Neuropsychologia 141 (2020) 107437

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: http://www.elsevier.com/locate/neuropsychologia

Turns during navigation act as boundaries that enhance spatial memory and expand time estimation

Iva K. Brunec[a,b,c,d,*], Jason D. Ozubko[e], Tovi Ander[a], Ruoran Guo[a], Morris Moscovitch[a,b,1], Morgan D. Barense[a,b,**,1]

[a] Department of Psychology, University of Toronto, Canada
[b] Rotman Research Institute, Baycrest Health Sciences, Canada
[c] Temple University, USA
[d] University of Pennsylvania, USA
[e] SUNY Geneseo, USA

ARTICLE INFO

Keywords:
Recollection
Spatial navigation
Event boundaries

ABSTRACT

Ongoing experience unfolds over time. To segment continuous experience into component events, humans rely on physical and conceptual boundaries. Here we explored the subjective representation of turns along travelled routes as boundaries. Across two experiments, turns selectively enhanced participants' subjective recollection of locations immediately preceding them, compared to their recollection of locations in the middle of a route straightaway or immediately following turns. In Experiment 2, we also observed a subjective expansion of the time spent at pre-turn, relative to post-turn, locations. These results highlight the influence of turns on memory for travelled routes and provide further evidence for a link between subjective episodic re-experiencing and temporal memory. Taken together, this evidence suggests that turns during navigation act much as boundaries do for events, enhancing memory and processing of pre-boundary locations.

1. Introduction

To retrieve events from our lives, we rely on the ability to reinstate the context of the originally experienced event, possibly due to cognitive reconstruction of past events and mental time travel (Tulving, 1983, 1985). We often retrieve events from our lives based on partial cues – for example, we might see a single photograph from our holiday which triggers the retrieval of events surrounding the one in the photo. This ability to retrieve contextual information of an event has been described by William James (1890, pp.658), and Endel Tulving as *recollection*, a vivid sense of re-experiencing an event and the ability to recover details not present in the cue itself (Tulving, 2002). In contrast to recollection, *familiarity* with a cue corresponds to a mere sense of knowing that an event took place, but an inability to reconstruct event details and mentally travel back in time. Fully recollecting an event thus entails the ability to recover its spatial and temporal context, as well as the details of the experience.

Recollection has typically been associated with hippocampal activation, and familiarity with activation in the medial temporal cortex (Diana et al., 2007; Ranganath et al., 2004). Recent evidence suggests that the hippocampus supports a pattern completion mechanism underlying recollection by representing multi-component events (Horner et al., 2015), such as the associations between the person/location/object involved (Horner et al., 2015; Horner and Burgess, 2014). A recent view has further delineated this process by decomposing recollection into its operation of pattern completion and its representational content that involves highly detailed, associative, spatiotemporal, and contextual information (Cowell et al., 2019). According to this view, different types of content may be represented by different brain structures, with the hippocampus preferentially supporting the representation of the complex, multi-dimensional information that underpins the phenomenological experience of recollection. While hippocampal involvement in the recollection of spatial information and associations between individual stimuli is relatively well established (Eichenbaum, 2017a, 2017b), it is not well known whether locations along travelled routes have different rates of recollection depending on

---

[*] Corresponding author. University of Toronto, Department of Psychology, 100 St George Street, Toronto, ON, M5S 3G3, Canada.

[**] Corresponding author. Department of Psychology, University of Toronto, Canada.

E-mail addresses: iva.kristlbrunec@mail.utoronto.ca (I.K. Brunec), barense@psych.utoronto.ca (M.D. Barense).

[1] Shared senior authorship.

https://doi.org/10.1016/j.neuropsychologia.2020.107437
Received 3 July 2019; Received in revised form 25 February 2020; Accepted 10 March 2020

their navigational utility.

To address this issue, we took our cue from studies of event segmentation in episodic memory. Much as changes in spatial and temporal contexts can serve as boundaries to segregate the continuous flow of events into segments or episodes and make them memorable, we reasoned that locations at turns are especially informative as they can serve as spatial boundaries that can aid navigation by splitting a route into segments. That is, the segmentation of events in the temporal flow of experience may share key mechanisms with the segmentation of physical space (Brunec et al., 2018a). In the present experiments, we aimed to test whether turns along navigated routes are especially memorable, akin to contextual shifts in event segmentation.

Spatial features, such as the number of turns and environmental complexity, affect spatial and temporal memory and produce memory biases (Bellmund et al., 2020; Bonasia et al., 2016; Brunec et al., 2017a). As participants approach turns, they engage in planning and seek additional navigational information (Brunyé et al., 2018). Further, items at turns are recognized more rapidly than those not at turns (Janzen and van Turennout, 2004). The prominence of spatial structure as an organizing principle during navigation is also reflected in neural representations in the hippocampus (Howard et al., 2014) and parahippocampus (Janzen and van Turennout, 2004). Recent neuroimaging evidence suggests that as participants enter a road segment, hippocampal activity represents the structure of the environment, specifically possible future turns (Javadi et al., 2017). Similarly, rodent neurophysiology findings suggest that turns elicit forward 'sweeps' in hippocampal firing (Johnson and Redish, 2007) and segment spatial representations (Bos et al., 2017; Gupta et al., 2012).

Greater hippocampal activity at turns, which appears to represent potential future states, may also enhance the encoding of turn locations into long-term memory. Given the key role of turns in navigational planning, locations associated with turns along a newly learned route should be remembered better. Based on the importance of turns for spatial 'chunking' (Gupta et al., 2012), we speculated that turns along a route also allows humans to extract regularities from the environment and segment temporally extended experiences (Schapiro et al., 2013, 2016). This prediction would be consistent with neuroimaging evidence of peaks in hippocampal activity at movie clip offsets (Ben-Yakov et al., 2013; Ben-Yakov and Dudai, 2011) or at boundaries during movie watching (Baldassano et al., 2017; Ben-Yakov and Henson, 2018), which are thought to highlight changes in context and retroactively integrate the just-experienced information into cohesive events.

Spatial boundaries also affect memory for the temporal order of sequentially presented stimuli. Memory for the order of objects presented in different virtual rooms was found to be impaired relative to those experienced within the same room (Horner et al., 2016). A computational model of this cross-boundary memory disruption suggests that the rate of temporal context drift is increased immediately following boundaries (Horner et al., 2016), effectively adding noise to information essential for temporal order judgments. This evidence fits with findings in non-spatial domains, in which contextual shifts were found to affect episodic memory, such that both temporal order (DuBrow and Davachi, 2013, 2014) and associative memory (Ezzyat and Davachi, 2011) are impaired when stimuli belong to different contexts (Davachi and DuBrow, 2015). However, boundaries can improve memory for individual events by providing structure (Pettijohn et al., 2016). This indicates that boundaries can differentially affect different aspects of memory.

Here, we aimed to investigate whether turns as contextual boundaries are represented more richly in episodic memory and whether these boundary representations might produce mnemonic biases. We provide novel behavioural evidence in humans to suggest that pre-turn intersections are remembered more richly than non-turn intersections (Experiment 1). Further, we found that participants show an inflation in time estimates for pre-turn, relative to post-turn intersections (Experiment 2).

2. Experiment 1: increased recollection rates for intersections preceding turns

In the first experiment, we aimed to investigate whether turns along a newly learned route are recollected better than non-turn locations. In this task, participants learned a novel route and stopped at equal numbers of pre-turn and mid-segment intersections, after which they reported subjective recollection for images of each of the intersections where they had waited. We hypothesized that rates of recollection would be higher for pre-turn intersections. We based this prediction on behavioural evidence that turns promote planning and decision-making processes (Brunyé et al., 2018; Janzen and van Turennout, 2004), and neural evidence suggesting that boundaries promote retroactive hippocampal binding (Ben-Yakov et al., 2013).

2.1. Experiment 1 methods

Navigation task. We recruited 22 participants (20 F; $M_{age} = 20.6$ years, $SD_{age} = 3.03$) based on the sample sizes in our prior related study (Brunec et al., 2018b). None of the participants in either experiment reported neurological or psychiatric conditions and all had normal or corrected-to-normal eyesight. All participants provided informed consent. This study was approved by the University of Toronto ethics board.

