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Research Report

Memory consolidation affects the interplay of place and response navigation





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ABSTRACT

Navigation through space is based on memory representations of landmarks ('place') or movement sequences ('response'). Over time, memory representations transform through consolidation. However, it is unclear how the transformation affects place and response navigation in humans. In the present study, healthy adults navigated to target locations in a virtual maze. The preference for using place and response strategies and the ability to recall place and response memories were tested after a delay of one hour (n = 31), one day (n = 30), or two weeks (n = 32). The different delays captured early-phase synaptic changes, changes after one night of sleep, and long-delay changes due to the reorganization of navigation networks. Our results show that the relative contributions of place and response navigation changed as a function of time. After a short delay of up to one day, participants preferentially used a place strategy and exhibited a high degree of visual landmark exploration. After a longer delay of two weeks, place strategy use decreased significantly. Participants now equally relied on place and response strategy use and increasingly repeated previously taken paths. Further analyses indicate that response strategy use predominantly occurred as a compensatory strategy in the absence of sufficient place memory. Over time, place memory faded before response memory. We suggest that the observed shift from place to response navigation is context-dependent since detailed landmark information, which strongly relied on hippocampal function, decayed faster than sequence information, which required less detail and depended on extrahippocampal areas. We conclude that changes in place and response navigation likely reflect the reorganization of navigation networks during systems consolidation. © 2024 The Author(s). Published by Elsevier Ltd. This is an open access article under the CC

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1. Introduction

Memory consolidation is an essential skill for survival that allows us to retrieve information even after extended time periods. Consolidation is not just the long-term storage of information but instead is a transformative, flexible, and lingering process that qualitatively alters the encoded information (Dudai et al., 2015; Roüast & Schönauer, 2023; Winocur & Moscovitch, 2011). With the passage of time, detailed representations that require contextual reinstatement fade quickly (Sadeh et al., 2014), while abstract gist-like representations emerge (Winocur & Moscovitch, 2011) and schemas form through generalization across multiple experiences (Farzanfar et al., 2023). These qualitative changes are based on network changes (Winocur & Moscovitch, 2011), particularly in hippocampal-neocortical connections (Moscovitch et al., 2005; Squire & Alvarez, 1995). Memory consolidation theories propose that consolidation works on different time scales, starting with synaptic changes immediately after encoding, followed by memory reactivations during the first night of sleep and continuing with long lasting brain-network reorganization (Dudai et al., 2015). These changes occur dynamically in a non-linear, flexible, and reversible manner (Roüast & Schönauer, 2023).

Memory consolidation also affects spatial memories that are acquired during navigation. Spatial memories can be formed based on the subject's position in space, either in relation to environmental features or movement sequences ('response learning' or 'egocentric representation') or independent of the subject's position in space and based on relations between external environmental features only ('place learning' or 'allocentric representation') (Goodman, 2021; Newcombe, 2018). Initial work in rodents and humans suggested that place and response navigation have dissociable neural substrates in the hippocampus and striatum/posterior parietal cortex (Iaria et al., 2003; Marchette et al., 2011; Packard & McGaugh, 1996). Recent studies complement that place and response navigation rely on widespread and partially overlapping networks (Ekstrom et al., 2017; Genzel, 2020), both involving the hippocampus (Cabral et al., 2014; Iglói et al., 2010). Behaviourally, human navigators show a high variability in strategy use (Marchette et al., 2011). One study found a shift from place to response navigation with continued training, presumably due to habit formation (Iaria et al., 2003), while others reported parallel acquisition of strategies with flexible and bi-directional shifts (Iglói et al., 2009; Marchette et al., 2011). The use of place and response navigation also depends on factors such as sex, age, arousal, the environment, and task instructions (Boone et al., 2019; Goodman, 2021; Hegarty et al., 2021). However, it remains less clear how the passage of time influences place and response navigation.

Spatial memory consolidation has distinct effects on navigation across different time scales. In the initial hour after encoding during synaptic consolidation, a short wakeful rest can improve immediate and one-week spatial memory retention (Craig et al., 2015, 2016, 2019). Another study found selective impairments for human place and response navigation when post-encoding neural activity was modulated. Impairments were observed when a GABA_A-ergic agent was administered immediately after learning but not after delays of more than one hour, thus emphasizing the causal role of the initial hour for consolidation (Iggena et al., 2022). Sleep can further enhance spatial memories (Ferrara et al., 2008; Samanta et al., 2021; Simon et al., 2022) and have positive effects on strategy flexibility and memory integration (Noack et al., 2021) via memory reactivations (Rasch & Born, 2013). After sleep, humans showed increased navigation-related striatal activity, suggesting a shift from hippocampusdependent to striatum-dependent navigation over time (Orban et al., 2006). In rodents, sleep deprivation can lead to a preference for response over place navigation (Hagewoud et al., 2010).

Only few studies have investigated the impact of systems consolidation on spatial memories after weeks and months. For spatial memories, consolidation theories predict a reorganization from hippocampal to neocortical areas (Moscovitch et al., 2005; Squire & Alvarez, 1995), accompanied by transformations from detailed to abstract representations (Moscovitch et al., 2005; Winocur & Moscovitch, 2011). Neurobiological studies further indicate that the hippocampus may have a time-limited role for memory storage (Barry & Maguire, 2019), because of factors such as dendritic spine turnover in the hippocampus with an average lifespan of one to two weeks (Attardo et al., 2015). Correspondingly, empirical studies found reduced hippocampal and increased neocortical activation for remote spatial memory in humans (Hirshhorn et al., 2012; Patai et al., 2019; Rosenbaum et al., 2004). Behaviourally, spatial location memory deteriorated faster than spatial gist within a one-month period and afterwards location memory was biased towards gist (Zeng et al., 2021). Additionally, a rodent study found that spatial gist abstractions that allowed for faster learning emerged first after two weeks of time and spatial schemas that allowed for onesession learning emerged only after three months of time (Alonso et al., 2021). It is less clear how consolidation affects navigation strategy use after long delays. One study found that rodents shift their strategy from hippocampusdependent place navigation to striatum-dependent response navigation after continuously training for at least two weeks due to habit formation (Packard & McGaugh, 1996). It is unclear, however, how the mere passage of time affects place and response navigation strategies and the underlying memory representations.

