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Reference frames for spatial navigation and declarative memory: Individual differences in performance support the phylogenetic continuity hypothesis

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ABSTRACT

Recent experimental evidence has led to the idea that the neural mechanisms supporting spatial navigation have been flexibly adapted to organize concepts and memories through spatial codes. The "phylogenetic continuity hypothesis" (Buszáki & Moser, 2013) further proposes that the mechanisms supporting episodic and semantic memory would have respectively evolved from self-based (i.e. egocentric) and map-based (i.e. allocentric) spatial navigation mechanisms. Recent studies have observed traces of this phylogenetic continuity in human behavior, but the full original model has not yet been tested. Here, we evaluated the relationships between the four model components by using two sets of tasks in the spatial navigation and declarative memory domains based on complex materials and emphasizing the self vs. map-based processing (i.e. route vs. survey component for spatial navigation and episodic vs. semantic component for declarative memory). Consistent with the model predictions, the results of a multiple multivariate regression analysis revealed a specific across-domain relationship, such that route-based navigation performance specifically predicted episodic memory performance (self-based, egocentric components), while survey navigation performance specifically predicted the semantic memory one (map-based, allocentric components). The results of an additional regression analysis on the within-domain transformation process from self-based to map-based representations confirmed that route-based navigation specifically predicted survey navigation, while episodic memory specifically predicted semantic memory. Our results provide further behavioral evidence in support of the general hypothesis that the neural machinery evolved to map the physical world might have been recycled to organize memory and conceptual knowledge. Crucially, they also support the more specific hypothesis that the organizational principles involved in higher-level processing of information have inherited the fundamental distinction between different reference frames (egocentric vs. allocentric) for navigation in the physical world.

1. Introduction

In mammals, the ability to represent and navigate the outside world is supported by the activity of the medial temporal lobe. A series of groundbreaking studies have demonstrated that the hippocampal-entorhinal system contains the fundamental machinery to accomplish these goals in the forms of place-cells (O'Keefe & Dostrovsky, 1971) and grid-cells (Hafting, Fyhn, Molden, Moser, & Moser, 2005) that code for positions, displacement, and features of the environment (McNaughton, Battaglia, Jensen, Moser, & Moser, 2006a, 2006b; O'Keefe & Nadel, 1978). More recently, several researchers have further proposed that the neural mechanisms identified in spatial navigation may operate across different information domains to organize concepts and memories through spatial codes (for a review see Bellmund, Gärdenfors, Moser, & Doeller, 2018 and Bottini & Doeller, 2020). According to this framework, the information processing of place and grid cells – with their peculiar firing patterns – provides a representational format to map dimensions in cognitive, in addition to physical, spaces.

The general hypothesis that neurocognitive structures and algorithms that are recruited to represent and navigate the physical space are also recruited to represent and navigate non-spatial conceptual knowledge (for a review see Bottini & Doeller, 2020) has been tested in

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humans using functional magnetic resonance imaging. For example, Constantinescu, O'Reilly, and Behrens (2016) have found that the set of brain regions recruited during spatial navigation show a similar hexagonal grid-like pattern also when participants navigate within conceptual knowledge. Similarly, Viganò and Piazza (2020) have shown that the same neuronal coding for representation of distance and direction in the physical space might also underlie navigation in abstract semantic spaces during a symbolic categorization task. Specifically, the latter study showed that the medial prefrontal cortex and the entorhinal portion of the hippocampal formation represent distances and directions between concepts in the same way as they represent these dimensions in the physical world (McNaughton et al., 2006a, 2006b). Therefore, a given stimulus can be located inside a cognitive map along a set of quality dimensions in the same way as landmarks are located inside a spatial map (Bellmund et al., 2018).

The fact that the hippocampal-entorhinal circuitry is preserved along evolution has also supported the idea of a phylogenetic continuity between mechanisms for mapping physical and mental spaces, as reported in the pivotal review work by Buzsáki & Moser, 2013. The hypothesis of a phylogenetic continuity between navigation and memory was delineated based on the anatomical and physiological properties of the hippocampal-entorhinal system in which the enlarged representational capacity and neuronal growth through evolution from insects, rats, monkey and humans is highly compatible with a mechanism of storing of large quantities of seemingly unrelated representations. The basic observation is indeed that insects navigate in the environment using simple circuits and few neurons while rats and humans map the local environment through progressively more complex and larger neural assembly. According to the theory, therefore, the neuronal growth supporting complex representations of space and environmental details in the mammalian brain may also support non-spatial knowledge.

This evolutionary theory also proposes that higher-level mechanisms for navigating the mental space may have inherited a fundamental distinction between the different coordinates systems or reference frames for navigating the physical world. The hypothesis indeed stands that mechanisms supporting episodic and semantic memory have respectively evolved from self-based or egocentric and map-based or allocentric spatial navigation mechanisms (Buzsáki & Moser, 2013, Fig. 1).

