Environmental overlap and individual encoding strategy modulate memory interference in spatial navigation

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ABSTRACT

There has been great interest in how previously acquired knowledge interacts with newly learned knowledge and how prior knowledge facilitates semantic and "schema" learning. In studies of episodic memory, it is broadly associated with interference. Very few studies have examined the balance between interference and facilitation over the course of temporally-extended events and its individual differences. In the present study, we recruited 120 participants for a two-day spatial navigation experiment, wherein participants on Day 2 navigated virtual routes that were learned from Day 1 while also learning new routes. Critically, half of the new mazes overlapped with the old mazes, while the other half did not, enabling us to examine interference and facilitation in the context of spatial episodic learning. Overall, we found that navigation performance in new mazes that overlapped with previously-learned routes was significantly worse than the new non-overlapping mazes, suggesting proactive interference. Interestingly, we found memory facilitation for new routes in familiar environments in locations where there was no direct overlap with the previously-learned routes. Cognitive map accuracy positively correlated with proactive interference. Moreover, participants with high self-report spatial ability and/or a preference for place-based learning experienced more proactive interference. Taken together, our results show that 1) both memory interference and facilitation can co-occur as a function of prior learning, 2) proactive interference within a route varied as a function of the degree of overlap with old knowledge, and 3) individual differences in spatial ability and strategy can modulate proactive interference.

1. Introduction

Daily life depends on learning or inferring relationships between knowledge acquired across different episodes. However, we also need to uniquely remember individual events in order to, for example, retrace a navigational route to work. How newly learned knowledge interacts with the old, either as a source of memory interference or providing facilitation, has been systematically and extensively studied since the 1950s (Underwood, 1957). Memory interference has been widely observed in perceptual, procedural, semantic and episodic memory systems (Craig, Dewar, & Sala, 2015; Neath & Surprenant, 2015). However, many paradigms for examining memory interference in episodic memory use discrete pairs of experimental stimuli, which presents a challenge for generalizing findings to survival important scenarios like spatial learning and for understanding how interference and facilitation may change over the time-course of an event. Furthermore, although several studies have shown age and working memory

capacity are related to memory interference (Bowles & Salthouse, 2003; Darby & Sloutsky, 2015; Kail, 2002; Kane & Engle, 2000), there is relatively scant knowledge of the basis for individual differences in how overlap between experiences affects long-term memory. In the current study, we aimed to investigate memory interference in a virtual spatial navigation task and to characterize the individual differences of memory interference in healthy young adults.

There are two prominent forms of memory interference: proactive and retroactive. Proactive interference is when previously learned knowledge attenuates the learning rate of new information, and retroactive interference is when newly learned knowledge disrupts memory of the previously-learned information. In episodic memory research, a standard task for examining memory interference is paired-associates learning. Participants in such tasks typically first study a list of arbitrarily paired items (e.g., a female face [A] and the name EE [B]), such that A can later be presented as a memory cue and B is a memory target. After learning the first list, participants will learn a second list of

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similarly arbitrarily paired items, which includes completely new pairs (e.g., a male face [D] named JJ [E]) and pairs with an overlapped item with the first list (e.g., the same female face A in list 1 is now paired with the name SS [C]). In such a paradigm, proactive interference is typically operationalized as the performance difference between learning AC pairs and AB pairs, or between learning AC pairs and DE pairs. Retroactive interference is typically operationalized as the performance decrease in retrieving AB pairs after AC learning. Both forms of interferences have been widely studied (for reviews, see Craig et al., 2015; Neath & Surprenant, 2015; Wixted, 2004).

In contrast to the deep literature on episodic memory interference, very few studies have examined the individual differences in how new and old knowledge interact. Lifespan developmental work has emphasized that children exhibit more severe proactive and retroactive interferences than young adults, and older adults have been shown to exhibit more severe proactive interference than young adults (see, e.g., Bowles & Salthouse, 2003; Darby & Sloutsky, 2015; Kail, 2002). Additionally, working memory capacity was also shown to related to short-term memory interference (Kane & Engle, 2000). Important for the current study, there is evidence that different degrees of configural encoding, in which disparate information is integrated into a complex structure, may influence both proactive and retroactive interference (Darby & Sloutsky, 2015).

In the current study, we used a virtual spatial navigation task to investigate interactions between new and old episode memories for two reasons: First, spatial navigation reflects a naturalistic behavior that is fundamental for survival across species – our paradigm was developed (Brown, Hasselmo, & Stern, 2014; Brown & Stern, 2014; Brown, Whiteman, Aselcioglu, & Stern, 2014) to parallel work on memory integration and discrimination in rodents (Agster, Fortin, & Eichenbaum, 2002; Ferbinteanu, 2016; van der Meer, Johnson, Schmitzer-Torbert, & Redish, 2010; Wood, Dudchenko, Robitsek, & Eichenbaum, 2000). Our neuroimaging work with this paradigm has previously implicated hippocampal-dependent memory processes in navigating overlap between spatial experiences; although we observed individual differences in these smaller imaging samples, the present study was needed to examine the underlying cognitive processing of navigating overlapping routes and these individual differences. Second, spatial navigation provides a unique opportunity to investigate the relationship between the level of interference and the degree of overlap within segments of an episode memory in a parametric way. In the current study, we manipulated the degree of overlap between pairs of temporally-extended route memories (one old/familiar and one newly learned), such that – as with most routes through our real world environments - some segments of the pairs of paths were unique, some segments partially-overlapped with the other route, and some segments shared completely identical spatial and perceptual information. With this design, we could test how the level of interference between new and old route memories changed as a function of naturalistic changes in overlap, which has been rarely investigated in previous studies.

Another important aim of the current study was to characterize how several related individual differences influence how new and familiar route knowledge interact. Firstly, we found the configural encoding account (Darby & Sloutsky, 2015; Humphreys, Bain, & Pike, 1989) particularly interesting and relevant in the current study, because in spatial navigation, individuals differ substantially in acquiring configural knowledge of the environment (He, McNamara, Bodenheimer, & Klippel, 2019; Siegel & White, 1975). Therefore, we could test a configural encoding account of spatial memory interference through three related measures: 1) Correlation between proactive interference and *task-specific configural knowledge,* which was measured by the cognitive map accuracy of the environment (Tolman, 1948). 2) Correlation between proactive interference with *general spatial ability,* which was reflected by self-report spatial sense of direction. Research from our lab has shown that individuals with high self-report sense of direction (SOD; Hegarty, Richardson, Montello, Lovelace, & Subbiah, 2002; Pazzaglia &

De Beni, 2001) take advantage of certain environmental cues or neural resources to improve their navigation and cognitive map formation whereas low SOD individuals do not (He, McNamara, & Brown, 2019; He & Brown, 2020; He et al., in press). 3) Correlation between proactive interference and *endogenous navigation strategy,* which was measured by Y-Maze task (Rodgers, Sindone, & Moffat, 2012). Prioritizing configural knowledge acquisition (encoding the layout of the environment as opposed to landmark-action associations) could affect both route and configural knowledge acquisition of the environment (He, McNamara, Bodenheimer, & Klippel, 2019), which in turn could influence memory interference. By examining each of these correlations separately and having them compete for variance in a multiple linear regression model, we aimed to reveal the relative importance of each factor in explaining memory interference at the individual level.