Participants were instructed that the experiment would simulate the experience of training a bus driver to learn a new bus route in downtown Chicago. They were informed that they would be stopped at several 'bus stop' intersections along the route to help them learn where they would have to stop their bus to pick up passengers. These bus stop intersection locations were marked with red bars at the top and bottom of the screen (Fig. 1A). Participants were asked to pay attention to the scenery and to the locations of the bus stops along the route. There were 12 bus stop intersections in total, 6 immediately preceding turns (*pre-turn intersection)*, and 6 not immediately preceding or following turns (*mid-segment intersection)*, but all bus stop locations were placed at intersections where turns were possible (Fig. 1B). The durations spent waiting at different bus stop intersections were counterbalanced across participants (range 1–12 s). All bus-stop intersections immediately preceded turns, meaning that participants experienced the turn (boundary) immediately after each bus stop wait.

The route learning portion of the experiment was implemented in MATLAB (The Mathworks, Inc., 2017), using images from Google Street View. Panoramic images along the selected routes were presented for 200 ms each and cross-faded as the car advanced to make the movement appear smoother. As these tasks required no active navigation, these routes appeared as videos from a first-person perspective. The same platform was used in prior studies we reported (Brunec et al., 2017b; Brunec et al., 2018b). The retrieval portion of the experiment was programmed in Psychtoolbox in MATLAB (Brainard, 1997). The tasks were presented on a Windows laptop with a 14-inch screen.

Participants traversed the route 7 times to help them learn the route in as much detail as possible. The wait duration associated with each intersection was kept the same across 7 traversals for each participant. After the final traversal, they were immediately tested on a recognition memory task. They were presented, in a random order, with images of the 12 bus stop intersections where they had waited, one at a time, as well as images of 12 new intersections not from the route. For each image, they were asked to report their sense of *re-experiencing* the wait or *knowing* that they had waited at the intersection, or whether the image was *new* (Fig. 1C). 'Re-experience' responses should capture participants' subjective *recollection* of the experience associated with each location, while 'know' responses should capture a sense of *familiarity* that an event had occurred. These measures have previously been linked to temporal memory in a navigation paradigm (Brunec et al., 2017b).

Baseline memorability control with no navigational component. To control for baseline levels of memorability for our chosen intersections, we first calculated a memorability score for each image using an

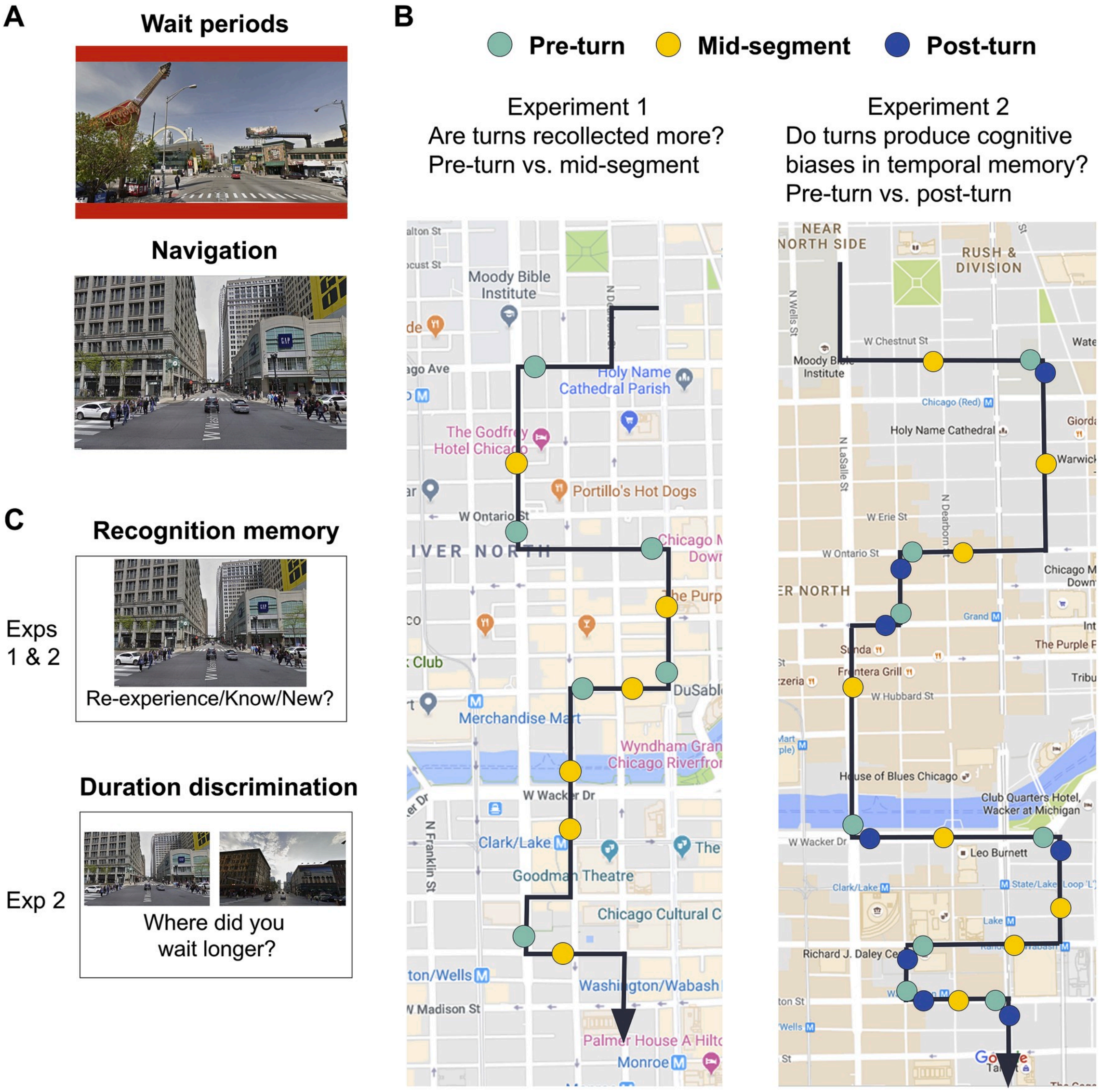

Fig. 1. A) Schematic representation of the navigation vs. wait periods. During wait periods, participants were presented with red horizontal bars at the top and bottom of the screen. B) Overhead maps of the two routes used in Experiments 1 and 2 with marked pre-turn (teal), mid-segment (yellow), and post-turn (blue) intersections. C) Tasks performed by participants after learning the routes. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

extensively validated model using convolutional neural networks (http://memorability.csail.mit.edu/demo.html; Khosla et al., 2015). There was no significant difference in memorability scores between pre-turn ($M_{\text{Pre-turn}} = 0.359$, $SD_{\text{Pre-turn}} = 0.069$) and mid-segment intersections ($M_{\text{Mid-segment}} = 0.411$, $SD_{\text{Mid-segment}} = 0.084$): t (10) = 1.17, p = .268.

To further control for baseline levels of recollection of our chosen intersections, we recruited a group of 27 participants who completed a control memory task with no navigational component (18 F; $M_{\text{age}} = 19.33$, $SD_{\text{age}} = 2.63$). In this task, participants were simply shown the images of the ‘bus stop’ intersections in a random order, devoid of navigational context, for 4 s each. Immediately following this encoding phase, participants were tested on a re-experience/know task for those images. They were instructed that a ‘re-experience’ response would refer to a rich, vivid sense of being able to remember small details and any thoughts or feelings they may have had when they first viewed the image. The term ‘know’, in contrast, would refer to a sense that they have seen the image before, but that does not entail any detail beyond what is in the picture. The proportion of ‘re-experience’ responses was calculated for each image to derive its baseline recollection rate. This value was added as a covariate in the linear model we ran in the experimental sample. A total of 27 participants completed the control task. However, we noticed early on that one of the bus stop images had a disproportionately high recollection rate, and swapped it for a different bus stop image halfway through. This swapped image was ultimately used in the navigational task described above. Of the 12 bus stop images, we thus have 27 responses for 11 of the images, and 13 responses for the 12th image. The results of the regression model in the navigation task remain the same regardless of whether the covariate values are calculated based on the full sample of 27 or the smaller sample of 13 control participants.