In this study, we investigate the impact of time on spatial navigation, in particular the influence of the duration of the memory delay on place and response navigation in humans. Healthy adults navigated to target locations in a virtual maze and were asked to remember the position of target locations. After a delay of either one hour, one day, or two weeks, we tested the preference for using place and response strategies and the ability to recall place and response memories that guide navigation. The time windows aligned with distinct consolidation phases: While the onehour delay represented behaviour during early-phase synaptic changes, the one-day delay additionally assessed sleeprelated changes, and the two-week delay reflected long-delay network reorganization changes (e.g., due to dendritic spine turnover in the hippocampus). The existing evidence suggests that perceptually detailed spatial information stored in

hippocampal-neocortical connections declines within days. In contrast, abstract or gist-related spatial information stored in cortico-cortical connections prevails or even improves with time. In our experimental scenario, place navigation required memory of detailed landmark information while response navigation required memory of less detailed sequence information. Thus, we predicted that the relative contributions of place and response navigation change as a function of the memory delay, and more specifically, that place navigation declines faster than response navigation over time.

2. Materials and methods

2.1. Sample

We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. The study procedures and study analyses were not pre-registered prior to the research being conducted.

We included 93 participants in our study which were recruited via online advertisement. All participants spoke German fluently, had normal or corrected-to-normal vision, reported to be in good health and had no history of neurological disorders, or acute psychiatric disorders. Prior to the appointment, participants were assigned to one of three groups (one-hour delay (1h), n = 31; one-day delay (1d), n = 30; two-week delay (2wk), n = 32), based on their personal scheduling availability. The groups were matched for sex, age, years of education, handedness, and self-reported spatial abilities (Table 1). Sample size was estimated prior to analysis based a previous study on place and response navigation (Iggena et al., 2022). This study used a similar navigation task and experimental design and reported effect sizes between Cohen's d = .25 and d = .52. A priori power analysis using WebPower (Zhang et al., 2018) was conducted for a 3-by-2 repeated-measures design with an effect size of d = .35, a significance level of a = .05, statistical power 1 - b = .8, and non-sphericity correlation coefficient of 1. The power analysis recommended a total sample size of at least 82 participants. We recruited more study participants to compensate for potential dropouts. Inclusion/exclusion criteria were established prior to data analysis. Of 118 participants screened for study

inclusion, 25 were excluded from study participation. Fifteen participants did not meet the learning criterion of correctly remembering at least ten of sixteen locations in the final block of probe trials, two participants were excluded because they did not follow the task instructions, six participants were excluded due to incomplete data/technical issues and two participants due to initially undisclosed neurological and/or acute psychiatric disorders. The final sample included 93 participants.

All participants gave written informed consent. The study was approved by the ethics committee of the Charité – Universitätsmedizin Berlin and conducted in accordance with the Declaration of Helsinki. Participants received a monetary compensation for their participation.

2.2. General experimental procedure

We tested memory-guided place and response navigation in two sessions. Place navigation was operationalized as landmark learning and response navigation was operationalized as sequence learning (Iglói et al., 2009; Rondi-Reig et al., 2006). We used a mixed between-within subjects experimental design. All subjects were tested twice (within-subjects) and the second session occurred after a delay of either 1h, 1d or 2wk (between-subjects). We used a between-subjects design for the delay groups to avoid carryover effects of learning. The first session ('learning') began with a practice trial, where participants were put in a simple virtual rectangular arena to practice using the keyboard controls for navigation (e.g., moving forward, rotating) without any time constraints. This was followed by an exploration trial, where participants were placed into the main virtual maze environment and encouraged to walk and look around freely. The rationale behind the exploration trial was to standardize exposure to the environment and ensure that participants had seen all landmarks and maze alleys. Target objects were not visible during the exploration trial. Afterwards, the main task started, and participants were requested to find and remember the location of sixteen target objects (repeated blocks with training and probe trials; details in section 2.3.2.).

The second session ('retrieval') occurred after a delay of either 1h, 1d, or 2wk. We assessed two aspects, first, navigation strategy preference, and second, memory ability (details in section 2.3.2.). Lastly, we asked participants to draw a map of the environment from memory (see Supplement A.2 and B.2) and to complete a demographical questionnaire and the

Table 1 – Demographic data for the three delay groups.

1h delay (n = 31)	1d delay (n = 30)	2wk delay (n = 32)	р
18/13/0	17/13/0	17/15/0	.932 ¹
25.48 (5.88)	25.83 (6.04)	25.81 (5.35)	.965 ²
15.95 (2.21)	16.50 (2.45)	16.18 (2.15)	.640 ²
28/3	26/4	28/4	.925 ¹
27/4	27/3	27/5	.926 ¹
4.66 (.98)	4.76 (.89)	4.84 (1.15)	.790 ²
	1h delay (n = 31) 18/13/0 25.48 (5.88) 15.95 (2.21) 28/3 27/4 4.66 (.98)	$\begin{array}{c c} \mbox{1h delay (n = 31)} & \mbox{1d delay (n = 30)} \\ \hline 18/13/0 & \mbox{17/13/0} \\ 25.48 (5.88) & \mbox{25.83 (6.04)} \\ 15.95 (2.21) & \mbox{16.50 (2.45)} \\ 28/3 & \mbox{26/4} \\ 27/4 & \mbox{27/3} \\ 4.66 (.98) & \mbox{4.76 (.89)} \end{array}$	$\begin{array}{c c c c c c c c c c c c c c c c c c c $

Note. 1h = one-hour delay; 1d = one-day-delay; 2wk = two-week delay. SBSOD = Santa Barbara Sense of Direction scale (German version; Hegarty et al., 2002). Absolute frequency for categorical data. Mean and standard deviation for continuous data. Statistical tests for group comparisons were 1 = Fisher's exact test; 2 = one-way ANOVA.

German version of the Santa Barbara Sense of Direction scale (SBSOD; Hegarty et al., 2002). Participants were free to follow their daily activities in between the learning and retrieval session but were instructed to avoid additional active learning (e.g., exam studying) on the experiment days.

