Rapid improvement of cognitive maps in the awake state

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Acknowledgments

Abstract

Post-navigation awake quiescence, relative to task engagement, benefits the accuracy of a new 'cognitive map'. This effect is hypothesised to reflect awake quiescence, like sleep, being conducive to the consolidation and integration of new spatial memories. Sleep has been shown to improve cognitive map accuracy *over time*. It remained unknown whether awake quiescence can induce similar *time-related improvements* in new cognitive maps, or whether it simply counteracts their decay. We examined this question via two experiments. In Experiment 1, using an established cognitive mapping paradigm, we reveal that map accuracy for a virtual town was significantly better in people whose memory was probed after 10mins of post-navigation awake quiescence *or* ongoing cognitive engagement, relative to those whose memory was probed shortly after initial navigation. In Experiment 2, using a newly-developed cognitive mapping task that involved a more complex and real-life virtual town, we again found that map accuracy was superior in those whose memory was probed after 10mins of awake quiescence than those who were tested soon after navigation. These findings indicate that actual improvements in human memories are not restricted to sleep. Thus, contrary to conventional wisdom and theories, the passage of (day)time need not always result in forgetting.

Keywords

Spatial navigation, Spatial memory, Memory consolidation

The ability to navigate flexibly depends on the formation of accurate cognitive maps – flexible mental representations of the spatial relationships between objects in the world that can be accessed from any perspective and vantage point. These observer-independent mental representations are formed via the integration of new memories pertaining to a novel spatial experience (for review see: Wolbers and Wiener, 2014; Morton et al., 2017). In our recent human behavioural work we revealed that, when probed at a delayed stage, a cognitive map of a navigated virtual environment is more accurate if participants experience awake quiescence for several minutes after being trained on a novel route than if they engage in an unrelated perceptual task in the minutes after route training (Craig et al., 2016a; b). We hypothesised that this effect was because awake quiescence is conducive to the consolidation and integration of new spatial memories into an accurate cognitive map, possibly by supporting neural reactivation (see below) (Craig et al., 2016a).

Neural reactivation of novel experiences has been demonstrated in rodents and humans (e.g. Peigneux et al., 2004; Karlsson and Frank, 2009; Carr et al., 2011; Staresina et al., 2013). In rodents, place and grid cells in the hippocampus and entorhinal cortex, which were first activated during initial navigation, are automatically reactivated in the minutes that follow the navigation experience, especially when these minutes comprise sleep or awake quiescence (Buzsáki, 1989; Wilson and McNaughton, 1994; Hasselmo, 1999; Karlsson and Frank, 2009; Gupta et al., 2010; Carr et al., 2011; Mednick et al., 2011; Ólafsdóttir et al., 2016). This neural reactivation, which is well suited to induce synaptic plasticity (Buzsáki, 1986, 1989), has been shown to be critical for the consolidation and integration of new spatial memories (e.g. Buzsáki, 1989; Gupta et al., 2010), and cognitive map formation (Gupta et al., 2010). The role of neural reactivation in spatial memory is further evidenced by (i) a positive correlation between the degree of reactivation and subsequent spatial memory performance in humans and rodents (Peigneux et al., 2004; Karlsson and Frank, 2009; Carr et al., 2011; Jadhav et al., 2012; Deuker et al., 2013), and (ii) poor subsequent spatial memory performance in rodents following electrophysiological disruption of neural reactivation (Ego-Stengel and Wilson, 2010; Jadhav et al., 2012). Moreover, given that neural reactivation can involve the generation of novel, never directly travelled, trajectories (Gupta et al., 2010), it is likely to aid the active development of cognitive maps *over time*.

In keeping with this prediction, research in humans shows that cognitive map accuracy improves over time during an extended period of sleep, relative to an equivalent period of wakefulness filled with engaging cognitive tasks (Ferrara et al., 2008; Coutanche et al., 2013; Nguyen et al., 2013). This effect is believed to reflect the consolidation and integration of spatial memories into a new cognitive map during post-navigation sleep, resulting in time-related improvement in map precision/completeness.

