Does a turn in the road mark a turn of events? Turns along travelled routes provide contextual boundaries during navigation

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Research Article

Abstract

Physical or conceptual boundaries segment continuous experience into component events. Boundaries accentuate differences between events that occur on either side of them, and reduce differences among events within them. Here we show that turns during navigation have the same effect on memory for routes as they do for episodes. Across three experiments, turns selectively enhanced participants' recollection of locations immediately preceding them. In addition, in Experiments 1 and 2, the presence of an intervening turn enhanced participants' ability to discriminate between event durations across boundaries, but impaired their ability to discriminate between their ordinal positions. In Experiment 3, the reported increase in recollection of pre-turn locations was also reflected in subjective dilation of the time spent at pre-turn, relative to post-turn, locations. Together, these results highlight the fundamental role of turns in the segmentation of spatial and temporal memory and indicate a potential mechanism for the segmentation of experience generally.

Introduction

Our lives entail a continuous stream of experience, yet we can retrieve memories as individual events by relying on changes in spatial and temporal contexts to segregate them. Similarly, we can plan a route from one location to another by splitting it into segments, relying on spatial boundaries. The segmentation of events in the temporal flow of experience may therefore share key mechanisms with the segmentation of physical space. In the present studies, we aimed to test whether turns along navigated routes promote spatial segmentation, akin to contextual shifts in event segmentation.

Spatial features, such as the number of turns and route complexity, affect spatial and temporal memory and produce memory biases (Bonasia, Blommestein, & Moscovitch, 2016; Brunec, Javadi, Zisch, & Spiers, 2017). In navigation, the prominence of spatial structure as an organizing principle is also reflected in neural representations in the hippocampus (Howard et al., 2014) and parahippocampus (Janzen & van Turenout, 2004). Similarly, rodent neurophysiology findings suggest that turns elicit forward 'sweeps' in hippocampal firing (Johnson & Redish, 2007) and segment spatial representations (Bos et al., 2017; Gupta, Van Der Meer, Touretzky, & Redish, 2012).

While neural evidence highlights the important role of turns in navigation, their role in structuring long-term representations in episodic memory is unclear. Here, we seek to address this gap. Prior evidence suggests that humans rely on perceptual and conceptual shifts in contexts to integrate information from the past and use it to guide future decisions (Kurby & Zacks, 2008; Pettijohn & Radvansky, 2015). Contextual shifts also affect episodic memory (Davachi & DuBrow, 2015), such that both temporal order (DuBrow & Davachi, 2013, 2014) and associative memory (Ezzyat & Davachi, 2011) are impaired when stimuli belong to different contexts.

In the spatial domain, temporal order memory for objects presented in different virtual rooms was impaired relative to those experienced within the same room (Horner, Bisby, Wang, Bogus,

& Burgess, 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 judgements. However, when information on either side of a boundary represents a cohesive unit, boundaries actually improve memory by providing structure (Pettijohn, Thompson, Tamplin, Krawietz, & Radvansky, 2016), which might be supported by a peak in hippocampal activity between events (Baldassano et al., 2017; Ben-Yakov & Dudai, 2011). Boundaries therefore differentially affect different memory aspects.

Here, we aim to bridge the literatures on event segmentation and spatial navigation by exploring the effect of turns on memory for information acquired along a spatial trajectory. 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, Rogers, Cordova, Turk-Browne, & Botvinick, 2013). We provide the first behavioural evidence in humans to suggest that turns act as boundaries between spatial contexts during navigation, akin to boundaries between events.

Experiment 1

If turns serve as boundaries, their impact on memory for routes should be similar to that of contextual boundaries on events, with separable effects on different aspects of episodic memory. A critical comparison made here was that between memory for *temporal order* of locations (*ordinal discrimination*) and *event duration* associated with particular locations (*duration discrimination*) (Howard & Eichenbaum, 2013) (Fig. 1). If turns temporarily perturb temporal context drift (Horner et al., 2016), they should impair ordinal memory for events across boundaries, which requires the ability to compare relative event positions within a temporal sequence (DuBrow & Davachi, 2013). In contrast, the perturbation in contextual drift caused by a boundary should accentuate details specific to an event, such as event duration. Durations of individual events should therefore be more discriminable from one another when the events are separated by a boundary (Pettijohn et al., 2016).