2.3. Task

2.3.1. Virtual maze setup

We created a virtual navigation task which was inspired by the 'starmaze' task (Iggena et al., 2022; Iglói et al., 2009, 2010; Rondi-Reig et al., 2006) and the human Y maze (Rodgers et al., 2012). The virtual maze consisted of seven symmetrically arranged peripheral alleys connected by seven central alleys. It was surrounded by a large mountain range and several distant landmarks (Fig. 1A; see also Supplementary Fig. A.1). We opted for a starmaze variant with seven rather than the traditional five alleys, because we wanted to create a more challenging task for healthy young adults with a larger number of target locations. Inside the maze, there were sixteen target locations. We had one original start location for the learning session, and six new start locations for probe trials in the retrieval session (Fig. 1B). The virtual environment and landmarks were custom-made in Blender (version 2.79b, Blender Foundation) or downloaded from the Unity Asset Store. Additionally, we used sixteen 3D objects (soccer ball, chair, dumbbell, table, telephone, book, scissors, bike, violin, hammer, umbrella, wine bottle, suitcase, globe, watering can, piano) from a validated database (Peeters, 2018) as visual cues for locations. The navigation task was implemented in Unity3D (version 2018.2.14f, Unity Technologies) using the Unity Experiment Framework (Brookes et al., 2020). The target and start locations were presented in random order for each participant. Participants navigated from a first-person perspective and controlled their movement within the virtual environment with the keyboard (arrow keys for forward/backward movement and left/right rotation, space bar as response key in probe trials).

2.3.2. Navigation task

We instructed participants that they should find and remember the exact position of sixteen target locations marked by 3D objects using both place information (operationalized as landmark use) and response information (operationalized as sequence use). We used sixteen target locations, in contrast to prior navigation studies that only required learning a single target location (Iglói et al., 2009; Packard & McGaugh, 1996). This was a conscious design choice to increase task difficulty. In each trial, only one objectlocation-pair was tested. At the beginning of each trial, we presented an image of the to-be-remembered object as a cue. During 'training' trials, the 3D object was visible at the correct location (Fig. 1C) and the location could be remembered based on either place and/or response information. Only one object was visible in each trial. Participants were asked to find the location as quickly and directly as possible and collect the object. To ensure that participants found the most direct route to each location, we displayed a floating arrow above the target region during the first trial for each object-location-pair. During 'probe' trials, the 3D object was not visible (Fig. 1C).

Participants were asked to go back to the target location that they remember and press a key at this remembered location. No feedback was provided in probe trials.

During the learning session, participants always started from the original start location in training and probe trials ('regular' probe trials). We told participants to pay attention to and memorize their paths as well as the surrounding environmental cues, thus emphasizing the encoding of both place and response information. The learning session consisted of 80 training trials and 32 regular probe trials (Fig. 1D; details in Supplementary Table A.1).

At the end of the learning session, we also included dedicated 'memory' probe trials to test the ability to recall place and response information (Fig. 1D; 16 trials each). These trials ensured that participants had acquired a sufficient level of place and response memory at the end of the learning session. In 'response memory' probe trials, participants had to navigate to target locations while the sky and landmark cues were removed, thus requiring the recall of sequences of path segments. In 'place memory' probe trials, we presented 2D images of target locations with the surrounding sky and landmark cues and asked them to identify the target object at this location, thus requiring the recall of landmarks. Response memory probe trials were presented before place memory probe trials. The final block of probe trials in each condition (regular, response, and place; 16 trials each) was used to assess baseline performance and to test if there were any differences in place and response learning between the delay groups at baseline.

In the retrieval session, participants started from new start locations within the maze ('strategy' probe trial). Participants were asked to go back to the target location that they remember and press a key at this remembered location. No feedback was provided. We did not explicitly inform participants about the new start location before the trial but mentioned in the general instructions at the beginning of the learning session that this may happen during the experiment. This manipulation allowed us to assess whether participants preferentially used landmark information (place strategy) or sequence information (response strategy) for locating targets (example in Fig. 2A). We did not include trials with the original start location in the retrieval session because we wanted to prevent re-learning and maximize the number of trials that allow for a distinction between place and response strategy use. At the end of the retrieval session, we again presented the 'memory' probe trials to test the ability to recall place and response information. The retrieval session consisted of 60 strategy probe trials, 16 place memory probe trials, and 16 response memory probe trials (Fig. 1D; details in Supplementary Table A.1).

2.4. Data analysis

We recorded positions within the maze as x-, y-coordinates and z-rotations in a Cartesian coordinate system together with a timestamp. All data were downsampled to 20 Hz. We preprocessed the navigation data in MathWorks® Matlab (v2021a). We computed several variables to capture three aspects of navigation: memory recall, strategy use, and efficiency.

For the assessment of memory recall, we used the *memory* score [%] (Bellmund et al., 2020; Iggena et al., 2023). This variable

A Top-view of the maze environment



B Overview of start and target locations



C First-person view in trial types

Original start in training/probe







Target location in probe



D Trial order in both sessions



Fig. 1 – Overview of the navigation task and trial types. Note. A) Top-view of the virtual maze environment. B) Overview of start and target locations. The black circle is the original start, the blue circles are the new starts in strategy probe trials, and the stars are the target locations. C) First-person view in trial types. Left: View from original start in training and probe trials. Middle: View at target location in training trials where the object is visible at the correct location. Right: View at target

captures the spatial accuracy of remembered locations in probe trials in a standardized score that ranges from zero to one, with one indicating high performance and .5 corresponding to chance level. First, we calculated the memory error i.e., the Euclidean distance between the remembered location and the location Memory Error [vu] = reference target (Eq.: $\sqrt{(x_{reference} - x_{remembered})^2 + (y_{reference} - y_{remembered})^2}$), and a random error distribution for each target location. The random error distribution was obtained by computing the Euclidian between each target location and distance 1000 randomly sampled locations. The memory score [%] then corresponds to the percentile rank of the memory error on the random error distribution (Eq.: Memory Score [%] = 1 - 1(proportion of random error scores < memory error)). We also calculated the memory score for place memory probe trials where participants did not navigate but select target objects. Here, we used the x- and y-coordinates of the selected target object as the remembered location.

For the assessment of navigation strategies in strategy probe trials, we computed three variables. First, we calculated a variant of the memory score called strategy score [%]. In strategy probe trials, there were two reference target locations, one based on a place strategy (using landmark information), and one based on a response strategy (using sequence information; example in Fig. 2A). Correspondingly, we calculated two strategy scores for each participant (i.e., one for the place reference target location and one for the response reference target location) with the memory score formula described above. The strategy score ranges from zero to one, with one indicating that a participant preferentially navigated towards the respective reference location and .5 corresponding to chance level. Note that the strategy score is suitable for ambiguous spatial situations i.e., if the two reference locations are in close proximity (e.g., in neighbouring alleys of the maze), the two strategy score values will be similarly high, thus accounting for uncertainty in determining a participant's strategy preference.

