have examined the relationship between these measures. Environmental spatial knowledge may consist of metrically accurate survey knowledge (i.e. a map-like representation) or labelled graph knowledge with rough metric information. Here we ask how geometrically accurate spatial knowledge needs to be in order for participants to take novel shortcuts in a learned environment. In two experiments (Ns = 56, 60) participants learned a route through a virtual maze and were asked to make direction estimates and then to travel to maze locations by the shortest possible route. Results indicated that their spatial knowledge was imprecise such that direction estimates were above chance but had an average angular error of more than 70 degrees. This imprecise but partially accurate knowledge enabled participants to find novel paths to the targets, which were shorter than the learned route, but not always the shortest paths. These results cast doubt on the necessity of metrically accurate survey knowledge for taking shortcuts and support a theory of labeled graph knowledge such that with limited spatial knowledge, people are still able to take novel efficient paths.

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Finding our way in new environments: the role of landmark- direction associations

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It has been proposed that humans find their way through a new environment by memorizing distinctive buildings or other objects along the way, and associating them with the direction to take (e.g., "at the gas station, I must turn right"). To scrutinize the role of such landmark-direction associations, we asked 29 healthy participants (40.4 ±3.7 years of age) to learn a route across nine T-shaped intersections. Each intersection featured a unique architectural landmark, and each required participants to turn left or right. On trial 1, participants were guided along the route by the experimenter. On trial 2 & 3, they walked without guidance and the experimenter immediately corrected any errors. Group L could only use landmark- direction associations to find their way. Group S could only use the serial order of directions (e.g., "first left, then right, then right"), and Group LS could use both. We found that the number of wayfinding errors decreased from trial 2 to trial 3. More importantly, the number of errors was similar in group S and LS, but was significantly higher in group L. These group differences persisted in a subsequent trial where all landmarks were removed. Taken together, these findings suggest landmark-direction associations played a minor role for wayfinding in the present study.

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Integrating episodic and spatial context signals in the hippocampus

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Episodic and spatial memory are two core forms of memory. Episodic memory allows remembering events from the past whereas spatial memory allows forming a map-like representation of the environment. Interestingly, these two memory forms are supported by the same brain structure: the hippocampus. However, it remains unclear what the relationship between episodic and spatial memory processes is and how the hippocampus can support both at the same time. Here, we test two different models assuming that the hippocampus supports both memory forms either via a common coding or a parallel processing mechanism, respectively. To this end, we combined fMRI with a life-simulation task and a virtual reality game to manipulate episodic and spatial context associations between objects. In the life-simulation task, participants watched two different stories whereby objects were associated with one of the two stories (episodic contexts). In the virtual reality game, participants delivered objects to stores in two different neighborhoods of a virtual city whereby objects were associated with one of the two neighborhoods (spatial contexts). Ultimately, this resulted in a 2×2 design with pairs of objects sharing both an episodic and a spatial context, pairs of objects sharing only one (either episodic or spatial) context and pairs of objects sharing no context. Preliminary results show neural adaptation effects in the hippocampus which scale with overlapping episodic and spatial contexts between objects. At the same time, we find no evidence for differences between episodic and spatial adaptation effects in hippocampal subregions (neither across hemispheres nor along the anterior-posterior axis). This indicates that our experimental approach is powerful enough to induce neural similarity between objects sharing episodic and / or spatial contexts. Furthermore, our preliminary results are more in line with the model of a common coding mechanism for both memory forms in the hippocampus.

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Developmental changes in AD mouse organization of exploratory behavior under dark conditions

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Wandering is observed in 60% of Alzheimer's disease (AD) patients and has the potential to become life threatening if patients are not found within the first 24 hours. Specific genetic mutations increase AD-related neuropathology and cognitive impairments that may contribute to spatial disorientation. AD patients exhibit an impairment in radial optic flow which underlies self-movement cue processing. Previous work has demonstrated a role for self-movement cue processing in organizing exploratory behavior; however, it remains to be determined whether genetic mouse models of AD exhibit performance consistent with impaired processing of self-movement cues. In the current study, seventeen female mice (n=9 wildtype control, n=8 human APP transgenic) explored a circular table for 40 minutes under dark conditions at two and four months of age. Sequential analysis of exploratory behavior was used to characterize components of movement during progressions and stops throughout the environment. Distance and peak speed are more general measures of locomotion, while path circuitry, movement scaling, change in heading, and home base establishment are more specific measures that are sensitive to hippocampal and vestibular pathology. Initially, at two months of age, AD mice traveled further distances with greater peak speeds relative to wildtype mice; however, differences in general measures of locomotion were absent at four months. Developmental deficits were observed in specific measures of movement at four months, including distance ratio, movement scaling, and change in heading, while home base establishment remained stable across time. These observations are consistent with a developmental impairment in processing self-movement cues. This work establishes a sensitive behavioral tool to characterize spatial orientation deficits which may be used to detect the onset and progression of AD pathology in other genetic models.

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Navigational frame of reference during idiothetic path integration in humans.

