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Travel in the Physical and Mental Space: A Behavioral Assessment of the Phylogenetic Continuity Hypothesis Between Egocentric Navigation and Episodic Memory

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Abstract

Based on the neuro-functional association between navigation in the physical and the mental space at the level of the hippocampal-entorhinal system, Buzsáki and Moser (2013) have hypothesized a phylogenetic continuity between spatial navigation and declarative memory functions. According to this proposal, mechanisms of episodic and semantic memory would have evolved from mechanisms of self-based and map-based navigation in the physical space, respectively. Using classic versions of path integration and item recognition tasks in human subjects, we have recently described a correlation and a predictive relationship between abilities in egocentric navigation and episodic memory. Here we aim at confirming and extending this association to the dynamic component of sequential updating in the physical (egocentric navigation) and mental (episodic memory) space, and at investigating the relationship of these self-centered abilities with semantic memory. To this aim, we developed three new experimental tasks in which the dynamic component of updating information is particularly emphasized in the spatial, the temporal, and the semantic domain. The contribution of visual short-term memory to the three tasks was also controlled by including an additional task. The results confirmed the existence of a direct and predictive relationship between self-based spatial navigation and episodic memory. We also found a significant association between egocentric navigation and semantic memory, but this relationship was explained by short-term memory abilities and was mediated by episodic memory functions. Our results support the hypothesis of an evolutionary link between mechanisms that allow spatial navigation in the physical space and time travel in the mental space.

Keywords

spatial navigation, egocentric navigation, episodic memory, semantic memory

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Introduction

Recent studies have suggested that basic spatial navigation mechanisms provide coding principles that operate across non-spatial domains to support a wide spectrum of cognitive functions, including declarative memory first of all (Buzsáki & Moser, 2013) but also conceptual knowledge and abstract thought (Bellmund et al., 2018; Viganò & Piazza, 2020).

Human navigational abilities are traditionally thought to rely on two interlinked mechanisms for the representation of the spatial environment: one is typically referred to as map-based or allocentric navigation and the other is known as self-based or egocentric navigation (Boccia et al., 2014; Iaria et al., 2003; Igloi et al., 2009). While map-based navigation is based on fixed coordinates extracted from external landmarks,

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self-based navigation is based on a continuous updating of the observer's position in space. During self-based navigation, the current body position is used as a reference frame, and spatial coordinates are calculated based on the continuous integration of body-motion signals along the locomotion trajectory (Klatzky, 1998). To more clearly describe mechanisms of self-based navigation, previous studies have proposed that egocentric representations can be thought of as high-resolution visual "snapshots" linked to current behavior and that coherent egocentric representations are formed by integrating these static body-referenced snapshots in series (Ekstrom & Isham, 2017).

In a similar vein, declarative memory functions have been traditionally decomposed into two main components characterized by different spatio-temporal coordinates (Tulving, 1983). Specifically, while semantic memory is defined as the explicit knowledge of living things, objects, facts, and events of the world independently of their spatio-temporal context, episodic memory is typically conceptualized in terms of the explicit recollection of spatially and temporally contextualized first-person experiences. Episodic memory functions, in particular, are thought to be responsible for the binding of disparate and often arbitrary details into a coherent event. Even if recollection can be chunked into shorter sub-episodes, the feeling of a continuous process is normally always well preserved (Tulving, 2002). It is now well established, that the conscious recollection of unique personal experiences in terms of their details and temporal occurrence relies on the ability to subjectively sense time and the internal creation of a personal timeline (Bonato et al., 2012; Dere et al., 2006; Weger & Pratt, 2008), intended as an imaginary line passing through our body and extending forward and backward across future and past time portions. As argued in classic memory studies, indeed, it is along this subjective timeline that the most sophisticated form of episodic memory, known as mental time travel, is thought to take place (Tulving, 2002).

At the neurobiological level, both navigation and declarative memory strictly depend on a dedicated network centered on the medial temporal lobe (MTL), which includes the hippocampal formation and cortical regions of the retrosplenial and posterior cingulate cortex (Kravitz et al., 2011). As shown by several neurophysiological works, hippocampal activity reflects information about both locations in space and moments in time (Eichenbaum, 2014; Ekstrom & Ranganath, 2018; Epstein et al., 2017; Moser et al., 2017). The neuro-functional correspondence between navigational and memory functions at the level of the MTL has led to the proposal of a phylogenetic continuity between neural mechanisms for navigation in the physical and the mental space (Buzsáki & Moser, 2013). Accordingly, episodic and semantic memory would have respectively evolved from egocentric self-based and allocentric map-based navigation. In the hippocampus, such a phylogenetic continuity would be supported by cell assembly sequences driven by external inputs (i.e., environmental or body-derived cues originally used to track movements of the body in the environment during physical travel), which provide the basis for the subsequent development of internally driven sequences allowing mental time travel. In other words, physical movement in the real world might represent the primary source of the brain's ability to remember past experiences and plan future actions.