Second, we computed visual landmark exploration as a proxy for place strategy use. Here, we calculated the *initial rotation velocity* [rad/sec] (also called initial angular velocity; Hasz & Redish, 2020; Papale et al., 2012; Santos-Pata & Verschure, 2018) which represents the extent of horizontal head movements up until the first decision point. This measure is associated with place learning, deliberate path planning and hippocampal function (Iggena et al., 2023; Schmidt et al., 2013). Initial rotation velocity was calculated as the cumulative change in z-rotation [rad] from the beginning of the trial up until the first decision point and divided by latency [sec] to obtain velocity (Eq.: Initial Rotation Velocity [rad/sec] = $\sum_{i=1}^{n_{initial}} |(z_i - z_{i+1})| / t_{initial})$. The value ranges from zero to infinity with higher values denoting more visual landmark exploration, and thus the use of a place strategy.

Third, we computed path repetition as a proxy for response strategy use. Here, we calculated the trajectory distance [vu] (Iggena et al., 2023) between two aligned path trajectories, namely the original trajectory in response memory probe trials at the end of the learning session and the trajectory in strategy probe trials in the retrieval session. Path repetition is associated with response learning (Iggena et al., 2023). Trajectory distance was calculated with the dynamic time warping algorithm (DTW; Berndt & Clifford, 1994). DTW aligns two signals by minimizing the sum of squared distance between pairs of points on stretched vectors (Tao et al., 2021; see also Fig. 2B). We first rotated the two paths to the same origin, computed the sum of squared distance with DTW (Eq.: Nonnormalized Trajectory Distance $[vu] = \sum_{k=1}^{K} (original XY_{k,m} -$ $XY_{k,n}$)*(original $XY_{k,m} - XY_{k,n}$)), and then normalized the DTW according to Tao et al. value (2021) (Eq.: Trajectory Distance $[vu] = \sqrt{DTW/max(m,n)}$. The value ranges from zero to infinity with lower values denoting more path repetition, and thus the use of a response strategy.

Lastly, we calculated two variables for overall navigation efficiency. First, *latency* [sec], as the time to complete the trial in seconds (Eq.: Latency [sec] = $t_n - t_1$). Second, *excess path length* [vu] (Bellmund et al., 2020), which was calculated by subtracting the length of the participant's path trajectory (Eq.: Path Length [vu] = $\sum_{i=1}^{n} \sqrt{(x_i - x_{i+1})^2 + (y_i - y_{i+1})^2}$)) from the ideal path length (Eq.: Excess Path Length [vu] = (path length – path length_{ideal})), thus a higher values denote taking less direct paths.

2.5. Statistical analysis

All statistical analyses were performed in R Studio (v4.2.1; R Core Team 2021). The data were analyzed with linear mixed models (LMM) in *afex* (Singmann et al., 2022). LMM explicitly

location in probe trials where the object is not visible. Participants go back to the remembered target location and press a key. D) Trial order in both sessions. *Left*: The trial order in the learning session consisted of three blocks of training trials, where participants started from the original start and the target object was visible, followed by one block of regular probe trials, where participants also started from the original start, but the target object was not visible. In probe trials participants were asked to go back to the remembered target location and press a key. Afterwards, we presented two more blocks of training trials and one block of regular probe trials. The session ended with one block of response memory probe trials and one block of place memory probe trials to assess baseline place and response memory recall. In response memory probe trials, participants navigated to target locations from the original start while the landmark cues were removed. In place memory probe trials, we presented 2D images of target locations with the surrounding landmark cues and asked participants to identify the target object at this location. *Right*: The trial order in the retrieval session consisted of five blocks of strategy probe trials where participants started from new start locations within the maze. This manipulation allowed us to assess whether participants preferentially used landmark information (place strategy) or sequence information (response strategy) for locating targets. Afterwards, we presented one block of response memory probe trials and one block of place memory probe trials to assess place and response memory probe trials and one block of place memory probe trials to assess started from new start locations within the maze. This manipulation allowed us to assess whether participants preferentially used landmark information (place strategy) or sequence information (response strategy) for locating targets. Afterwards, we presented one block of response memory probe trials and one block o

model dependencies in the data (e.g., repeated observations) as random effects, resulting in a high statistical power and low risk of Type I errors (Singmann & Kellen, 2019). For the withinsession analyses (i.e., baseline memory at the end of the learning session, visual landmark exploration and path repetition in the retrieval session), we ran LMM with the fixed effect group (between-subjects factor with 3 levels: 1h, 1d, and 2wk). For the between-session analyses (i.e., change in place and response memory), we ran LMM with the fixed effects group (1h, 1d, and 2wk), and session (within-subjects factor with 2 levels: learning session, retrieval session). For the analysis of the strategy score, we ran LMM with the fixed effects group (1h, 1d, and 2wk), and reference location (within-subjects factor with 2 levels: place, response) and we included the baseline performance as model covariates to account for variations in encoding strength. All LMM included sex as a covariate. All LMM included participant id, target location id and, if applicable, block number as random effects and were modelled with the maximal random effects structure (Barr, 2013; Matuschek et al., 2017). The LMM were estimated using Restricted Maximum Likelihood (REML). Degrees of freedom were computed using Satterthwaite's method in ImerTest (Kuznetsova et al., 2017). For all significant fixed effects, we computed post-hoc contrasts with emmeans (Lenth, 2022), using Bonferroni corrections for multiple comparisons. To assess the effect size of significant fixed effects, we used the omega squared (ω^2) from effectsize (Ben-Shachar et al., 2020).

To investigate the relationship between strategy use and memory ability, we also computed Spearman's rank correlations between the strategy variables from the retrieval session and the memory variables from both the learning and the retrieval session. Additionally, we calculated Spearman's rank correlations between those variables with navigation efficiency variables and demographical factors. Sex was used as a control variable in partial correlations. The *p*-values for the correlation analyses were Bonferroni-corrected. Plots were created with afex (Singmann et al., 2022) and ggplot2 (Wickham, 2016). The results section of this manuscript was written with the *papaja* package (Aust & Barth, 2022).

2.6. Data availability

The digital study materials, the data that support the findings of this study, and the analysis code are openly available on the Open Science Framework https://osf.io/2a6hu/.

3. Results

3.1. No differences between delay groups at baseline

First, we wanted to investigate if the delay groups had a comparable baseline performance at the end of the learning session. There was no significant effect of delay group on the memory score in final probe trials from the original start $[M_{1h} = .95 (SD = .13); M_{1d} = .96 (SD = .11); M_{2wk} = .95 (SD = .13); p = .892; full results in Supplementary Table B.1], in response memory probe trials <math>[M_{1h} = .95 (SD = .14); M_{1d} = .95 (SD = .11); M_{2wk} = .94 (SD = .16); p = .664], and in place memory probe trials <math>[M_{1h} = .82 (SD = .28); M_{1d} = .83 (SD = .27);$

 M_{2wk} = .81 (SD = .29); p = .771]. The three delay groups thus had a comparable place and response memory at the end of the learning session.