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The ability of organisms to track their location in space using only self-motion cues, termed Path Integration (PI), has been shown to form a framework for more complex navigation processes (Schatz et al. 1999; Biegler, 2000). This fundamental aptitude has been the focus of mathematical modeling for decades and one consistently debated question is: from which frame of reference (FoR) is PI conducted? Among the many competing hypotheses, there are two broad categories which are the Egocentric FoR and the Allocentric FoR. In short, the Egocentric FoR uses the organism's own position and orientation as a reference for external locations in the environment, whereas the Allocentric FoR uses the spatial relationship between external locations to calculate the organism's location and orientation in space.

We add evidence to this debate by evaluating the fit of 3 generative Bayesian models on data obtained from a blind-folded triangle-completion task. We evaluated an Egocentric Model (EM), an Allocentric Model (AM) and a Trigonometric Model (TM). The last of these was inspired by experiments where subjects had to retrace or report their outgoing paths (Loomis et al. 1993; Sadalla & Montello, 1989) and proposes that spatial location is maintained by remembering the geometry of outgoing paths. All three models posit the use of Bayesian priors, which bias predictions and lead to characteristic errors. The strength and pattern of these errors depend on how the priors are represented in the models and therefore can be used to distinguish between them.

Interestingly, the EM's predictions matched our data best; with the least average unsigned prediction error, the highest correlation between model errors and behavioral errors, and the most similar trends in response variance. Thus, our results indicate that blind-folded triangle completion by Idiothetic PI may be executed from an Egocentric FoR.

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Human navigation in 3D

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Up to now, the studies of navigation have mostly focused on navigational performance on 2D horizontal planes. However, the last two decades have seen the emergence of studies investigating human's ability to navigate in three-dimensional space, i.e., horizontal and vertical planes. The main question is to understand whether human space processing is isotropic (properties of the horizontal and vertical dimensions are identical) or anisotropic (properties vary systematically according the dimension).

Our study investigates the nature of human space processing by comparing navigational performances on vertical and horizontal terrains. We tested the ability of humans to walk back home after walking over different terrains, even and uneven. The ability to get home, captured by the accuracy of distance reproduction, shows that humans are able to walk back home correctly on a horizontal surface (flat). Surprisingly, uneven terrains with different vertical information do not lead to similar performances. Humans walked back home correctly after going up and down stairs, however, they largely undershoot the distance home after walking over a hill. This difference is mostly explained by a biased perception of the slope inclination: in addition to the behavioral task, participants were also asked to estimate the inclination and the height of the hill.

Our results suggested that participants undershoot the distance home after crossing the hill because they had perceived the hill higher and steeper than it actually was. Therefore, we explain the anisotropic nature of space processing by a perceptive bias: if people accurately perceived and represented the size of a hill, they would walk back home correctly. Challenging previous perceptual studies, we demonstrated that this tendency to greatly exaggerate the slope inclination has a direct consequence on spatial behavior.

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Online Virtual Navigation Experiments with the Landmarks Unity Package

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One challenge commonly faced by navigation researchers involves the 3-dimensional (3D) nature of the stimuli used in their experiments. In a recent article, published in Behavior Research Methods (Starrett et al., 2020), we describe an open-source package for the Unity game engine, Landmarks. Our software reduces the programming requirements that often impede the design of 3D navigation experiments. Landmarks is also one of the only 3D experimental design solutions that includes support for immersive virtual reality hardware (currently the HTC Vive head-mounted display as well as KatVR and Cyberith omnidirectional treadmills, with support for additional hardware planned). With the ongoing COVID-19 pandemic largely rendering in-person experiments using VR and even desktop interfaces difficult, one approach researchers can take is pivoting to web-based variants of 3D experiments. To facilitate this, we have added support for Microsoft Azure cloud-based storage to Landmarks. All that is required for researchers is Unity, the Landmarks Unity project (from GitHub), and a Microsoft Azure account; this integration requires no knowledge of the C# programming language used with Unity. When built as standalone apps (Windows/macOS), experiments will automatically transmit all experimental data to the user's Azure storage account in addition to storing the data on the local machine where they are run (as a redundancy in the event of data transmission errors). These experiment applications can be integrated into common pipelines for online research along with Qualtrics, SONA, Amazon Mechanical Turk, Prolific, and others. With Landmarks, online experiments can also be deployed in virtual reality, but this requires participants to own or have access to the required hardware (e.g., an HTC Vive). We outline the process for adding Azure functionality to an existing Landmarks experiment and present preliminary data from one of our lab's first forays into online navigation experiments.

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Travel Direction as a Fundamental Component of Human Navigation

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In daily life, one's travel direction is typically correlated with head direction, but from first principles, these two factors can offer different spatial information. Although head direction has been found to be a crucial part of human navigation, it is unclear whether travel direction plays a primary role in navigation. To test this, we adopted a visual motion adaptation paradigm, which allowed probes for selectivity of travel direction. To do so, we first adapted people to visual self-motion in one direction in a virtual hallway, and then tested people during a series of visual back and forth movements, toward and away, from the initial travel direction. In both phases, the head direction was reversed occasionally to be dissociated from the travel direction, precluding optic flow from contributing to any observed adaptation effects. We then asked subjects to report their net travel direction, measuring psychometric functions for perceived travel direction, under conditions of adaptation and no-adaptation. We found high-level motion aftereffects of travel direction, suggesting that travel direction is a fundamental component of human navigation. Interestingly, subjects had a higher frequency of reporting net travel toward the adapted direction, indicating that the aftereffect is opposite to the traditional motion aftereffect. The same aftereffect was found after controlling for response biases. We propose that the travel direction system is composed of separate sensory inputs and feed-forward high-level motion processing pathways, which may overlap or interact with the head direction system.