To foreshow our results, at the group level, we found the level of proactive interference within a route varied as a function of the degree of overlap: When a new route shared a familiar environment with an old route, in a unique segment of the route, memory facilitation from the familiar environment was observed. In segments of the new route that partially or completely overlapped with the alternative, previously-learned route through the environment, marginal and significant (respectively) proactive interference effects of the old route on new event learning were observed. Our analysis of individual differences revealed that proactive interference was positively correlated with configural knowledge. Proactive interference was also predicted in part by cognitive traits - high SOD individuals experienced more interference than low SOD, and within low SOD individuals, the preference for a place-based strategy further positively correlated with proactive interference.

2. Methods

2.1. Participants

Because few studies have examined the proactive and retroactive interference in spatial navigation, we conducted the power analysis by assuming a medium effect size (d' = 0.5), which would require a sample size of 34 participants to reach a power of 80%. We set our sample size to enable us to detect reliable individual differences and compare subgroups of at least that size. One-hundred twenty-seven participants, primarily Georgia Tech undergraduates, were recruited for this experiment. Four participants dropped out due to motion sickness and three were removed from the analysis because of incomplete data. This resulted in one-hundred twenty participants (sixty males and sixty females) for the navigation and Y-Maze task and one-hundred nineteen participants for the pointing task. The average participant age was 21 (standard deviation of 3 years). All recruited participants were healthy with good vision and without previous neurological disorders. All but 20 participants were compensated with either credit or at a rate of $10 per hour (20 participants, who also completed an MRI component of the same paradigm received $15 per hour). Participants gave informed consent using procedures approved by the Georgia Tech Institutional Review Board.

2.2. Virtual navigation task and environmental design

Twenty virtual mazes were built with POV-Ray Version 3.66 (http://www.povray.org), a 3D ray tracer modeling program (see Fig. 1A). The mazes were described to participants as routes. The participants were instructed to pay critical attention to the unique identifying artwork at each starting room, patterns on the floor and column texture (see Fig. 1B). While navigating the mazes, the participants had a ground level perspective and their accuracy and reaction time was recorded with *E*-prime 2.0 (Psychology Software Tools, Inc., Pittsburgh, PA, USA). Each maze consisted of three hallways with three decision points. To distinguish each intersection within and between each maze, each
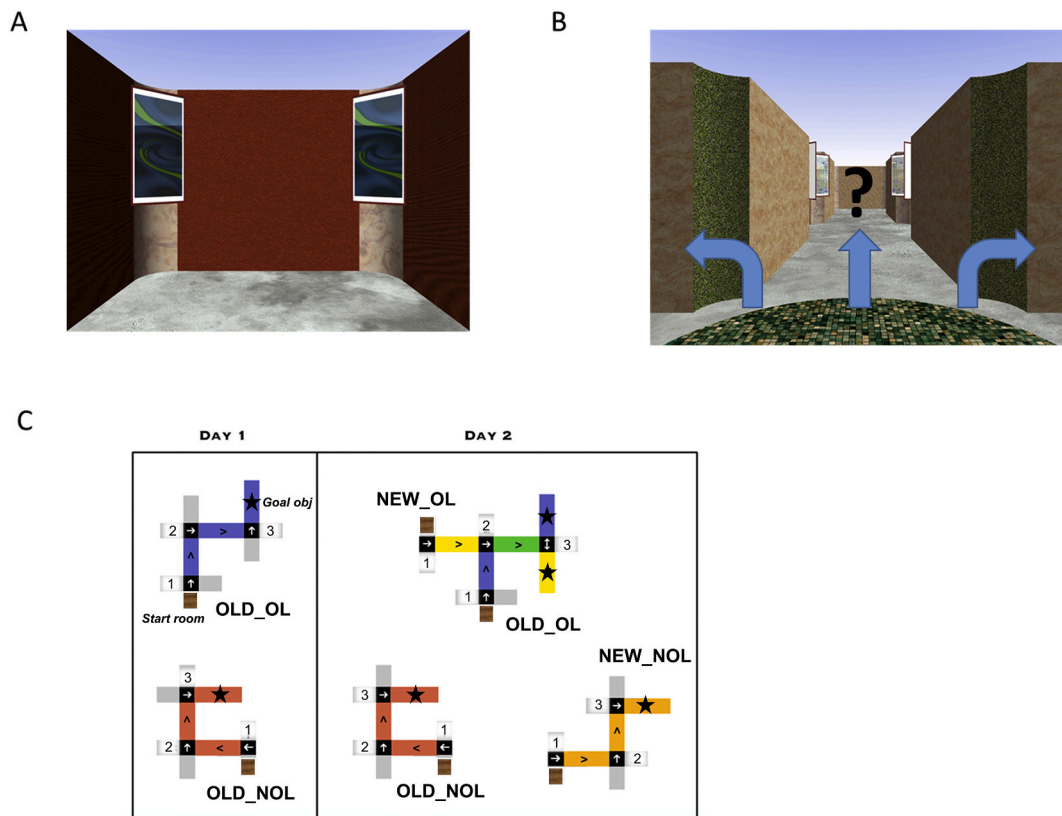
Q. He et al.

Fig. 1. Experimental Design. A. Example of participant's ground level perspective of unique starting intersection (with the wooden gates up). B. Example of participant's ground level perspective at either second intersections with arrows showing possible directional choices. Note that the floor tiles and textures of the columns are different at each interaction. C. Bird's eye view of example maze layouts for each maze type. The Old_OL (blue path) and Old_NOL (red path) mazes are both learned equivalently on Day 1 as if they were NOL routes. Old_OL becomes overlapping at the shared hallway (green path) when participants learn the New_ OL maze (yellow path) on Day 2. The New_NOL mazes (orange path) acts as an individualized baseline for new maze learning from which to measure OL interference and facilitation effects. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

intersection had unique tile patterns on the floor and corresponding unique column texture (see Fig. 1B). These abstract texturing details – although not objects, per se, served as landmarks, and were used instead of objects to minimize perceptual confounds when decoding patterns of brain activity in an fMRI variant of this study. After the third and final intersection, the participant would "discover" a hidden goal object (a person or piece of fruit) in the middle of the final hallway. These categorically distinct goal objects were used for the purpose of a separate analysis of a subset of participants, who completed an expanded fMRI version of this reported task.