Finally, we predicted that spatial locations preceding turns would be more likely to be recollected based on evidence suggesting that items preceding boundaries are better remembered than non-boundary items (Swallow, Zacks, & Abrams, 2009; Zacks, Speer, Vettel, & Jacoby, 2006). We also manipulated the degree of active engagement in the task as an attentional control during both navigation (active vs. passive navigation) and waiting periods (active vs. passive wait).

Figure 1. A) Sample views from the route at one of the intersections (top) and during navigation (bottom). Participants were informed that the car would stop at several intersections along the way as if waiting at a red traffic light which would be indicated by horizontal bright red bars on the top and bottom of the screen. B) The two route configurations used in the three experiments presented here. The circles depict the intersections where participants waited. In Experiments 1 and 2, intersections were paired depending on whether they were separated by a turn (1 turn) or not (0 turns). In Experiment 3, we compared pre- vs. post-turn locations where wait times were equal. C) The three memory tasks and the experiments in which they were used.

Methods

Participants

Ninety-five participants (69 female) were recruited from University of Toronto introductory first-year psychology course classes or from the student community and participated in the experiment for course credit or payment. We conducted a power analysis assuming a medium effect size ($f = .3$). This assumption was based on the effect size obtained by Horner et al. in a similar task (2016; approximately $f = .5$ across three experiments), but the estimate was made more conservative due to the addition of the duration discrimination task. Our power analysis indicated that $N = 68$ would be sufficient to achieve 90% power in a within-between factorial design with no assumed correlation between measures, making our sample size adequate (calculation performed using G*Power v 3.1.9.2; Faul, Erdfelder, Lang, & Buchner, 2007). None of the participants in any of the experiments reported neurological or psychological 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 randomly allocated to one of four conditions: Active navigation/Active wait ($N = 24$), Active navigation/Passive wait ($N = 23$), Passive navigation/Active wait ($N = 24$), and Passive navigation/Passive wait ($N = 23$; conditions described below). Two female participants were excluded from the Active navigation/Active wait condition due to extremely low hit rates on the recognition memory task ($< 20\%$ correct), suggesting that the task was not completed accurately. Both participants were excluded before group-level statistical analyses were conducted. An additional female participant was excluded from the Passive navigation/Active wait condition due to a data writing error. These exclusions resulted in a total of 92 participants (66 female; mean age 19.6 years, $SD = 2.49$ years).

Experimental Design and Procedure

A route in a virtualized city unfamiliar to our participants (downtown Chicago) was created using images from Google Street View (Fig. 1A). Panoramic images were extracted and a three-dimensional route was reconstructed. The program was run in MATLAB, using PsychToolBox (Brainard, 1997), to allow a first-person perspective view of the environment as the car navigated through city streets. The route was 4.04 km long. Participants waited at 12 intersections on the route; four were followed by right turns, four by left turns, and four by no turns (straightaways; Fig. 1B). At each stop, the wait duration lasted between 1 – 12 seconds, with a 1-second interval. Participants repeated the route 7 times before their memory was tested. The order of the wait durations was randomized across participants, but remained the same across all seven repetitions of a route for each participant.

