

RAPID COMMUNICATION

Memory and Navigation: Compression of Space Varies with Route Length and Turns

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ABSTRACT: For memory to be efficient and useful during recall, problem-solving, and planning, retrieval must be compressed in time. Evidence from rodents suggests that neural compression during replay of spatial memories varies widely, with a range of compression ratios reported from 6:1 to 64:1. Anecdotal evidence suggests that similar compression occurs during mental navigation in humans: we recall how to get from one place to another countless times almost every day of our lives, and this recall never takes as long as physically travelling those routes would take. In this experiment we sought to determine whether this behavioural compression could be measured during mental navigation in humans (spatial memory replay), and which factors might affect the compression of such spatial memories. To this end, thirty participants mentally navigated routes between two landmarks, which varied in length and number of turns, as we measured replay times and recorded ratings of familiarity, detail, and presence. A multi-level model was used to determine which factors were associated with variation in compression. Route length and number of turns emerged from this model as significantly correlated with compression, such that longer routes were more compressed while compression was attenuated as the number of turns in a route increased. This suggests that compression during recall may be affected by specific features of a route, especially those that may act to segment the space or event being represented. © 2015 Wiley Periodicals, Inc.

KEY WORDS: spatial memory; compression; navigation; mental simulation; segmentation

INTRODUCTION

In rodents, the compressed replay of hippocampal (HC) firing patterns has been investigated extensively and is thought to underlie consolidation and recall of spatial memories (O'Neill et al., 2010; Hartley et al., 2014). Since the HC is also thought to support memory and spatial cognition (Scoville and Milner, 1957; O'Keefe and Nadel, 1978;

Ekstrom et al., 2003), our goal was to demonstrate behavioural compression during replay of spatial memories in people, and to investigate potential influencing factors. In this study we asked participants to navigate mentally between two points along well-known routes while we recorded how long it took to them to do so. To anticipate our results, we found that compression of routes in memory was strongly correlated with route length, such that longer routes were more compressed, and was negatively correlated with the number of turns in a route.

In neuronal replay, the sequence of HC neurons that fired during an event fire in the same or reversed sequence during subsequent wake or sleep (Lee and Wilson, 2002; Foster and Wilson, 2006). Preplay has also been documented, where cell ensembles fire in sequence before learning, in anticipation of a run, or before turns and decision points (Diba and Buzsáki, 2007; Johnson and Redish, 2007). Such neuronal replay and preplay are considered a possible substrate of not only physical navigation, but also of episodic and spatial recall and planning (Buzsáki and Moser, 2013). Notably, in these cases of replay and preplay, HC neuronal sequences fire more rapidly than they do during the original event (Skaggs et al., 1996; see also Hebb, 1949). Recently, HC neural reinstatement was also reported in epilepsy patients; place cell activity that was recorded during virtual navigation was reinstated during subsequent recall of spatial memories, independent of active navigation (Miller et al., 2015).

A 'compression factor' indicates how much more rapidly a sequence is enacted during replay than during the initial event of interest. In rodents, compression factors such as 10:1 (Skaggs et al., 1996) and a range of 6:1 to 64:1 (median of 20:1; Lee and Wilson, 2002) have been reported. These results suggest that, at least in rodents, the neural sequences representing different spatial information may be compressed to varying degrees. However, up to this point there has been a lack of systematic investigation into how human spatial memories may be compressed.

To investigate the compression of spatial memories in humans, we focused on a behavioural compression factor. In particular, we hoped to determine the nature of compression during mental navigation, how

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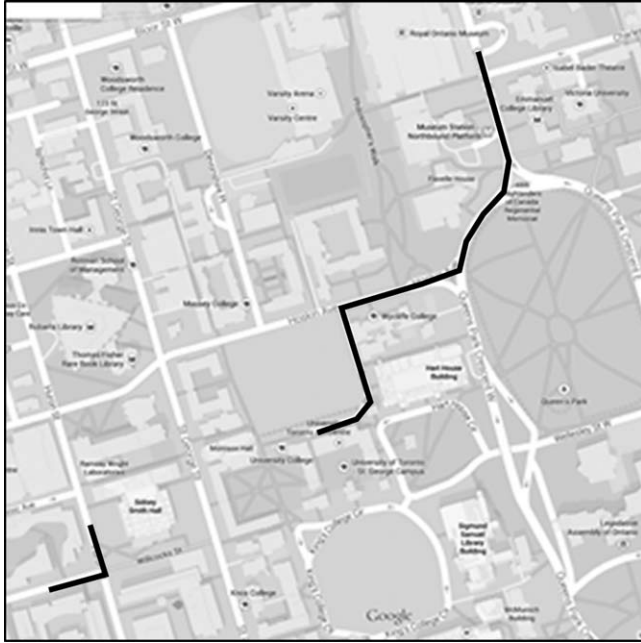


FIGURE 1. One of the shortest and one of the longest routes used in this study, depicted on a map of the University of Toronto campus.

compression might vary, and which factors might influence this variation. The factors we chose to assess were route length, number of turns, familiarity, detail, and presence, which is defined as a sense of re-experiencing actual navigation. Since we asked participants to complete each route in the way that was most natural to them and did not instruct them to attend to particular aspects of the imagined experience, we predicted that compression would be related to route length and number of turns, but weakly-related, if at all, to the other factors.