Importantly, it remained unknown whether the recently reported benefit of post-navigation awake quiescence (Craig et al., 2016a; b) reflects (i) consolidation-related *improvement* in cognitive map accuracy over time, as is the case with post-navigation sleep, or (ii) *reduced decay* of a new cognitive map over time. Research in humans suggests that awake quiescence benefits *verbal memories* by reducing their decay (Dewar et al., 2012, 2014; Craig et al., 2014) rather than by inducing improvements, and this is assumed to be the case for sleep and awake quiescence effects in declarative memory overall (Mednick et al., 2011). To the best of our knowledge, no research, in humans or rodents, has investigated whether awake quiescence improves cognitive map accuracy over time. If, like sleep, awake quiescence induces actual consolidation-related improvements in the precision of a cognitive map, then map accuracy should be *superior* following a period of post-navigation quiescence than shortly after navigation. If, on the other hand, awake quiescence reduces/counteracts the decay of a cognitive map over time, then map accuracy should be *poorer* following the 10-minute delay than shortly after navigation, but less so after quiescence than an engaging task.

We conducted two experiments to examine whether post-navigation awake quiescence improves cognitive map accuracy over time or reduces their decay. In Experiment 1, we used an established cognitive mapping paradigm (Craig et al., 2016a; b) to probe participants' memory (i) shortly after

navigating a virtual town or (ii) after a 10-minute delay of awake quiescence or task engagement. Experiment 2 was conducted to establish whether the key finding of Experiment 1 could be replicated when using a newly developed cognitive mapping paradigm (see later).

Sixty healthy young adults (mean age = 20.83 years, SD = 2.41; 33F:27M) were recruited as participants in Experiment 1. All participants were trained to criterion on a route through a virtual town environment before experiencing one of three delay conditions: (i) no delay (participants moved directly to the subsequent testing phase) (N=20), (ii) 10 minutes of an engaging perceptual task (a spot-the-difference game) (N=20), or (iii) 10 minutes of awake quiescence (quiet resting) (N=20). They then performed a cognitive map test (for detailed Methods see: Craig et al., 2016a), which required participants to point in the direction of various landmarks from different locations encountered on the trained route. Superior pointing accuracy (i.e. a smaller angle of error) in this test should reflect a more accurate cognitive map of the environment. Post-study, all participants completed the Santa Barbara Sense of Direction (SBSOD) questionnaire, a reliable self-reported measure of spatial ability (Hegarty et al., 2002), as well as a detailed questionnaire which probed whether participants actively thought about and/or rehearsed the learned route during quiescence, and their experience using computer and virtual reality games/equipment (Moffat et al., 2001). Figure 1 provides an overview of the experimental procedure. Ethical approval was granted by The University of Edinburgh and Heriot-Watt University, where this research was conducted. The participant data for the 10-minute quiescence and 10-minute task groups came from our recently published work (Craig et al., 2016a). Given that we previously reported a significant difference in pointing error scores between these two conditions (Craig et al., 2016a), where those who experienced awake quiescence demonstrated better pointing accuracy than those who experienced task condition, the key comparisons in the current study were: (i) no delay vs. 10min awake quiescence, and (ii) no delay vs. 10min task. This allowed us to examine whether (a) cognitive map accuracy improves over time during awake quiescence, and (b) such improvement is specific to awake quiescence or observed also during task engagement (albeit to a lesser extent).
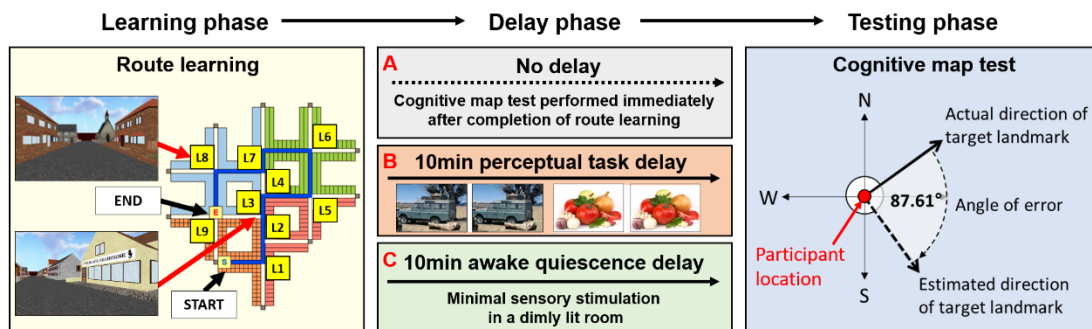

Figure 1. Experiment 1 procedure: Participants (i) learned a route (see blue line) through a virtual town containing nine distinctive landmarks (L1 = Gas station, L2 = Bank, L3 = Convenience store, L4 = Restaurant, L5 = Hotel, L6 = Pet store, L7 = Pub, L8 = Church, L9 = Hardware store), and (ii) underwent one of three delay conditions (**A**: no delay (N=20), **B**: 10 minutes of an engaging spot-the-difference game (N=20), **C**: 10 minutes of awake quiescence (N=20)), before (iii) performing a cognitive map test (Craig et al., 2016a). In this 16-trial test, participants were presented a landmark from the environment on screen and asked to rotate to point towards a second (target) landmark. We calculated, for each trial, the absolute deviation (in degrees) between the actual direction of the target landmark and the participant's estimated direction, where superior pointing accuracy (i.e. small angle of error) should reflect a more accurate cognitive map. Participant and group means were computed subsequently.