Participants were instructed that their task would be to learn a novel route in downtown Chicago by traversing it several times. They were informed that the car would stop at several intersections along the way as if waiting at a red traffic light which would be indicated by horizontal bright red bars on the top and bottom of the screen. In the *active navigation* conditions, participants had active control over the direction that the car travelled, and used the arrow keys as controls to turn left or right, or to continue straight ahead. Despite having control over navigation, participants were prevented from navigating away from the predetermined

route. Participants in the active navigation conditions were told that during the first trial, navigation would be passive, and during all subsequent times, navigation would be active. Those in the *passive navigation* conditions had no control over navigation; instead, they passively watched as the car navigated on its own. In the *active wait* conditions, participants were asked to actively press the "brake pedal" (space bar), when the red bars appeared at intersections (Fig. 1A). Participants were told that they should hold down the brake pedal for the entire wait, until the red bars disappeared. Participants in the *passive wait* conditions were not instructed to press any keys at intersections. The red bars during the wait periods were presented, but no green bars were shown during navigation.

Participants were told that their main task was to remember as much as possible about the route, the environment, and their experience in general. To promote incidental learning, we did not direct the participants' attention to the order or duration of intersections. All participants were asked to indicate in which direction navigation should proceed on every route repetition, after waiting at two randomly chosen intersections. This procedure was implemented to ensure that participants in all conditions were paying attention to the route.

After traversing the route seven times to ensure learning of duration information, participants completed a series of tasks (Fig. 1C). The first was a recognition memory task in which participants saw images of the 12 intersections that had been on the route randomly intermixed with 12 images of intersections from downtown Chicago that had not been on their route. Participants were instructed to respond, for each image, whether they could explicitly recall waiting at the intersection ('Re-experience'), whether they simply knew they waited there, without any associated contextual information ('Know'), or whether they believed it was a new intersection that was not on the route they had learned ('New'). The 're-experience' responses served as a measure of subjective recollection and therefore memory richness (Fig. 1C) (Tulving, 1985; Yonelinas, 2002). Participants used the R, K, and N keys, respectively, to make their responses.

Participants then completed two discrimination tasks (Fig. 1C). Their order was counterbalanced across participants. In the duration discrimination task, they were shown all possible pairs of images of intersections where they had waited one at a time in a randomized order. They were asked to indicate at which intersection they had waited longer, using the arrow keys. In the ordinal discrimination task, participants again saw all pairs of intersections in a newly randomized order, and were now asked to indicate which intersection was closer to the end of the route.

Results

Recognition memory. We first analyzed participants' ability to recognize pre-turn intersections, relative to mid-segment intersections (Fig. 1B). There was no significant difference in the proportion of pre-turn vs. mid-segment intersections correctly recognized as old ($\chi^2(1) = 1.18$, $p = .277$, Cramer's $V = .032$). On average, 96.5% (SD = 6.5%) of pre-turn intersections were correctly identified as old, and 95.2% (SD = 12.3%) of mid-segment intersections were correctly identified as old. The corrected recognition score (d') across all trials was 2.51 (SD = .74).

Where false alarm rates were 0 and hit rates were 1, we applied a standard correction procedure and replaced rates of 0 with $0.5/n$ and rates of 1 with $(n-0.5)/n$ (where n is the number of lures and old trials, respectively; Stanislaw & Todorov, 1999). False alarm data were not recorded for two participants.

To further explore participants' subjective memory richness for accurately recognized intersections, we examined their recollection rates for pre-turn vs. mid-segment intersections. Within items correctly recognized as old, we found significantly greater rates of recollection for intersections followed by turns, relative to those not followed by turns ($\chi^2(1) = 9.43$, $p = .002$, Cramer's $V = .093$). Therefore, the presence of a turn seems to boost recollection for information encountered immediately before a turn, even though the proportion of correctly recognized locations was overall equivalent (Fig. 2A).

Duration and ordinal discrimination. We next focused on how the presence of a turn differentially affected participants' ability to discriminate between the ordinal positions and wait durations of neighbouring intersections. We carried out an omnibus 2 (intervening turn: 0 turns vs. 1 turn) $\times$ 2 (task: ordinal vs. duration discrimination) $\times$ 2 (wait: passive vs. active wait) $\times$ 2 (navigation: passive vs. active navigation) ANOVA, where the discrimination task and presence of a turn were within-subjects factors, and wait and navigation (passive vs. active) were between-subjects factors.