In support of this neurophysiologically based model, we have recently described a specific and predictive relationship between human abilities in egocentric navigation and episodic memory (Committeri et al., 2020). In particular, we have shown that performance on a classic path integration task based on proprioceptive cues was significantly correlated with performance on a classic item recognition task. On the other hand, no significant correlation was observed between the performance in the egocentric navigation and the semantic memory tasks, suggesting a specific relationship between the egocentric components of episodic memory and spatial navigation.

The present study sought to investigate whether the conclusions drawn from our previous study could be confirmed and generalized to the dynamic component of sequential updating of information during egocentric navigation and episodic memory. To this aim, a new set of experimental tasks were designed in which the dynamic component of the spatio-temporal updating was emphasized in both the physical (Travel in Space [TS]) and the mental (Travel in Time [TT]) domain. Compared to the traditional tasks used in our previous work, performance in the self-based egocentric navigation and episodic memory tasks more strongly reflected the individual ability to linearly travel back and forth in the physical and the mental space. A semantic memory task was also included in the design with a similar structure and a similar emphasis on dynamic processing within the semantic memory (Travel in Categories [TC]). Specifically, compared to the episodic memory task, in which the dynamic updating of information was performed along a linear sequence and on a self-based reference frame, the semantic memory task was based on a nonlinear process of updating of nonself/allocentric information about semantic categories.

Based on the aforementioned hypothesis of a phylogenetic continuity and the results of our previous study, we predicted a positive correlation between performance in the egocentric navigation and the episodic memory task, as they both imply a sequential travel component and a dynamic updating of information in self-based/egocentric coordinates. Alongside, on the basis of the phylogenetic continuity model and the allocentric reference frame of the semantic memory task, a null or indirect relationship was expected between performance in the egocentric navigation and the semantic memory task. Finally, since the three tasks shared a similar structure that involves the online maintenance of information from the initial video-clip/pictures stream in short-term memory, a control visual short-term memory task (STM) was also included in the design to control for a potential confounding effect of this component to the hypothesized relationship between navigational and memory functions.

Materials and Methods

Participants

A total of 141 healthy and right-handed volunteers (mean age = 21.5 ± 2.7 years, 119 females), recruited from the University

G. d'Annunzio of Chieti-Pescara, participated in the study. All participants were naïve as to the purpose of the experiment, reported normal or corrected-to-normal vision, and were enrolled in the study after providing informed consent. None of the participants reported having previously watched the television series "Grandfathered" before the experiment. The study was conducted following the ethical standards of the 1964 Declaration of Helsinki and was approved by the University Ethics Committee (prot. #1932 approved on July 11, 2019).

Pilot Study for Stimuli Selection

Trial selection for each of the four tasks was conducted through pilot studies collected before the main experiment in independent samples of subjects. Specifically, trials with extreme values of mean accuracy in the four tasks were excluded from the selection and a final set of 34 trials with a medium-high difficulty level was included in each task design.

TT task. To assess the time travel component of the episodic memory performance, we developed a temporal order memory task based on movie scenes. The episodic memory task, hereafter defined as the "Travel in Time" task, was designed to emphasize the self-based component of sequential updating and temporal ordering in the mental space and included an encoding and a retrieval session separated by a ~50 min interval. At encoding, a full episode of the American television series "Grandfathered" dubbed in Italian (Season 1, Episode 1, "Pilot"; duration: 21:20 min) was shown to participants. The episode portrays a character's real-life-like actions and contains ordinary events (e.g., breakfast at home, a walk in the park, a visit to the hospital). Participants were instructed to pay attention to the movie but were not informed about the nature of the following tasks. In the retrieval session, they provided a temporal order judgment on the encoded audio-visual material. Each trial began with the presentation of a 6 s video clip extracted from the same episode, followed by a 500 ms red fixation cross and a target picture of 1-s duration (Figure 1A). Target pictures were extracted from movie scenes occurring 1–2 min earlier or after the onset-offset of the corresponding video-clip, with a 1:1 ratio. Participants had 3 s from the onset of the target image to indicate whether the target picture was extracted from a scene occurring before or after the video-clip (i.e., "z" key for "before", "m" key for "after"). A 1-s ITI preceded the following trial. The retrieval session included 34 trials and was preceded by four practice trials.