Specifically, the storage of ordered sequences of elements appears to be a key aspect of both self-based egocentric navigation and episodic memory. During self-based navigation, location sequences are linked

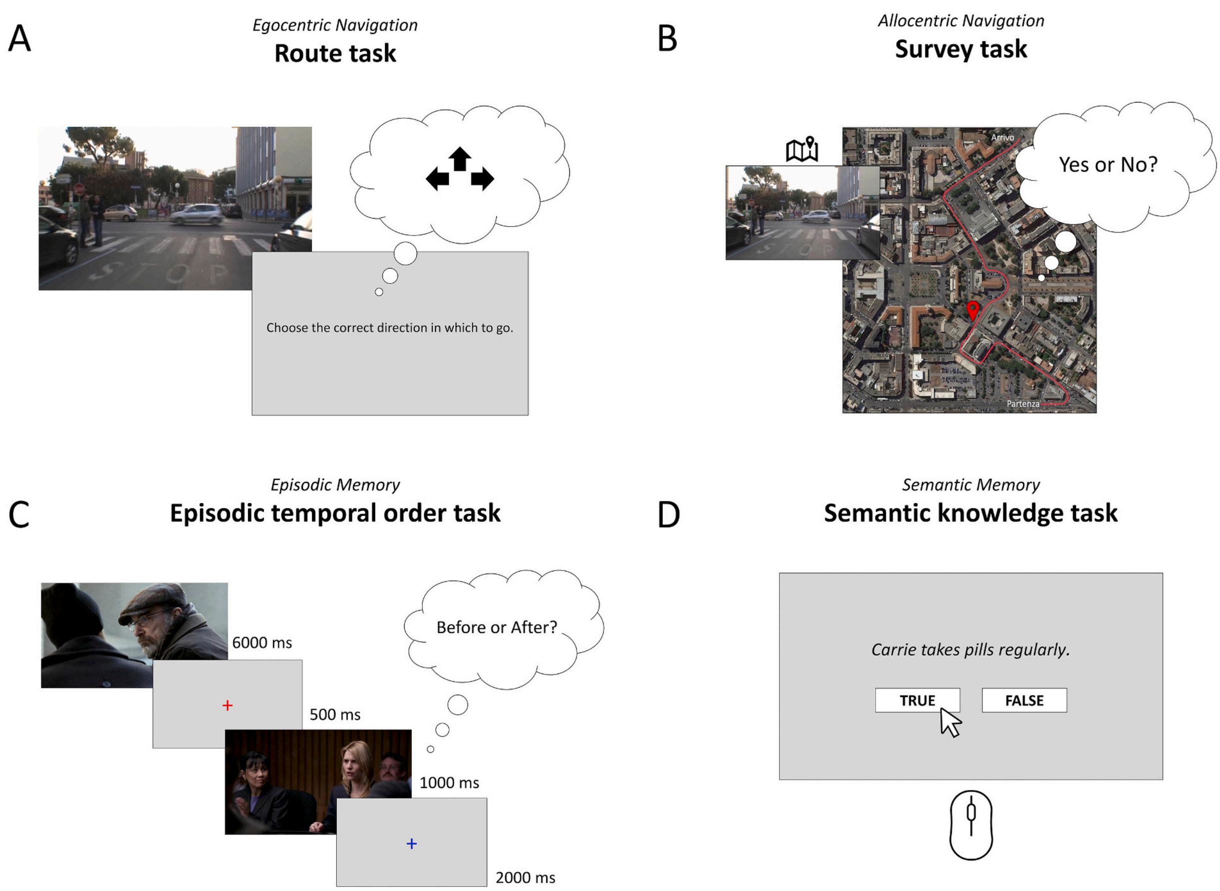

Fig. 1. A) *Route task*. Participants watched a first-perspective video of a path through the streets of a city. At each crossroad, the video stopped and participants had to choose the correct direction where going by pressing the arrow keys on the keyboard. **B)** *Survey task*. Each trial presented a screenshot depicting one of the crossroads encountered along the path and the real map of the city area surrounding the path. The path was indicated on the map by a red line, and a placeholder was shown in one of the crossroads. Participants had to indicate whether the position of the presented crossroad corresponded to that occupied on the map by the placeholder or not. **C)** *Episodic temporal order task*. The temporal order memory task included an encoding and a retrieval session separated by a 30 min interval. At encoding, a full episode of a television series was shown to participants. 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, a target picture of 1 s duration, and a blue cross indicating other 2 extra seconds to provide a response: indicate whether the target picture was extracted from a scene occurring before or after the video-clip. **D)** *Semantic knowledge task*. After completing the Episodic temporal order task, participants watched episode 2, 3 and 4 of the same television series every other day in a week. One week after, a task of general knowledge about the encoded television series was administered in which a true/false response was provided on a series of affirmations about general knowledge of the movie plot. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