Of the twenty mazes, ten of the mazes were non-overlapping (NOL) and the other ten mazes were overlapping (OL). The OL mazes did not differ from the NOL mazes in their appearance other than each sharing a hallway with one of the other OL mazes (see Fig. 1C). The OL mazes were split into five pairs. All OL mazes had unique starting rooms and goal hallways. However, for each of the five pairs, the hallway between the second intersection and third intersection overlapped between each other. Participants could recognize the overlapping hallways by the unique appearance of the floor tiles and column textures/artwork at each intersection.

Because OL mazes physically overlapped in the middle, retrieving the correct turn at overlapping intersections required disambiguation of the navigational episode based on contextual memory (specifically, the current intersection is identical, but the turn/route can be distinguished by memory for preceding distinctive maze elements including headings and the non-overlapping starting location artwork that cued each overlapping (and non-overlapping) maze; Fig. 1A).The second intersection was the first of two overlapping hallway decision-points and the third intersection was the overlapping hallway decision-point where the

two routes diverged again (Fig. 1C). Because of natural physical constraints, the second intersection therefore presented as a choice point with two different turn behaviors for the same location, but the approaching orientation varied depending on which overlapping maze pair was being navigated from its unique starting room. For this reason, the memories for the second intersection had partial contextual overlap. The third intersection was objectively the most difficult retrieval point because it was the exact same for either of the overlapping maze route pair, in terms of both approaching orientation and artwork (see Fig. 1C). For this reason, the third intersection had complete overlap and distinguishing the different memories required temporal context (i.e., association between the most recent preceding contextual cues and future action). In particular, the participant was instructed that it was imperative to use the starting artwork because it would help them distinguish between mazes. As such, our design varied the extent of overlap, whereby the starting intersection shared a global environment with another route but had no local interfering cues for the turn memory; the second intersection had partial overlap, and the third intersection would present maximal interference between memories.

2.2.1. Task timeline

Before each maze, the participant began in a room recessed back from the first intersection. They had a two-second period to view the starting location's unique artwork before they indicated which direction they would go through the intersection in front of them. Wooden gates were up in this period such that the only visual information available to the participant was the unique artwork of the starting location (Fig. 1A). After the two second period, the gates dropped, and the participant chose to navigate left, straight, or right with a button press of 1, 2, or 3

respectively (Fig. 1B). They would then move forward into the first intersection and traverse in their selected direction.

To control timing and isolate behavioral choices in the task, navigation in the virtual environment was largely passive and automated, and participants only needed to press a directional button to decide which direction to go at the starting point and subsequent intersections (i.e., no body-based movement). This was done to enable us to directly link the behavioral and cognitive insights from this study to our prior fMRI work using this general tightly-controlled navigation paradigm (Brown, Hasselmo, & Stern, 2014; Brown & Stern, 2014; Brown, Whiteman, et al., 2014). After the participant responded at each intersection, there was an automatic transversal of the intersection in two steps (1 s duration). The 90-degree turn had two 45-degree steps with the first immediate to the button press and then a 1 s pause before the next 45-degree turn. Traveling the subsequent hallway was automatic (2 s duration) and simulated through a video of POV Ray images. If the response at an intersection was incorrect, the participant first received a feedback image and their response was automatically corrected before the turn-hallway sequence began. In the feedback image, red letters that read "Wrong" appeared on the screen and a green arrow displayed the correct response. Error feedback was provided during all runs for both Day 1 and Day 2. On Day 2, there was an inter-trial-interval (ITI) between each completed maze (black screen with a fixation point) for eight seconds.

2.3. Procedure

2.3.1. Day 1

On Day 1, after consent, participants first completed a survey on their sense of direction (SOD; Hegarty et al., 2002).

2.3.1.1. "Old" route training. Participants were then trained on ten of the twenty total mazes, with five being NOL mazes and the other five being half of each OL maze pairs. The five OL mazes participants learned on Day 1 were completely distinct from each other but would later overlap with the five paired New OL mazes that participants would learn on Day 2 (see Fig. 1C). Participants were made aware that some mazes would remain NOL while others would become OL on Day 2 and were shown in an overhead map example of two OL routes (unused in the actual task), but importantly participants were not told which of these "Old" mazes would become OL. Therefore, to the participants on Day 1, all mazes were experienced as non-overlapping and learned identically. The ten Old mazes were learned in a pseudo-randomized order for each participant, only ensuring that five were one from each of an OL pair and the other five were NOL. During training, participants first had to learn the mazes serially, navigating each maze correctly four consecutive times before learning the next maze. After learning each Old maze in series, participants then completed four training runs, with the run order counterbalanced across participants, in which they navigated all ten of the mazes once per run in a randomized order. The training runs helped the participants reinforce their learnings of the mazes.

2.3.1.2. Y-maze task. After training on the 10 "Old" mazes for the navigation task, participants completed an endogenous navigation strategy preference task, (a Y-Maze task, based directly on procedures established by the Moffat lab; Rodgers et al., 2012). The details of this procedure are provided in Rodgers et al., 2012. In brief, during the Y-maze task, participants first navigated five unique Y-Mazes in series, following four consecutive correct trials per Y-Maze. The instructions for how to navigate were carefully designed so to be vague and not to suggest a particular strategy (i.e., a to-place or response-based strategy) to the participant. Participants were told to move down a corridor and make a choice at the fork in the road, using arrow keys. After each trial, the participant received auditory feedback. A guitar chord signaled they had made a correct choice at the fork and a buzzer signaled they had

made an incorrect choice. Participants were simply instructed to make the choice that would result in the guitar sound. After four consecutive correct runs within one environment, unique background landmark objects were rotated around the maze by 180 degrees, without any explicit notification to the navigator. If the participant's encoding of the guitar sound was place-based, they would change which arm they navigated down to follow the landmark on a critical 5th probe trial. If the participant's strategy was instead response-based, they would continue to navigate the same arm as during the four correct encoding trials. Neither response strategy would receive feedback on this probe trial (i.e., there was no "correct" strategy). Therefore, the Y-Maze provided 5 measures of endogenous navigational strategy preference prior to any testing/learning of overlapping routes on Day 2. We combined this measure with the SOD measures to better understand how individual differences may predict route navigation performance and interference effects.