Table 1. Experiment 1: Background information, mean number of learning cycles required to learn the route, and mean time to respond (seconds) in the cognitive map test as a function of delay condition group. Standard deviations are shown in parentheses.

Delay group	Gender	Age	Years in education	Computer experience	SBSOD questionnaire	Learning cycles	Cognitive map time to respond (s)
No delay (N=20)	8M:12F	21.70 (3.15)	15.85 (1.46)	12.20 (3.02)	3.81 (1.05)	2.00 (0.00)	15.72 (6.27)
10min quiescence (N=20)	9M:11F	20.20 (1.85)	16.05 (1.76)	10.80 (2.82)	3.54 (0.71)	2.05 (0.22)	16.94 (4.17)
10min task (N=20)	10M:10F	20.75 (1.86)	16.30 (1.66)	11.60 (3.08)	3.45 (0.86)	2.00 (0.00)	15.48 (3.66)

Groups were matched in participants' background, including gender ratio, age, years in education, self-reported computer experience, self-reported spatial ability (SBSOD), and number of learning cycles required to learn the route (see Table 1; no delay vs. 10min quiescence: all p > .075; no delay vs. 10min task: all p > .231). Groups were also matched in the time that it took participants to respond in the cognitive map test (no delay vs. 10min quiescence: $F_{,38}$ = 14.778, P = .475; $\eta\rho^2$ = .014; no delay vs. 10min task: $F_{1,38}$ = 0.027, P = .871; $\eta\rho^2$ = .001).

We did, however, find group differences in the *accuracy* of participants' cognitive map test responses. Critically, comparison of mean pointing error scores revealed a significant difference between the no delay and 10min quiescence groups ($F_{1,38}$ = 17.974, P < .001; $\eta\rho^2$ = .321, Figure 2a) *and* the no delay and 10min task groups ($F_{1,38}$ = 4.810, P = .034; $\eta\rho^2$ = .112, Figure 2b). In both cases the significant difference was because those who experienced a 10-minute delay (of awake quiescence or cognitive engagement) between learning and testing demonstrated significantly superior pointing accuracy than those who performed the cognitive map test shortly after route learning (no delay group).
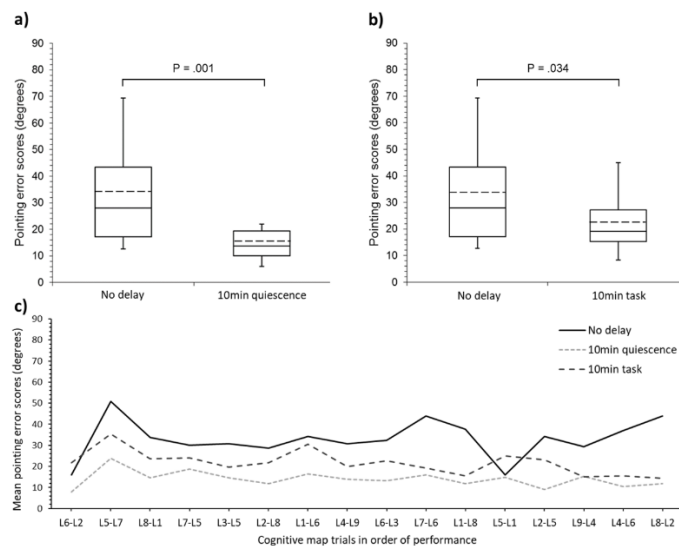

Figure 2. Experiment 1 results: Box-whisker plot showing pointing error scores (degrees) in the cognitive map test when performed after **(a)** no delay and 10 minutes of awake quiescence (both N=20), and **(b)** no delay and 10 minutes of a perceptual task (both N=20). The solid centre line in each box shows the median pointing error score for that group. The upper and lower boundaries of boxes represent the interquartile ranges. Box whiskers show the upper and lower quartiles of pointing error scores. The dashed centre line in each box shows the mean pointing error score for that group. **(c)** Trial-by-trial distribution of mean pointing error scores for the no delay (solid line), 10min task (dashed line), and 10min quiescence (dotted line) groups. The presented and target landmarks are noted for each trial, e.g. Trial 1 = L6-L2, which corresponds to the presentation of landmark 2 (Bank) and landmark 6 (Pet store) being the target landmark.