Statistical analysis. We ran trial-wise analyses of participants’ recognition accuracy and recollection estimates in relation to whether each location was a pre-turn or a mid-segment intersection. We performed separate multi-level logistic regression analyses on accuracy and recollection data, implemented in R (R Core Team; https://www.R-project.org/) using the *glmer* function in the *lme4* package (Bates et al., 2015). A type II Wald chi-square test was then performed on the output to determine the significance of the factors using the *Anova* function in the *car* package (Fox and Weisberg, 2011). The binary outcome variables for each trial were 1) correct vs. incorrect recognition accuracy, and 2) for correctly recognized images, whether the response on each trial was classified as 're-experience' or 'know'. The predictors in both analyses were the intersection category (pre-turn vs. mid-segment), the ordinal position of each intersection and the duration of the wait at each intersection. To control for potential differences in intersection memorability, we analyzed participants' subjective recollection following route learning by including a covariate for the baseline recollection rate for each intersection obtained in a separate group of participants who completed the task with no navigational component.

2.2. Experiment 1 results and discussion

2.2.1. Recognition accuracy

The average *d*' was 2.51 (SD = 0.50), suggesting that the participants were highly accurate at discriminating lures from targets. Performance was near-ceiling across the board ($M_{\text{Pre-turn}} = 0.99$, $SD_{\text{Pre-turn}} = 0.087$, $M_{\text{Mid-segment}} = 0.95$, $SD_{\text{Mid-segment}} = 0.21$). Correct responses consisted of both 're-experience' and 'know' responses to old images. After controlling for baseline recognition rates, we found no significant difference between pre-turn and mid-segment intersections. These results are reported in the Supplementary Materials (Fig. S1A).

2.2.2. Baseline recollection with no navigational component

In the separate sample of participants who completed a recognition memory task for the individual intersection images without ever having learned them in any navigational context, we found no difference in baseline recollection rates between pre-turn and mid-segment intersections ($M_{\text{Pre-turn}} = 0.709$, $SD_{\text{Pre-turn}} = 0.247$, $M_{\text{Mid-segment}} = 0.770$, $SD_{\text{Mid-segment}} = 0.246$; t (26) = 1.15, p = .260). These baseline recollection values are depicted as black circles in Fig. 2A.

2.2.3. Recollection of locations following route learning

We next ran a logistic regression on the 're-experience' and 'know' responses for correctly recognized intersections following route learning. Only intersections correctly recognized as old were included. As above, we included both wait duration at each intersection (1–12 s) and the ordinal position of each intersection (1–12) as continuous covariates. To ensure that all reported statistics accounted for potential differences in baseline memorability across intersections, we also included intersection-specific baseline recollection values, obtained from the control sample, as a regressor (for unadjusted values, please see Table S1 in the Supplementary Materials). We found a significantly greater proportion of 're-experience' responses for pre-turn intersections, compared to mid-segment intersections (χ^2 (1) = 7.26, p = .007; Fig. 2A). It is important to emphasize that this main effect of intersection category was significant despite the fact that baseline recollection scores were also a significant predictor of recollection in this sample of participants (χ^2 (1) = 6.69, p = .010). This indicates that intersection category affected recollection over and above any baseline differences in the memorability of the images. We found no effect of ordinal position (χ^2 (1) < 1; Fig. S3B). We did observe a significant effect of wait duration (χ^2 (1) = 15.75, p < .001; Fig. 2B), due to the fact that intersections where participants waited longer were significantly more likely to be recollected. This suggests that intersection category and wait duration both independently predicted subjective recollection following route learning, and that baseline recollection rates did not contribute to the difference in recollection between pre-turn and mid-segment intersections.

In this experiment, we also investigated participants' ability to distinguish between the durations and ordinal positions of individual intersections, based on a prior observation that turns differentially affected memory for duration and temporal order (Brunec et al., 2018b). In this previous work, we found that memory for the temporal order of intersections separated by turns was worse relative to those not separated by turns. In contrast, memory for the wait duration of intersections separated by turns was improved relative to those not separated by turns, suggesting that different aspects of memory can be differentially affected by turns. In the present experiment, we were unable to replicate these findings (Fig. S2), and instead found no significant accuracy differences between the duration and ordinal discrimination tasks, and no modulation by turns. It is unclear why we were unable to replicate our original effects, as the routes were similar in length (4.04 km, 3.23 km), number of turns (11, 12), average distance between stops (274 m, 194), and image memorability scores (0.385, 0.356). We have planned further experiments to investigate the conditions under which turns modulate duration and ordinal discrimination.

2.2.4. Experiment 1 discussion

In summary, in Experiment 1 we found higher rates of recollection for locations preceding turns along a newly learned route, compared to mid-segment ones. This finding suggests richer memory for events near turn points, which may serve to aid in navigational planning following spatial learning. If turns act as boundaries along navigated routes in a manner similar to how event boundaries act for temporally extended

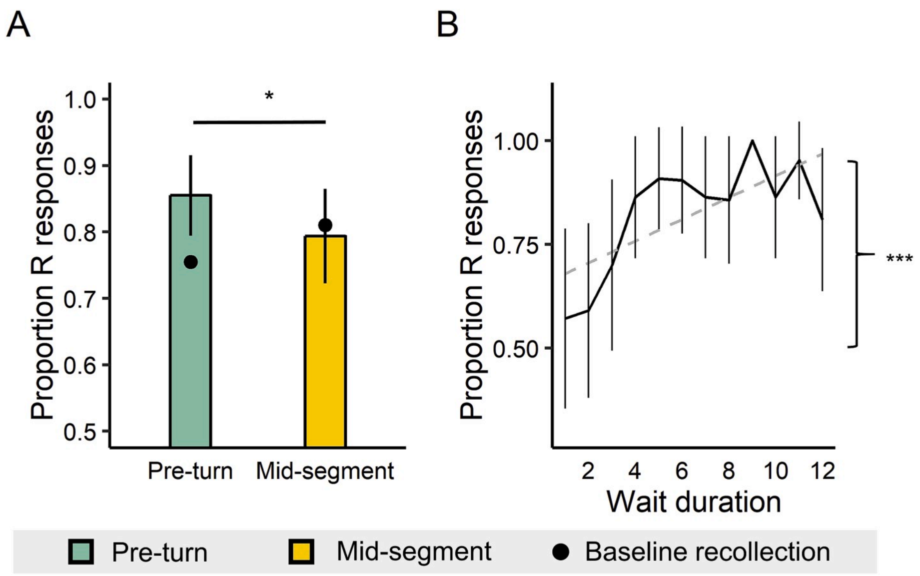

Fig. 2. Experiment 1. A) For images correctly identified as old, participants were significantly more likely to report re-experiencing their wait at pre-turn, relative to mid-segment intersections. B) 'Proportion of R responses' reflects the proportion of images correctly identified as old that were subjectively 're-experienced'. The proportion of 're-experience' responses increased with wait duration. Baseline recollection rates (black circles) observed in a control experiment with no navigational component served as a covariate for these analyses. *p < .05. Error bars reflect 95% confidence intervals (CI) around the mean. The dashed line in panel B reflects the linear fit.

episodes, higher recollection rates for pre-turn locations might be due to the peak in hippocampal activation observed at boundaries (Ben-Yakov et al., 2013; Ben-Yakov and Henson, 2018). Because mid-segment locations are not associated with such a boundary, their lower recollection rates may be due to the absence of such a boundary-related peak in hippocampal activity. It is possible that the effects observed in this experiment could result from participants' proactive attempts to memorize turn locations over the course of multiple route traversals, as turns are especially salient change points. To address this issue, in our next experiment participants traversed the route only once prior to completing the memory test. With just a single traversal, participants had no way of knowing of when a turn was coming and thus could not attempt to memorize turn locations.