TS task. To assess the egocentric component of the spatial navigation performance, we developed a spatial positioning task based on street-view images extracted from Google Earth. The egocentric navigation task, hereafter defined as the "Travel in Space" task was designed to emphasize the self-based component of sequential ordering and spatial updating in the physical space. To this aim, the Google Earth Pro software was used to generate a series of 6-s video-clips displaying the first-person perspective of a navigational path extracted from different streets of several cities around the world. Each video-clip included 10 consecutive screenshots of the same street covering a total distance of 100 m in the real environment (i.e., ~10 m for each snapshot). Each trial began with the presentation of a 6-s video clip, followed by a 500 ms red fixation cross and a target picture of 1-s duration (Figure 1B). Target pictures were extracted from street-view images photographed at a distance of ~50–100 m backward or forward from the corresponding video-clip, with a 1:1 ratio. Participants had 3 s from the target image onset to indicate whether it was extracted from a backward or a forward position with respect to the video-clip ("z" key for "backward", "m" key for "forward"). A 1-s ITI preceded the following trial. The task included four practice and 34 experimental trials.

TC task. As for the TT and the TS tasks, the dynamic component of semantic memory was assessed using a semantic categorization task based on images extracted from the web. The semantic task, hereafter defined as the "Travel in Categories" task, was designed to emphasize the dynamic updating of nonself/allocentric conceptual knowledge about semantic categories. As for the TT and the TS tasks, each trial of the TC task began with the presentation of six consecutive pictures for 6 s (1 s for each picture), followed by a 500 ms red fixation cross and a target picture of 1-s duration (Figure 1C). Participants had 3 s from the target image onset to indicate whether it belonged to the same semantic category of the six preceding elements ("m" key for "yes", "z" key for "no"). A 1-s ITI preceded the following trial. The six elements of the initial stream were selected from a given semantic category, with categories including pictures of both living and nonliving elements (e.g., *reptiles, European countries, famous singers, farm animals*). Target pictures were either selected from the same semantic category of the preceding stream of pictures or a different semantic category, with a 1:1 ratio. As an example of a "no" trial, six pictures of flying animals were presented at the beginning of the trial (i.e., *a toucan, a hawk, a butterfly, a dragonfly, a bat, an eagle*) and a picture of a *penguin* was presented as target picture. Participants were not explicitly informed about the unifying semantic feature. Instead, they were invited to continuously integrate information during the stream of pictures to update their hypothesis about the category definition (from birds to flying animals in the example). Notably, while the TT and the TS tasks were intrinsically based on sequential ordering and updating of information (both stimulus presentation and task performance), the TC task was designed to emphasize the dynamic but not the sequential updating of conceptual knowledge about semantic categories (i.e., the order of stimulus presentation was designed to be irrelevant to task performance). The task included four practice and 34 experimental trials. For a complete list of the experimental trials included in the experiment, see Supplemental Table 1.

STM task. Given that the three main tasks (TT, TS, and TC) shared a similar structure and were all based on online maintenance and updating of visual information from the initial video-