Figure 2c shows trial-by-trial pointing error scores in the cognitive map test as a function of group. The data indicate that the group differences between the no delay and 10min quiescence groups, and no delay and task groups, were due to a general superiority in the overall precision/completeness of participants' cognitive maps in the 10min quiescence and 10min task groups, opposed to (e.g.) better associations of a specific subset of landmarks to their correct locations. Given that pointing was relatively accurate overall (all mean angles of error were less than 51 degrees in the three groups), the data further suggest that (i) participants did not find any specific trials especially demanding, and (ii) guessing was not a major factor as participants had at least a broad idea of target landmark locations.

As in related work (Dewar et al., 2014; Craig et al., 2015, 2016a; b), the accuracy benefit of awake quiescence, relative to no delay, could not be explained by mnemonic strategies (e.g. active rehearsal of the trained route) during the 10-minute quiescence delay because the effect remained when excluding participants (N = 6/20, 30.00%) from this group who reported such strategies ($F_{1,33}$ = 13.770, P = .001; $\eta\rho^2$ = .294). It is also unlikely that participants performed poorer in the no delay group due to a fatigue associated with recent route learning as: (i) participants did not find this task especially demanding (as evidenced by the low number of learning cycles required to learn the route), (ii) it was not excessive in duration (typically 10-15mins), and (iii) if cognitive fatigue was responsible for poorer performance in the no delay group, pointing accuracy should have been *further reduced* following 10 minutes of additional cognitive engagement (task group), which was not the case.

Importantly, as noted earlier, some of the reported data (10min quiescence group and 10min task group) came from an already published study (Craig et al., 2016a) and the new data for the no delay group were collected at a different time point and location. Despite groups being matched in participants' background, it is possible that these factors influenced our findings. Moreover, the virtual town environment used in Experiment 1 was relatively basic, and therefore it remained unknown whether the effects observed would replicate in more real life-like, complex environments. To this end, Experiment 2 was conducted to examine whether the time-dependent improvement of post-navigation awake quiescence in cognitive map accuracy was replicable in a new set of participants and within a more complex real life-like environment.

Experiment 2 used the same general procedure as Experiment 1 (see Figure 1), thus, only key methodological details and changes are noted below. Fifty new healthy young adults (mean age = 21.98 years, SD = 2.79; 13F:35M) were trained to criterion on a route through a new, more complex, virtual town environment (see Figure 3a). Training comprised learning cycles. In the first learning cycle, participants completed two learning trials, where the participant travelled the route as a 'passenger' in a car, and one probe trial, where memory for the direction turned at each junction was probed. If participants made one or more errors in this first probe trial, they completed an undefined number of further learning cycles, each of which involved one learning trial and one probe trial, until zero errors were made in a probe trial. Participants then experienced one of two delay conditions: (i) no delay (participants moved directly to the subsequent testing phase) (N=25) or (ii) 10 minutes of awake quiescence (quiet resting) (N=25), which they were randomly assigned to pre-experimentally. They then performed a cognitive map pointing test, where they were required to point from each landmark experienced along the trained route (N = 5) to all other landmarks (total trials = 20). Trials were presented in a random order, and the same random order was used across all participants. Finally, participants completed the Santa Barbara Sense of Direction (SBSOD) questionnaire and a detailed questionnaire (see Experiment 1).

Unlike Experiment 1, which used a relatively basic virtual town environment and a route that comprised equidistant junctions (decision points), linear tracks and 90 degree turns, the environment used in Experiment 2 comprised a more real life-like, rich and detailed virtual town and a more complex route that included sweeping turns and varied distances between junctions (see Figure 3). All experimental procedures for Experiment 2 were cleared by the ethics committee of Heriot-Watt University, UK, where this research was conducted. Data from two participants were lost due to one

individual performing more than two standard deviations above (i.e. poorer) than the group mean (no delay group) and a second individual not abiding by task instructions (10min quiescence group). Therefore, Table 2 reports data from a sample of N = 24 per group (total N = 48) and the analyses reported in the subsequent section were conducted on this sample.