In Experiment 1, we compared only pre-turn locations to mid-segment locations which were separated by a noticeable spatiotemporal distance. Prior evidence suggests that immediately following boundaries such as doorways, the speed of temporal context drift is transiently increased (Horner et al., 2016). Further, turns along routes expanded the time participants needed to mentally navigate familiar routes (Bonasia et al., 2016). As temporal drift has been directly linked to participants' estimates of elapsed time (Lositsky et al., 2016), the introduction of a contextual boundary may induce biases in temporal representations immediately following boundaries. To test whether boundaries affect participants' temporal perception during large-scale navigation, we added bus stop locations immediately following each turn in Experiment 2. Based on evidence provided by Bonasia et al. (2016), turns should produce a bias in the subjective perception of elapsed time. To test this prediction, we matched all wait durations in Experiment 2, which enabled us to investigate biases in temporal perception.

3. Experiment 2: contextual boundaries trigger biases in temporal memory

In Experiment 2, we constructed a novel route to test 1) whether the recollection effect observed in Experiment 1 would generalize to a different route, 2) whether it can be observed after a single route traversal, and 3) whether turns produce biases in temporal discrimination. We set 8 pre-turn and mid-segment locations comparable to Experiment 1, and further added bus stop locations immediately following each turn to test whether these locations would be susceptible to biases in temporal perception. Participants waited for an equal amount of time at locations immediately before a turn, immediately after a turn, and in the middle of a road segment.

In addition to collecting participants' self-reported recollection ratings for each location, we also tested whether pre-turn locations were associated with cognitive biases. Because the times were objectively equal, unbiased participants should report having waited longer before and after a turn on approximately equal proportions of trials. If, however, pre-turn durations became temporally dilated due to the hypothesized retroactive memory boost, they should be biased towards reporting longer waits at pre-turn than post-turn locations. We tested participants on the same memory tasks twice. The first test occurred after a single route traversal, when participants had no expectations about the route. The second test occurred after their fourth route traversal. We acknowledge that repeated testing likely improved participants' performance by drawing their attention to the aspects of the task on which they were tested, but this enabled us to test whether any of the observed effects persisted even after the route became well learned.

3.1. Experiment 2 methods

Navigation task. Twenty-one participants (19 F; $M_{age} = 21.1$, $SD_{age} = 3.27$ years) took part in this experiment. One female participant was excluded due to an error in data saving.

The number of 'bus stop' intersections in Experiment 2 was increased from 12 to 24. The stops were placed at different locations along the route. Eight of the stops occurred immediately before a turn (teal circles in Fig. 1B; *pre-turn* intersections); 8 of the stops occurred immediately following each of the turns (blue circles in Fig. 1B; *post-turn* intersections), and 8 of the stops occurred at intersections not immediately preceding or following a turn (yellow circles in Fig. 1B; *mid-segment* intersections). In this experiment, participants waited for the same amount of time (4 s) at each stop. Navigation and wait were passive for all participants. Participants were again instructed that the experiment would simulate the experience of training a bus driver to learn a new bus route in downtown Chicago, where they would be stopped at several locations along the route. These bus stop intersections were marked with red bars at the top and bottom of the screen. Participants were asked to pay attention to the scenery and to the locations of the bus stops along the route.

After a single route traversal, participants completed a recognition memory task and a duration discrimination task. In the recognition memory task, participants saw each of the 24 old bus stop intersections and 24 new intersections and had to indicate whether they could re-experience waiting at each, only knew that they had waited, or whether they thought it was a new intersection. In the duration discrimination task, on each trial, participants were shown images of each pair of pre-turn and post-turn bus stops at which they had waited side-by-side and were asked to use the right or left arrow key to select the bus stop where they had waited longer.

Upon completing these two tasks following a single route traversal, participants were told that they would need to become experts of the bus route before they could earn their Chicago bus driver's certification and were taken through the exact same route three more times. Participants were also told that, following all three repetitions, they may receive the same set of tests as before, or they may receive a new set of tests to see how well they could learn other aspects of the bus route. Although all participants would receive the identical test as before, this manipulation was used with the aim of preventing participants from narrowing their focus to only those aspects of the route that had been previously tested. Participants completed the same two recognition memory and duration discrimination tasks, with identical instructions, but a newly randomized order in which the images were shown.

Baseline memorability control with no navigational component. As in Experiment 1, we first calculated the memorability score for each image (Khosla et al., 2015). There was no significant difference between pre-turn, post-turn, and mid-segment intersections ($F(2, 21) = 0.377$, $p = .691$; $M_{\text{Pre-turn}} = 0.360$, $SD_{\text{Pre-turn}} = 0.065$, $M_{\text{Post-turn}} = 0.341$, $SD_{\text{Post-turn}} = 0.044$, and $M_{\text{Mid-segment}} = 0.366$, $SD_{\text{Mid-segment}} = 0.072$).

As in Experiment 1, we also recruited a separate group of 20 participants (10 F; $M_{age} = 18.8$, $SD_{age} = 1.1$ years) who were shown the images of the intersections in a random order devoid of navigational context and then tested on their memory for those images. The procedures were identical to those described in Experiment 1. We again calculated the average proportion of reported recollection responses for each intersection and entered it as a covariate in each of the logistic regression models in the navigation task. With this approach, we could account for differences in baseline memorability. The presence of a significant effect of intersection category, regardless of the significance of the covariate, would suggest that the variance explained by the location of an intersection is not explained by the baseline memorability of that intersection.

Statistical analysis. We conducted the same set of analyses as in Experiment 1 on recognition accuracy and recollection data. Trial-wise logistic regression analyses were run on participants' recognition accuracy (correct vs. incorrect) and recollection responses on correctly recognized images ('re-experience' vs. 'know'). The predictors in both analyses were the intersection category (pre-turn vs. post-turn vs. mid-segment) and the ordinal position of each intersection. As the wait durations were equal at all intersections, they were not included as a covariate in this experiment. As in Experiment 1, to control for potential differences in intersection memorability, we included the covariate of baseline recollection rate for each intersection obtained from a separate group of participants who completed the task with no navigational component. The data following 1 vs. 4 traversals were modelled in separate mixed effects models.

To test for the presence of bias in participants' duration discrimination, we calculated the proportion of trials where the pre-turn intersection was chosen and compared these values against 0.5 in a one-sample *t*-test.

3.2. Experiment 2 results and discussion

3.2.1. Recognition accuracy

After a single route traversal, the average *d*' score across all trials was 1.27 (SD = 0.56) and after three additional route repetitions, it was 1.90 (SD = 0.87). Participants were accurate at recognizing old images ($M_{\text{Pre-turn}} = 0.84$, $SD_{\text{Pre-turn}} = 0.37$, $M_{\text{Post-turn}} = 0.67$, $SD_{\text{Pre-turn}} = 0.47$, $M_{\text{Mid-segment}} = 0.71$, $SD_{\text{Mid-segment}} = 0.45$). Correct responses consisted of both 're-experience' and 'know' responses to old images. As in Experiment 1, we found no significant differences in recognition memory for different intersection locations, after controlling for baseline recognition rates. These results are reported in the Supplementary Materials (Fig. S1C).

3.2.2. Baseline recollection with no navigational component

In the separate sample of participants who completed a recognition memory task for the individual intersection images without ever having learned them in any navigational context, we found a significant difference in baseline recollection (F (2, 38) = 4.61, p = .016; $M_{\text{Pre-turn}} = 0.729$, $SD_{\text{Pre-turn}} = 0.229$, $M_{\text{Post-turn}} = 0.702$, $SD_{\text{Post-turn}} = 0.251$, and $M_{\text{Mid-segment}} = 0.593$, $SD_{\text{Mid-segment}} = 0.274$). These baseline recollection rates are depicted as black circles in Fig. 3A. This effect was driven by significantly higher recollection rates for images of pre-turn than mid-segment intersections (t (19) = 3.15, p = .005). There was no difference in recollection for images associated with pre-turn and post-turn locations (t (19) = 0.612, p = .548), but while there was a trend between mid-segment to post-turn baseline recollection (t (19) = 2.0, p = .060); the latter was not a contrast of interest.