2.3.2. Day 2

2.3.2.1. Maze route navigation task. On Day 2, participants performed a navigation task during which they navigated all 10 Old (familiar) maze routes and learned the 10 remaining "New" mazes (five more NOL mazes and the five OL mazes paired with those learned on Day 1). These New mazes were learned on Day 2 after one complete sleep cycle to ensure that the memories of the Old mazes from Day 1 could be consolidated. Before any new learning trials began, participants completed a warm-up run during which they navigated the ten Old mazes in a randomized order. After the warm-up run, participants completed ten runs of the maze route navigation task. This included 10 runs through all 20 mazes. Each run included all 10 Old mazes and all 10 new mazes. Participants learned the New mazes through the same automated feedback as Day 1. The order of mazes within each run on Day 2 was randomized except for the first run in which a random maze order was adjusted to ensure that each New OL maze came before its Old OL maze pair counterpart. This ensured that the Old OL maze would be subjected to retroactive interference (if any) from the first trial onward.

Following the above procedure, the 20 mazes were divided into four subjectively and mnemonically distinct conditions for analysis: Overlapping old mazes (Old_OL), Non-overlapping old mazes (Old_NOL), Overlapping new mazes (New_OL), and Non-overlapping new nazes (New_NOL). Reaction times and accuracy for each intersection were recorded for each maze condition to assess overall performance and learning curves.

2.3.2.2. Pointing task. After completion of the maze route navigation task, participants completed an additional "pointing task" in each of the 20 maze environments (see the layout of each maze in Fig. S1). Participants were placed in the starting room of each maze, looking forward into the first intersection, and were asked to imagine that they were standing at the location and heading indicated by the image. Then participants used the 9-button array on a numerical keypad to indicate the closest direction, in 45-degree increments, to the maze's end goal object's location, relative to their bearing in the virtual environment. Although our static environment task design (Brown, Hasselmo, & Stern, 2014; Brown & Stern, 2014) did not lend itself to continuous orientation probes as used in our other recent work (He, McNamara, Bodenheimer, & Klippel, 2019; He, McNamara, & Brown, 2019; He et al., in press), this task nevertheless enabled us to probe participants' configural knowledge of the approximate goal location at the other end of the circuitous route. Directions for this probe were defined egocentrically, as if their starting facing orientation was defined as "North". The center button of the numerical pad (Button 5) was unused and represented the participants' 2D starting position in the maze's map. Button 2 was South, 8 was North, 6 was East, 4 was West, and 1, 3, 7, and 9 were southwest, southeast, northwest and northeast, respectively.

2.4. Data analysis

Overall participant accuracy was calculated by averaging all intersection decision-points and all runs of the navigation task on Day 2. This was done separately for each of the four maze conditions (Old_NOL, Old_OL, New_NOL and New_OL). Likewise, within each maze condition, accuracy for the post-navigation pointing task was calculated by averaging the pointing error which was calculated by the discrepancy between the correct response and the participant's "closest heading" response (see the correct pointing response of each maze in Fig. S1). For example, if the correct response was north (number 8), the pointing error would be 45° if the actual response was northeast (number 9) or northwest (number 7). Note that the pointing error was incremental because the response precision was 45°, but this approach has the benefit of weighing larger errors relative to ground truth more strongly than a purely categorical scoring. Linear mixed models of the data that treated participants as a random effect and tested for interactions between intersection (start, second, third), New/Old, and NOL/OL, and block number factors.

We focused our analysis on evidence for interference and facilitation within each intersection. Interference and facilitation were assessed by comparing New_OL performance against the baseline New_NOL performance at each intersection (where perceptual and response demands were identical except for the critical OL manipulation). If New_NOL performance was worse than New_OL performance, this was evidence for facilitation due to prior knowledge of the environment. If New_NOL performance exceeded New_OL performance, this was evidence of proactive interference from Old_OL memories. Similarity between environments can cause interference either proactively (Old_OL affects memory of New_OL maze) or retroactively (New_OL maze affects memory of Old_OL maze). In this paradigm, as the routes naturally increased in similarity/overlap from the start to the third intersection, the interference effect would be predicted to increase. Correlations across participants were also completed to predict interference or facilitation on an individual level.