Table 2. Experiment 2: Background information, mean number of learning cycles required to learn the route, and mean time to respond (seconds) in the cognitive map test as a function of delay condition group. Standard deviations are shown in parentheses.

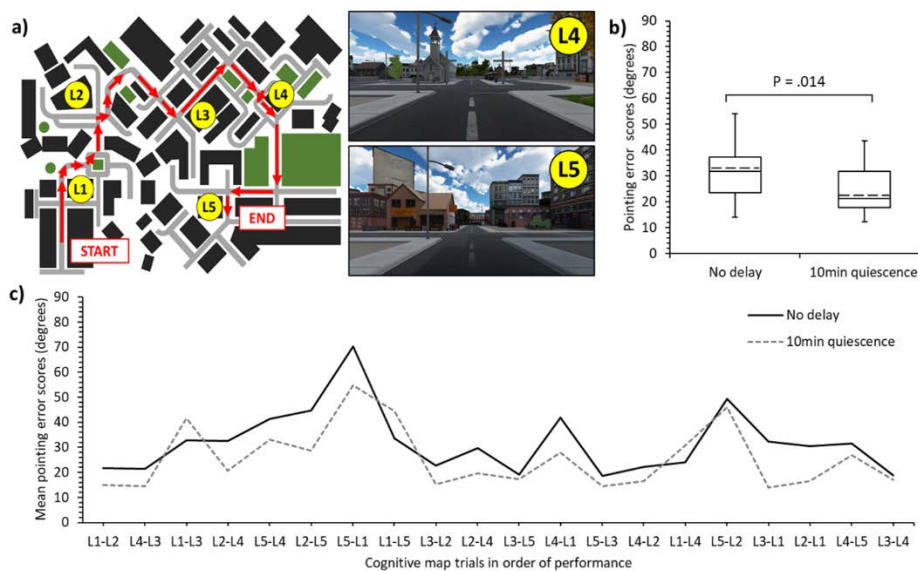| Delay group	Gender	Age	Years in education	Computer experience	SBSOD questionnaire	Learning cycles	Cognitive map time to respond (s)
No delay (N=24)	17M:7F	22.54 (2.62)	16.33 (2.18)	13.83 (4.65)	4.08 (1.35)	1.75 (0.79)	17.93 (9.70)
10min quiescence (N=24)	18M:6F	21.42 (2.90)	16.25 (2.55)	13.59 (3.86)	3.73 (1.13)	1.50 (0.59)	19.04 (8.43)

Figure 3. Experiment 2: (a) Bird's eye map of the virtual town and two screenshots from the learned route, showing landmark 4 (Church) and landmark 5 (Restaurant). The learned route is shown via the red arrows between the 'START' and 'END' labels. Yellow circles show the locations of salient landmark buildings (L1 = Hotel, L2 = Convenience store, L3 = Gas station, L4 = Church, L5 = Restaurant) that were used in the pointing task. Black shapes represent other, generic town-like buildings (e.g. apartment blocks) and green shapes represent areas of green space (i.e. grass and trees) **(b)** Box-whisker plot showing pointing error scores (degrees) in the cognitive map test when performed after no delay and after 10 minutes of awake quiescence (both N=24). The solid centre line in each box shows the median pointing error score for that group. The upper and lower boundaries of boxes represent the interquartile ranges. Box whiskers show the upper and lower quartiles of pointing error scores. The dashed centre line in each box shows the mean pointing error score for that group. **(c)** Trial-by-trial distribution of mean pointing error scores for the no delay (solid line) and 10min quiescence (dotted line) groups. The presented and target landmarks are noted for each trial, e.g. Trial 1 = L1-L2, which corresponds to the presentation of landmark 1 (Hotel) and landmark 2 (Convenience store) being the target landmark.

Groups were matched in participants' background, including gender ratio, age, years in education, self-reported computer experience, self-reported spatial ability (SBSOD), and number of learning cycles required to learn the route (see Table 2; all p > .164). Groups were also matched in the time to respond in the cognitive map test (see Table 2; $F_{1,46}$ = 0.179, p = .674, $\eta\rho^2$ = .004). However, as in Experiment 1, we found a significant between-group difference in the *accuracy* of cognitive map test responses ($F_{1,46}$ = 6.494, P = .014, $\eta\rho^2$ = .124). Those who experienced a 10-minute delay of awake quiescence between learning and testing demonstrated significantly more accurate pointing than those who experienced no delay between learning and testing (Figure 3b). As in Experiment 1, the data indicate that better performance in the 10min quiescence group over the no delay group was due to a general superiority in the overall precision/completeness of participants' cognitive maps (figure 3c). This accuracy benefit of awake quiescence could not be explained by mnemonic strategies during the 10-minute awake quiescence delay because the effect remained when excluding participants (N = 7/24, 29.17%) from this group who reported such strategies ($F_{1,39}$ = 5.015, P = .031; $\eta\rho^2$ = .114).