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Gender differences in spatial learning and navigation: the mediation role of spatial self-efficacy and visuo-spatial abilities

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Introduction: Research has documented gender differences in spatial learning and navigation, showing an advantage for men. Little, however, is known about why women perform worse in navigation and other spatial tasks. To date, studies have focused mainly on cognitive variables (e.g. visuo-spatial ability, VSA). A few studies, however, have suggested that even motivational factors (e.g. spatial self-efficacy; SE) might be involved. The current study aims to explore the role of VSA and SE in mediating the relationship between gender and spatial learning in a virtual environment. We assessed VSA, general, and specific-to- task SE of a sample of participants who underwent a number of spatial tasks - navigation (route retracing), pointing and sketch a map - in virtual environment. We expected that gender would correlate with all the spatial tasks, and VSA and SE mediate such relationship.

Method: A sample of 173 young adults (age range: 19-33 years) learned a route in a virtual environment. Afterwards, each participant was required to: indicate the starting point (pointing), retrace the route, and locate landmarks on a map. Before performing each spatial task, participants reported their self-efficacy referred to the task (specific SE). General SE and VSA were assessed using, respectively, a questionnaire and two tests (Jigsaw Puzzle and Mental Rotation).

Results: Structural equation model showed that general and specific SE, and VSA, fully mediated the association between gender and map location. General SE fully mediated the relationship between gender and pointing. No relationship between gender and navigation was found.

Conclusion: Our findings suggest that both motivational and cognitive factors should be taken into account in research on gender differences in spatial learning.

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Landmark-based representations of spatial context in postrhinal cortex

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Animals use visual landmarks to establish a sense of orientation and spatial context. This process requires the brain to integrate visual inputs with information about the animal's head direction (HD). The rat postrhinal cortex (POR), which receives inputs from visual brain areas as well as areas carrying a vestibular-driven HD signal, may play a role in this integration. We recorded from single HD cells in POR and found that, while they had a single preferred firing direction (PFD) in the presence of a single visual landmark (a large white cue card placed along one wall of the square enclosure), they adopted a second PFD when a second identical landmark was placed into the environment, with the orientation of the second PFD depending on the placement of the second landmark. These cells showed higher firing rates for a more familiar landmark, and they generally did not respond to a novel landmark (a black cue card) that was visually distinct from the familiar landmark. When the familiar landmark was removed from the environment, the cells still fired relative to the previous location of the landmark but with reduced firing rates, suggesting that they retained a memory for the familiar landmark. In contrast, HD cells recorded from the anterior thalamic nuclei (ATN) maintained a single PFD under all circumstances. In addition, we could use the firing of a few co-recorded POR HD cells to discriminate among different spatial contexts (landmark configurations). In contrast again, ATN HD cells did not provide adequate information for the same contextual decoding. This study provides insight into how visual landmarks are integrated into a spatial framework that enables the neural encoding of landmark-based orientation and spatial context.

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Effects of aging on encoding of walking direction in the human brain

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Human aging is characterized by declined spatial cognition and reduced distinctiveness of fMRI activation patterns. One possible mechanism behind the decline of spatial cognition in older age could be changes in neural distinctiveness of information that humans use when navigating spatial environments. We asked if neural representations of walking direction, which inform spatial navigation, are less distinct in older compared to younger adults. To this end, we developed a novel method to measure fMRI pattern similarity during free, virtual navigation and estimate neural direction tuning specificity. We expected lower tuning specificity in older adults, i.e. that activation patterns reflecting neighboring directions are less distinct compared to non-adjacent directions. Because loss of distinctiveness leads to more confusions when information is read out by downstream areas, we analyzed predictions of a decoder trained on directional fMRI patterns and asked (1) whether decoder confusions between two directions increase proportionally to their angular similarity, and (2) how this effect may differ between age groups. We expected that the number of confusions followed a Gaussian tuning function, and that the tuning width would be wider in older adults.

Evidence for these tuning-function-like signals was found in the retrosplenial complex and early visual cortex, reflecting the primarily visual nature of directional information in our task. Significant age differences in tuning width, however, were only found in early visual cortex, suggesting that less precise visual information could lead to worse directional signals in older adults. At the same time, only directional information encoded in RSC, but not visual cortex, correlated with memory on task. These results shed new light on neural mechanisms underlying age-related spatial navigation impairments and introduce a novel approach to measure tuning specificity using fMRI.