together by a neural path integrator along one-dimensional space with no need for a map-like representation. Analogously, during episodic memory formation, sequentially occurring items are thought to be assembled into a coherent memory episode (Buzsáki, 2005; Eichenbaum, Dudchenko, Wood, Shapiro, & Tanila, 1999). In contrast, allocentric maps define a location inside a two-dimensional space independently of the navigator's position or the paths performed, in the same way as semantic memory defines concepts inside associative maps independently of a particular temporal or spatial context. Indeed, while the orthogonal organization of concepts within semantic maps shares the same omni-directional distance relationships found between landmarks inside a map (Bellmund et al., 2018), the aggregation of elements within an event shares the same sequential and linear processing that characterizes positions inside a path.

In previous studies, we have searched for evidence in favor of this neurophysiologically-based hypothesis by looking at human behavior. We described a specific and predictive relationship between egocentric navigation and episodic, but not semantic memory performance, further demonstrating that this relationship is independent of other basic cognitive abilities, such as attention and working memory (Committeri et al., 2020). This result was replicated in a second study in which the dynamic component of updating of information in navigation and memory tasks was particularly emphasized (Fragueiro et al., 2021). Notably, in this second study, we also found an unexpected association between egocentric navigation and semantic memory performance which, however, was explained by episodic and working memory abilities. In summary, the direct relation between egocentric navigation and episodic, but not semantic, memory is consistent with the existence of a common mechanism for the processing of spatial and temporal information.

No behavioral study in humans, however, has yet tested the full navigation/memory model proposed by Buzsáki and Moser (2013) by assessing both the episodic and semantic component of declarative memory and both the egocentric and allocentric component of spatial navigation. The first straightforward hypothesis that stems from the model is that specific *across-domain* relationships should exist between performance in tasks requiring a self-dependent (egocentric navigation and episodic memory) or a self-independent (allocentric navigation and semantic memory) reference frame. Interestingly, the model architecture also suggests the hypothesis that specific *within-domain* relationships should exist between performance during navigational (egocentric and allocentric) or memory (episodic and semantic) tasks. The latter hypothesis is based on the consideration that higher-level representations (i.e., map-based allocentric navigation, semantic memory) largely derive from their respective lower-level counterparts (i.e., self-based egocentric navigation, episodic memory). Specifically, allocentric maps are based on repeated self-based explorations of the environment (Lever, Wills, Cacucci, Burgess, & O'Keefe, 2002; Siegel & White, 1975). In a similar vein, semantic knowledge is progressively acquired through the repeated encoding of similar information by the episodic memory system (Eichenbaum et al., 1999; Moscovitch et al., 2005). Repeated coding might be employed in building higher-level map-based representations in each domain. Nodal cells may encode the intersections among otherwise distinct navigational paths or events (Eichenbaum et al., 1999) in a continuous and dynamic process to build networks inside a mental space: allocentric spatial maps in one case, context-independent semantic memories in the other.

The present work aims at testing the full evolutionary model proposed above by examining the behavioral performance of human participants engaged in different spatial navigation and memory tasks which emphasize the transformation process from self-based to map-based representations. We used two spatial navigation tasks sharing the same material to assess the learning of a path from a route (self-based) perspective and the subsequent use of survey knowledge from a map-view of the same environment (Bonavita et al., 2022). We also developed two memory tasks sharing the same audio-visual material, one assessing the temporal order component of episodic memory for movie scenes (i.e. episodes of a TV series, also see Fragueiro et al., 2021) and the other testing for the consequent semantic knowledge acquired through the encoding of multiple episodes from the same TV series. Based on the *across-domain* hypothesis mentioned above, we expected that route-based navigation performance should predict order memory (episodic) performance whereas survey navigation performance should predict semantic memory performance. Moreover, according to the *within-domain* hypothesis, we expected that route-based navigation should specifically predict survey navigation performance whereas episodic memory should specifically predict semantic memory performance. The two hypotheses were tested through multiple multivariate regression models that allowed us to assess the specificity of the observed relations.

2. Materials and methods

2.1. Participants

A total of 74 healthy participants (mean age = 21.7±2.5 years, 57 females, 71 right-handed), 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 "Homeland" 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 (protocol #1932 approved on July 11, 2019).

2.2. Spatial navigation tasks

To assess the two components of spatial navigation we used the online tasks developed by Bonavita et al. (2022, study 2), as implemented in testable (https://www.testable.org/). These are adapted versions of previous paradigms for the assessment of route and survey navigation in both normal (Boccia, Guariglia, Sabatini, & Nemmi, 2016) and pathological populations (Boccia, Silveri, Sabatini, Guariglia, & Nemmi, 2016), and the identification of individual differences in environmental navigation (Nemmi, Boccia, & Guariglia, 2017; Teghil, Boccia, Bonavita, & Guariglia, 2019).