3.2. Participants preferred place strategies after a delay of up to one day, whereas they equally relied on place and response strategies after the two-week delay

Next, we evaluated strategy use after the delay in strategy probe trials, where participants were starting from new locations. First, we looked at the strategy score which captures the preference for using a place strategy (landmark information) or a response strategy (sequence information) based on the remembered target location (example in Fig. 2A). The LMM had significant main effects for delay (p = .003; full results in Table 2), and reference location (p < .001), and a significant interaction between delay and reference location (p = .004). For all delays, participants exhibited above-chance place strategy use (all $p_{Bonferroni(6)} < .003$) which was significantly decreased after the 2wk delay compared to the 1h delay $[t(85.50) = 3.55, p_{Bonferroni(9)} = .006]$ and the 1d delay [t(85.57) = .006]3.32, $p_{Bonferroni(9)}=$.012]. Conversely, we observed abovechance response strategy use only after the 2wk delay $(p_{\text{Bonferroni(6)}} < .001)$ but not after the shorter delays (all $p_{\text{Bonferroni(6)}}$ > .999). Further post-hoc comparisons for the interaction effect revealed that participants preferentially used place over response strategies after the 1h delay $[t(89.00) = 3.65, p_{Bonferroni(9)} = .004]$ and the 1d delay [t(88.99) = .004]3.65, $p_{Bonferroni(9)}\,=\,.004]$ but there was no clear preference anymore after the 2wk delay [t(89.00) = -.45], $p_{\text{Bonferroni(9)}} > .999$]. Two of the model covariates i.e., baseline memory in the final probe trials from the original start (p =.013) and baseline place memory (p < .001) had a significant effect on the strategy score. There were no sex differences for the strategy score (main effect p = .965; interaction with reference location p = .364). Exemplary path trajectories are provided in Supplementary Fig. B.2. In a supplementary analysis we also explored the percentage of trials where participants ended in locations other than place and response ("don't remember" trials; details in Supplement B.3). We found that the percentage of "don't remember" trials was significantly higher after the 2wk delay compared to the 1h delay $[t(90)\,=\,-$ 3.84, $p_{Bonferroni(18)}\,=$.004]. After the 2wk delay, there was an equal amount of place, response, and "don't remember" trials (all $p_{Bonferroni(18)} > .999$).

Second, we looked at visual landmark exploration as a marker for place strategy use (Fig. 2B). For the LMM with the initial rotation velocity, we found a significant main effect of delay (p = .029; full results in Table 3). Initial rotation velocity decreased with increasing delay and was significantly higher after the 1h delay compared to the 2wk delay [$t(89.01) = 2.71, p_{Bonferroni(3)} = .024$]. Third, we looked at path repetition as a marker for response strategy use (Fig. 2B). For the LMM with the normalized trajectory distance (i.e., the dissimilarity between the retrieval path and the response baseline path), we found a significant effect of delay (p = .019; full results in Table 3). The normalized trajectory distance decreased with increasing delay and was significantly lower after the 2wk delay compared to after the 1h delay [$t(89.00) = 2.43, p_{Bonferroni(3)} = .052$] and the 1d delay [t(88.99) = 2.53,

A Delay effects on strategy use

Place and response strategy score



Fig. 2 — Delay effects on memory-guided navigation. Note. A) Delay effects on strategy use. First row: Place and response strategy score. Participants preferentially used place strategies after the one-hour (1h) or one-day (1d) delay but not after the two-week (2wk) delay, when place strategy use decreased, and participants equally relied on place and response strategies. Second row, left to right: Navigation was characterized by high visual landmark exploration (high initial rotation velocity) after the 1h or 1d delay and high path repetition (low normalized trajectory distance between the retrieval path and the response baseline path) after the 2wk delay. B) Delay effects on memory recall. Place memory was preserved after the 1h or 1d delay but deteriorated after the 2wk delay. Response memory decreased between learning and retrieval but remained at a high level. Response memory was preserved equally across delays.

Variable Strategy score Fixed effects df^s df_{res}^{S} ω^2 F р 6.39 2 85.06 .003 .11 Delay Group **Reference** Location 15.82 1 89.00 <.001 .14 Delay Group × Reference 5.79 2 89.00 .004 .09 Location .00 Covariate Sex 1 85 01 965 00 Covariate Sex × Reference .83 1 89.00 .364 .00 Location Covariate Baseline Memory 6 4 0 1 85 49 013 06 <.001 Covariate Baseline Place 14 97 1 85.41 .14 Memory Covariate Baseline Response .72 1 85.76 .399 .00 Memory Random effects SD r Participant ID (intercept) .03 .19 Participant ID \times Reference (slope) Participant ID × Reference -.08 (correlation)

 $p_{\text{Bonferroni(3)}} = .039$]. Lastly, we analyzed navigation efficiency. There were no differences in latency (p = .156) and excess path length (p = .153) between the three delays. For latency, we found a sex difference (p = .038) with male participants completing the trials faster than female participants. There were no sex differences for initial rotation velocity, normalized trajectory distance, and excess path length (full results in Table 3).

.06

.01

.24

Taken together, we observed that participants preferentially used place strategies after a short delay of one hour and one day. After a longer delay of two weeks, place strategy use decreased; participants now equally relied on place and response strategies and increasingly repeated previously taken paths. While the delay affected strategy use, it did not influence navigation efficiency.

3.3. Place memory was preserved after a delay of up to one day but declined after two weeks, while response memory was equally preserved across delays

Next, we investigated memory recall after the delay. Here, we computed one LMM with the memory score from place memory probe trials, and one LMM with the memory score from response memory probe trials (Fig. 2C). For place memory, we found a significant interaction between delay and session (p < .001; full results in Table 4). After the 2wk delay, participants had significantly lower place memory compared to the 1h delay [t(89.13) = 2.98, $p_{\text{Bonferroni}(9)}$ = .033] and the 1d delay $[t(89.10) = 3.37, p_{Bonferroni(9)} = .010]$. Place memory declined significantly between learning and retrieval sessions in the 2wk delay group only $[t(90) = 4.55, p_{Bonferroni(9)} < .001]$. There was no sex difference in place memory (p = .819). For response memory, we found a significant decrease between the learning and retrieval session (p < .001) even though response memory remained at a high level (see Fig. 2B). The decrease was independent of the memory delay (p = .102), indicating that response memory was equally preserved across delays. There was no sex difference in response memory (p = .322).