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Pathfinder: open source software for analyzing spatial navigation search strategies

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Spatial navigation is a universal behavior that varies depending on goals, experience and available sensory stimuli. Spatial navigational tasks are routinely used to study learning, memory and goal-directed behavior, in both animals and humans. One popular paradigm for testing spatial memory is the Morris water maze. Researchers typically express learning as a function of the latency to escape, though this reveals little about the underlying navigational strategies. Recently, a number of studies have begun to classify water maze search strategies in order to clarify the precise spatial and mnemonic functions of different brain regions. However, despite their usefulness, strategy analyses have not been widely adopted due to the lack of software to automate analyses. We developed Pathfinder, an open source application for analyzing spatial navigation behaviour. Here we show Pathfinder's performance on a sample dataset, where it effectively characterized highly-specific spatial search strategies used during the trials. Our software provides support for inputs from commonly-used, commercially-available and open-source software packages, is optimized for classifying search strategies, and can also be expanded easily to work with other species and spatial navigation tasks. Pathfinder has the ability to automatically determine the platform location as well as the size of the pool and related pool parameters. It can generate heatmaps of trials, analyze navigation with respect to multiple goal locations, and can be easily updated to accommodate future developments in spatial navigation behaviours.

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Blink-related brain activity of pedestrians in real-world indicates the advantage of landmark-based navigation instructions for spatial knowledge acquisition

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Navigation assistance systems support users while navigating through novel but also known environments. However, the increasing use of navigation aids diminishes orienting abilities. Users tend to process less of the available spatial information than needed for orienting without system support. Landmarks are one important part for the acquisition of spatial knowledge. This research aims at fostering incidental spatial knowledge acquisition by including landmark-related information in auditory navigation instructions. Pedestrians equipped with mobile EEG navigated a predefined route through Berlin. The control group received auditory navigation instructions comparable to commercial navigation aids. The experimental group received auditory navigation instructions including a landmark name and further related information alongside with the directions. Without prior knowledge of the participants, recall performance was measured in a free map drawing and a cued-recall task afterwards. To investigate brain activity underlying incidental spatial knowledge acquisition during the navigation task, accompanying blink-related measures were extracted from the EEG. Performance measures of both spatial tasks revealed an advantage for the experimental group using landmark-related navigation instructions compared to the control, especially in recalling the route information at decision points. Blink-related potentials could be extracted from the mobile EEG data in the real-world and revealed for the experimental group increased activity at frontal leads during instruction provision and simple walk phases compared to baseline. The results indicate that landmark-related navigation instructions enhance incidental spatial knowledge acquisition during assisted navigation. More general, this study demonstrated that it is possible to utilize blink-related brain activity for investigating cognitive processes during ongoing tasks in fully uncontrolled environments.

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Place and view selectivity in the hippocampus of the non-human primate

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Across several mammalian species, spatial memory has been shown to be critically supported by the hippocampus and parahippocampal regions. However, while neurons separately and jointly selective for coordinate, orientation, and metric representations of allocentric space have been reliably demonstrated in rodents, evidence of such selectivity has been sparse in behaving non-human primates. Compared to rodents, primates have much greater visual acuity and spend more time visually, rather than physically, exploring their environment. In support of the importance of visual exploration in primates, cells selective for coordinate representation of view have been discovered (Georges-Francois et al 1999; Wirth et al 2017). While past work has not allowed for the dissociation of physical and visual reference frames, it is important to understand the separate or joint contributions of body position and gaze to the activity of a single neuron during navigation. The present study recorded hippocampal activity in the right hemisphere of a male non-human primate (*macaca fascicularis*) with a 124-channel chronically implanted microelectrode array, while the animal performed a continuous, goal-directed navigation task within a virtual open maze with 6 fixed goal locations. Eye gaze was tracked concurrently with location in the maze. Spatial information content was calculated to assess place and view selectivity. 74 putative hippocampal cells were recorded, 10 of which were jointly selective for place and view, 4 selective for place only, and 3 selective for view only. Our results suggest that cells exhibiting mixed selectivity may be more prevalent than cells exhibiting exclusive selectivity for space or view in the primate hippocampus.

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Presubicular layer III neurons receive convergent input from anterior thalamus and retrosplenial cortex

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The presubiculum is a key structure for spatial orientation coding. It is part of the brain wide head direction circuit, and its neurons are sensitive to an animals' head direction. The presubiculum (PrS) integrates vestibular sensory input and visual landmark information via the anterior thalamic nuclei and the retrosplenial cortex (RSC) respectively. Here we investigated the functional connectivity between the PrS and afferent regions using anatomical tracing, optogenetics and electrophysiological patch clamp recordings in mouse brain slices.

Retrograde tracing revealed that neurons in the anterior thalamus and in the retrosplenial cortex (RSC) are major input regions of the PrS. Using optogenetics, we found that both thalamic and RSC axons innervated the superficial layers of the dorsal PrS. Photostimulation of thalamic or RSC axons monosynaptically initiated excitatory postsynaptic events in principal neurons of PrS layer III. To investigate the convergence of thalamic and retrosplenial inputs onto single layer III PrS neurons, we used two different viral vectors inducing expression of blue and red shifted opsins, Chronos and Chrimson, in the thalamus and the RSC, respectively. The axons originating from either region were stimulated independently, using brief pulses of 470 or 627 nm light, within a range of low light intensities (up to 0.5 mW). Excitatory postsynaptic responses were elicited in layer III neurons when stimulating either set of afferents. Coincident activation of RSC and thalamic axon terminals could lead to supralinear summation of subthreshold EPSPs or action potential firing.