We found a significant interaction between the presence of an intervening turn (0 turns or 1 turn; Fig. 2B) and task (duration or ordinal discrimination) ($F(1, 88) = 16.54$, $p < .001$, $\eta_p^2 = .158$; Fig. 2B). For adjacent intersections separated by a turn, duration discrimination was improved, whereas ordinal discrimination was impaired. This interaction had a large effect size (Cohen, 1988), suggesting that turns exert powerful, yet separable, influences on memory for event order and duration. Based on this significant interaction, we ran paired samples t-tests for duration and ordinal discrimination separately. We found that an intervening turn significantly improved duration discrimination ($t(91) = 3.29$, $p = .001$, $d = .350$; corrected for dependence between means). We also observed a marginal impairment in ordinal discrimination when the two intersections were separated by a turn ($t(91) = 1.92$, $p = .059$, $d = .202$). As there was no significant main effect of active vs. passive navigation ($F(1, 88) = .091$, $p = .763$, $\eta_p^2 = .001$) or waiting ($F(1, 88) = .830$, $p = .365$, $\eta_p^2 = .009$) and no significant interactions, we collapsed the data for participants across all four conditions in Fig. 2. The breakdown by condition can be found in Supplementary Materials (Figs. S1 and S2). There was no significant main effect of intervening turn ($F(1, 88) = 1.03$, $p = .312$, $\eta_p^2 = .012$), no significant intervening turn by navigation interaction ($F(1, 88) = 3.32$, $p = .072$, $\eta_p^2 = .036$) and no significant intervening turn by wait interaction ($F(1, 88) = .295$, $p = .588$, $\eta_p^2 = .003$), as well as no significant three-way interaction between turn, wait, and navigation ($F(1, 88) = .712$, $p = .401$, $\eta_p^2 = .008$).

We also found a main effect of task, with significantly better performance in the ordinal discrimination task, relative to the duration discrimination task ($F(1, 88) = 52.03$, $p < .001$, $\eta_p^2 = .372$). There was no significant task by navigation interaction ($F(1, 88) = .164$, $p = .687$, $\eta_p^2 = .002$) and no significant task by wait interaction ($F(1, 88) = .148$, $p = .702$, $\eta_p^2 = .002$), as well as no significant three-way interaction ($F(1, 88) = .681$, $p = .412$, $\eta_p^2 = .008$). There was no

significant three-way interaction between turn, task, and navigation ($F(1, 88) = .845$, $p = .361$, $\eta_p^2 = .010$) or turn, task, and wait ($F(1, 88) = 1.28$, $p = .261$, $\eta_p^2 = .014$), as well as no significant four-way interaction between turn, task, wait, and navigation ($F(1, 88) = .079$, $p = .779$, $\eta_p^2 = .001$).

Figure 2. A) Intersections followed by turns were significantly more likely to be reported as recollected, relative to those not followed by turns. B) Participants were significantly more accurate at discriminating between the durations of two intersections separated by a turn, relative to two intersections not separated by a turn. † $p = .059$, * $p < .05$, ** $p < .01$, *** $p < .001$. Error bars reflect 95% confidence intervals (CIs).

Experiment 1 Discussion

Experiment 1 provides evidence of enhanced memory for locations immediately preceding turns, and opposing effects of turns on duration and ordinal discrimination. Memory for temporal duration specific to each event benefited from the presence of a boundary, likely due to increased discriminability of event-specific information (Pettijohn et al., 2016; Zacks, Tversky, & Iyer, 2001). In contrast, when comparing two ordinal positions, the presence of a boundary numerically disrupted discrimination (DuBrow & Davachi, 2013; Horner et al., 2016).

While the effect on duration discrimination was significant and robust, the effect on ordinal discrimination only approached significance and showed a small effect size. One possibility is that after seven route repetitions, the order of intersections was well learned, making effects of turns less prominent. We addressed this in Experiment 2, in which participants traversed the route only once before completing the same memory tasks (Fig. 1C).