Participants had to first learn a path within the environment from a first-person perspective (Route task), and subsequently to relate this path to a map-view representation of the same environment (Survey task). The two navigational tasks were specifically chosen to emphasize a self-based (egocentric) vs. a map-based (allocentric) component of spatial navigation using the same navigational material and requiring a self-to-map transformation process. The landmark task was exclusively included to confirm the recognition of the target landmarks by the participants before the survey task.

Route task. Participants watched a first-perspective video which gave the viewer the feeling of driving a car through the streets of a city. At each of the 9 crossroads included in the movie, the video stopped, and the participant was requested to select the correct direction to go (straight, right, or left) by pressing the arrow keys on the keyboard (Fig. 1A). After each choice, participants received feedback about their accuracy (i.e., "Correct!" or "Wrong! The correct direction is left/right/straight") before the video started again. The video was presented three times sequentially. Participants guessed during the first presentation (first exposure) and were expected to improve in subsequent presentations based on previous feedback. An accuracy score based on the second and third attempts (correct responses of the second and third attempts/18) was used for the analysis.

Landmark task. Participants were asked to recognize the crossroads encountered along the path among 18 screenshots (9 representing the crossroads encountered along the path and 9 distractors representing parts of the same city that were not presented in the video). The landmark recognition accuracy (HITS = old landmarks effectively recognized/9) was used to confirm that participants effectively acknowledged the landmarks presented in the subsequent Survey task.

Survey task. Each trial presented a screenshot depicting one of the crossroads encountered along the path and the real map of the city area surrounding the path. The path was indicated on the map by a red line, and a placeholder was shown in one of the crossroads (Fig. 1B). Participants were required to indicate whether the position of the presented crossroad corresponded to that occupied on the map by the placeholder by pressing the 'S' key to say yes or the 'N' key to say no. Participants were presented with a total of 18 trials and an accuracy score (correct responses/18) was used for the analysis.

2.3. Declarative memory tasks

As for the navigational domain, for declarative memory we developed two different tasks emphasizing a self-based vs. a map-based component by using the same audio-visual material (i.e. a TV series) and requiring a self-to-map transformation process.

Participants had to first watch the initial episode of a TV series and perform a temporal order memory task on the newly acquired material (episodic memory); subsequently, they watched other episodes of the same TV series and performed a task of general knowledge about it (semantic memory).

Episodic temporal order task. Episodic memory was assessed through the same temporal order memory task for film-based material employed in our previous study on the topic (Fragueiro et al., 2021). The task included an encoding and a retrieval session separated by a 30 min interval. At encoding, participants watched a full episode of the American television series "Homeland" dubbed in Italian (Season 1, Episode 1, "Pilot"; duration: 53:03 min), without being informed about the nature of the following task. At retrieval, a temporal order judgment on the encoded audio-visual material was required. On each trial, participants first viewed a 6 s segment (video clip) extracted from the same episode, followed by a 500 ms red fixation cross; then, they viewed a single screenshot of 1 s duration (target picture) depicting an event that happened before/after the segment presented in the video clip (from 2 to 6 min earlier or after the onset-offset of the video clip, with a 1:1 ratio). Participants were required to judge the temporal order of the screenshot in relation to the 6 s segment. Video clips and target pictures were selected by systematically moving along the episode with ~1 min sampling intervals. Note that during the selection of the target picture, uninformative frames (e.g. fuzzy images) were discarded. Participants were explicitly instructed to use *viewing* order rather than story order, also considering that the TV-series episode included few flashbacks and that a few trials contained a flashback scene in the clip or the screenshot (two trials/pairs contained a flashback in the clip, 2 trials/pairs contained a flashback in the target, and in one trial/pair both the clip and the target belonged to the same flashback line). Thus, participants had to judge whether the screenshot was extracted from a scene that had been viewed before or after the 6 s segment. They had a limit of 3 s from the onset of the target picture to provide their response (i.e., "z" key for "before", "m" key for "after") (Fig. 1C). A 1 s ITI preceded the following trial. The retrieval session included 46 trials presented in random order and was preceded by 4 practice trials. Accuracy scores were used for the analysis, and no-answered trials were counted as incorrect responses.

Semantic knowledge task. Semantic memory was assessed using a task based on general knowledge acquired through the encoding of multiple episodes ($N = 4$) of the "Homeland" TV series. After completing the first study session, indeed, participants were instructed to watch the next three episodes (2, 3, and 4) of the TV series every other day within a week (see Procedure below). Then, they provided true/false responses to different statements about the series ($N = 84$, with a 1:1 ratio) (Fig. 1D) developed by taking inspiration from the study by Renoult et al., 2016. Importantly, the sentences were formulated in such a way that the task did not require episodic memory about specific events or spatio-temporal contexts, but rather general knowledge acquired through the repetition of events and situations across the episodes. The statements in fact referred to general facts about the characters' life, habits, relationships, and personality. For example, "*Carrie uses methods not always approved by the CIA*", "*Brody's son doesn't get along with Mike*", "*Carrie takes pills regularly*". A complete list of the statements is provided in Supplementary Table 1. Participants had 6 s to respond starting from the onset of the sentence. Accuracy scores were used for the analysis, and no-answered trials were counted as incorrect responses.