Bayesian analyses reinforced the findings of Experiment 2. Specifically, a Bayesian one-sample t-test provided little/no (BF10 = less than 3) evidence (Jeffreys, 1961) for the alternative hypothesis that there was a between-group difference in the number of learning cycles required to learn the route (BF10 = 0.535). Indeed, there was more evidence in favour of the null hypothesis that there was no between-group difference in the number of required learning cycles (BF01 = 1.868), though we acknowledge that this evidence was not strong. In addition, a one-sample t-test provided some (BF10 = more than 3) evidence (Jeffreys, 1961) for the alternative hypothesis that there was a difference in pointing error scores between groups (BF10 = 3.705, BF01 = 0.270).

Furthermore, when removing those in the 10min quiescence group who reported rehearsal (N=7), as above, there was more evidence in favour of the null than alternative hypothesis for possible differences in the number of learning cycles (BF01 = 2.893, BF10 = 0.335), suggesting that groups were matched in route learning. There was also more evidence in favour of a between-group difference in pointing error scores (BF10 = 2.131) than for the null (BF01 = 0.469), though we acknowledge that this evidence, from a smaller N, is not as strong as when those who rehearsed were included. These findings reinforce that groups were well matched during route learning and that between-group differences were observed during testing.

Taken together, our data suggest that cognitive map accuracy *rapidly improves over time* (within minutes) in the awake state, and this appears to be especially true during post-navigation quiescence. In Experiment 1, participants who completed a cognitive map test for a recently-navigated virtual town after experiencing either (i) 10 minutes of awake quiescence or (ii) 10 minutes of ongoing cognitive engagement demonstrated significantly better pointing accuracy, relative to those who performed the cognitive map test shortly after navigating the virtual town. The difference following quiescence was more pronounced than that following ongoing cognitive engagement. In Experiment 2, we replicated the benefit of a post-navigation delay comprising awake quiescence in a different participant sample, using a more complex, real life-like virtual town. It is noteworthy that the benefit of awake quiescence, relative to no delay, was found in two different tasks of varying complexity and ecological validity, in studies conducted in different populations of young adults at different universities, and by different experimenters. Our findings cannot be explained by differences in participants' background or mnemonic strategies (e.g. active rehearsal) and are unlikely to be due to differences in cognitive fatigue. However, they can be explained via a consolidation account. We propose that map accuracy was superior in those who experienced a delay between learning and testing because of the consolidation and integration of new spatial memories over time, resulting in a *time-related improvement in the overall precision/completeness of a cognitive map for the navigated environment*.

Importantly, superior map accuracy after a wakeful delay, and especially awake quiescence, demonstrates that, at least in the case of new cognitive maps, awake quiescence does not merely reduce decay, and that actual improvements in (at least some types of) human memories are not

restricted to sleep. This resonates with (i) research in rodents demonstrating consolidation-related reactivation of place and grid cells in the hippocampus-entorhinal cortex during post-navigation awake quiescence and sleep (Karlsson and Frank, 2009; Carr et al., 2011; Ólafsdóttir et al., 2016), and (ii) research in humans demonstrating superior cognitive map accuracy following post-navigation sleep (Ferrara et al., 2008; Coutanche et al., 2013; Nguyen et al., 2013). It is possible that the benefit of time in the current study was because of neural reactivation in the wakeful minutes that immediately followed navigation. In addition, other research in rodents demonstrates the upregulation of genes that are strongly associated with very early neural plasticity, consolidation and the formation of cognitive maps, in the hippocampus and entorhinal cortex, shortly after navigation (Feldman et al., 2010; Barry and Commins, 2017). This further suggests that the immediate time that follows navigation is critical for the early cellular-level transformation of new memory representations and may at least partially account for our findings.