Thirty-three undergraduate students (18 female, mean age = 19.1 SD = 2.3) participated, all of whom had lived on the University of Toronto campus for at least one semester.

The data of three participants were dropped since they took many unusual detours, determined through verbal report after the experiment, leaving a final sample of thirty participants. Participants were asked to imagine traveling twelve familiar routes between well-known campus landmarks, established in an earlier pilot study. The routes were 140m to 1000m in length, contained between zero and four turns, and did not overlap, see Figure 1. As participants were presented with a route, they indicated whether or not they were familiar with that particular route. If so, they were then instructed to close their eyes and mentally navigate between the two landmarks, indicating with a button press when they began and finished the route. After each trial, participants rated, on a scale of 1 – 10, their familiarity with the route, the level of detail they recalled during navigation, and their “presence”. Unfamiliar routes were skipped. Compression of routes was calculated by dividing the time it would take to walk each route (length divided by average walking pace, 1.39 m/s) over the time taken to navigate each route mentally. At the end of each trial, participants were asked to report verbally how they navigated the route. This study was approved by the University of Toronto Research Ethics Board and all participants gave written informed consent.

Compression was modelled as a function of route length, number of turns, detail, familiarity, and presence. Prior to analysis, all independent variables were centered. With respect to the compression of routes, scores were log-transformed in order to account for non-normality in the raw data distribution. A 2-level multilevel model was used to account for routes being nested within participants, and a random intercept was estimated for each participant to account for baseline differences in compression between participants. An unstructured covariance matrix was used, along with the between-within method of estimating degrees of freedom.

Participants were familiar with (and thus navigated) a mean of 8.0 (SD = 3.0) routes out of twelve. Mean ratings for these

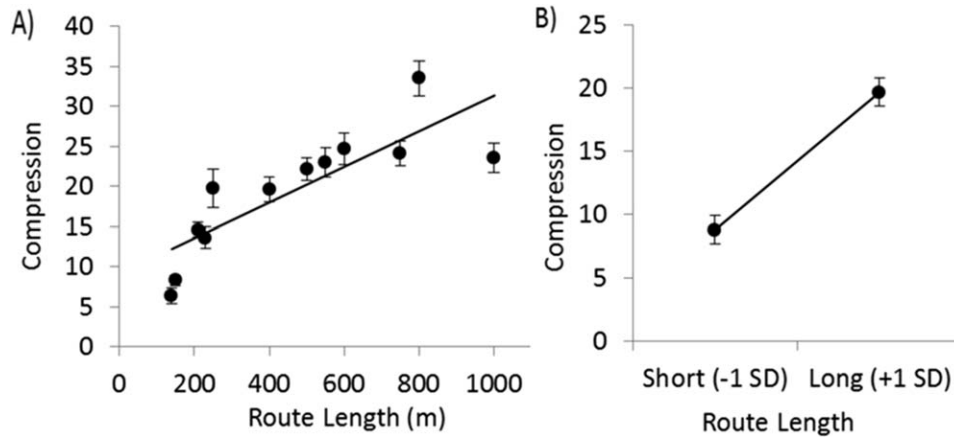


FIGURE 2. The interaction between route length and compression. A) Route length versus mean compression. B) Mean compression for short and long routes, after controlling for all other variables. ‘Short’ is defined as one standard deviation below the mean route length (210.4 m) and ‘Long’ is defined as one standard deviation above the mean route length (729.6 m). Error bars represent standard error of the mean.

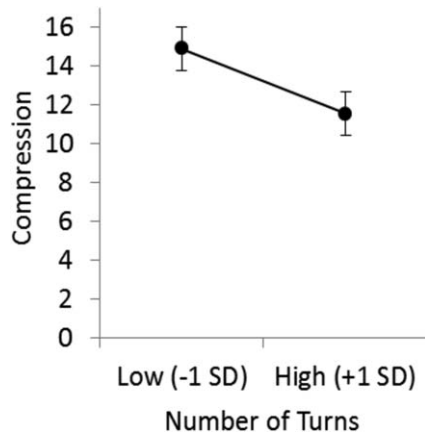


FIGURE 3. The interaction between number of turns and compression, after controlling for all other variables. ‘Low’ is defined as one standard deviation below the mean (0 turns) and ‘High’ is defined as one standard deviation above the mean (3 turns). Error bars represent standard error of the mean.

routes were 8.5 for familiarity ($SD = 1.8$), 7.4 for detail ($SD = 1.9$), and 7.2 for presence ($SD = 2.1$); each with a range of 1–10. All participants demonstrated consistently compressed replay. The lowest compression factor recorded was 1.1, while the highest compression factor recorded was 100.8, with a mean range within participants of 32.8 ($SD = 23.6$).