Taken together, we observed that place memory was well preserved after delays of one hour and one day but deteriorated after two weeks. In contrast, response memory was equally preserved across delays.

3.4. Strategy use after the delay correlated with baseline memory and delayed memory

To investigate the relationships between variables, we computed several correlations (Table 5, Bonferroni-corrected for multiple comparisons). First, we assessed the correlations between strategy variables. More visual landmark exploration (i.e., higher initial rotation velocity) correlated with a higher place strategy score. More path repetition (i.e., lower normalized trajectory distance) correlated with a higher

Table 3 -	 Fixed effects 	s and random	effects fo	r navigation	variables in	strategy probe	e trials after	the delay.
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Variable	Strategy use									Efficiency								
	Initia	Initial rotation velocity (Place) Norm. trajectory distance (Response)								Latency				Excess path lengt			ngth	
	 Fixed effects																	
	F	df ^s	$df_{\rm res}^{\rm S}$	р	ω^2	F	df ^s	$df_{\rm res}^{\rm S}$	р	ω^2	F	df ^s	$df_{\rm res}^{\rm S}$	р	F	df ^s	$df_{\rm res}^{\rm S}$	р
Group	3.67	2	89.00	.029	.05	4.13	2	89.00	.019	.06	1.90	2	88.92	.156	1.92	2	89.00	.153
Covariate Sex	1.11	1	89.00	.295	.00	1.39	1	89.00	.241	.00	4.46	1	88.92	.038	1.51	1	88.99	.223
	Random effects																	
	SD					SD					SD				SD			
Participant ID	.56			_		.68					4.16				.07			
Target ID	.04					.35					.64				.01			
Block	.11					.21					1.28				.01			
Residual	1.17					.92					6.79				.19			

Table 2 – Fixed effects and random effects for the strategy score in strategy probe trials after the delay.

Target ID (intercept)

Block (intercept)

Residual

Variable	Memory recall												
	Place memory score						Response memory score						
					Fixed	d effects							
	F	df ^s	$df_{\rm res}^{\rm S}$	р	ω^2	F	df ^s	$df_{\rm res}^{\rm S}$	р	ω^2			
Group	3.01	2	89.03	.055	.04	1.09	2	89.48	.339	.00			
Session	1.87	1	90.02	.175	.01	19.09	1	90.19	<.001	.16			
Group \times Session	10.38	2	90.02	<.001	.17	2.34	2	90.19	.102	.03			
Covariate Sex	.05	1	89.00	.819	.00	.99	1	89.08	.322	.00			
					Randor	n effects							
	SD	r				SD	r						
Participant ID (intercept)	.11					.08							
Participant ID × Session (slope)	.02					.02							
Participant ID $ imes$ Session (correlation)		54					72						
Target ID (intercept)	.04					.02							
Residual	.25					.13							

Table 4 – Fixed effects and random effects for the memo	ory score in probe trials before and after the delay
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response strategy score. This confirms that the chosen strategy variables reliably capture place and response strategy use. We found an inverse correlation between place strategy and response strategy variables, implying that participants predominantly used either place or response strategies rather than other strategies (e.g., random walk).

Next, to investigate the relationship between strategy use and memory ability, we computed correlations between the strategy variables and memory variables (across delay groups). Participants with higher place memory at baseline and higher place and response memory after the delay were more likely to use place strategies after the delay. Participants with lower place memory at baseline and after the delay were more likely to use response strategies after the delay. There was no association between response memory and response strategy use. Additionally, we found a positive correlation between place memory and response memory after the delay, suggesting the possibility of a common underlying factor for the ability to recall consolidated spatial memory.

We also computed correlations between strategy use and memory ability with efficiency variables and demographical factors. Participants with a faster latency after the delay were more likely to use response strategies, less likely to use place strategies, and they had lower place memory after the delay. There were no significant associations with excess path length. Likewise, there were no significant correlations between age, years of education, self-rated spatial abilities, and any of the strategy variables or memory variables.

Taken together, we found that strategy use after the delay was associated with baseline and delayed memory, in particular place memory, and correlated with the speed of navigation. Place memory and response memory were positively correlated, suggesting partially overlapping cognitive functions.

Table 5 - Correlation table.

Variable		Strategy use	after delay	Memory re	М	SD		
	1. Place Strategy Score	2. Response Strategy Score	3. Initial Rotation Velocity	4. Norm. Trajectory Distance	5. Place Memory Score	6. Response Memory Score		
1. Place Strategy Score	-						.74	.22
2. Response Strategy Score	92***	-					.58	.19
3. Initial Rotation Velocity	.49***	52***	_				2.48	.58
4. Norm. Trajectory Distance	.89***	93***	.53***	-			1.60	.72
5. Place Memory Score	.78***	68***	.37*	.66***	-		.81	.15
6. Response Memory Score	.37*	24	.16	.26	.43**	-	.91	.11
7. Baseline Memory Score	.27	18	.14	.19	.29	.82***	.96	.05
8. Baseline Place Memory Score	.66***	55***	.21	.54***	.73***	.33	.82	.12
9. Baseline Response Memory Score	.32	21	.07	.21	.33	.81***	.95	.07
10. Latency	.38*	40**	.37*	.38*	.43**	.22	16.72	4.39
11. Excess Path Length	.11	20	.20	.26	.22	06	.12	.08
12. Age	18	.11	.04	08	22	16	25.74	5.72
13. Years of Education	07	.02	.01	01	17	03	16.22	2.26
14. SBSOD	06	.00	05	03	.07	.11	4.75	1.01

Note. Spearman's rank correlation coefficients. Significance levels *p < .05; **p < .01; ***p < .01 (Bonferroni-corrected). M = mean; SD = standard deviation. SBSOD = Santa Barbara Sense of Direction scale. Variables from the retrieval session: place strategy variables (1, 3); response strategy variables (2, 4); memory variables (5–6); variables from the learning session: baseline memory variables (7–9); efficiency variables (10–11); demographical factors (12–14). Sex was used as a control variable in partial correlations.