3. Results

We used JASP (JASP Team, 2020) for statistical analyses and Matplotlib (Hunter, 2007) and Seaborn for data visualization. We tested our ideas about the interactions between prior route knowledge, new route learning, and degree of experiential overlap at the group (average) level and in the context of individual differences. Cohen's *d* for independent *t*-test was computed as $(m_A - m_B)/SD_{pool}$, where m_A and m_B represented
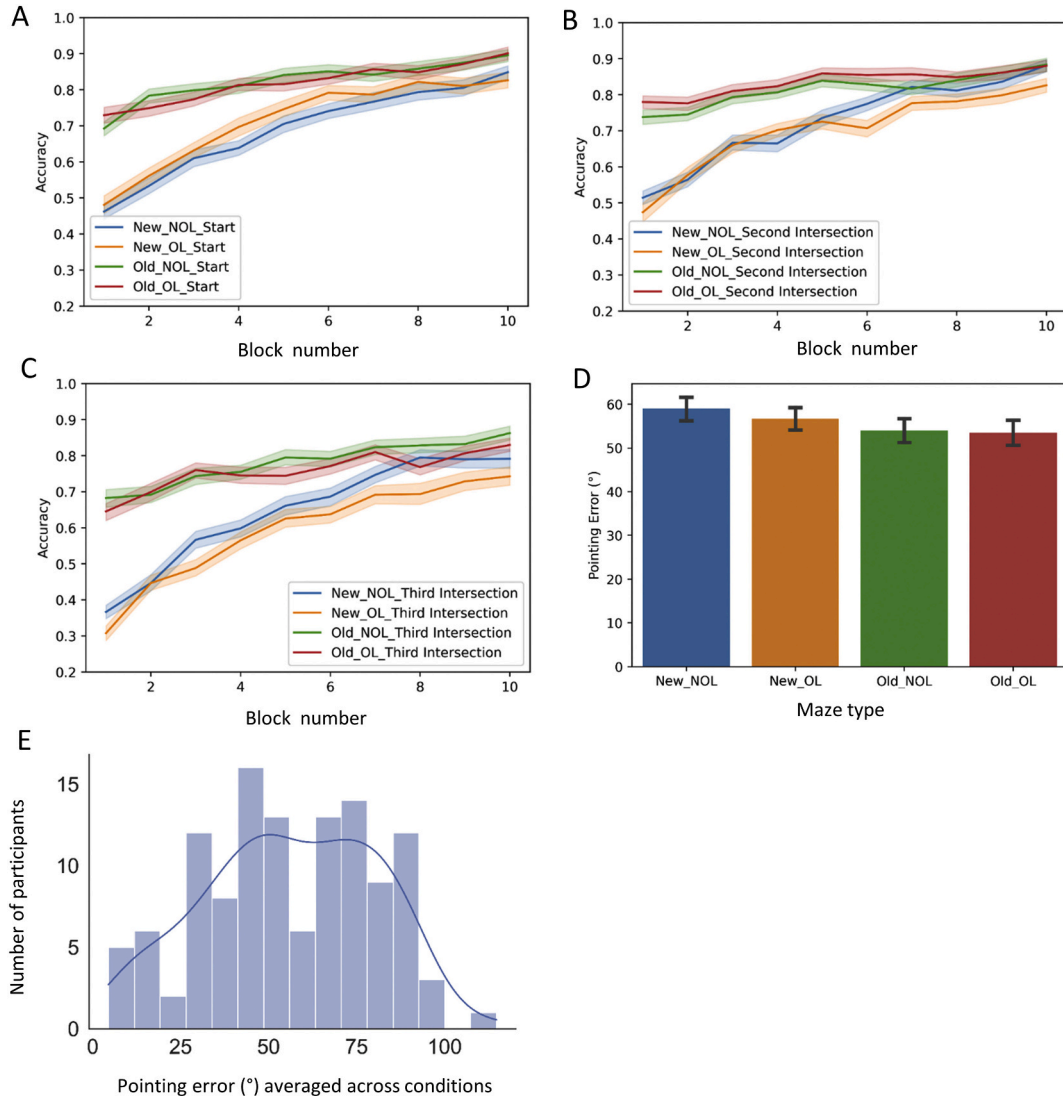

Fig. 2. Learning curves in the new/old and NOL/OL mazes in the start (A), second intersection (B), and third intersection (C). D) Pointing task performance separated by new/old and NOL/OL mazes. E) Pointing error distribution across participants. Error bars denote ± SEM.

the mean value of the group A and B, respectively, and SD_{pool} was an estimator of the pooled standard deviation of the two groups. Cohen's d for pair t-test was computed as $mean_D/SD_D$, where D was the differences of the paired samples values.

3.1. Group level

We first examined the accuracy at each decision point (start, second intersection and third intersection) as a function of new/old, NOL/OL and block number (Fig. 2A-C). We then submitted the data to a linear mixed model (Bates et al., 2015) with new/old, NOL/OL, decision point and block number as fixed factors and participant ID as random intercept. The main effects of new/old, decision point, and block number were significant ($ps < 0.001$), verifying that retrieval demands and learning effects influenced cognition. The two-way interactions between new/old and block number, between NOL/OL and block number, between new/old and NOL/OL, between decision point and block number, and between new/old and decision point were significant ($ps < 0.005$). Critical for our question of whether interference effects vary as a function of degree of overlap with prior experiences, the three-way interaction between new/old, NOL/OL and decision point was significant ($F(2,14113) = 4.15, p = 0.016$). The four way-interaction (new/old, NOL/OL, decision point and block number) was not significant ($F(2,14113) = 0.27, p = 0.76$), suggesting that the observed significant three-way interaction was not dependent on block number. Pointing task data were analyzed in a two-way, repeated-measure ANOVA (new/old, NOL/OL). Results showed that there was no main effects of New/Old ($F(1,119) = 3.35, p = 0.07, \eta^2 = 0.011$) or NOL/OL ($F(1,119) = 0.910, p = 0.34, \eta^2 = 0.002$) nor was there a significant interaction ($F(1,119) = 0.12, p = 0.73, \eta^2 < 0.001$), suggesting configural knowledge was broadly matched, within a participant, across route-learning scenarios (Fig. 2D; see Fig. S2 for reaction time of each condition). Importantly, however, although the pointing errors across conditions were high in general, all of them were significantly lower than chance level ($90°$; $ts > 10$, $ps < 0.001$) and displayed substantial individual differences (Fig. 2E).

3.1.1. Proactive interference and facilitation in the new mazes

Because the three-way interaction between new/old, NOL/OL and decision point was significant, and was not modulated by block, we averaged the accuracy across blocks (Fig. 3A). Simple main effects showed that for the new mazes (Left, Fig. 3A), the accuracy in the NOL was overall significantly lower than the OL ($F(1,118) = 5.56, p = 0.02$, Cohen's $d = 0.21$) at the starting decision point, indicative of a facilitation effect for new OL routes from old mazes. This pattern shifted for subsequent intersections as overlap between the experiences increased: in the second intersection, the accuracy in new NOL was marginally significantly higher than the OL ($F(1,118) = 3.66, p = 0.06$, Cohen's $d = 0.17$). In the third intersection, the accuracy in NOL became significantly higher than the OL ($F(1,118) = 15.76, p < 0.001$, Cohen's $d = 0.36$), indicative of proactive interference. To visualize these interference effects more directly, we computed the accuracy difference between NOL and OL, with negative difference reflecting facilitation and positive reflecting interference, and replotted the data in Fig. 3B. Consistent with our conceptual framework of how overlap varies over the spatiotemporal course of the OL routes, in the new mazes (Fig. 3B, yellow line) there was a linear change from start to the third intersection, which transitioned from facilitation to interference.

3.1.2. No retroactive interference in the old mazes

To follow up on the above three-way interaction, we also calculated the simple main effects in the old mazes (Right, Fig. 3A). There was no significant difference between NOL and OL at any of the decision point ($Fs < 2.72, ps > 0.10$; Fig. 3B, purple line), suggesting little retroactive interference or facilitation from the new mazes in old OL routes (which again had been learned a sleep cycle + day prior).