2.4. Procedure

The experiment was conducted in two different online sessions. During the first session, the participants were shown the first episode of the television series "Homeland" (~50 min). Immediately after, they completed the spatial navigation tasks (~30 min) and then the episodic memory task (~10 min). Participants were subsequently instructed to watch episodes 2, 3, and 4 of "Homeland" every other day within a week. Exactly one week after the first session, participants completed the semantic memory task (~10 min). The spatial navigation tasks were developed and administrated via "Testable", the Episodic temporal order task was constructed using "Inquisit Lab 5" and administrated using "Inquisit Web", and the Semantic knowledge task was administrated via "QualtricsXM".

2.5. Statistical analysis

Statistical analyses were conducted on a total sample of 62 participants after the exclusion of outlier subjects with an accuracy score exceeding two standard deviations (±) from the group mean in any task. Normal distribution of data was evaluated using the parameters of skewness and kurtosis of data distribution (Kendall & Stuart, 1958). Following the check for normal distribution, we tested whether performance (i.e. accuracy) was above chance in each task through a one-sample *t*-test against chance level (0.50).

To test the across-domain hypothesis, we conducted a multiple multivariate regression analysis including spatial navigation (i.e. route and survey scores) as predictors and declarative memory (i.e. episodic and semantic memory scores) as dependent variables. In the same vein, the within-domain hypothesis was tested with a multiple multivariate regression model including higher-level map-based representations as dependent variables (i.e. survey and semantic memory scores) and their respective lower-level self-based counterparts as predictors (i.e. route and episodic memory scores).

For each regression analysis, a Variable Inflation Factors (VIF) method was employed to control for the multicollinearity of the data. Effect size and observed power (1–β error probability) were calculated setting the α error probability at a value of 0.05. Both unstandardized β coefficient describing the individual effect of each predictor on the dependent variables, and standardized β coefficients allowing to compare the strength of the effects of different predictors on each dependent variable, are reported in the results section (Siegel & Wagner, 2022).

Finally, a "generalization" index was obtained for each domain in which higher values indicated better performance in higher-level vs. lower-level task components (i.e., positive ratio in the spatial navigation or memory index indicated higher performance scores during allocentric/map-based vs. egocentric/self-based spatial navigation or memory). For this purpose, an asymmetry score was calculated within each domain using the formula (survey–route)/(route+survey) for spatial navigation, and the formula (semantic-episodic)/(semantic+episodic) for declarative memory functions. The presence of a significant relation between the two generalization indexes was assessed using Pearson's correlation test.

All analyses were conducted on IBM SPSS Statistics 25.

3. Results

Analysis of the skewness and kurtosis parameters indicated that all variables were normally distributed (skewness: all values <0.34 and > -0.87; kurtosis: all values <0.40 and > -0.87). The performance was above chance in all tasks (Route task: 0.78 [SD = 0.17], Survey task: 0.72 [SD = 0.15], Episodic temporal order task: 0.55 [SD = 0.11], Semantic knowledge task: 0.80 [SD = 0.08]) as confirmed by one-sample *t*-tests against chance-level (all *p*-values <0.01). Furthermore, as indicated by the landmark HIT scores (mean = 0.90, SD = 0.10), all participants effectively recognized the landmarks that were subsequently located in the Survey task.

The first *across-domain* regression model (Fig. 2, continuous lines), including spatial navigation scores (i.e. Route and Survey tasks) as predictors, was statistically significant for both dependent variables: episodic memory (i.e. Episodic temporal order task) ($R^2 = 0.14$, $F_{(2, 59)} = 4.91$, $p = 0.01$, power = 0.79, VIF = 1.26) and semantic memory (i.e. Semantic knowledge task) ($R^2 = 0.13$, $F_{(2, 59)} = 4.20$, $p = 0.02$, power = 0.72, VIF = 1.26). Specifically, the results indicated that episodic memory performance was significantly predicted by route navigation scores (unstandardized $\beta = 0.23$, standardized $\beta = 0.34$, $t = 2.517$, $p = 0.01$) (Fig. 3A), but not by survey navigation scores (unstandardized $\beta = 0.05$, standardized $\beta = 0.07$, $t = 0.525$, $p = 0.60$) (Fig. 3B). On the other hand, semantic memory performance was significantly predicted by survey navigation scores (unstandardized $\beta = 0.18$, standardized $\beta = 0.37$, $t = 2.735$, $p = 0.008$) (Fig. 3D), while a negative relationship was observed with route navigation scores (unstandardized $\beta = -0.13$, standardized $\beta = -0.29$, $t = -2.091$, $p = 0.04$) (Fig. 3C).