4. Discussion

We investigated the effects of memory consolidation on navigation in a virtual maze, focussing on strategy use and memory recall. The delay between learning and retrieval varied between one hour, one day, and two weeks. We predicted that the relative contributions of place and response navigation change as a function of the delay, more specifically, that place navigation declines before response navigation. Strategy use was assessed by letting participants navigate from new start locations in a virtual maze, thus participants exhibited different navigation patterns and ended up at different target locations if they used distal landmark cues (place) or a sequence of turns (response). Memory recall was assessed in separate trials where only either place or response information was available.

We observed distinct differences in strategy use and memory recall after short delays (1h and 1d delay) compared to the 2wk delay. After short delays, participants preferentially used place strategies, which was evident by a higher amount of visual landmark exploration during the initial orientation phase and a stronger preference for locating targets based on landmark information, compared to the 2wk delay. Conversely, after the 2wk delay, participants showed a decrease in place strategy use and instead also relied on response strategies. This was evident by a higher amount of path repetition, a decrease in locating targets based on landmark information and a relative increase in locating targets based on sequence information after the 2wk delay compared to the shorter delays. The delay did not affect navigation efficiency i.e., the speed and directness of movement. For memory recall, we found that place memory was well preserved after the 1h and 1d delay but significantly deteriorated after the 2wk delay. Response memory, on the other hand, declined slightly immediately after learning but then remained stable across delays. Strategy use after the delay correlated with baseline memory and delayed memory but not demographical factors. Taken together, we show that the passage of time, and thus memory consolidation, has a differential impact on place and response navigation in humans.

4.1. Delay effects on memory-guided navigation vary after hours, days, and weeks

Memory consolidation is a reorganization process during which newly encoded information is reactivated, abstracted, and integrated (Dudai et al., 2015; Farzanfar et al., 2023). We chose three memory delays to capture distinct consolidation phases: The 1h delay for early-phase synaptic changes (Dudai et al., 2015), the 1d delay for additional sleep-related changes (Rasch & Born, 2013), and the 2wk delay for network reorganization changes (e.g., due to dendritic spine turnover in the hippocampus; Barry & Maguire, 2019).

We did not observe any differences in navigation after earlyphase consolidation compared to sleep-related consolidation. At first glance, this contrasts with previous studies who found that sleep promotes navigation flexibility (Noack et al., 2021) and performance (Ferrara et al., 2008; Samanta et al., 2021; Simon et al., 2022). One explanation for the absence of differences may be ceiling effects, as participants were trained extensively during the learning session. Another reason may be that wakeful rest may have had a positive effect on memoryguided navigation, too. Because we did not include a one-day wake condition, we cannot draw definitive conclusions on this matter. However, this would be in line with studies showing that navigation benefits from a short wakeful rest (Craig et al., 2015, 2016, 2019), and the observation that navigation-related early consolidation processes occur already within the first hour after encoding (Iggena et al., 2022).

When comparing navigation after two weeks with the shorter delays, we did find clear differences in memoryguided navigation. The distinct changes after the 2wk delay may provide a behavioural correlate for reorganization processes that occur because of neurobiological storage constraints of the hippocampus (Barry & Maguire, 2019). Here, animal studies revealed a substantial synaptic turnover in the hippocampus within the first one to two weeks after encoding (Attardo et al., 2015). Reorganization of spatial memory may involve a relative shift from hippocampal to neocortical areas (Moscovitch et al., 2005; Squire & Alvarez, 1995), in particular to the parahippocampal, retrosplenial and posterior parietal cortex (Hirshhorn et al., 2012; Patai et al., 2019; Rosenbaum et al., 2004), and alter spatial memory representations that guide place and response navigation. Thus, delays that extend beyond a single day may be particularly relevant for spatial memory consolidation, although only few studies (e.g., Alonso et al., 2021; Patai et al., 2019; Zeng et al., 2021) have systematically investigated them.

4.2. Decrease in place navigation and relative stability of response navigation over time

Navigation trajectories provide rich information on behaviour, allowing for inferences about navigation strategies, the accuracy of spatial memory representations, and navigation efficiency (Iggena et al., 2023; Iglói et al., 2009; Marchette et al., 2011; Simon et al., 2022). We predicted that the relative contributions of place and response navigation change over time due to reorganization processes in hippocampal-neocortical networks. In line with this, we observed that place strategies were preferentially used in the first hours to days after encoding. During this time window, response strategies were not used systematically (i.e. not above chance level). After two weeks, place strategy use decreased, and participants equally relied on place and response strategies. The strategy shift coincided with a decline in place memory after two weeks, while response memory remained stable across delays. Response strategy use was negatively correlated with place memory (but not response memory), indicating that response strategies were used to compensate for insufficient place memory. Thus, in our experimental context, place and response navigation were both present and retrievable initially. Over time, place navigation faded before response navigation.

We observed a shift in the relative contributions from hippocampus-related place to striatum-related response navigation over time. The direction of this shift aligns with studies investigating the effect of continued training on strategy use in rodents (Packard & McGaugh, 1996) and humans (Iaria et al., 2003 but note that Iglói et al., 2009 report bi-directional shifts). Reasons behind the training-related shift from place to response navigation were habit formation and the use of a more cost-effective strategy. Likewise, a shift from place to response navigation was observed in rodents when consolidation was impaired by sleep deprivation (Hagewoud et al., 2010). Here, the shift allowed compensating for impaired hippocampal function due to sleep deprivation. We complement these findings by showing a shift from place to response navigation in humans as a function of time. Here, shifting to response navigation likely serves to compensate for the forgetting of perceptual landmark details that are required for place navigation. Our results align with the proposal that forgetting depends on the nature of memory representations (Sadeh et al., 2014), which states that memories are particularly vulnerable to time-dependent decay if they require contextual reinstatement in the hippocampus.

The observation of distinct forgetting curves for place and response navigation aligns with the traditional view that they are acquired in parallel 'memory systems', in the hippocampus and striatum respectively (Marchette et al., 2011; Packard & McGaugh, 1996). We further observed compensatory response strategy use when place memory was insufficient, indicating these memory systems are flexibly used according to preferences and task demands (Iglói et al., 2009; Marchette et al., 2011). Notably, there was a positive correlation between place and response memory, suggesting that the cognitive functions for spatial memory ability are partially overlapping. This corresponds to recent work emphasizing that place and response navigation (or 'allocentric' and 'egocentric' representations) are not distinct entities but share overlapping brain network activations (Cabral et al., 2014; Ekstrom et al., 2017; Gasser et al., 2020; Iglói et al., 2010) and undergo similar behavioural and neural changes during sleep-related consolidation (Bastian et al., 2022; Samanta et al., 2021). Please note that explicitly testing place and response memory at the end of the learning session may have influenced participant's strategy choices after the delay. We tried to mitigate this risk by completing all training trials beforehand and by emphasizing the importance of using both place and response information in the instructions.