3.2. Individual level

3.2.1. Proactive interference positively correlated with configural knowledge

Because we demonstrated significant proactive interference effect in learning to navigate the third intersection (maximal overlap), we next
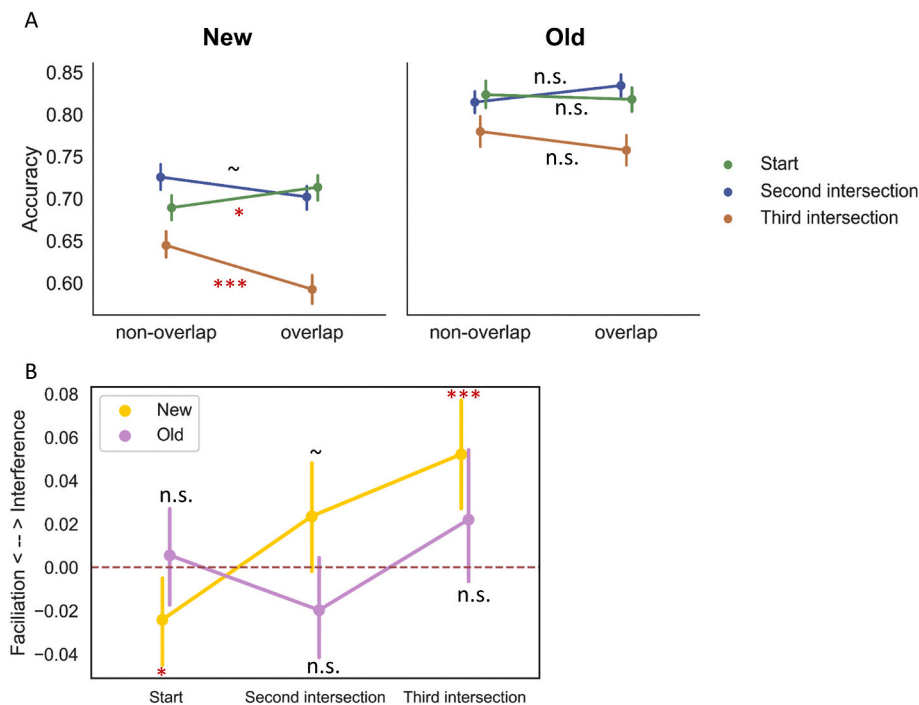

Fig. 3. A) Accuracy separated by new/old, OL/NOL and decision points. B) Memory interference and facilitation (accuracy difference between NOL and OL) in the new and old mazes, separated by decision point. ~ $p < 0.1$, *$p < 0.05$, ***$p < 0.001$, n.s. not significant. Error bars denote $\pm$ SEM in A) and 95% CI in B). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

asked whether the amount of proactive interference was correlated with configural knowledge. We probed this theorized relationship in several ways: first reflected directly through pointing task performance in the maze environments themselves. Similar to Darby and Sloutsky (2015), we divided the pointing task performance into Old_NOL, Old_OL, New_NOL and New_OL to further assess how proactive interference was associated configural knowledge in different mazes. We found that in general, stronger proactive interference was associated with lower pointing error or better configural knowledge for our environments (Table 1), especially in the old OL mazes (no such patterns in reaction time; Table S1). This pattern may be expected by a number of ideas surrounding navigational learning, but we also note this differed from the pattern in Darby and Sloutsky (2015), in which the authors showed a non-significant, but negative correlation between proactive interference and configural knowledge in a non-navigation task. We discuss the potential reasons for these differing findings in the Discussion.

3.2.2. Proactive interference was predicted by the interaction of SOD and Y-Maze

We next asked whether the self-report spatial ability and navigational strategy preference could contribute to individual differences in proactive interference. Descriptive statistics of SOD and Y-Maze are presented in Table 2 (one missing datapoint in SOD and in Y-Maze). Consistent with our hypothesis, proactive interference was significant higher in individuals with high SOD than those with low SOD ($t(118) = 2.36$, $p = 0.02$, Cohen's $d = 0.43$; high and low SOD individuals were categorized by median-split of SOD scores). Individual Y-Maze scores, which reflected spatial vs response-based strategy preference, did not significantly correlated with proactive interference ($r(119) = 0.147$, $p = 0.11$; N indicated number of participants) and were, interestingly, found to be independent of SOD ($r(118) = -0.02$, $p = 0.84$) (i.e., reporting a strong sense of direction does not predict preferring a place-based navigation strategy). Moreover, the correlations between Y-Maze scores and proactive interference were very different for high vs low SOD groups of individuals: Within high SOD, the correlation between proactive interference and Y-Maze scores was close to zero ($r(57) = -0.045$, $p = 0.74$; Fig. 4A), but this correlation was much higher and positive in the low SOD ($r(61) = 0.341$, $p = 0.007$; Fig. 4B), and these correlations were significantly different from each other ($Z = 2.14$, $p = 0.03$).

To test whether there was an interaction between SOD and Y-Maze scores and whether cognitive map accuracy played an independent role in predicting interference when these traits were accounted for, we ran two multiple linear regressions: One with SOD (high or low), Y-Maze scores, and the interaction between SOD and Y-Maze as predictors (Table 3). Given a theoretical common cognitive substrate for pointing performance and SOD, we then ran a regression adding pointing performance for the old OL mazes (Table 4). The results showed both SOD and Y-Maze were significant predictors ($ps < 0.01$), and importantly, the interaction was also significant ($p = 0.028$). However, in the context of multiple regression pointing performance became only a marginal predictor ($p = 0.098$) of interference (with a modest impact on the significance of the SOD-Y-Maze interaction). Together, these results suggested that 1) high SOD individuals were more likely to experience proactive

Table 1
Correlations between proactive interference and pointing task performance.

	1	2	3	4	5
1. Proactive interference					
2. Pointing_New_NOL	−0.142				
3. Pointing_New_OL	0.109	0.560***			
4. Pointing_Old_NOL	−0.162	0.461***	0.565***		
5. Pointing_Old_OL	−0.223*	0.505***	0.456***	0.588***	

* $p < 0.05$,
*** $p < 0.001$.

Table 2
Descriptive statistics of SOD and Y-Maze.

	SOD	Y-Maze
Mean	4.223	2.387
Median	4.27	2
Std. deviation	0.916	2.051
Skewness	0.091	0.058
Kurtosis	0.069	−1.667
Minimum	2.067	0
Maximum	6.67	5

interference than low SOD individuals. 2) Within low SOD individuals, the more a place-based strategy was preferred (perhaps maladaptively, given their poor sense of direction), the more likely proactive interference was to be experienced. 3) Individual differences in self-report spatial ability and strategy appear to account for some of the ability of objectively measured spatial integration to predict proactive interference.