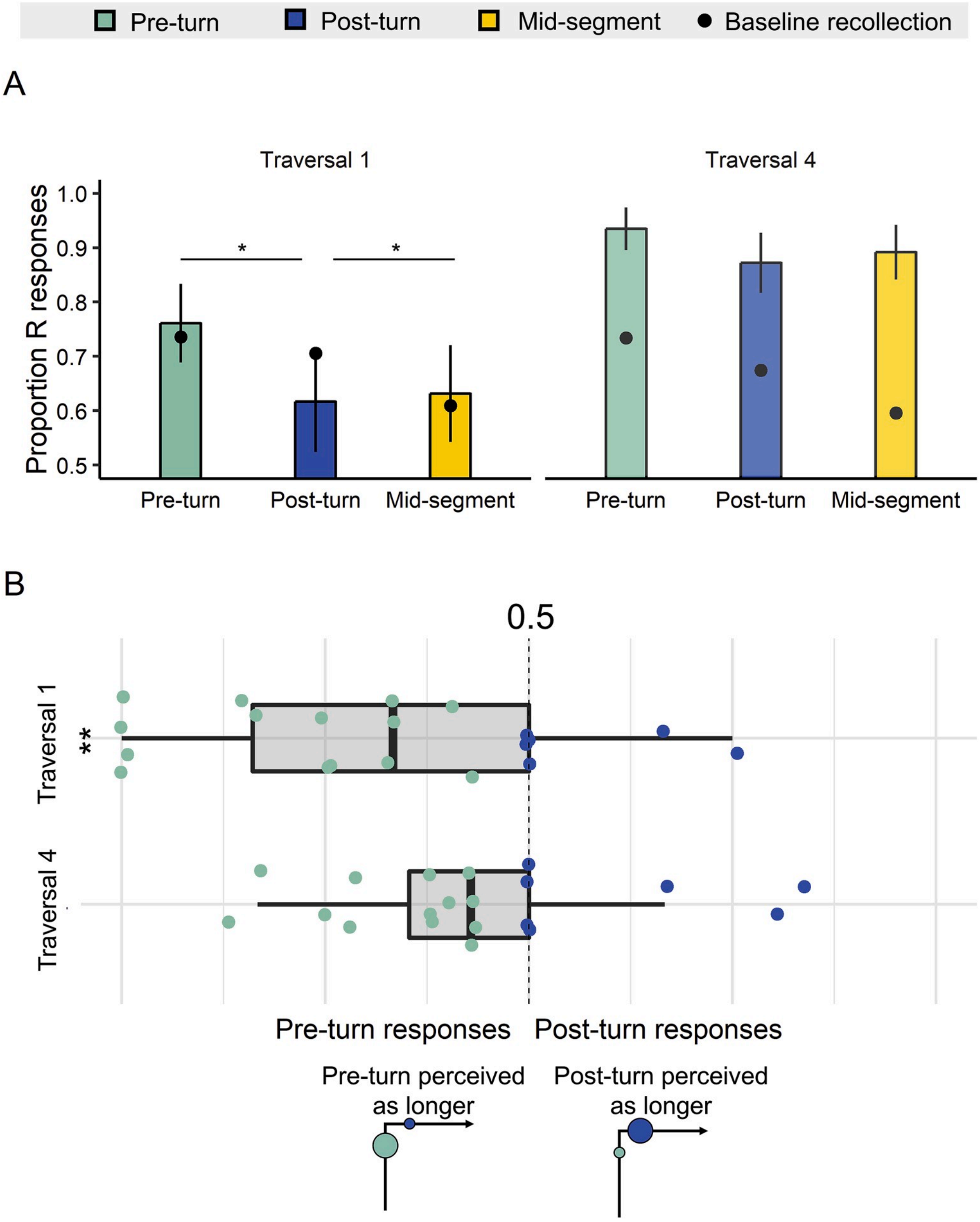

Fig. 3. Experiment 2. A) After a single route traversal, intersections followed by turns were significantly more likely to be recollected than post-turn intersections, but not than mid-segment intersections. The label 'Proportion of R responses' reflects the proportion of images correctly identified as old that were subjectively 're-experienced'. The effect was not significant after four route traversals and a second memory test. Baseline recollection rates (black circles) observed in a control experiment with no navigational component served as a covariate for these analyses. B) Participants showed a bias towards perceiving waits at pre-turn intersections as longer than post-turn intersections, despite the durations being objectively equal. *p < .05, **p < .01. Error bars reflect 95% CIs.

3.2.3. Recollection of locations following route learning

We next ran a logistic regression on participants' 're-experience' and 'know' responses for correctly recognized intersections following route learning. All analyses included the baseline recollection covariate described above, and we again modelled the ordinal position of each intersection. After traveling the route once, there was a significant main effect of location on recollection rates (χ^2 (2) = 6.82, p = .033; Fig. 3A). It is important to note that this was observed even despite a significant effect of baseline recollection (χ^2 (1) = 53.86, p < .001; denoted as black circles in Fig. 3A), indicating that intersection category significantly predicted recollection following navigation while accounting for baseline differences in memorability. There was no significant effect of ordinal position (χ^2 (1) < 1; Fig. S3D) and no interaction between location and ordinal position (χ^2 (2) = 1.35, p = .508). Follow-up contrasts revealed that after a single route traversal, participants were more likely to recollect waiting at pre-turn, compared to post-turn locations (χ^2 (1) = 5.34, p = .021). There was no difference between pre-turn and mid-segment locations (χ^2 (1) < 1). There was also a difference in recollection rates between post-turn and mid-segment locations (χ^2 (1) = 4.18, p = .041). In all three follow-up contrasts, baseline recollection significantly predicted recollection following route learning (all p-values < .001; see Table S1 for effects of location with and without the baseline recollection covariate). These results suggest that the difference between pre-turn and post-turn locations for our navigational participants was significant despite the difference in baseline recollection for our control participants, but that the difference in baseline recollection accounted for most of the variance in the comparison between pre-turn and mid-segment intersections for our navigational participants. The effect of ordinal position and the interaction between location and ordinal position were non-significant in all three follow-up contrasts (χ^2 (1) < 1).

After three more exposures to the route, the main effect of location on recollection was abolished (χ^2 (2) = 2.19, p = .335; Fig. 3A), but baseline recollection was still a significant predictor (χ^2 (1) = 27.86, p < .001), with no significant effect of ordinal position (χ^2 (1) = 1.63, p = .201) and no significant interaction between location and ordinal position (χ^2 (2) = 3.29, p = .193; Fig. S3D).

3.2.4. Duration discrimination bias

We conceptualized the measure of pre-turn bias as the proportion of trials on which participants reported waiting longer before the turn, relative to after the turn, despite the wait times being objectively equal. A proportion of 0.5 would therefore indicate no bias, as this would mean that participants reported waiting longer before the turn on exactly half of the trials. We conducted two one-sample t-tests comparing participants' responses after the first route traversal and after the fourth traversal against 0.5. We were not interested in participants' accuracy, as neither wait was truly longer – instead, we were interested in participants' duration discrimination biases as a proxy for 'weight' of representation. If a location is represented more strongly in one's mind, participants might infer or be biased to report that they waited there longer.

After the first route traversal, participants showed a significant pre-turn bias (t (19) = 3.73, p = .001, Cohen's d = 0.834; Fig. 3B), but while it was numerically in the same direction, this effect did not significantly persist after 4 route traversals (t (19) = 1.66, p = .112, Cohen's d = 0.373). A paired samples *t*-test indicated that there was a non-significant reduction in this bias from the 1st to the 4th traversal (t (19) = 1.71, p = .104, d = 0.382). Together, these results suggest that participants had stronger mental representations of pre-turn intersections than of post-turn intersections.