In our study, place memory deteriorated significantly within the two-week period. This contrasts with Packard and McGaugh (1996), where rodent's place memory remained intact after the two-week delay. A major difference between the two studies is that we manipulated time only, whereas Packard and McGaugh (1996) manipulated time in combination with training. Other potential explanations are cross-species differences between humans and rodents and differences in experimental design (e.g., more explicit instructions for humans, real-life navigation in rodents versus virtual navigation in humans).

For navigation efficiency i.e., the speed and directness of navigation, we did not necessarily expect delay effects, because previous studies found that consolidation benefits spatial memory accuracy but not navigational variables like latency and path length (Simon et al., 2022). In line with this, participants navigated as quickly and directly after the 2wk delay as after shorter delays. Place strategy use and place memory in the retrieval session correlated with slower navigation speed, whereas response strategy use correlated with faster navigation speed. This could indicate that place navigation is a deliberate mode of navigation, while response navigation involves automation (Goodman, 2021; Iaria et al., 2003; Marchette et al., 2011; Schmidt et al., 2013).

4.3. Contextual factors modulate the relative contributions of place and response navigation

The use of place and response navigation is modulated by contextual factors such as the environmental design (Goodman, 2021), task instructions (Boone et al., 2019), task demands (Gardner et al., 2013), and stress (Goodman, 2021). For example, visually heterogeneous environments with multiple landmarks increase the likelihood that navigators use place navigation (Goodman, 2021; Packard & Goodman, 2013). Similarly, the presence of multiple rather than a single target location may bias navigation towards place navigation. Correspondingly, we observed a preference for place navigation in an environment that contained multiple perceptually detailed landmarks and multiple target locations, at least after short delays. This differs from prior studies that report an overall preference for response navigation in environmental contexts with fewer landmarks and a single target location (Iglói et al., 2009; Maier et al., 2023).

Environmental heterogeneity may also be an important modulator of consolidation. Consolidation theories predict that memory representations deteriorate quickly over time if they require the recollection of detailed information but prevail if they require a sense of familiarity or abstract information only (Sadeh et al., 2014; Winocur & Moscovitch, 2011). These representational changes coincide with neural activation shifts from the hippocampus to neocortical areas (Winocur & Moscovitch, 2011). Thus, it is plausible that hippocampus-dependent place navigation deteriorates fast in environments with a heterogeneous and detailed landmark structure where abstract information (e.g., the semantic landmark category) is not sufficient for place navigation. Correspondingly, we observed a significant decrease in place navigation after two weeks. In contrast, response navigation remained stable and was increasingly used after two weeks. The reason behind might be that successful response navigation did not require as much detailed recollection as place navigation and could be solved based on habitual responses (e.g., short sequences of turns) or even a sense of familiarity (e.g., directional information that target was 'just to the right').

We suggest that the shift from place to response navigation over time in our study is also a context-dependent effect. This is in line with recent evidence showing a reversed shift from response to place navigation in rodents, when they were tested in a stressful rather than appetitive context (Asem & Holland, 2013; Gasser et al., 2020). Further research is necessary to examine the generalizability of our findings across experimental contexts. For example, it should be assessed whether response navigation declines more strongly over time if it requires remembering long sequences of turns (e.g., paradigm by Rauchs et al., 2008) and, on the other hand, whether place navigation remains more stable if it only requires remembering coarse landmark information. Besides contextual factors, individual characteristics will likely play a role. Previous studies found a higher inherent preference for response navigation in women and older navigators (Boone et al., 2019; Hegarty et al., 2021) that may persist after consolidation. In contrast, we did not find any sex and age effects on place and response navigation after the delay, indicating that they were no relevant predictors for the strategy choice after the delay in our experimental context.

4.4. Open questions for future research

In our navigation task, which was inspired by the starmaze (Iglói et al., 2009; Rondi-Reig et al., 2006) and human Y maze (Rodgers et al., 2012), landmark learning was used as a proxy for place navigation and sequence learning as a proxy for response navigation. Please note, though, that response navigation can also occur as a function of landmark learning (e.g., when remembering to turn left/right at a specific landmark). Future studies are thus required to disentangle consolidation effects on reference frames versus cue types (e.g., proximal and distal landmarks, boundary). Furthermore, our navigation task was desktop-based and thus provided visual but not multisensory information and did not require physical movement. Previous studies found that navigation benefits from multisensory input (Iggena et al., 2023) and physical movement (Hegarty et al., 2021); thus, it would be important to validate our findings in a more ecologically relevant context with real-life navigation. Future studies should also include neuroimaging techniques to elucidate hippocampal and neocortical contributions for remote place and response navigation. Lastly, consolidation studies should include extended time windows beyond the initial days (see e.g., Hirshhorn et al., 2012; Patai et al., 2019; Rosenbaum et al., 2004), given our finding that relevant behavioural changes may only appear after several weeks.

4.5. Conclusion

Our study shows that the consolidation of memory-guided navigation is a dynamic process that gradually unfolds in the hours, days and weeks after encoding. Relevant changes in navigation behaviour occurred particularly after delays that extended beyond a single day, thus emphasizing that consolidation involves ongoing and long-lasting transformations that go beyond early synaptic and sleep-related changes. We found that the choice of the time delay between encoding and retrieval critically determined the use of navigation strategies and the availability of memory representations for navigation. In an experimental setting that was inspired by animal research, we observed a shift from place navigation to response navigation after two weeks, indicating that hippocampusdependent landmark information decayed faster than striatum-dependent sequence information. Response navigation occurred predominantly as a compensatory strategy in the absence of sufficient place memory. The changes in place and response navigation likely reflect the reorganization of hippocampal-neocortical networks during systems consolidation. Future studies should further investigate how contextual factors modulate the interplay between place and response navigation across experimental settings and explore the nature of the underlying network changes.

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CRediT authorship contribution statement

Patrizia M. Maier: Writing – review & editing, Writing – original draft, Visualization, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Deetje Iggena**: Writing – review & editing, Visualization, Software, Project administration, Methodology, Formal analysis, Conceptualization. **Christoph J. Ploner**: Writing – review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Carsten Finke**: Writing – review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Open practices

The study in this article has earned Open Data and Open Material Badges for transparent practices. The data and materials used in this study are available at: https://osf.io/2a6hu/.

Declaration of competing interest

None.

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Supplementary data

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