4. Discussion

The current study aimed to investigate how new and old episode memories interact in a spatial navigation task and to test a theoretical framework for understanding individual differences in such interference. At the group level, we found that proactive interference increased over the course of a route as a function of the degree of overlap with a previously-learned route: learning facilitation from environment familiarity was observed in spatially-perceptually unique starting segments of routes, but marginal and significant interference effects from previously-learned routes were observed when learning to navigate the partial and completely overlapping segments, respectively. These interference effects were asymmetrical: we did not observe significant retroactive interference in the old routes. At the individual level, we found that configural knowledge of the environment measured by the pointing task was positively correlated with proactive interference. High SOD individuals experienced stronger proactive interference than low SOD individuals. Within low SOD individuals, the more they preferred for a more place-based strategy, the stronger the proactive interference.

One important contribution of our study is that it examined patterns of interference as they unfold across events over space and time – something that is naturally experienced in route navigation in our daily lives and difficult to address in traditional paired-associates designs. One more surprising outcome was the facilitation effect in the unique starting segment. To the best of our knowledge, no studies have reported this dynamic shift across an episode from learning facilitation due to a familiar environment to interference due to direct overlap with previous experiences, which highlights the benefits of studying how old and new learning interact with complex and temporally-extended events over discrete paired-associate paradigms. Several mechanisms could contribute. Proactive interference has been linked to inhibitory processes in executive control (Anderson, 2003; Jonides & Nee, 2006), with proposals that to learn a new response associated with the old cue, the brain must inhibit the activation of the old cue – old response association, requiring additional attentional resources. Based on this active control account of memory interactions, one possibility of the facilitation effect was that participants' attention was more aroused across the entire overlapping route than the non-overlapping route, which could increase encoding efficiency at the starting decision point where inhibition of a competing response was not required. Another possibility, based on the configural encoding account (Darby & Sloutsky, 2015; Humphreys et al., 1989), was that participants could generate a richer mental representation of the environment when there were multiple routes, and therefore enhanced learning efficiency in the unique segment of the overlapping route. Such a view shares features with ideas surrounding spatial schemas, which have been shown in rodents and humans can facilitate new learning (McKenzie et al., 2014; Tse et al.,
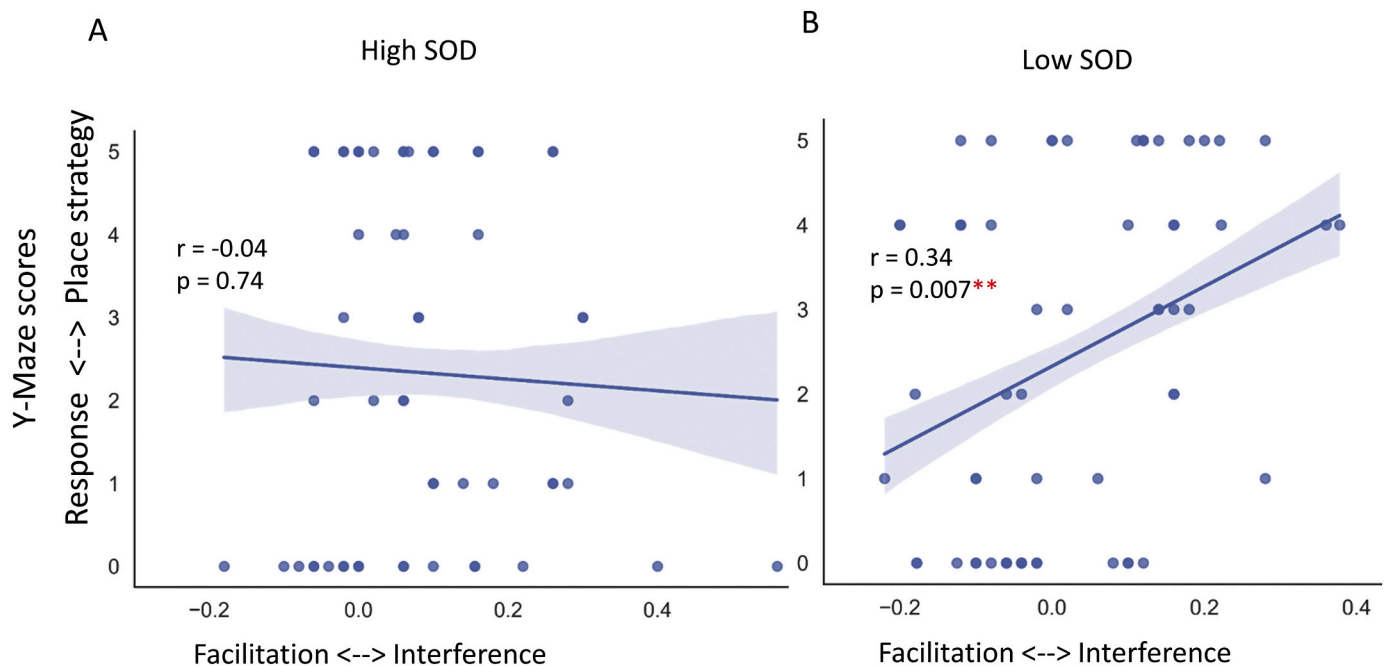
Fig. 4. Correlations between proactive interference and Y-Maze scores (the higher the Y-Maze score, the more a place-based strategy is preferred), separated by high (A) and low (B) SOD individuals. **$p < 0.01$. Error bars denote ± SEM.

Table 3
Multiple regression with SOD, Y-Maze and SOD X Y-Maze as predictors.

	Unstandardized	Standard Error	Standardized	t	p
SOD	0.130	0.04	0.454	3.362	0.001**
YMaze	0.052	0.02	0.743	2.661	0.009**
SOD X YMaze	−0.028	0.012	−0.657	−2.228	0.028*

* $p < 0.05$,
** $p < 0.005$.

2007; van Kesteren, Brown, & Wagner, 2018). A novel finding from our study is that the balance between facilitation and interference can shift over the course of a temporally-extended event, suggesting different learning mechanisms may contribute based on situational factors. Alternatively, this shift from facilitation to interference may reveal the mechanism which learning facilitation from prior knowledge could be endogenous or automatic when we encounter familiarity in our world, but their effect on behavior can be masked by more powerful interference processes. Noting that these possibilities relate to several major theories of memory interference, so building on our design here in future research could help distinguish these theories and shed further light on the mechanisms of memory interference.