We suggest that in the PrS, thalamic head direction signals may be matched by convergent visual input from the RSC, to stabilize the attractor and avoid drift of the head direction signal. The analysis of optical stimulation experiments should help our understanding of multisensory information processing in single neurons in the presubiculum.

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Investigating Age-Related Decline and Compensation in Memory Mechanisms Using Human Intracranial EEG

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Age-related decline in cognitive function, particularly in spatial memory, occurs even in the absence of neurodegenerative disorders (i.e., Alzheimer's Disease). Most studies on the aging human brain have used functional MRI or scalp EEG. In this study, we used intracranial EEG to investigate the functional changes in neural mechanisms underlying spatial memory that occur with age. 69 presurgical epilepsy patients (19 to 61 years of age, median age 34) performed a computer-based spatial memory task. Over two encoding periods, the subject was automatically driven directly to a target location from a random starting position in a virtual environment. The subject was then asked to use a joystick to freely navigate back to the target location. Neural oscillations in frequency bands between 1 to 70Hz were compared across the younger (age<41) and older (age>44) subjects. As expected, spatial memory accuracy decreased with age; surprisingly, however, the neural predictors of successful memory differed across the two groups. In the left hippocampus, despite the fact that younger subjects generally had higher oscillatory power in the 3.5- 26Hz range, older subjects had higher power in the 1-3.5Hz frequency range, which was also a marker of successful memory. In the right hippocampus, older subjects showed higher oscillatory power in the most part of the frequency band especially during the encoding period; but younger subjects showed higher theta power (5-10Hz) during the retrieval period. Interestingly, in the striatum, which is involved in associative memory and route-based navigation, higher power throughout the 5-26Hz frequency band was observed, with theta power correlated with successful memory retrieval. We interpret our results to show both an age-related impairment in memory function (in the hippocampus), alongside potential compensatory mechanisms in the left hippocampus and striatum.

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Spatial navigation and scene exploration in biomarker-defined early Alzheimer's disease

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Background: Spatial navigation deficits are typical for early Alzheimer's disease (AD). Individuals with AD have altered scene exploration during spatial navigation. We evaluated potential of a virtual spatial navigation task and scene exploration assessment to differentiate individuals with early AD from those with cognitive deficit of other etiology.

Methods: In total, 59 participants: amnesic mild cognitive impairment (aMCI) with positive (aMCI+, n=22) and negative (aMCI AD-, n=15) AD-biomarkers and cognitively normal older adults (CN, n=22) underwent clinical and cognitive evaluation, MRI brain scan, biomarker assessment and spatial navigation testing in a virtual realistic-looking "Intersections" test. The test consisted of three tasks: i) egocentric "route repetition", where participants repeated the route through a virtual city, ii) allocentric "route retracing", where participants indicated their way back, and iii) allocentric "different approach direction" combined with eye-tracking, where participants indicated their original position from a different perspective at each intersection with two same and two unique houses. Number of fixations and length of fixation of unique houses were analyzed.

Results: In the "route repetition" and "different approach direction" tasks, the aMCI+ group scored lower compared to the CN ($p < 0.001$) and aMCI AD- ($p < 0.024$) groups. In the "route retrace" task, the aMCI+ group scored lower than the CN group ($p < 0.001$) but similar to the aMCI- group. Duration and number of fixations of unique landmarks was similar across all groups regardless of the task performance in the "different approach direction" task ($p > 0.05$).

Discussion: The egocentric and allocentric tasks from the virtual "Intersection" test detected spatial navigation impairment typical for early AD. Spatial navigation unlike scene exploration can differentiate aMCI individuals with AD from those with non-AD etiology.

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Training Visual-Vestibular Integration in Older and Younger Adults

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When navigating our environment, our brains process and integrate several different sensory inputs, including dynamic visual and vestibular cues. Multisensory integration during self-motion allows us to interpret the world around us and our own movement through it. In this study we investigated how younger ($n = 7$) and older adults ($n = 11$) use visual and vestibular information (alone and in combination) to perceive their heading direction during passive movement. Participants were seated in a 6 degrees-of- freedom motion simulator and reported the direction of their movement (left or right of straight ahead) after they were moved forward and to the left or forward and to the right in three conditions: 1) physically (vestibular alone), 2) visually (through a virtual cloud of dots via a head-mounted display; visual alone), or 3) bimodally (vestibular and visual combined). We also investigated whether training could improve the accuracy and/or precision of their heading estimates by providing participants with feedback on their responses (correct or incorrect) and then re-testing their heading judgements. Transfer of any training effects were explored by evaluating the effects of training on a standing balance task. Although data collection is still underway, preliminary analyses suggest that older adults may be less precise than younger adults when estimating the heading of passive movements in both unimodal and bimodal conditions. Training effects were observed in both groups, in the form of increased visual heading precision. Together, these results provide additional insight into visual-vestibular self-motion perception and how it may be influenced by training or age-related factors.

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A homing task that could not be done by image matching

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Returning to a previously visited location can be done by image matching or by 3D reconstruction of the scene. Previously, we have shown that participants' errors are better predicted by image-matching. Here we restrict participants' view to prevent them using this strategy.