Experiment 2

Experiment 2 was largely identical to Experiment 1, except that participants completed a single traversal of the same route, after which they were tested on identical tasks as above. We aimed to determine whether a single route traversal is sufficient to produce increased recollection for pre-turn locations and to test whether the effect of intervening turns on ordinal discrimination in Experiment 1 might have been attenuated due to overlearning. Due to the difference in difficulty on the ordinal and duration discrimination tasks, we did not expect participants' performance to be above chance on the duration discrimination task following a single route traversal.

Methods

Participants

Based on the observed effect size for the task by turn presence interaction in Experiment 1 ($\eta_p^2 = .158$, $f = .433$), an a priori power analysis indicated that $N = 20$ would be sufficient to achieve 90% power in a within participants design (power calculation performed using G*Power v 3.1.9.2; Faul, Erdfelder, Lang, & Buchner, 2007). We recruited 20 participants from the University of Toronto student community (14 F, mean age = 22.0 years, SD = 1.73 years). No participant was excluded from this experiment.

Experimental Design and Procedure

The methods in Experiment 2 were largely identical to Experiment 1, with two key differences. First, participants only traversed the route once, enabling us to investigate whether the trend in poorer ordinal discrimination between locations separated by a boundary which was observed in Experiment 1, where multiple trials may have dampened the effect, would be more clearly evident after a single route traversal. Second, given that we found no significant differences between active and passive navigation and wait conditions in Experiment 1, all participants both navigated and waited passively, as this setup enabled us to most closely control the timing. All other aspects of the task protocol were identical.

Results

Recognition memory. There was no significant difference in the proportion of pre-turn vs. mid-segment intersections correctly recognized as old ($\chi^2(1) = .147$, $p = .701$, Cramer's $V = .025$). On average, 85.6% (SD = 14.8%) of pre-turn intersections were correctly identified as old, and 83.8% (SD = 16.8%) of mid-segment intersections were correctly recognized as old. The d' score across all trials was 1.23 (SD = .75).

Within items correctly recognized as old, we found significantly greater rates of recollection for intersections followed by turns, relative to those not followed by turns ($\chi^2(1) = 13.78$, $p < .001$, Cramer's $V = .260$) (Fig. 3A). Therefore, the presence of a turn boosted recollection for information encountered immediately before a turn, replicating the result from Experiment 1.

Figure 3. A) Intersections followed by turns were significantly more likely to be reported as recollected, relative to those not followed by turns. B) Participants were significantly more accurate at discriminating between the ordinal positions of two intersections along the same road segment, relative to two intersections separated by a turn. * $p < .05$, ** $p < .01$, *** $p < .001$. Error bars reflect 95% CIs.

Duration and ordinal discrimination. We conducted a 2 (task: ordinal vs. duration discrimination) x 2 (intervening turn: 0 turns vs. 1 turn) repeated measures ANOVA. We found a significant interaction between the presence of an intervening turn and task ($F(1, 19) = 4.64, p = .044, \eta_p^2 = .20$; Fig. 3B). This effect size was moderate-to-large and comparable across Experiments 1 and 2, indicating that turns produced effects of a similar magnitude across two experiments. We found no main effect of task, despite numerical performance being greater in the ordinal discrimination task, relative to the duration discrimination task ($F(1, 19) = 1.61, p = .219, \eta_p^2 = 0.08$). There was no significant main effect of intervening turn ($F(1, 19) = .975, p = .336, \eta_p^2 = 0.05$).

Based on this significant interaction, we ran paired samples t-tests for duration and ordinal discrimination separately. After a single route traversal, there was no effect of turns on duration discrimination ($t(19) = .916, p = .371, d = .205$). However, duration discrimination performance was not significantly above chance for comparisons separated by a turn ($t(19) = .684, p = .502, d = 0.15$), nor those not separated by a turn ($t(19) = .444, p = .662, d = 0.10$), with 95% confidence intervals crossing chance levels in both cases, making this comparison impossible to interpret. Importantly, however, we found that an intervening turn significantly impaired ordinal discrimination ($t(19) = 2.51, p = .021, d = .581$).