Interestingly, the findings of Experiment 1 indicate that consolidation-related improvements can occur during ongoing cognitive engagement because, relative to experiencing no delay, cognitive map accuracy was significantly better even when people performed a 10-minute spot-the-difference game after initial navigation. We propose that the consolidation and integration of new spatial memories can occur *during* ongoing task engagement, but might be less efficient than during awake quiescence, possibly due to additional demands on the memory system/hippocampal network. Indeed, the spot-the-difference game used in our task group is likely to have resulted in novel memory encoding, and recent findings demonstrate that the number of fixations made during the visual exploration of novel stimuli - as in the spot the difference game - positively predicts hippocampal activity (Liu et al., 2017). The hypothesised increased demand/co-current activity during task engagement may have a quantitative and/or qualitative impact on the coordinated reactivation of place and grid cells, resulting in a diminished improvement in cognitive map accuracy over time. Furthermore, increased demand on the memory system over a much longer period of time (~8 hours) may explain, to some degree, why previous studies, which have shown a sleep-related improvement in spatial memory, have failed to show an improvement in spatial memory over time when participants are wakefully engaged in ongoing tasks (Ferrara et al., 2008; Coutanche et al., 2013; Nguyen et al., 2013). Indeed, consolidation has been proposed to be an opportunistic process that occurs especially during periods of reduced sensory input and cognitive engagement (i.e. sleep and awake quiescence) (Wilson and McNaughton, 1994; Hasselmo, 1999; Wixted, 2004; Mednick et al., 2011). Our findings support this hypothesis and the view that consolidation benefits from states of reduced sensory processing more generally, rather than being restricted to sleep (Wilson and McNaughton, 1994; Hasselmo, 1999; Wixted, 2004; Mednick et al., 2011). We acknowledge that further work is required to establish the specific neural mechanisms underlying the rapid development of cognitive maps and the memory benefit of post-navigation awake quiescence.

Can the observed time-related improvement in memory be reconciled with decay and interference theories of forgetting? Our findings indicate that new declarative memories might not only be forgotten over time via decay and/or interference. Instead, they suggest that actual improvements in (at least some types of) new memories are possible, at least over the shorter term, i.e. in the wakeful minutes that immediately follow encoding. However, we acknowledge that the forgetting of a newly formed cognitive map is likely to occur over a longer period (e.g. days to weeks) filled with potentially interfering activities, though it is worth noting that recent work has shown no reliable decay of allocentric pointing scores over the course of one week in a similar cognitive mapping paradigm (Bennett and Giudice, 2017). Thus, we do not suggest that our findings are at odds with decay and interference theories of forgetting. In contrast, we suggest that they potentially offer new insights into the early processing of new memories in forming a cognitive map. Further work is needed to characterise the timeline of cognitive map development and forgetting in the minutes to weeks that follow initial encoding.

In summary, our results provide behavioural evidence of the rapid consolidation-related improvement

of cognitive map accuracy over time in the awake state. Furthermore, they suggest that contrary to conventional wisdom and theories, actual improvements in (at least some types of) memories are not restricted to sleep, and the passage of (day)time need not always result in forgetting, at least over the shorter term.

References

Barry DN, Commins S. 2017. Temporal dynamics of Immediate Early Gene expression during cellular consolidation of spatial memory. Behav Brain Res 327:44–53.

Bennett CR, Giudice NA. 2017. Evaluating age-related cognitive map decay using a novel time-delayed testing paradigm. In: Barkowsky T., Burte H., Hölscher C. SH, editor. Spatial Cognition X. Vol. 10523. Springer London.

Buzsáki G. 1986. Hippocampal sharp waves: Their origin and significance. Brain Res 398:242–252.

Buzsáki G. 1989. Two-stage model of memory trace formation: A role for "noisy" brain states. Neuroscience 31:551–570.

Carr MF, Jadhav SP, Frank LM. 2011. Hippocampal replay in the awake state: A potential substrate for memory consolidation and retrieval. Nat Neurosci 14:147–153.

Coutanche MN, Gianessi CA, Chanales AJH, Willison KW, Thompson-Schill SL. 2013. The role of sleep in forming a memory representation of a two-dimensional space. Hippocampus 23:1189–1197.

Craig M, Dewar M, Harris M, Della Sala S, Wolbers T. 2016a. Wakeful rest promotes the integration of spatial memories into accurate cognitive maps. Hippocampus 26:185–193.

Craig M, Dewar M, Della Sala S, Wolbers T. 2015. Rest boosts the long-term retention of spatial associative and temporal order information. Hippocampus 25:1017–1027.