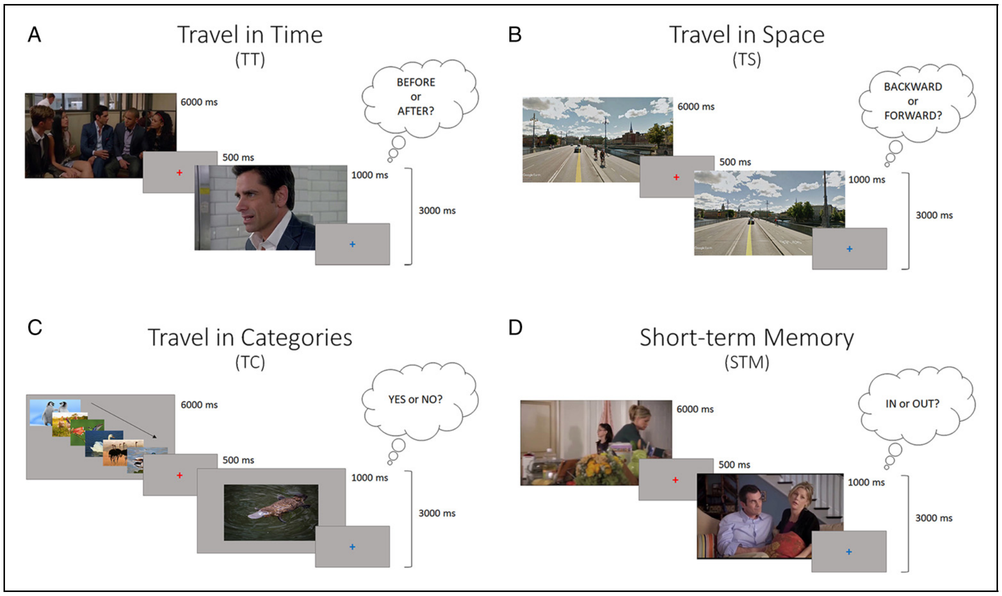

Figure 1. (A) In the TT task, participants indicated whether the target picture was extracted from a scene occurring before or after the one presented in the video-clip. (B) In the TS task, participants reported whether the target picture was extracted from a backward or a forward position with respect to the path seen in the video-clip. (C) In the TC task, participants indicated whether the target element belonged to the same semantic category of the six preceding elements. (D) In the STM task, participants reported whether the target picture was extracted from the previously presented video-clip.
Abbreviations: TT = Travel in Time; TS = Travel in Space; TC = Travel in Categories; STM = short-term memory.

clip/pictures stream, a visual STM task was additionally included in the design to control for the potential contribution of visual STM functions to the hypothesized relationship between tasks.

As for the previously described tasks, the STM task was composed of an initial 6-s video clip extracted from an episode of the television series "Modern Family" (Season 1, Episode 1, "Pilot"; duration: 22 min), followed by a 500-ms red fixation cross and a target picture of 1-s duration extracted from the same episode (Figure 1D). Target pictures were extracted from movie scenes included in the presented video clips or from movie scenes occurring 1–2 s earlier or after the onset-offset of the presented video clip, with a 1:1 ratio. Participants had 3 s from the target image onset to indicate whether the target picture was extracted from the previously presented video clip ("m" key for "yes", "z" key for "no"). A 1-s ITI preceded the following trial. The task included four practice trials and 34 experimental trials.

Procedure

The experiment was conducted in a single experimental session of ~2 h duration (including instructions and pauses) with the following order: TT-encoding (22 min), interval (50 min), TT-retrieval (~10 min), TS (~10 min), TC (~10 min), and STM (~10 min). The TT-retrieval session was collected as first, following the TT-encoding session and the subsequent interval to reduce potential interference effect (e.g., movies scenes from the STM task). The task paradigms were developed on Inquisit Lab 5 and administrated via Inquisit Web.

Statistical Analysis

Statistical analyses were conducted on a total sample of 124 participants after the exclusion of outlier subjects with a mean accuracy performance of two standard deviations (*SD*) below of the group mean in each of the four tasks. Normal distribution of data was evaluated using the parameters of skewness and kurtosis of data distribution (Kendall & Stuart, 1958). Following controls for normal data distribution, we tested whether performance (i.e., accuracy) in each task was above chance through a one-sample *t*-test against chance level (0.50). Significant differences in performance across tasks were also assessed through one-way ANOVA and post-hoc tests (Bonferroni).

The relationship between accuracy in the spatial navigation (i.e., TS) and the episodic memory (i.e., TT) task was firstly assessed by conducting a robust correlation analysis implemented in Matlab R2020a (Pernet et al., 2013, robust correlation analysis toolbox). Correlation values were obtained through skipped correlation analyses, which estimate the robust center of the data and associated Pearson correlation values after the automatic removal of bivariate outliers (Rousseeuw, 1984; Rousseeuw & Van Driessen, 1999; Verboten & Hubert, 2005).

The predictive power of the association between the behavioral scores in the TS and the TT tasks was also assessed using a leave-one-out cross-validation analysis implemented in Matlab (R2020a). Specifically, we used a leave-one-subject-out cross-validation scheme in which individual scores in the TS task were used to predict the corresponding TT scores based on a regression curve estimated from the remaining (N–1) subjects. A Pearson correlation analysis was conducted between the observed and the predicted episodic memory scores. To account for the nonindependence of the leave-one-out folds, a permutation test was conducted by randomly shuffling the TS scores 1,000 times and rerunning the prediction pipeline to create a null distribution of r values. The resulting p-value was derived from the proportion of null distribution r values higher or equal to the corresponding empirical correlation value (see Beaty et al., 2018; Shen et al., 2017).

As a second analysis step, the specificity of the relationship between spatial navigation (TS) and episodic memory (TT) performance was examined using robust correlation analysis between the accuracy scores in the semantic memory task (TC) and both the TS and the TT tasks. Robust correlation analyses were also conducted between the short-term memory task (STM) and the other tasks (TT, TS, and TC). A series of partial correlation analyses were then conducted to examine whether the correlation between the spatial navigation and the episodic memory performance was explained by common variance in short-term memory or semantic memory performance. To this aim, two partial correlation analyses were performed between the TS and TT tasks using the STM or the TCscores as a covariate. Similarly, two partial correlation analyses were used to test whether the correlation between spatial navigation and semantic memory scores was explained by common variance in STM or TT performance. Partial correlations were performed on IBM SPSS Statistics 25 after the exclusion of the bivariate outliers identified in the original robust correlation analyses between the two main variables.