Experiment 2 Discussion

After a single route traversal, ordinal discrimination was significantly worse for adjacent intersections separated by a turn, relative to intersections not separated by a turn. Even after a single learning experience, turns act as spatial boundaries between events and locations, akin to doorways or abstract contextual boundaries (DuBrow & Davachi, 2013; Horner et al., 2016). As in Experiment 1, pre-turn intersections were more likely to be subjectively recollected. Memory for pre-boundary locations is enhanced rapidly, as this boost in subjective recollection was present after a single route traversal.

Because Experiments 1 and 2 compared pre-turn locations only to mid-segment locations, we cannot rule out the possibility that turns increase recollection for locations immediately preceding *and* following them. If pre-turn locations continue to have greater recollection rates than post-turn locations positioned equally far from the turn, it would provide evidence that turns retroactively enhance the representation of experiences immediately preceding them. Further, if increased recollection rates for pre-turn, relative to post-turn, locations represent subjectively richer memory, this boost should be reflected in a cognitive bias, such that pre-turn durations would be subjectively dilated. In Experiment 3, we directly compared locations immediately preceding turns with those immediately following them.

Experiment 3

In Experiment 3, participants navigated along the same route, but waited at an equal number of locations immediately before a turn, immediately after a turn, and in the middle of a road segment (Fig. 1B). Second, all wait durations were made equal. We tested participants on the same 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, to

determine whether any biases that were observed in the first test would persist after route repetition.

In addition to collecting participants' self-reported recollection ratings for each location, we also tested whether increased recollection rates for pre-turn locations were reflected in 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.

Methods

Participants

To match the sample size to Experiment 2, twenty-one participants (mean age = 21.1 years, SD = 3.27; 19 F) took part in this experiment. One female participant was excluded due to an error in data saving, resulting in the same sample size as Experiment 2.

Experimental Design and Procedure

The same overall route as in Experiments 1 and 2 was used in this experiment. The number of stops was increased from 12 to 36, and the stops were placed at different locations along the route, this time in groups of three (A, B, C). The criteria for this placement were as follows: stop A always occurred immediately before a turn (teal circle in Fig. 1B); stop B always occurred immediately after a turn (blue circle in Fig. 1B), and stop C occurred somewhere along the following segment, provided it was not immediately preceding or following a turn (yellow circle in Fig. 1B). In this experiment, participants waited for the same amount of time (4 seconds) at each stop. Navigation and wait were passive for all participants.

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 locations along the route to help them learn where they would have to stop their bus to pick up passengers. These "bus stop" locations 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. At every bus stop, participants were stopped for four seconds.

After a single route traversal, participants completed a recognition memory task and a duration discrimination task. In the recognition memory task, participants saw a total of 36 old intersections and 36 new intersections and had to indicate whether they could re-experience waiting at each, only knew 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 two 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. Participants saw 8 different pairs of intersections. As we wanted to conduct a pure test of temporal perception biases, participants did not complete an ordinal discrimination task in this experiment.

Upon completing these two tasks following a single route traversal, participants were told that they would need to become an 'expert' 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 same test as before, this manipulation was used to ensure that participants would refrain from narrowing their focus to only the aspects of the route that had been previously tested. We did this with the aim of making the second test, in as much as possible, a reflection of how added experience with the route affected duration discrimination, and to discourage participants from using strategies, such as counting, to learn the wait times. Participants completed the same two tasks, with identical instructions, but a newly randomized order in which the images were shown.