Participants viewed a naturalistic indoor scene in immersive virtual reality. During the learning phase, participants viewed the scene from one zone of the room (binocular vision and limited head movements) with a restricted field of view (90° cone) and only one viewing direction permitted (e.g. North). After participants became familiar with the view ('home') they were teleported to another location and had to return 'home' (search phase). The FOV was again restricted, but the direction could be 0°, 90° or 180° different from the learning phase. Some objects were visible in both phases, ensuring the task was possible.

Participants' errors (end locations relative to 'home') increased as a function of the angle between the learning and search phase viewing directions. When the search phase orientation differed by 90° or 180°, errors tended to be shifted in the viewing direction in the learning phase (Model 1 assumes only this shift). However, a model based on the path participants took to reach 'home' (Model 2), provided a better explanation of the data (RMSEs: Model 1: 0.46m, 2 d.f., Model 2: 0.39m, 1 d.f.). Residuals with respect to the two models are highly correlated ($r=.71$, $p<.001$).

The fact that participants can do this task at all rules out the hypothesis that they use a simple image-matching strategy. On the other hand, a 3D reconstruction hypothesis does not predict these systematic biases. Either type of model would need to be adjusted to explain these data. Generative adversarial networks and latent representations offer one possible adaptation of an 'image-based' strategy.

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Multi-modal representation of self-motion in the retrosplenial cortex

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Successful navigation depends on animals' ability to reliably track their orientation and heading direction. The internal representation of such directional sense requires angular head velocity (AHV) information. However, despite numerous studies on head direction, place, and grid cells, little is known about the computations underlying AHV signalling, and in particular, how this is achieved in higher order cortical regions in the mammalian brain. Using high-density single-unit recordings, we describe the activity of AHV neurons in the retrosplenial cortex (RSP) of mice exploring a large arena, and in response to vestibular and visual motion stimuli under controlled head-fixed conditions. We find that many AHV neurons display similar tuning properties during active (freely moving) and passive motion (head-fixed rotations in yaw), and combine vestibular and visual inputs to increase the gain and signal-to-noise ratio of angular velocity coding during navigation. Further, using a novel go/no-go task and computational methods, we demonstrate that vestibular-visual combination increases the perceptual accuracy of own velocity, and the fidelity of its representation by RSP neuronal ensembles. These findings provide novel insights into cortical computations underlying representation of self-motion during navigation.

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Human spatial memory in the real world - Augmented Reality and chronic neural implants

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Spatial memory research and rehabilitation in humans is typically performed either in real environments, which is challenging practically, or in Virtual Reality (VR), which has limited realism. Here we explored the use of Augmented Reality (AR) for studying spatial cognition. AR combines the best features of real and VR paradigms by allowing subjects to learn spatial information in a flexible fashion while walking through a real-world environment.

To compare these methods, we had subjects perform the same spatial memory task in VR and AR settings. Although subjects showed good performance in both, subjects reported that the AR task version was significantly easier, more immersive, and more fun than VR. Importantly, memory performance was significantly better in AR compared to VR.

We then ran the AR experiment on a patient with a chronic neural implant, focusing on neural representations of task stage, spatial memory and movement. Our findings validate that integrating AR can lead to improved techniques for spatial memory research and suggest their potential for rehabilitation. Our results also demonstrate the ability to generalize from the wider body of VR based neuroscience research, but also the importance of naturalistic conditions.

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A selective role for the mPFC during choice and deliberation, but not spatial memory retention over short delays

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Spatial-working memory tasks require important interactions between working memory and decision-making processes to maintain high-levels of task performance. Past research has revealed that the medial prefrontal cortex (mPFC) and hippocampus (HPC) are both vital structures involved in these processes. Recent evidence suggests interactions between these two structures are dynamic and task dependent. However, there exists uncertainty surrounding the specific time points of proposed mPFC functions and contributions during these tasks, specifically regarding its role in retaining information online during delay periods. To address this issue, we ran rats on a spatial-delayed alternation task in which we utilized a closed-loop optogenetic system to transiently disrupt mPFC activity during different task epochs (delay, choice, return). By analyzing the effects of mPFC disruption on choice accuracy and a deliberative behavior known as vicarious-trial-and-error (VTE), our study revealed several interesting findings surrounding the role of the mPFC in spatial working memory tasks. The main findings include: 1) choice accuracy in the spatial-delayed alternation task was impaired only when the mPFC was disrupted at the choice epoch and not delay or return epochs, 2) mPFC disruption resulted in a non-epoch specific reduction in VTE occurrence which correlated with impairments in task performance. Taken together, findings from this study suggest that, in spatial decision-making, contributions made by the mPFC are specific to points of deliberation and choice and that VTEs are a deliberative behavior which relies on intact mPFC function.