There was a significant main effect of route length on compression ($t(205) = 10.06$, $P < 0.001$; see Figs. 2A,B). There was also a significant main effect of number of turns on compression ($t(205) = -2.70$, $P = 0.007$; see Fig. 3). No other predictors were associated with a significant effect on compression (for detail $t(205) = 1.44$, $P = 0.15$; for familiarity $t(205) = -0.69$, $P = 0.49$; for presence $t(205) = -1.23$, $P = 0.22$). Figures 2B and 3 show the interaction between each significant predictor and compression when controlling for the effects of all other variables, as is done in the multi-level model. High and low values reflect one standard deviation above and below the mean of each predictor. This method was chosen since the relationship between each predictor and compression is not necessarily apparent in the raw data. For example, since number of turns is correlated with route length, when raw compression scores are plotted against turns the slope is flat, while after controlling for route length, number of turns is negatively correlated with compression, as seen in Figure 3.

As predicted, detail and presence both demonstrated negligible effects on compression. One might expect to find larger effects of detail or presence if participants were asked to focus on specific details along the route, or to put particular effort into vividly re-experiencing some routes, but not others. We did not investigate these possibilities since we were interested in how participants navigate when recalling routes in the way that is most natural to them. With respect to familiarity, since all participants had lived on campus where the routes were located, the variation in familiarity was too small to yield good correlations. One might find larger effects of familiarity on compression during mental navigation if very familiar routes

were compared with fairly unfamiliar routes. Critically, even after controlling for all of these subjective factors, route length and number of turns still had significant, independent, effects on compression: when a route is longer it is more compressed, while turns attenuate compression.

The correlation between route length and compression is consistent with evidence from estimations of distance in humans and from single cell studies in rodents. Behaviourally, human spatial estimation has been found to vary with distance; when participants are asked to estimate how long it would take to travel various distances by starting and stopping a stopwatch while looking at a person between 20 and 120 feet away, underestimation increases with increasing distance (Plumert et al., 2005). With respect to neural compression in the rodent literature, Dragoi and Buzsaki (2006) found that the ratio of real distances to neuronal representations of distances increased as the distance between place fields increased. This demonstrates a similar increase in compression with increasing distance. Though we cannot be sure that similar mechanisms mediate compression during mental navigation in humans, they provide a plausible neural account of our findings and encourage further investigation.

It is unlikely that the correlation between route length and compression is due to participants spending a relatively fixed time on each trial, since the time taken to mentally navigate increased consistently as route length increased (correlation between route length and raw mental navigation times: $r = 0.23$, $p < .001$). Furthermore, navigation times varied widely with a mean range of 45.2 seconds within participants.

The negative correlation between number of turns in a route and compression is also consistent with previous literature. More than 30 years ago, Thorndyke (1981) demonstrated that human estimations of distance increase linearly with the number of intervening points along a route on a map. Since turns are natural intervening points by which a route might be parsed, this evidence fits with our demonstration of attenuated compression when routes have more turns in them. We hypothesize that this effect is due to the segmentation of space into shorter, less compressed chunks. As discussed above, shorter routes are less compressed than longer routes. A neural basis for this proposal is suggested by Gupta et al. (2012), who demonstrated such segmentation of spatial paths in the firing patterns of rodent HC neurons. They found that replay represents discrete chunks while a rat travels between two landmarks, then jumps to the next chunk once each landmark is passed. Assuming there is a limit to compression in memory, this segmentation of routes may be critical. In this way, routes could be broken up into smaller segments based on turns, landmarks, or other salient details once the limit is reached.

The relevance of turns is also emphasized in rodent research demonstrating that, when rats reach a choice point in a familiar maze, HC firing sweeps ahead in the direction of the reward location (Johnson and Redish, 2007). Similarly, Ozubko et al. (under review) found greater HC activation at decision points in humans during a virtual navigation task.

Segmentation at boundaries seems to be critical in non-spatial domains as well. For instance, neural activity is time-locked to salient event boundaries when participants watch film clips of everyday events (Ben-Yakov et al., 2014; Zacks et al., 2001). Memory is also enhanced for information from within an event, over information from across event boundaries or context shifts (DuBrow and Davachi, 2013; Ezzyat and Davachi, 2011). More recently, Faber and Gennari (2015) demonstrated, using short events involving geometric shapes, that both duration judgements and mental replay times increased when clips contained more sub-events. Together, these data, along with our demonstration that turns in a route attenuate compression, suggest that salient ‘boundaries’ modulate memory, both at encoding and retrieval.

We suggest that compression supports more than just efficient recall during navigation. Compressed replay may also support the consolidation and re-combination of different ‘chunks’ of information, encouraging the establishment of higher order associations and the organization of information in memory. Studying spatial memory and mental navigation allows us to investigate compression in a systematic way, since we have a clear objective measure of how long it takes to physically walk a route and can manipulate different characteristics of the route. However, such compression also seems to be present in episodic memory, and may be similarly affected by features of an event such as the number of salient sub-events. Furthermore, whereas the correspondence between human and rodent episodic memory is unclear, navigation seems similar in both species. Thus, studying spatial compression in humans allows us to draw clear, and testable, links between rodent models of cognition and the human neuropsychological processes they are meant to model.

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