Results

Recognition memory. We first examined the proportion of correctly vs. incorrectly identified old locations. After a single route traversal, we found a significant effect of location (pre-turn, post-turn, mid-segment) ($\chi^2(2) = 12.74$, $p = .002$, Cramer's $V = .163$; Fig. 4A). Significantly more intersections were correctly recognized as old when they preceded turns than both when they followed turns ($\chi^2(1) = 12.25$, $p < .001$, Cramer's $V = .196$) or when they were in the middle of a road segment ($\chi^2(1) = 7.17$, $p = .007$, Cramer's $V = .150$). There was no difference in error rates between the post-turn and mid-segment locations ($\chi^2(1) = .717$, $p = .397$, Cramer's $V = .047$). On average, 83.8% (SD = 16.3%) of pre-turn locations were correctly recognized as old, 66.9% (SD = 33.1%) of post-turn locations were correctly recognized as old, and 70.7% (SD = 29.3%) of mid-segment locations were correctly recognized as old. After a single route traversal, the d' score across all trials was 1.27 (SD = .56).

After three additional route repetitions, the main effect of location remained significant ($\chi^2(2) = 6.23$, $p = .044$, Cramer's $V = .114$; Fig. 4A). Significantly more intersections were correctly recognized as old when they preceded turns than when they followed turns ($\chi^2(1) = 6.03$, $p = .014$, Cramer's $V = .137$), but not when they were in the middle of a road segment ($\chi^2(1) = 1.40$, $p = .237$, Cramer's $V = .066$). There was no difference in error rates between the post-turn and mid-segment locations ($\chi^2(1) = 1.75$, $p = .186$, Cramer's $V = .074$). On average, 95.6% (SD = 7.3%) of pre-turn locations were correctly recognized as old, 88.1% (SD = 11.9%) of post-turn locations were correctly recognized as old, and 92.5% (SD = 8.5%) of mid-segment locations were correctly recognized as old. After three additional route traversals, the d' score across all trials was 1.90 (SD = .87).

We next examined the proportion of subjectively recollected locations within the correctly identified images. After traveling the route once, there was a significant main effect of location on self-reported recollection rates ($\chi^2(2) = 7.18$, $p = .028$, Cramer's $V = .142$; Fig. 4B). Pre-turn locations were more likely to be recollected than both post-turn ($\chi^2(1) = 5.87$, $p = .015$, Cramer's $V = .156$) and mid-segment locations ($\chi^2(1) = 4.94$, $p = .026$, Cramer's $V = .141$). There was no difference in recollection rates between post-turn and mid-segment locations ($\chi^2(1) = .051$, $p = .821$, Cramer's $V = .015$).

After three more exposures to the route, there was no main effect of location ($\chi^2(2) = 3.36$, $p = .186$, Cramer's $V = .087$; Fig. 4B). However, the pre-turn locations were still marginally more likely to be recollected than post-turn locations ($\chi^2(1) = 3.31$, $p = .069$, Cramer's $V = .106$), but not mid-segment locations ($\chi^2(1) = 1.74$, $p = .187$, Cramer's $V = .076$). The difference between post-turn and mid-segment locations remained non-significant ($\chi^2(1) = .266$, $p = .606$, Cramer's $V = .030$).

A **B** **C**

Pre-turn duration discrimination bias

Figure 4. A) Intersections followed by turns were significantly more likely to be correctly identified as old than both post-turn and mid-segment intersections, after a single route traversal. After 4 traversals, pre-turn intersections were more accurately recognized as old relative to post-turn, but not mid-segment, intersections. B) Intersections followed by turns were significantly more likely to be recollected than both post-turn and mid-segment intersections, after a single route traversal. The effect was not significant after four route traversals. C) When discriminating between durations of intersections, participants showed a bias towards perceiving pre-turn intersections as longer than post-turn intersections, despite the durations being objectively equal. † $p = .069$, * $p < .05$, ** $p < .01$, * $p < .001$. Error bars reflect 95% CIs.**

These data together suggest that, not only were locations preceding turns more often correctly recognized as old, but also that memories for these locations had a stronger recollective subjective quality. While the accuracy of recognition memory persisted even after repeated exposure to the route, recollection rates were no longer significantly different, though the trend remained the same.

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.