The second *within-domain* regression model (Fig. 2, dashed lines), including route navigation and episodic memory as predictors, was statistically significant for both dependent variables: survey navigation ($R^2 = 0.21$, $F_{(2, 59)} = 7.79$, $p = 0.001$, power = 0.94, VIF = 1.16) and semantic memory ($R^2 = 0.17$, $F_{(2, 59)} = 5.86$, $p = 0.005$, power = 0.86, VIF = 1.16). Specifically, survey navigation performance was significantly predicted by route navigation scores (unstandardized $\beta = 0.38$, standardized $\beta = 0.43$, $t = 3.435$, $p = 0.001$), but no significant relationship was found with episodic memory (unstandardized $\beta = 0.09$, standardized $\beta = 0.07$, $t = 0.525$, $p = 0.60$). On the other hand, semantic memory performance was significantly predicted by episodic memory (unstandardized $\beta = 0.28$, standardized $\beta = 0.42$, $t = 3.279$, $p = 0.002$), while a negative relation was found with route navigation scores (unstandardized $\beta = -0.12$, standardized $\beta = -0.27$, $t = -2.13$, $p = 0.04$).

Finally, we found a significant across-domains correlation between the asymmetry scores (i.e. between the generalization indexes from lower-level to higher-level representations), calculated within each domain (spatial navigation and declarative memory). The asymmetry score within the navigation domain positively correlated with the asymmetry score within the memory domain ($r = 0.42$, $p = 0.001$) (Fig. 4).

4. Discussion

The present study tested the general hypothesis of spatial codes for conceptual knowledge (Bellmund et al., 2018; Bottini & Doeller, 2020) and, more specifically, a human model of the phylogenetic continuity hypothesis between mechanisms for spatial navigation and memory (Buzsáki & Moser, 2013). To this aim, we examined the performance on tasks emphasizing (not exclusively tapping on) the egocentric/allocentric and episodic/semantic components of spatial navigation and memory functions, respectively. The evolutionary model proposed by Buzsáki and Moser (2013) in fact hypothesizes a specific phylogenetic continuity between egocentric navigation and the episodic component of declarative memory on one side, and allocentric navigation and semantic memory on the other. Although previous behavioral studies have looked for traces of this neurophysiologically-based model in human behavior (Committeri et al., 2020; Fragueiro et al., 2021), here we tested for the first time the complete model including all four components. We employed two sets of tasks in the spatial navigation and memory domain, each based on the same study material, and a design in which the self-based component of spatial navigation and memory was collected before the map-based component of the two functions. In this way, we also emphasized the transformation process from self-based to the subsequent development and use of higher-level map-based representations.

As expected, the first regression model confirmed the presence of a specific *across-domain* relation, according to which route-based navigation predicts episodic memory performance whereas survey navigation predicts semantic memory performance. These findings support the hypothesis of a specific *across-domain* relationship between performance in tasks emphasizing a self-based (i.e. egocentric navigation and episodic memory) versus a more self-independent or map-based (i.e. allocentric navigation and semantic memory) reference frame. According to the hypothesis, higher-level mechanisms for navigating in the mental space appear to have inherited a fundamental distinction between different coordinate systems: while unidimensional sequences of elements appear to be a key aspect of both self-based egocentric navigation and episodic memory, allocentric spatial and mental maps define locations and knowledge inside a two-dimensional context-free coordinates system.

The second regression model confirmed the presence of a specific *within-domain* relationship, according to which route navigation predicts survey navigation performance whereas episodic memory predicts semantic memory performance. Thus, our results support the well-established notion that higher-level representations like map-based