Finally, to examine the existence of an indirect behavioral association between spatial navigation and semantic memory mediated by episodic memory, a mediation analysis was conducted using the PROCESS toolbox for SPSS (Hayes, 2013). Specifically, a mediation model was tested (template model number 4) in which the spatial navigation performance (TS) was modeled as the independent variable, the episodic memory performance (TT) as a mediator, and the semantic memory performance (TC) as the dependent variable.

All the correlation results were corrected for false discovery rate (Benjamini & Hochberg, 1995) using the *fdr_bh* script running on Matlab (R2020a). In addition, a two-tailed post hoc power analysis (1–β error probability) was conducted for each reported effect size (i.e., Pearson's r) using the G*Power toolbox (3.1.9.7). Power analyses were conducted setting the α error probability at a value of 0.05.

Results

Analysis of the skewness and kurtosis parameters indicated that all variables were normally distributed (skewness: all values <−0.14 and >−1.2; kurtosis: all values <1.29 and > −0.58). Consistent with the selection criteria in the pilot studies, performance was above chance in all tasks (TT: 0.62 [$SD = 0.15$], TS: 0.65 [$SD = 0.12$], TC: 0.67 [$SD = 0.12$], STM: 0.72 [$SD = 0.12$]); one-sample t-tests against chance performance, all p-values <.001)]. An across-task comparison using a one-way ANOVA, however, revealed significant differences between performance in the four tasks. In particular, post-hoc comparisons (Bonferroni) conducted on the significant main effect of the task ($F = 14.825$, $p < .001$) indicated that the STM was slightly easier than the other three tasks (all p-values <.01), and that the TC was easier than the TT ($p = .007$).

The robust correlation analysis indicated a statistically significant positive correlation between the scores in the egocentric navigation (TS) and the episodic memory (TT) tasks ($r = .23$, $p = .005$, FDR = 0.0133, power = 0.73) (Figure 2A). As indicated by the leave-one-out cross-validation analysis, moreover, individual scores in the TT task were reliably predicted by scores in the TS task ($p = .004$, FDR = 0.0133) thus indicating not only a correlational structure but also a predictive relationship between these two measures of performance. Since the two tasks shared an analogous structure, these findings not only confirm the association between egocentric navigation and episodic memory performance shown in our previous study (Committeri et al., 2020) but also demonstrate that this association is likely mediated by common mental components associated with time travel and sequential updating of information in the two domains.

Consistent with our previous findings, moreover, a significant positive correlation was found between the episodic and the semantic memory scores ($r = 0.24$, $p = .003$, FDR = 0.0133, power = 0.77) indicating a statistical dependence between the two forms of declarative memory. A significant correlation, however, was also found between the egocentric navigation (TS) and the semantic memory (TC) scores ($r = .16$, $p = .03$, FDR = 0.04, power = 0.43) (Figure 2B) indicating a weaker specificity compared to our previous findings. As indicated in the Methods section, however, the specific contribution of the episodic, semantic and spatial components to the observed correlational structure was addressed by conducting a series of partial correlation analyses with each of the variables used as a covariate in separate analyses. Furthermore, as the STM performance positively correlated with all three tasks (TT, TS, TC: for all tasks, $p < .05$), partial correlation analyses were employed to estimate the visual short-term memory contribution to the observed correlation results.

Consistent with the predictions, the results indicated that the correlation between egocentric navigation and episodic memory remained significant also when controlling for semantic memory ($r = .20$, $p = .02$, FDR = 0.032, power = 0.61) or short-term memory ($r = .21$, $p = .02$, FDR = 0.032, power = 0.65) performance. In contrast, no significant correlation was observed between egocentric navigation and semantic memory performance when controlling for episodic memory ($r = .11$, $p = .22$, FDR = 0.22, power = 0.23) or short-term memory ($r = .12$, $p = .18$, FDR = 0.21, power = 0.26) performance. Notably, while these results support the robustness of the relationship between egocentric navigation and episodic memory, they also suggest the hypothesis of a spurious/indirect relationship between egocentric navigation and semantic memory.