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Feedback-based medial temporal lobe signals mediate developmental differences in spatial map precision

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The medial temporal lobe (MTL) is central to building a map of our environment. The hippocampus (HPC), entorhinal cortex (ERC), parahippocampal cortex (PHC) and retrosplenial cortex (RSC) together form maps that represent relationships between objects, landmarks, and locations, which are refined across multiple navigational experiences. Behaviorally, children are less proficient at spatial navigation than adults, which may relate to the immaturity of MTL function at younger ages. Here, we identified age-related differences in the neurocognitive mechanisms that guide spatial memory representation. Children (6-12 years) and adults (18-33 years) completed a virtual navigation task by learning the locations of objects within a virtual arena. On test trials, participants were cued with an object and had to navigate to its remembered location. During corrective feedback, participants moved to the correct location in the environment. We hypothesized that feedback-driven learning signals critical for refinement of spatial memories would differ between children and adults. Behaviorally, spatial memory precision increased with age; distance error and angular error during test trials decreased with age. HPC, ERC, PHC, and RSC responses were increased in adults relative to children during feedback. Moreover, we found that magnitude of MTL responses during feedback tracked behavioral improvements in spatial memory precision on a trial-by-trial basis. Importantly, the relationship between MTL signaling and behavior was age-dependent; feedback-based MTL signals in adults were more tightly coupled to behavioral improvement in spatial memory than in children. These findings indicate functional development of the MTL circuit underlies age-related differences in spatial memory performance. In particular, feedback-based MTL learning signals that support iterative refinement of spatial representations are not functionally mature in childhood.

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Representation of 3D space in the hippocampus of freely moving marmosets

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The hippocampus plays a role in spatial navigation. Place cells increase their firing rate when an animal occupies a certain region of space, these cells have been identified in rodents and primates. However, place cells have been mainly identified in 2 dimensions. Less is known about representations of space in the hippocampus of animals that move in 3 dimensions (3D) such as the common marmoset. Moreover, whether these representations are modulated by variables such as spatial view or movement velocity has yet to be determined. Here, we sought to identify the firing properties of neurons in the hippocampus of freely navigating marmosets in 3D.

For this purpose, we habituated marmosets to freely move inside a plexiglass recording chamber with four vertical levels while wearing reflective markers on skull implants. We tracked the animals' head position and orientation in 3D using motion capture. We chronically implanted 32ch microwire arrays in the hippocampus and wirelessly recorded single unit activity during free navigation.

To calculate the animal's spatial view, head orientation was projected linearly to the walls of the maze starting from the current position of the animal. Rate maps of position and spatial view were constructed independently and the spatial information content (SIC) for both conditions was calculated for (n=154) neurons. Significantly modulated cells were defined as $SIC > .05$ corrected alpha value of the null distribution. Cells significantly modulated by spatial view were more prevalent than cells modulated by the animal's location (66.4% vs 46% of the total). Additionally, using a nested generalized linear model, we found that head angular velocity modulates the firing of a subpopulation of neurons to a greater extent than body translational velocity.

Our results indicate that gaze/view representations seem to be more prevalent than place. Representations of head velocity seem to be also more prevalent than those of body velocity.

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The perception of visually simulated self-motion is altered by body posture

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The perception of self-motion is a multisensory process involving visual and vestibular cues, among others. Visual cues may become more important in visual-vestibular tasks when vestibular cues are attenuated, for example in determining the perceptual upright while lying supine[1]. We tested whether this effect might generalize to self-motion perception, where a higher effectiveness of visual cues should lead to an overestimation of traveled distance. We immersed participants in a virtual hallway and showed them targets at different distances ahead of them. The targets disappeared and participants experienced optic flow simulating straight-ahead self-motion. They indicated by button press when they felt they had reached the position of the target previously viewed. Participants also performed a control task to assess biases in depth perception. We showed them virtual boxes at different distances and they judged on each trial if the height of the box was bigger or smaller than a ruler in their hands. Perceived distance can be deduced from biases in perceived size. They performed both tasks sitting upright and lying supine. For the main task, we found that participants needed less optic flow to perceive they had reached the target's position when supine than when sitting (by 4.4%, 95% CI=[2.9%;6.3%], using Mixed Modelling). For the control task, participants underestimated the distance slightly less when supine (by 2.5%, 95% CI = [0.05%;5.00%], as above). When supine, participants needed to travel less far compared to sitting, even though they overestimated distance while supine versus sitting. The bias in traveled distance can thus not be reduced to a bias in perceived distance. Our experiment provides evidence that visual information is more important for the perception of self-motion when gravity is not aligned with the long body axis.

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Age-related differences in visual-vestibular integration over time of exposure in VR simulated driving environments

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Vestibular function is known to change with age, but the effects of these changes on functional activities requiring self-motion perception is largely unknown. Driving is a complex task that involves the use of vestibular inputs to guide self-motion perception and behaviours. However, the degree to which age-related changes in vestibular function affect driving performance has yet to be studied in an experimental setting. Driving simulators are an increasingly common tool for examining driving performance in a safe and controlled way, yet they differ widely in fidelity, including a high level of variability regarding motion capabilities. Using Toronto Rehabilitation Institute's state of the art driving simulator, we measured the driving performance of older and younger drivers across three different physical motion conditions: no motion, rotational motion (yaw), and full motion (yaw, pitch, roll and translational motion) using a between-subjects design (age x type of motion). We tested 34 younger adults aged 18 – 35 and 32 adults aged 65+ using three, 15-minute driving scenarios for each motion condition with driving performance measured across 14 variables. We hypothesized an additive and beneficial effect of motion on driving performance, with older adults demonstrating greater performance differences across motion conditions than younger adults. Our results, however, demonstrate a more nuanced effect of motion on driving performance with younger and older adults responding to motion cues significantly differently over drives. Furthermore, although older adults drove comparatively more poorly on their first drive, they demonstrated greater improvements in performance over time than did younger adults. These findings suggest that age-related differences in how different motion types affect driving performance should not be viewed in terms of decrements in function, rather in unique perceptual and cognitive strategies in integrating multisensory information.