To relate the observed pre-turn bias to recollection, we also conducted a post hoc trial-wise logistic regression, predicting participants' responses on each trial in the duration discrimination task from their responses on the recollection task. We compared trials where the pre-turn location was re-experienced and the post-turn location was familiar to trials where both were re-experienced. We removed all other trials (i.e., pre-turn familiar/post-turn re-experienced, and both familiar) due to very low trial numbers. We also included the ordinal position of each pair as a continuous covariate. Interestingly, there was no significant main effect of recollection (χ^2 (1) < 1) or of ordinal position (χ^2 (1) < 1), but there was a significant interaction between the two (χ^2 (1) = 5.39, p = .020; Fig. S4). Recollection rates for individual locations did not increase with ordinal position (Fig. S3). However, the interaction between ordinal position and recollection observed on the duration discrimination task suggests participants' sense of recollection differentially affected duration estimates early vs. late on the route. For pairs of locations closer to the end of the route, participants were more likely to perceive the pre-turn wait as longer when only the pre-turn location was recollected, compared to when both were recollected. This was an unexpected interaction which warrants further investigation in future studies sampling a higher number of locations.

3.2.5. Experiment 2 discussion

Together, these data suggest that memories for intersections preceding turns had a stronger recollective quality. After three additional exposures to the route and a second identical memory test, these effects largely disappeared, which was likely due to the repeated testing session. Although we told participants that they may be asked about different aspects of the route on the second test, they likely benefited from being tested twice. However, comparing Experiment 2 results following a single route traversal to Experiment 1 results following seven route traversals suggests similar patterns, with slightly lower accuracy when the route is only seen once.

Further, participants tended to report that they had waited for a longer period of time at intersections preceding turns than those following them. This finding reflects an expansion of participants' subjective time estimates for experiences preceding turns, suggesting that turn points may have more cognitive 'weight'.

4. General discussion

Across two experiments, we observed greater rates of recollection for locations immediately preceding turns compared to either intersections in the middle of road segments (Experiment 1) or those immediately following turns (Experiment 2). We also observed that participants were more likely to report waiting for a longer period of time at locations immediately preceding turns compared to those following turns, even when the objective wait locations were equal (Experiment 2). This finding fits well with evidence reported by Bonasia et al. (2016), who found that the duration of mentally simulated routes scaled with the number of turns. The inflation of pre-boundary temporal information and increased subjective recollection may be produced by a post-boundary peak in hippocampal activity, which enables binding of pre-boundary information into a cohesive event (Baldassano et al., 2017; Ben-Yakov et al., 2013; Ben-Yakov and Henson, 2018). This retroactive signal might therefore result in an enhanced encoding of pre-boundary, relative to post-boundary, information. An alternative, potentially complementary explanation was proposed by Horner et al. (2016), who formulated a computational model suggesting that the speed of temporal context drift is increased immediately following boundaries. The present data do not allow us to distinguish between these alternatives. Results from Experiment 1 suggest that pre-turn locations are enhanced in memory relative to events not immediately preceding or following turns, which supports the retroactive binding explanation. However, in Experiment 2, higher subjective recollection was observed for pre-turn events relative only to post-turn, but not to mid-segment events due to differences in baseline memorability. Future studies are needed to distinguish between these explanations in the context of spatial navigation.

Turns represent points of navigational relevance, akin to transitions between contexts. A mechanism common to both spatial and event segmentation might therefore provide a cue that the content of information is changing, starting a new information-accumulation process (Clewett et al., 2019) or resulting in a prediction error that enables memory updating (Radvansky and Zacks, 2017). Decision points play a critical role in navigational planning and are reflected in hippocampal activity sequences (Erdem and Hasselmo, 2012; Foster and Knierim, 2012; Ólafsdóttir et al., 2015; Wood et al., 2000) and theta oscillation patterns (Gupta et al., 2012). Similarly, turns during spatial navigation elicit increased hippocampal and medial temporal lobe activation in humans (Howard et al., 2014; Janzen and van Turennout, 2004; Janzen et al., 2006).

The mechanism underlying the detection of navigationally relevant spatial locations may therefore be similar to the one used to detect contextual boundaries between events with no navigational component, such as narratives. Although Tulving did not explicitly take navigation into account in formulating his ideas on recollection and familiarity, they proved very useful in the present study, attesting to their wide applicability. Interestingly, the effect of spatial location was only reliably observed in recollection, but not overall recognition accuracy (i.e., both 're-experience' and 'know' responses). It is possible that the navigational relevance of turns to navigation is only reflected when memory is associated with the highly detailed, associative, spatiotemporal, and contextual source details that underpin recollective responses (Cowell et al., 2019). A key direction for future studies will be to establish the extent of overlap between regions sensitive to decision points along routes and those implicated in non-navigational event boundary detection to provide insight into whether the segmentation of events and space relies on the same mechanisms. One key difference between boundaries in navigational and non-spatial contexts is the nature of content at boundaries (Brunec et al., 2018a). Whether pre-boundary or post-boundary information is remembered better may depend on the task and material. In navigation, memory for pre-boundary information is favoured as it prepares one for upcoming directional decisions. In narratives, post-boundary processing may provide structure to a just-encoded memory. When stimuli are unrelated by narrative or navigational structure, cognitive/perceptual shifts also enhance binding across boundaries (Clewett et al., 2019; Heusser et al., 2018a; Rouhani et al., 2019; Swallow et al., 2011), but in the present experiments, we only observed an enhancement for the pre-boundary events.

The experiments presented here provide novel evidence that turns separate segments of space traversed during navigation, like contextual boundaries separating individual events in time. Mental time travel is a continuous process, which has recently been described as the activation of a distribution of past states when past events are recalled (Heusser et al., 2018b). Turns and boundaries might provide anchors to these past states, prioritizing points of spatiotemporal context change. As memory representations are commonly grounded in spatial context (Hassabis and Maguire, 2009; Robin et al., 2016), the hippocampal boundary-detection mechanism may have initially evolved to enable efficient spatial segmentation (Murray et al., 2018). Importantly, however, shifts in cortical patterns, particularly those implicating the angular gyrus and medial posterior cortex, were found to precede peaks in hippocampal activity during narrative perception (Baldassano et al., 2017). An outstanding question is whether this cortical shift precedes hippocampal activity only in the non-spatial domain, where schemas might guide perception more strongly and participants can anticipate event boundaries, or whether predictions in any domain are guided by neocortical patterns which trigger hippocampal boundary signaling.

Further investigation is necessary to establish whether turns are prioritized in memory even on frequently travelled routes in highly familiar environments, and how the representations of turn points might reconfigure over time. The hippocampus is critical for one-shot learning (Burgess et al., 1994; Lee et al., 2015), and is likely crucially involved in the representation of turns after a single exposure. Experiment 1 in the present study provides some evidence suggesting that turns are prioritized even after 7 route traversals, but participants were only familiarized with one route, with no context regarding the layout of the environment or connecting routes. With extended experience in an environment, goal coding becomes associated with retrosplenial cortical activity, which may support longer-term, context-independent representations (Patai et al., 2019). A similar pattern might be predicted for turn point representations, as participants learn connecting routes and each intersection may become associated with multiple routes. Alternatively, these route-specific patterns may persist, as only the goal state of the present route is brought online, and the relevant turn points are persistently activated more than non-turn points. Turn points during active navigation act as decision points, where the possible future routes from one's present location can be evaluated and the remaining route can be planned. In the present study, participants were passively led towards the goal, and even under such passive navigational conditions, turns were recollected more than post-turn locations. During active navigation, however, turns act as both 1) contextual boundaries associated with a shift in spatiotemporal context and 2) decision points, where participants must actively evaluate and decide which of the possible routes to take. An interesting open question is also how much this effect scales. In the present study, we found differences at the level of individual turns, but in well-learned environments, segmentation might operate at the level of neighbourhoods or larger regions within a city.

There are two caveats to consider in our direct comparisons between pre-turn and post-turn locations in Experiment 2. First, to be able to compare pre-boundary to post-boundary memory quality, we introduced stops that immediately preceded and followed turns. One possibility is that the pattern of results we observed is merely due to the close spatiotemporal proximity between the two stops. Future studies are needed to test whether the same pattern is observed between two successively sampled locations not immediately surrounding a turn (two mid-segment locations). The addition of such stops, however, may also introduce additional subjective contextual boundaries.