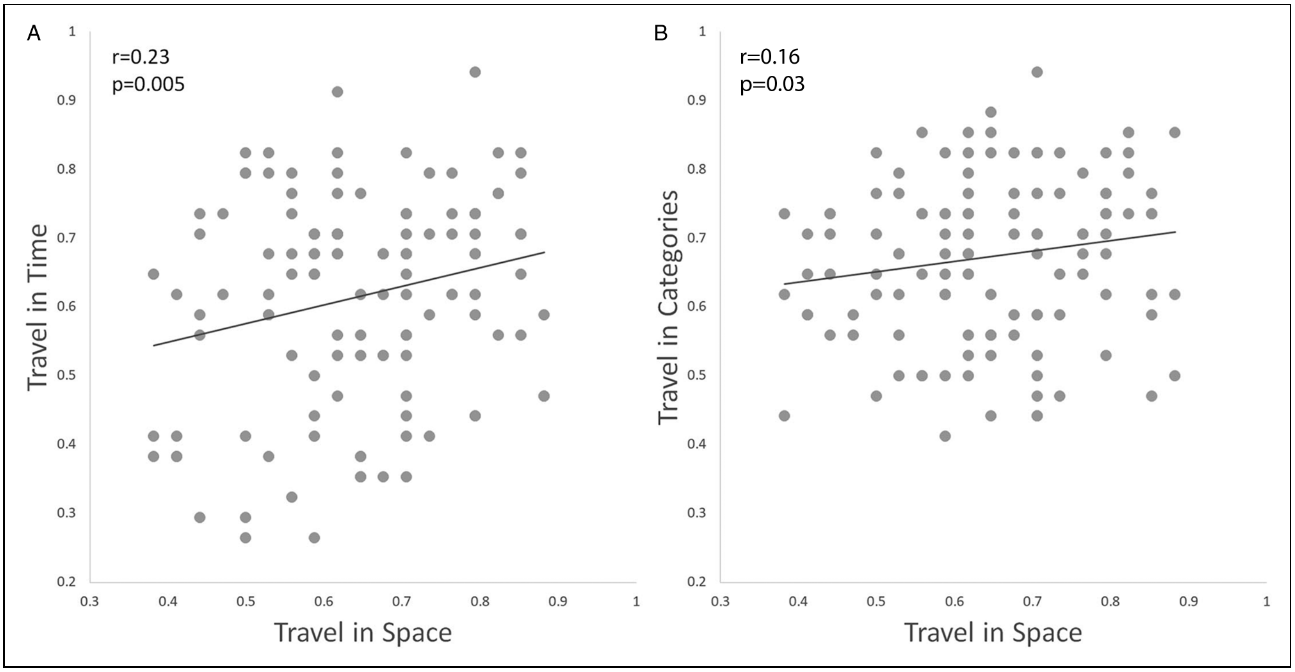

Figure 2. (A) Correlation between TS and TT and (B) Correlation between TS and TC excluding one bivariate outlier identified by the robust correlation analysis.
Abbreviations: TT = Travel in Time; TS = Travel in Space; TC = Travel in Categories.

This hypothesis was tested using a mediation analysis, which confirmed that the relationship between egocentric navigation and semantic memory was mediated by episodic memory ($R^2 = .05$, $F[1,122] = 6.68$, $p = .01$). As displayed in Figure 3, in particular, a bootstrap analysis with 5000 resamplings showed a statistically significant indirect effect of spatial navigation over semantic memory via episodic memory ($b = 0.0476$; 95% CI: LLCI = 0.006, ULCI = 0.109). Instead, the direct effect of spatial navigation over semantic memory without considering the mediation effect of episodic memory was not significant ($b = 0.0807$; $p = .34$, 95% CI: LLCI = −0.0875, ULCI = 0.2488). Furthermore, a statistically significant direct effect was obtained for egocentric navigation over episodic memory ($b = 0.2712$, $p = .01$, 95% CI: LLCI = 0.0636, ULCI = 0.4788), as well as for episodic memory over semantic memory ($b = 0.1756$, $p = .02$, 95% CI: LLCI = 0.0342, ULCI = 0.3169).