Craig M, Della Sala S, Dewar M, Sala S Della, Dewar M. 2014. Autobiographical thinking interferes with episodic memory consolidation. PLoS One 9.

Craig M, Wolbers T, Harris MA, Hauff P, Della Sala S, Dewar M. 2016b. Comparable rest-related promotion of spatial memory consolidation in younger and older adults. Neurobiol Aging 48:143–152.

Deuker L, Olligs J, Fell J, Kranz TA, Mormann F, Montag C, Reuter M, Elger CE, Axmacher N. 2013. Memory Consolidation by Replay of Stimulus-Specific Neural Activity. J Neurosci 33:19373–19383.

Dewar M, Alber J, Butler C, Cowan N, Della Sala S. 2012. Brief Wakeful Resting Boosts New Memories Over the Long Term. Psychol Sci 23:955–960.

Dewar M, Alber J, Cowan N, Sala S Della. 2014. Boosting long-term memory via wakeful rest: Intentional rehearsal is not necessary, consolidation is sufficient. PLoS One 9.

Ego-Stengel V, Wilson MA. 2010. Disruption of ripple-associated hippocampal activity during rest impairs spatial learning in the rat. Hippocampus 20:1–10.

Feldman LA, Shapiro ML, Nalbantoglu J. 2010. A novel, rapidly acquired and persistent spatial memory task that induces immediate early gene expression. Behav Brain Funct 6:1–11.

Ferrara M, Iaria G, Tempesta D, Curcio G, Moroni F, Marzano C, De Gennaro L, Pacitti C. 2008. Sleep to find your way: The role of sleep in the consolidation of memory for navigation in humans. Hippocampus 18:844–851.

Gupta AS, van der Meer MAA, Touretzky DS, Redish AD. 2010. Hippocampal Replay Is Not a Simple Function of Experience. Neuron 65:695–705.

Hasselmo ME. 1999. Neuromodulation: acetylcholine and memory consolidation. 3:351–359.

Hegarty M, Richardson AE, Montello DR, Lovelace K, Subbiah I. 2002. Development of a self-report measure of environmental spatial ability. Intelligence 30:425–447.

Jadhav SP, Kemere C, German PW, Frank LM. 2012. Awake Hippocampal Sharp-Wave. Sci Mag 336:1454–1458.

Jeffreys H. 1961. Theory of probability. 3rd ed. Oxford: Oxford University Press, Clarendon Press.

Karlsson MP, Frank LM. 2009. Awake replay of remote experiences in the hippocampus. Nat Neurosci 12:913–918.

Liu Z-X, Shen K, Olsen RK, Ryan JD. 2017. Visual Sampling Predicts Hippocampal Activity. J Neurosci 37:599–609.

Mednick SC, Cai DJ, Shuman T, Anagnostaras S, Wixted JT. 2011. An opportunistic theory of cellular and systems consolidation. Trends Neurosci 34:504–514.

Moffat SD, Zonderman AB, Resnick SM. 2001. Age differences in spatial memory in a virtual environment navigation task. Neurobiol Aging 22:787–796.

Morton NW, Sherrill KR, Preston AR. 2017. Memory integration constructs maps of space, time, and concepts. Curr Opin Behav Sci 17:161–168.

Nguyen ND, Tucker MA, Stickgold R, Wamsley EJ. 2013. Overnight Sleep Enhances Hippocampus-Dependent Aspects of Spatial Memory. Sleep 36:1051–1057.

Ólafsdóttir HF, Carpenter F, Barry C. 2016. Coordinated grid and place cell replay during rest. Nat Neurosci 19:792–794.

Peigneux P, Laureys S, Fuchs S, Collette F, Perrin F, Reggers J, Phillips C, Degueldre C, Del Fiore G, Aerts J, Luxen A, Maquet P. 2004. Are spatial memories strengthened in the human hippocampus during slow wave sleep? Neuron 44:535–545.

Staresina BP, Alink A, Kriegeskorte N, Henson RN. 2013. Awake reactivation predicts memory in humans. Proc Natl Acad Sci 110:21159–21164.

Wilson M a, McNaughton BL. 1994. Reactivation of hippocampal ensemble memories during sleep. Science (80-) 265:676–679.

Wixted JT. 2004. The Psychology and Neuroscience of Forgetting. Annu Rev Psychol 55:235–269.

Wolbers T, Wiener JM. 2014. Challenges for identifying the neural mechanisms that support spatial navigation: the impact of spatial scale. Front Hum Neurosci 8:1–12.