The second caveat is that due to the nature of the environment, post-turn locations were not intersections. We observed no differences in image memorability (Khosla et al., 2015) or baseline recollection rates between pre- and post-turn locations, making baseline memorability differences between the two location types an unlikely confound. However, the number of affordances or the structure of locations may have affected participants' responses. These potential issues should be addressed in future research. In addition to these task-related caveats, it is also important to note that the present studies included small numbers of participants, and the majority of our participants were women. While gender differences have been reported in spatial navigation (Coutrot et al., 2018; Nazareth et al., 2019), the present study did not require the participants to navigate freely, and we collected no spatial outcome measures. Nonetheless, it is possible that a more balanced sample would produce a different pattern of results.

5. Conclusions

In this paper, we present evidence that turns are prioritized in memory during later retrieval. We speculate that this mnemonic prioritization is produced by ongoing processes during navigation. Specifically, turns are points of particular relevance while navigating because decisions at each turn on route to the goal determine the efficiency of goal-directed navigation. Representing both the immediate local state at each turn (next road segment) as well as the more distant global goal state (final route goal), is therefore important, and may depend on the proximity to goal (Howard et al., 2014; Patai et al., 2019). The enhanced encoding of turn points during navigation may be related to more extensive processing and prediction of future states at those locations. Future studies are needed to investigate the relationship between turn point and goal representations on routes with different degrees of experience.

CRediT authorship contribution statement

Iva K. Brunec: Conceptualization, Formal analysis, Investigation, Methodology, Writing - original draft. **Jason D. Ozubko:** Conceptualization, Methodology, Software, Resources, Writing - review & editing. **Tovi Ander:** Investigation, Writing - review & editing. **Ruoran Guo:** Investigation. **Morris Moscovitch:** Conceptualization, Funding acquisition, Resources, Supervision, Writing - review & editing. **Morgan D. Barense:** Conceptualization, Funding acquisition, Resources, Supervision, Writing - review & editing.

Acknowledgements

The work reported in this manuscript was supported by Discovery and Accelerator grants from the Natural Sciences and Engineering Research Council of Canada (to M.D.B), a Scholar Award from the James S. McDonnell Foundation (to M.D.B.), Canadian Institutes of Health Research grants MOP49566 and MOP125958 (to M.M.), and a doctoral award from the Alzheimer Society of Canada (to I.K.B.).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2020.107437.

References

Baldassano, C., Chen, J., Zadbood, A., Pillow, J.W., Hasson, U., Norman, K.A., 2017. Discovering event structure in continuous narrative perception and memory. Neuron 95 (3), 709–721. https://doi.org/10.1016/j.neuron.2017.06.041 e5.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Software 67 (1). https://doi.org/10.18637/jss.v067.i01.

Bellmund, J.L., de Cothi, W., Ruiter, T.A., Nau, M., Barry, C., Doeller, C.F., 2020. Deforming the metric of cognitive maps distorts memory. Nat. Human Behav. 4 (2), 177–188.

Ben-Yakov, A., Dudai, Y., 2011. Constructing realistic engrams: poststimulus activity of Hippocampus and dorsal striatum predicts subsequent episodic memory. J. Neurosci. 31 (24), 9032–9042. https://doi.org/10.1523/JNEUROSCI.0702-11.2011.

Ben-Yakov, A., Eshel, N., Dudai, Y., 2013. Hippocampal immediate poststimulus activity in the encoding of consecutive naturalistic episodes. J. Exp. Psychol. Gen. 142 (4), 1255–1263. https://doi.org/10.1037/a0033558.

Ben-Yakov, A., Henson, R.N., 2018. The hippocampal film-editor: sensitivity and specificity to event boundaries in continuous experience. J. Neurosci. 38 (47), 10057–10068. https://doi.org/10.1101/273409.

Bonasia, K., Blommesteyn, J., Moscovitch, M., 2016. Memory and navigation: compression of space varies with route length and turns. Hippocampus 26 (1), 9–12. https://doi.org/10.1002/hipo.22539.

Bos, J.J., Vinck, M., van Mourik-Donga, L.A., Jackson, J.C., Witter, M.P., Pennartz, C.M. A., 2017. Perirhinal firing patterns are sustained across large spatial segments of the task environment. Nat. Commun. 8, 15602. https://doi.org/10.1038/ncomms15602.

Brainard, D.H., 1997. The psychophysics toolbox. Spatial Vis. 10 (4), 433–436. https://doi.org/10.1163/156856897X00357.

Brunec, I.K., Javadi, A.-H., Zisch, F.E.L., Spiers, H.J., 2017a. Contracted time and expanded space: the impact of circumnavigation on judgements of space and time. Cognition 166, 425–432. https://doi.org/10.1016/j.cognition.2017.06.004.

Brunec, I.K., Moscovitch, M., Barense, M.D., 2018a. Boundaries shape cognitive representations of spaces and events. Trends Cognit. Sci. 22 (7), 637–650. https://doi.org/10.1016/j.tics.2018.03.013.

Brunec, I.K., Ozubko, J.D., Barense, M.D., Moscovitch, M., 2017b. Recollection-dependent memory for event duration in large-scale spatial navigation. Learn. Mem. 24 (3), 104–114. https://doi.org/10.1101/lm.044032.116.

Brunec, I., Ozubko, J., Ander, T., Moscovitch, M., Barense, M., 2018b. Does a Turn in the Road Mark a Turn of Events? Turns along Travelled Routes Provide Contextual Boundaries during Navigation. Psyarxiv.

Brunyé, T.T., Gardony, A.L., Holmes, A., Taylor, H.A., 2018. Spatial decision dynamics during wayfinding: intersections prompt the decision-making process. Cognit. Res.: Princ. Implications 3 (1). https://doi.org/10.1186/s41235-018-0098-3.

Burgess, N., Recce, M., O'Keefe, J., 1994. A model of hippocampal function. Neural Network. 7 (6–7), 1065–1081.

Clewett, D., DuBrow, S., Davachi, L., 2019. Transcending time in the brain: how event memories are constructed from experience. Hippocampus. https://doi.org/10.1002/hipo.23074.

Coutrot, A., Silva, R., Manley, E., De Cothi, W., Sami, S., Bohbot, V.D., Wiener, J.M., Hölscher, C., Dalton, R.C., Hornberger, M., 2018. Global determinants of navigation ability. Curr. Biol. 28 (17), 2861–2866.

Cowell, R.A., Barense, M.D., Sadil, P.S., 2019. A roadmap for understanding memory: decomposing cognitive processes into operations and representations. ENeuro.

Davachi, L., DuBrow, S., 2015. How the hippocampus preserves order: the role of prediction and context. Trends Cognit. Sci. 19 (2), 92–99. https://doi.org/10.1016/j.tics.2014.12.004.

Diana, R.A., Yonelinas, A.P., Ranganath, C., 2007. Imaging recollection and familiarity in the medial temporal lobe: a three-component model. Trends Cognit. Sci. 11 (9), 379–386. https://doi.org/10.1016/j.tics.2007.08.001.

DuBrow, S., Davachi, L., 2013. The influence of context boundaries on memory for the sequential order of events. J. Exp. Psychol. Gen. 142 (4), 1277–1286. https://doi.org/10.1037/a0034024.

DuBrow, S., Davachi, L., 2014. Temporal memory is shaped by encoding stability and intervening item reactivation. J. Neurosci. 34 (42), 13998–14005. https://doi.org/10.1523/JNEUROSCI.2535-14.2014.

Eichenbaum, H., 2017a. On the integration of space, time, and memory. Neuron 95 (5), 1007–1018. https://doi.org/10.1016/j.neuron.2017.06.036.

Eichenbaum, H., 2017b. Time (and space) in the hippocampus. Curr. Opin. Behav. Sci. 17, 65–70. https://doi.org/10.1016/j.cobeha.2017.06.010.

Erdem, U.M., Hasselmo, M., 2012. A goal-directed spatial navigation model using forward trajectory planning based on grid cells. Eur. J. Neurosci. 35 (6), 916–931. https://doi.org/10.1111/j.1460-9568.2012.08015.x.

Ezzyat, Y., Davachi, L., 2011. What constitutes an episode in episodic memory? Psychol. Sci. 22 (2), 243–252. https://doi.org/10.1177/0956797610393742.