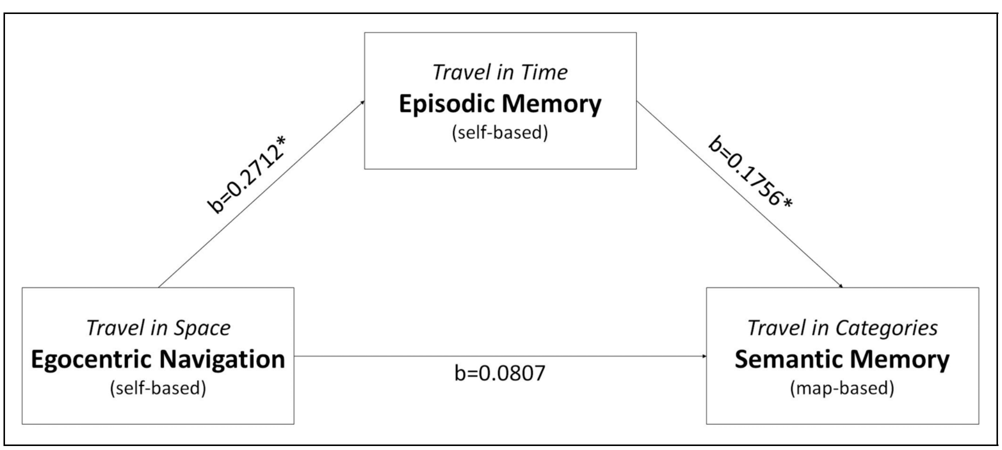

Figure 3. Mediation model testing the relationship between spatial egocentric navigation (TS) and semantic memory (TC) mediated by episodic memory (TT). While the indirect effect of spatial navigation over semantic memory via episodic memory was statistically significant ($b = 0.0476$; 95% CI: LLCI = 0.006, ULCI = 0.109), the direct effect of spatial navigation over semantic memory without considering the mediation effect of episodic memory was not significant ($b = 0.0807$; $p = .34$, 95% CI: LLCI = −0.0875, ULCI = 0.2488). [Note: $*p < .05$].
Abbreviations: TT = Travel in Time; TS = Travel in Space; TC = Travel in Categories.

Discussion

As outlined in the introduction, we have recently provided experimental support to the hypothesis formulated by Buzsáki and Moser (2013) of a phylogenetic continuity between neural mechanisms for navigation in the physical and in the mental space (Committeri et al., 2020). In particular, following the hypothesis that mechanisms for navigation in the mental space might have evolved from recycling mechanisms for navigation in the physical space, we found that participants' performance on a classic episodic memory task (i.e., item recognition) was reliably predicted by their performance on a classic egocentric navigation task (i.e., path integration). On the contrary, no correlation or predictive relationship was observed between the participants' performance on an egocentric navigation and a semantic memory task. Here we sought to extend these behavioral findings to the dynamic component of sequential updating and linear ordering (travel) of self-based egocentric navigation and episodic memory. Moreover, since episodic and semantic memory have been classically considered as closely interdependent functions (Greenberg & Verfaellie, 2010), directly or indirectly associated with egocentric navigation (Buzsáki & Moser, 2013), here we additionally sought to better elucidate the relationship between egocentric navigation and both forms of declarative memory. To this aim, we developed three new experimental tasks that shared a comparable experimental structure and an emphasis on the dynamic component of updating of information in different domains. Within this controlled setting, we compared the dynamic process of information updating across the spatial (TS), the temporal (TT), and the semantic (TC) domain. A visual short-term memory task (STM) with an analogous structure was additionally included in the design to control for the contribution of this function to the three main tasks.

The results confirmed our previous findings of a significant correlation and predictive relationship between measures of performance on egocentric navigation and episodic memory. Within the experimental context of the present study, in particular, the findings indicated that the participants' performance on traveling in space positively correlates and predicts the travel in time performance, with the correlation results indicating that this relationship was strongly independent of short-term memory abilities. We believe that the consistent relationship between egocentric navigation and episodic memory across studies is accounted for by a common mechanism for the processing and storing of spatial and temporal information. The storage of ordered sequences of elements, indeed, appears as a key aspect of both self-based egocentric navigation and episodic memory. During egocentric navigation, location sequences are linked together by a neural path integrator along with a one-dimensional space that does not require a map representation, similar to how sequentially occurring items are assembled into a coherent memory episode (Buzsáki, 2005). In contrast, allocentric maps define a location inside a two-dimensional space independently of the path performed to get there, similar to the way semantic memory defines concepts independently of their temporal or spatial context. Indeed, the orthogonal organization of concepts inside semantic maps shares many features with the omnidirectional distance relationships among landmarks inside a map (Bellmund et al., 2018; Viganò & Piazza, 2020).

The processing of time and space from a self-based perspective has led to the concept of mental lines (Bonato et al., 2012) and multiple studies have supported the association between linear time and space processing. For example, in a series of experiments using lateralized responses, Anelli et al. (2016, 2018) have described an intrinsic, or natural, disposition to map past and future events along a horizontal mental timeline with the former mapped leftward and the latter rightward. Importantly, such a reciprocal influence of spatial coding over time processing has been also evidenced when lateralization is induced in visuospatial processing through prismatic adaptation. Indeed, prismatic adaptation of spatial attention significantly modulated the processing of past and future concepts, for example by generating behavioral facilitation for recognition of past/future events that is consistent with the direction of the attentional shift, i.e., facilitation for past vs. future events associated with leftward vs. rightward shift of spatial attention respectively (Anelli et al., 2016). Even more paradigmatic, prismatic adaptation treatment inducing a leftward shift of spatial attention has been shown to induce a long-lasting amelioration of egocentric mental time travel abilities in patients with unilateral neglect for the left hemispace (Anelli et al., 2018). Finally, a recent study by Aksentijevic et al. (2019) has demonstrated that motion in space can significantly affect mnemonic processing. More specifically, the study has shown that backward motion can improve the mnemonic performance for different types of information relative to forward motion or no motion conditions, thus providing additional evidence of the close association between the processing of space and time.