Another interesting finding from the current study was that proactive interference was observed in route learning, which was represented by decision accuracy at each intersection, but not greater pointing error for New_OL than New_NOL (Fig. 2). In other words, overlapping routes

appear to introduce interference in turn responses to locations *en route*, but did not harm or benefit coarse larger-scale configural knowledge in our measures. Interference in landmark-action associations (e.g., turn left or right at the second intersection) may be elicited by perceptual cues in situ. Probes of survey learning, which may reflect a more abstract and higher-level of understanding of the environment (He, McNamara, Bodenheimer, & Klippel, 2019; Siegel & White, 1975), were conducted with non-overlapping cues (the starting view). However, because participants were not explicitly instructed to learn the layout of the environment, the interference in survey learning, which was measured after navigation, could be masked by the high difficulty of the pointing task. Future studies could explore interference/facilitation effects (if any) on configural knowledge probes that take place during navigation, when memory cues for different episodes may be present. Such findings could shed light on the interaction between memory interference and integration.

One important design aspect of the current project was that it was two-day study wherein all old mazes were learned as distinct routes one day before the new mazes. This enabled us to show interference/facilitation effects in new mazes without participants having allocated any extra attention or significance to their old OL counterparts during Day 1 learning, and it allowed us to test for an absence of retroactive interference on those old mazes due to sleep protection (Abel & Bäuml, 2014; Drosopoulos, Schulze, Fischer, & Born, 2007; Ekstrand, 1967; Wixted, 2004). Numerically, we did see hints of retroactive interference in the overlapping segment (Fig. 3), but the effect size was very small ($d' = 0.13$). Future studies investigating the retroactive interference in spatial navigation could implement a 12 h interval between old and new

Table 4
Multiple regression with SOD, Y-Maze, SOD X Y-Maze and pointing error for Old_OL mazes as predictors.*, **

	Unstandardized	Standard Error	Standardized	t	p
SOD	0.116	0.04	0.405	2.955	0.004**
YMaze	0.046	0.02	0.654	2.313	0.023*
SOD X YMaze	−0.024	0.012	−0.577	−1.939	0.055
Pointing_Old_OL	−7.09E-04	4.24E-04	−0.150	−1.669	0.098

* $p < 0.05$,
** $p < 0.005$.

learning sessions, wherein one group of participants would sleep during this interval while the other group did not to explicitly investigate the contribution of the sleep cycle in retroactive interference.

Another important topic we investigated in the current study was the individual differences in memory interference. Inspired by the configural encoding account (Darby & Sloutsky, 2015; Humphreys et al., 1989), we correlated the proactive interference with pointing task performance. We found that better configural knowledge, particularly in the old OL mazes, was associated with stronger interference, but the magnitude of the correlation was modest (r(119) < 0.23). These patterns were in sharp contrast to the findings from Darby and Sloutsky (2015), in which the authors found a non-significant, but negative correlation between proactive interference and configural knowledge. One potential reason of this discrepancy was the task difference. Another potential reason, perhaps more importantly, was the definition of 'configural knowledge': Darby and Sloutsky (2015) used the accuracy of the overlapping pairs as the index of configural knowledge, which was the same task to calculate memory interference. In this sense, configural knowledge was defined as the memory accuracy of individual episodic events in Darby and Sloutsky (2015). In our study, because 1) interference effects can be asymmetrical for new and old routes (which we indeed show here) and 2) navigational responses can be made according to different encoding strategies and mechanisms (e.g., the broadly discussed distinctions between stimulus-response-based and declarative memory (Goodroe, Starnes, & Brown, 2018), we chose to measure environmental configural encoding using a separate pointing task that challenges memory for spatial information integration beyond immediate perceptual cues. In this sense, configural knowledge was defined as the integration of multiple navigational events in the current study. If we correlated our proactive interference with the route learning (as opposed to pointing) accuracy in the old overlapping mazes similarly to Darby and Sloutsky (2015), we found that the correlation was close to zero. Together, our findings suggested that the way configural knowledge was defined played a critical role in determining the relationship between configural knowledge and memory interference.

Besides objectively-measured configural knowledge, self-report spatial ability and strategy also played important roles in predicting proactive interference from old to new spatial memories. Prior research has shown that higher SOD correlates with better performance of the task which required integration of spatial information (Arnold, Iaria, & Ekstrom, 2016; Hegarty et al., 2002; Ishikawa & Montello, 2006). Therefore, we probed SOD within the broader framework of the configural knowledge account of memory interference, and we indeed found that high SOD individual experienced stronger proactive interference. Because research from our lab has shown that high and low SOD individuals could utilize environmental cues and neural resources in very different ways (He & Brown, 2020; He, Han, Churman, & Brown, 2020; He, McNamara, & Brown, 2019), we correlated spatial strategy with proactive interference in high and low SOD separately. To our knowledge, there have been no studies examining the relationship between SOD and Y-Maze, so it was interesting to note that SOD and Y-Maze were independent measures according to our results. As it was still unclear whether SOD reflects ability or strategy or a combination of both, our finding of close-to-zero correlation between SOD and Y-Maze implies that SOD may reflect more of an ability than strategy. Nonetheless, we demonstrate that there was an interaction between SOD and strategy, in which a more place-based strategy (i.e., tend to encode the location of goals according to the layout of the environment rather than intersection-action associations) predicted stronger interference specifically among low SOD individuals – suggestive of adopting a maladaptive strategy for their spatial abilities. Although this analysis of SOD subgroups was exploratory, it coincided with and complemented our findings that efforts to integrate route experiences into configural knowledge of the environment increase risks of proactive interference.

The amount of prior research on individual differences in memory interference is limited, let alone research disentangling the contributions of abilities from strategies. In the current study, we conducted a multiple linear regression (Table 3, 4) to examine the relative importance of task-specific ability (pointing task performance), general spatial ability (SOD) and spatial strategy (Y-Maze) in explaining proactive interference. Our data imply that at the individual level, memory interference was more influenced by general spatial ability and encoding strategy than task-specific configural knowledge. Future studies, including measurements of other general cognitive abilities such as working memory capacity (Kane & Engle, 2000) and attention control, are much needed to test this conclusion further and reveal the how different cognitive abilities and encoding strategies influence memory interference in spatial and non-spatial domains.

In summary, the current study used a two-day spatial navigation task to investigate memory interference. We show that prior spatial memories can both facilitate and interfere with new learning, and we show this can dynamically shift across a navigation event depending on the amount of overlap between the experiences. Our study also shows that general spatial ability and encoding strategy modulate memory interference, and broadly touches on theories about how memories interact in naturalistic behaviors like navigation. Given that navigation abilities and interference effects change across the lifespan and with disease, these data may help us better understand both natural individual differences in memory interference and also give insight into how development and pathology can affect our ability to navigate our lives.

Declaration of Competing Interest
None.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cognition.2020.104508.

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