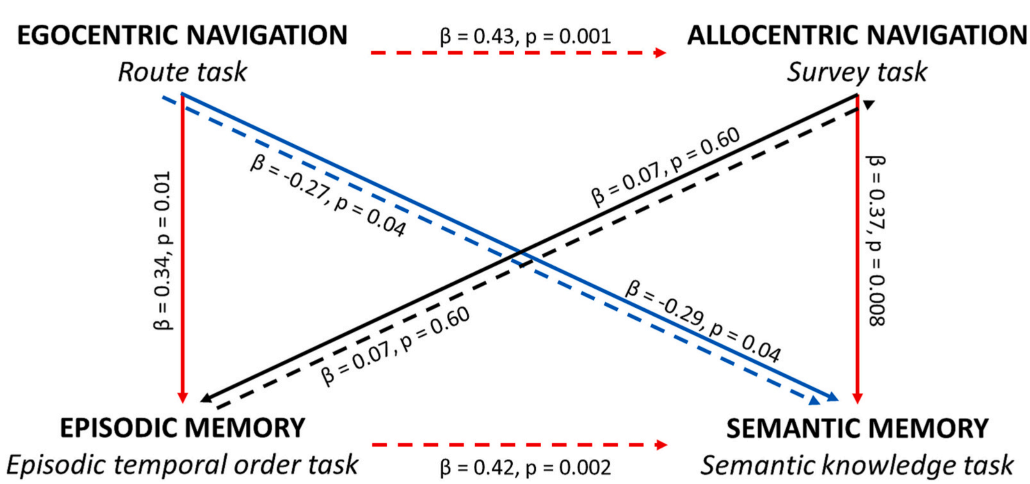

Fig. 2. Multiple multivariate regression models. Continuous lines correspond to the first regression model including spatial navigation scores (i.e. Route and Survey tasks) as predictors, and declarative memory scores as dependent variables (i.e. Episodic temporal order task and Semantic knowledge task). Dashed lines correspond to the second regression model including higher-level representations as dependent variables (i.e. survey and semantic memory scores), while their respective lower-level counterparts were included as predictors (i.e. route and episodic memory scores). β values reported correspond to the standardized coefficients.

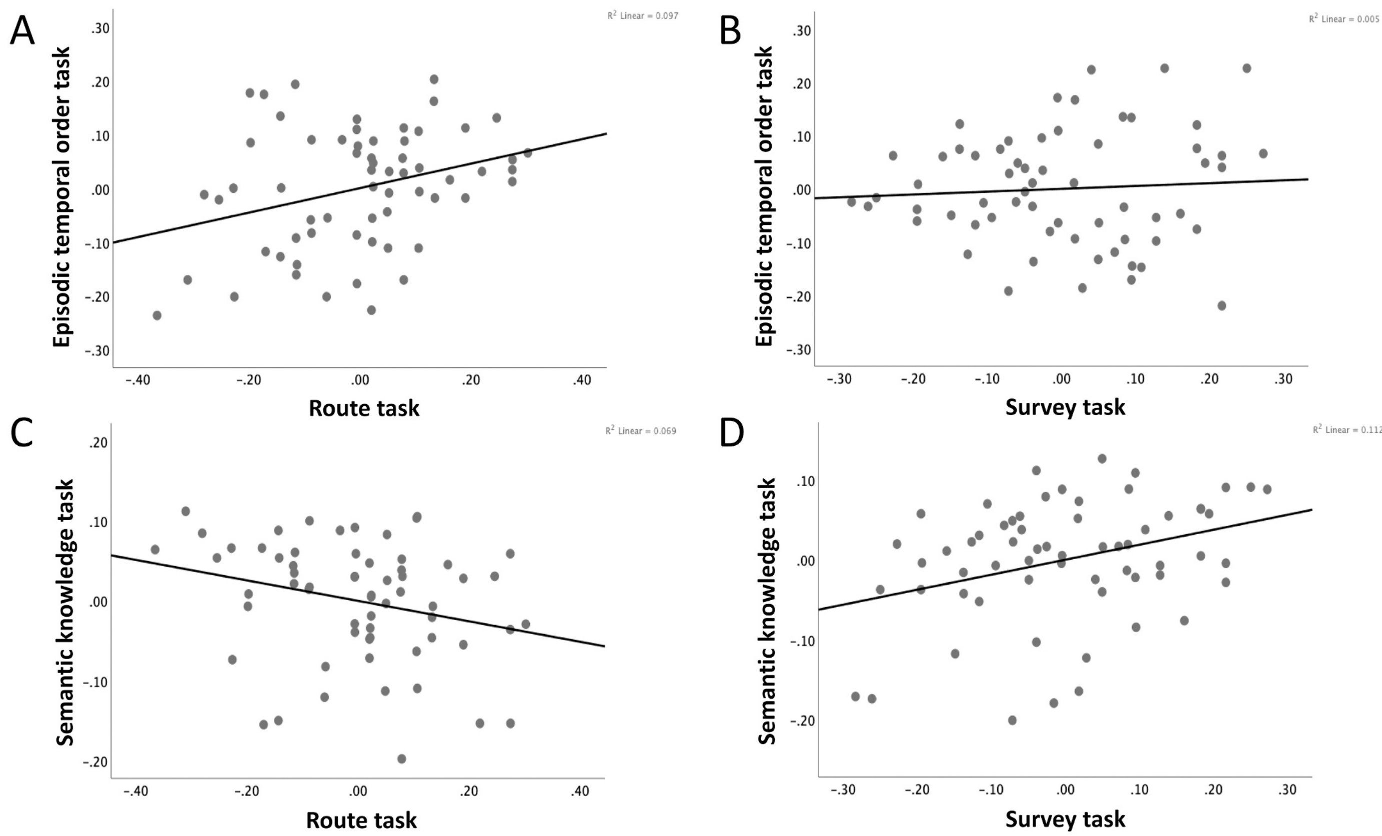

Fig. 3. A) Regression partial plot between route navigation and episodic memory scores ($\beta = 0.34$, $p = 0.01$); B) regression partial plot between survey navigation and episodic memory scores ($\beta = 0.07$, $p = 0.60$); C) regression partial plot between route navigation and semantic memory scores ($\beta = -0.29$, $p = 0.04$); D) regression partial plot between survey navigation and semantic memory scores ($\beta = 0.37$, $p = 0.008$).