Besides the relationship between self-based spatial navigation and episodic memory performance, the current results also indicate the presence of an association between egocentric navigation and semantic memory performance, which is partially inconsistent with our previous findings on the topic. With respect to this finding, however, the results of partial correlation and mediation analyses indicate that such a correlation was largely explained by other cognitive factors. Specifically, while the correlation between egocentric navigation and episodic memory was direct, predictive, and independent of short-term memory abilities, the correlation between egocentric navigation and semantic memory was significantly explained by the participants' scores in the STM task and, more relevantly, it turned out to be mediated by performance in the episodic memory task. Of note, the current findings of an association between egocentric navigation and semantic memory functions that are mediated by episodic memory abilities are highly consistent with the assumptions of the phylogenetic continuity model (Buzsáki & Moser, 2013): higher-level representations (i.e., map-based allocentric navigation, semantic memory) largely derive from their respective lower-level counterparts (self-based egocentric navigation, episodic memory). In accordance with the model, temporal- and context-free allocentric maps are thought to be based on repeated self-based explorations of the environment (Lever et al., 2002), very similar to how semantic knowledge is progressively acquired through the repeated encoding of similar episodes by the self-based episodic memory system, eventually becoming context-independent (Buzsáki, 2005; Eichenbaum et al., 1999). We thereby speculate that the ability to transform new episodic experience into long-term semantic memory might reflect the ability to transform spatial representations from an egocentric to an allocentric reference frame. Accordingly, as suggested by the original proposal of Buzsáki and Moser (2013), because old semantic knowledge does not rely on sequential or linear/ordered processing of information but rather on allocentric or map-based navigational mechanisms, the relationship between egocentric navigation and semantic memory would be necessarily mediated by episodic memory.

In this respect, we note that the current investigation only represents a test of the lower-level counterpart of the original model (i.e., egocentric navigation, episodic memory). A necessary addition to the investigation of the phylogenetic continuity hypothesis would be an assessment of the entire model/relationship, including map-based or allocentric navigation abilities, and a specific association of these abilities with the nonself, semantic memory performance (in contrast to self-based episodic memory performance). Future studies should therefore examine the higher-level counterpart of the model (i.e., map-based allocentric navigation, semantic memory), for example, by including allocentric navigation tasks in the experimental design and/or implementing ad-hoc data analysis methods capable of testing the degree of hierarchical relationships and reciprocal influence between memory (episodic and semantic) and navigational (egocentric and allocentric) abilities/functions.

Alongside, future studies should assess the contribution of potential overarching factors that might have influenced the observed relationship between navigation and memory functions. A similar approach was already employed in a previous study, in which the possible confounding effects of attentional and working memory abilities on the correlation between egocentric navigation and episodic memory were controlled for by including specific standardized tests in the experimental design (Committeri et al., 2020).

Finally, since the present study was based on a correlational approach to replicate and extend our original findings (Committeri et al., 2020), another future direction should be the assessment of the causal/directional relationship between spatial navigation and episodic memory. For example, future studies could consider alternative approaches, such as those based on training effects in which the causality (and phylogenetic continuity) hypothesis is examined on the basis of modulatory/plasticity effects of these cognitive functions. In alternative, the present model could be tested in the field of human development and aging research. It has been observed, indeed, that older adults, besides the well-known episodic memory deficits, exhibit marked deficits during spatial tasks requiring a first-person, egocentric perspective (e.g., Borella et al., 2015).

Conclusion

In conclusion, the results of the present study confirm our previous findings (Committeri et al., 2020) of a direct and predictive relationship between self-based, egocentric spatial navigation, and episodic memory. Moreover, they extend our previous findings to the dynamic component of sequential travel and updating of ordered/linear information in both the physical and the mental space/domain and support the hypothesis of a phylogenetic continuity and hierarchical relationship between self-based/egocentric and map-based/allocentric processing of information. This evidence, once again, is in agreement with the hypothesis of common mechanisms for the processing and storing of spatial and temporal information, and that the ability to navigate in the mental space may have evolved from recycling mechanisms developed for navigating in the physical space.

Open Practices Statement

The datasets generated during the current study are available from the corresponding author on reasonable request.

Declaration of Conflicting Interests

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Supplemental Material

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