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Conceptualizing Spatial Memory Gist

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Spatial memory of landmarks, areas, paths, and other structural elements is engaged when we plan a route between locations or try to orient ourselves within a space. We have conducted several studies with more than 300 participants using virtual environments (VEs) emulating a small urban community to evaluate how recall accuracy of landmarks, routes and districts (e.g. residential, commercial, industrial) relate. As we explored these data, we discovered a limitation in how districts within a city are recalled and evaluated using existing spatial memory constructs. We propose a new construct, which we call spatial memory gist (SMG), that we believe represents a higher-level, holistic understanding of spatial layout. We define SMG as the ability to form quick representations of the meaning of spaces (such as the categorization of different districts), as well as their relationships to one another to guide attention, object recognition, and spatial memory. We are currently exploring SMG to understand how meaning is derived through the identification of conceptual properties (e.g. shapes, objects, open/closed, etc.) and the relationships of these properties in space. This requires measuring both the amount of detail kept in working memory and the ability to conceive more abstract patterns of urban form within our VE. Thus far, we have developed techniques to measure both route and landmark accuracy and are now formulating metrics to assess SMG for districts. We draw from methods in environmental psychology, urban design, and immersive geovisualization, to determine the significance of SMG by implementing and measuring cues and real-time changes to urban form in VEs.

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Computing path integration with oscillatory phase codes in biological and artificial systems

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During spatial navigation, the frequency and timing of spikes from spatial neurons (e.g., place cells and grid cells) are temporally organized by continuous theta oscillations (6–11 Hz). The theta rhythm is regulated by subcortical structures including the medial septum, but it is unclear how spatial information from place cells may reciprocally organize subcortical theta-rhythmic activity. Here we recorded single-unit spiking from subcortical and hippocampal sites to study spatial modulation of rhythmic spike timing in freely exploring rats. Our analysis revealed a novel class of neurons that we termed ‘phaser cells,’ characterized by a symmetric coupling between firing rate and spike theta-phase. Phaser cells encoded space by assigning distinct phases to allocentric isocontour levels of each cell’s spatial firing pattern. In our dataset, phaser cells were predominantly located in the lateral septum, but also the hippocampus among other regions. Unlike the unidirectional late-to-early phase precession of place cells, bidirectional phase modulation acted to return phaser cells to the same theta-phase along a given spatial isocontour. Our dynamical models of intrinsic theta-bursting neurons demonstrated that experience-independent temporal coding mechanisms can qualitatively explain the spatial rate-phase relationships of phaser cells and the observed temporal segregation of phaser cells according to phase-shift direction. In open-field phaser cell simulations, competitive learning embedded phase-code entrainment maps into the weights of downstream targets, including path integration networks. Bayesian phase decoding revealed error correction capable of resetting path integration at subsecond timescales, this suggests that phaser cells may reset path integration errors. We then applied phaser cell dynamics to the control of bottom-up self-organized autonomous agents, revealing that multi-agent swarming dynamics can be expressed as a mobile form of Hebbian learning.

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Designing multi-variate research studies for exploring spatial navigation in humans

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Uncovering the neural mechanisms underlying human natural ambulatory behavior is a major challenge for neuroscience. Commercially available implantable devices that allow for recording and stimulation of deep brain activity in humans exist and can provide invaluable intrinsic brain signals but are not inherently designed for research and thus lack flexible control and integration capabilities. The same applies to various standalone wearable systems for body measurements that can offer important insight into human behavior. In this work we address the methods to utilize current technology in human-oriented spatial navigation research studies centered around intracranial encephalography (EEG) and stimulation. We put the emphasis on mobility and synchronization of multi-stream research setups. Experimental computers need a remote access to all devices, which often do not use the same communication protocols or are not designed to operate remotely. Further, it is often a challenge to synchronize wirelessly connected devices with different fixed or variable sampling rates. We review strategies to centralize the control into a single hub as well as the alignment methods in form of timestamping, marking, and capturing the same events with multiple streams. Finally, we unify optimal procedures into a mobile deep brain recording and stimulation (Mo-DBRS) platform that enables wireless and programmable intracranial EEG recording and electrical stimulation integrated and synchronized with virtual/augmented reality (VR/AR) and wearable sensors capable of external measurements (e.g., motion capture, heart rate, skin conductance, respiration, eye-tracking, and scalp EEG). When used in freely moving humans with implanted neural devices, this platform is adaptable to ecologically valid environments conducive to elucidating the neural mechanisms underlying ambulatory spatial navigation and other naturalistic behaviors while minimizing the equipment-induced uncertainty into results.

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