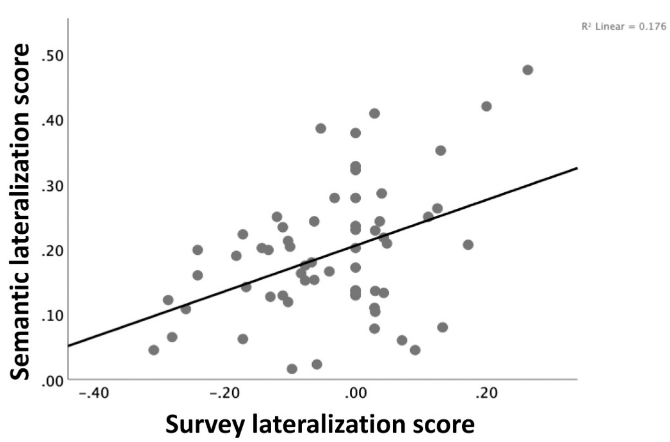

Fig. 4. Pearson's correlation ($r = 0.42$, $p = 0.001$) between generalization (i.e. from lower-level to higher-level representations) indices within each domain (spatial navigation and declarative memory), derived from asymmetry scores: (survey–route)/(route+survey) and (semantic–episodic memory)/(semantic+episodic), respectively.

allocentric navigation and semantic memory largely derive from their respective lower-level counterparts, respectively self-based egocentric navigation and episodic memory (Eichenbaum & Cohen, 2014). In other words, as repeated self-based exploration allows the construction of allocentric maps (Lever et al., 2002; McNaughton et al., 2006a, 2006b; Siegel & White, 1975), repetition of similar episodes allows the development of semantic knowledge (Cermak, 1984; Eichenbaum et al., 1999; Moscovitch, Cabeza, Winocur, & Nadel, 2016).

Our results also indicated a mild but negative relationship between route-based navigation and semantic memory performance, a result that might appear ad odd with the general model and the findings reported in Fragueiro et al. (2021), where a positive correlation was observed between spatial navigation and semantic memory. However, there are several explanations for this apparent discrepancy. Firstly, the positive correlation observed in our previous study was explained by working memory performance, and, more importantly, was mediated by episodic memory performance. Secondly, while the egocentric navigation and semantic memory tasks employed in our previous study emphasized the dynamic updating of information in the context of a similar stimulus presentation structure, in the current study the two tasks had distinct stimulus structures and modalities to match their within-domain counterpart. In particular, while egocentric navigation was assessed using a route learning navigation task based on a sequence of turns to create a path, semantic memory was assessed through a verbal semantic memory task based on abstract general knowledge about a TV series plot. On this basis, we hypothesize that the negative correlation observed between these two tasks might reflect different individual styles/strategies or preferences for the implementation of references frames. According to our hypothesis, individuals with a lower ability to produce context-independent general knowledge might emphasize a sequential mechanism for organizing information (i.e. better route navigation and lower semantic knowledge scores). This would agree with studies highlighting qualitatively distinct strategies for categorization learning (Little & McDaniel, 2015). Our results encourage future research on the individual styles/strategies for the implementation of reference frames, the individual differences in the transformation process from self-based lower-level to map-based higher-level representations, and the implications for general learning processing.

Finally, the correlation observed between the generalization indexes of spatial navigation and declarative memory further supports the hypothesis that participants with a preference/bias for an allocentric vs. egocentric frame of reference (i.e. survey vs. route) during spatial navigation also exhibit a bias for context-independent/semantic vs. temporally-specific/episodic memory processing. Said differently, some individuals may exhibit a preferred reference frame style (allocentric vs egocentric), and this preferred style may be transferred between domains (spatial navigation, declarative memory).

In conclusion, our results support the general model of spatial codes for high-level human cognition and the phylogenetic continuity hypothesis between mechanisms for spatial navigation and memory (Buzsáki & Moser, 2013). With respect to our previous findings, the current work further supports the specific levels by which this evolutionary hypothesis might take form in the human cognitive system. Our results indeed show that distinct spatial reference frames acquired within the physical world might have provided the organizational principles for structuring events (episodic memory) and knowledge (semantic memory) in the mental space.

Materials and data availability

Materials and datasets generated during the current study are available from the corresponding author on reasonable request

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.evolhumbehav.2023.08.001.

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