Here, 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 ($t(19) = 5.23$, $p < .001$, $d = 1.17$; Fig. 4C), which persisted even after 4 route traversals ($t(19) = 2.46$, $p = .024$, $d = .550$). A paired samples t-test indicated that there was a reduction in this bias from the 1st to the 4th traversal, which was trending towards significance ($t(19) = 1.93$, $p = .069$, $d = .432$). However, even after four route repetitions, confidence intervals did not cross 0.5, suggesting participants were still reliably biased to report pre-turn wait durations as lasting longer. Taken together, these results suggest that participants had stronger mental representations of pre-turn intersections than of post-turn intersections.

Experiment 3 Discussion

In Experiment 3, participants' responses reflected richer memory for pre-turn intersections. After a single traversal, the subjective recollective quality of pre-turn locations was greater than that of post-turn or mid-segment locations, thus replicating and extending the effect reported in Experiments 1 and 2. This effect was also reflected in participants' recognition memory accuracy, as pre-turn locations were more likely to be identified as old, compared to post-turn and mid-segment locations. Last, participants showed a significant bias when making duration

discriminations, such that they pre-turn wait durations were subjectively expanded relative to post-turn wait durations.

General Discussion

Across three experiments, we show that turns along a route contribute to how memories of events along its trajectory are formed. Across all experiments, participants showed enhanced memory for intersections immediately preceding turns. Turns between events also led to poorer ordinal discrimination of those events, but improved their duration discrimination, suggesting that contextual boundaries disrupt binding between events and enhance memory within events, respectively. Finally, we demonstrated that turns inflated the perceived time spent waiting at pre-turn, relative to post-turn locations.

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 & Dudai, 2011; Ben-Yakov, Eshel, & Dudai, 2013). This retroactive signal might therefore result in an enrichment of pre-boundary, relative to post-boundary information. Further, the finding that ordinal discrimination was impaired by the presence of a boundary, while duration discrimination was improved, corresponds with computational modelling evidence suggesting that the rate of temporal context drift is increased immediately following boundaries (Horner et al., 2016). The two explanations are compatible, as the retroactive hippocampal peak at the boundary may disrupt post-boundary temporal context drift. This disruption would impair the ordinal discrimination of events along a route. In contrast, duration discrimination would be enhanced because this perturbation in contextual drift accentuates details specific to events on either side of the boundary, increasing their discriminability (Pettijohn et al., 2016).

Turns represent points of particular 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, resulting in a prediction error that enables memory updating (Radvansky & Zacks, 2017). Decision points play a critical role in navigational planning and are reflected in hippocampal activity sequences (Erdem & Hasselmo, 2012; Foster & Knierim, 2012; Ólafsdóttir, Barry, Saleem, Hassabis, & Spiers, 2015; Wood, Dudchenko, Robitsek, & Eichenbaum, 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 & van Turenout, 2004; Janzen et al., 2007). We propose that the mechanism underlying the detection of navigationally relevant spatial locations is similar to the one used to detect contextual boundaries between events with no navigational component, such as narratives. 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.

The experiments presented here provide the first evidence that turns separate segments of space traversed during navigation, like contextual boundaries separating individual events in

time. As memory representations are commonly grounded in spatial context (Hassabis & Maguire, 2009; Robin, Wynn, & Moscovitch, 2015), the hippocampal boundary-detection mechanism may have initially evolved to enable efficient spatial segmentation (Murray, Wise, & Graham, 2016) and incrementally expanded to support the separation of events in both contextual, and physical, space.

Author Contributions

I.K.B., M.M., & M.D.B. developed the study hypotheses and concept. All authors contributed to the study design. I.K.B., J.D.O., and T.A. designed the experimental paradigms. I.K.B. and T.A. collected the data. I.K.B. performed the data analysis and interpretation under the supervision of M.M. and M.D.B. I.K.B. and T.A. drafted the manuscript, with revisions by J.D.O., M.M., and M.D.B. All authors approved the final version of the manuscript for submission.

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