Foster, D.J., Knierim, J.J., 2012. Sequence learning and the role of the hippocampus in rodent navigation. Curr. Opin. Neurobiol. 22 (2), 294–300. https://doi.org/10.1016/j.conb.2011.12.005.

Fox, J., Weisberg, S., 2011. An {R} Companion to Applied Regression, second ed. Sage http://socserv.socsci.mcmaster.ca/jfox/Books/Companion.

Gupta, A.S., van der Meer, M.A.A., Touretzky, D.S., Redish, A.D., 2012. Segmentation of spatial experience by hippocampal theta sequences. Nat. Neurosci. 15 (7), 1032–1039. https://doi.org/10.1038/nn.3138.

Hassabis, D., Maguire, E.A., 2009. The construction system of the brain. Phil. Trans. Biol. Sci. 364 (1521), 1263–1271. https://doi.org/10.1098/rstb.2008.0296.

Heusser, A.C., Ezzyat, Y., Shiff, I., Davachi, L., 2018a. Perceptual boundaries cause mnemonic trade-offs between local boundary processing and across-trial associative binding. J. Exp. Psychol. Learn. Mem. Cognit. 44 (7), 1075–1090.

Heusser, A.C., Fitzpatrick, P.C., Manning, J.R., 2018b. How is experience transformed into memory? *BioRxiv*. https://doi.org/10.1101/409987.

Horner, A.J., Bisby, J.A., Bush, D., Lin, W.-J., Burgess, N., 2015. Evidence for holistic episodic recollection via hippocampal pattern completion. Nat. Commun. 6 (1) https://doi.org/10.1038/ncomms8462.

Horner, A.J., Bisby, J.A., Wang, A., Bogus, K., Burgess, N., 2016. The role of spatial boundaries in shaping long-term event representations. Cognition 154, 151–164. https://doi.org/10.1016/j.cognition.2016.05.013.

Horner, A.J., Burgess, N., 2014. Pattern completion in multielement event engrams. Curr. Biol. 24 (9), 988–992. https://doi.org/10.1016/j.cub.2014.03.012.

Howard, L.R., Javadi, A.H., Yu, Y., Mill, R.D., Morrison, L.C., Knight, R., Loftus, M.M., Staskute, L., Spiers, H.J., 2014. The Hippocampus and entorhinal cortex encode the path and euclidean distances to goals during navigation. Curr. Biol. 24 (12), 1331–1340. https://doi.org/10.1016/j.cub.2014.05.001.

Janzen, G., van Turennout, M., 2004. Selective neural representation of objects relevant for navigation. Nat. Neurosci. 7 (6), 673–677. https://doi.org/10.1038/nn1257.

Janzen, G., Wagensveld, B., van Turennout, M., 2006. Neural representation of navigational relevance is rapidly induced and long lasting. Cerebr. Cortex 17 (4), 975–981. https://doi.org/10.1093/cercor/bhl008.

Javadi, A.-H., Emo, B., Howard, L.R., Zisch, F.E., Yu, Y., Knight, R., Pinelo Silva, J., Spiers, H.J., 2017. Hippocampal and prefrontal processing of network topology to simulate the future. Nat. Commun. 8, 14652. https://doi.org/10.1038/ncomms14652.

Johnson, A., Redish, A.D., 2007. Neural ensembles in CA3 transiently encode paths forward of the animal at a decision point. J. Neurosci. 27 (45), 12176–12189. https://doi.org/10.1523/JNEUROSCI.3761-07.2007.

Khosla, A., Raju, A.S., Torralba, A., Oliva, A., 2015. Understanding and predicting image memorability at a large scale. Int. Conf. Comput. Vis. (ICCV). https://doi.org/10.1109/ICCV.2015.275.

Lee, S.W., O'Doherty, J.P., Shimojo, S., 2015. Neural computations mediating one-shot learning in the human brain. PLoS Biol. 13 (4), e1002137 https://doi.org/10.1371/journal.pbio.1002137.

Lositsky, O., Chen, J., Toker, D., Honey, C.J., Shvartsman, M., Poppenk, J.L., Hasson, U., Norman, K.A., 2016. Neural pattern change during encoding of a narrative predicts retrospective duration estimates. Elife 5, e16070.

Murray, E.A., Wise, S.P., Graham, K.S., 2018. Representational specializations of the hippocampus in phylogenetic perspective. Neurosci. Lett. 680, 4–12. https://doi.org/10.1016/j.neulet.2017.04.065.

Nazareth, A., Huang, X., Voyer, D., Newcombe, N., 2019. A meta-analysis of sex differences in human navigation skills. Psychon. Bull. Rev. 1–26.

Ólafsdóttir, H.F., Barry, C., Saleem, A.B., Hassabis, D., Spiers, H.J., 2015. Hippocampal place cells construct reward related sequences through unexplored space. ELife 4. https://doi.org/10.7554/eLife.06063.

Patai, E.Z., Javadi, A.-H., Ozubko, J.D., O'Callaghan, A., Ji, S., Robin, J., Grady, C., Winocur, G., Rosenbaum, R.S., Moscovitch, M., 2019. Hippocampal and retrosplenial goal distance coding after long-term consolidation of a real-world environment. Cerebr. Cortex.

Pettijohn, K.A., Thompson, A.N., Tamplin, A.K., Krawietz, S.A., Radvansky, G.A., 2016. Event boundaries and memory improvement. Cognition 148, 136–144. https://doi.org/10.1016/j.cognition.2015.12.013.

R Core Team. (n.d.). R: a language and environment for statistical computing (Version 3.5.1) [Computer software]. R Foundation for Statistical Computing. https://www.R-project.org/.

Radvansky, G.A., Zacks, J.M., 2017. Event boundaries in memory and cognition. Curr. Opin. Behav. Sci. 17, 133–140. https://doi.org/10.1016/j.cobeha.2017.08.006.

Ranganath, C., Yonelinas, A.P., Cohen, M.X., Dy, C.J., Tom, S.M., D'Esposito, M., 2004. Dissociable correlates of recollection and familiarity within the medial temporal lobes. Neuropsychologia 42 (1), 2–13. https://doi.org/10.1016/j.neuropsychologia.2003.07.006.

Robin, J., Wynn, J., Moscovitch, M., 2016. The spatial scaffold: the effects of spatial context on memory for events. J. Exp. Psychol. Learn. Mem. Cognit. 42 (2), 308–315. https://doi.org/10.1037/xlm0000167.

Rouhani, N., Norman, K.A., Niv, Y., Bornstein, A.M., 2019. *Reward prediction errors create event boundaries in memory* [Preprint]. Neuroscience, 725440. https://doi.org/10.1101/725440 bioRxiv.

Schapiro, A.C., Rogers, T.T., Cordova, N.I., Turk-Browne, N.B., Botvinick, M.M., 2013. Neural representations of events arise from temporal community structure. Nat. Neurosci. 16 (4), 486–492. https://doi.org/10.1038/nn.3331.

Schapiro, A.C., Turk-Browne, N.B., Norman, K.A., Botvinick, M.M., 2016. Statistical learning of temporal community structure in the hippocampus. Hippocampus 26 (1), 3–8. https://doi.org/10.1002/hipo.22523.

Swallow, K.M., Barch, D.M., Head, D., Maley, C.J., Holder, D., Zacks, J.M., 2011. Changes in events alter how people remember recent information. J. Cognit. Neurosci. 23 (5), 1052–1064. https://doi.org/10.1162/jocn.2010.21524.

R2017a The Mathworks, Inc, 2017. The Mathworks, Inc [Computer software], version 9.2.

Tulving, E., 1983. Elements of Episodic Memory. Clarendon Press.

Tulving, E., 1985. Memory and consciousness. Canad. Psychol. Psychol. Canad. 26 (1), 1–11.

Tulving, E., 2002. Episodic memory: from mind to brain. Annu. Rev. Psychol. 53 (1), 1–25. https://doi.org/10.1146/annurev.psych.53.100901.135114.

Wood, E.R., Dudchenko, P.A., Robitsek, R.J., Eichenbaum, H., 2000. Hippocampal neurons encode information about different types of memory episodes occurring in the same location. Neuron 27 (3), 623–633. https://doi.org/10.1016/S0896-6273(00)00071-4.