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A study on episodic memory reconsolidation that tells us more about consolidation

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Abstract

Awake quiescence immediately after encoding is conducive to episodic memory *consolidation*. Retrieval can render episodic memories labile again, but *reconsolidation* can modify and re-strengthen them. It remained unknown whether awake quiescence *after retrieval* supports episodic memory reconsolidation. We sought to examine this question via an object-location memory paradigm. We failed to probe the effect of quiescence on reconsolidation, but we did observe an unforeseen 'delayed' effect of quiescence on *consolidation*. Our findings reveal that the beneficial effect of quiescence on episodic memory consolidation is not restricted to immediately following encoding but can be achieved at a delayed stage and even following a period of task engagement.

For labile new memories to be remembered they must be consolidated, i.e. strengthened and stabilised, over time (Wixted 2004; Dudai 2004). Extensive research demonstrates that post-encoding sleep and awake quiescence (quiet rest) are conducive to human episodic memory consolidation (Ferrara et al. 2008; Dewar et al. 2012; Craig and Dewar 2018; Mercer 2015; Sacripante et al. 2019; Brokaw et al. 2016; Craig et al. 2019; Wamsley et al. 2010; Clemens et al. 2005; Lahl et al. 2008; Gaskell et al. 2014; Dewar et al. 2014). Sleep and wakeful rest are hypothesised to support consolidation by providing a state of reduced sensory input and task engagement (Mednick et al. 2011; Wixted 2004; Hasselmo 1999; Dewar et al. 2012; Craig and Dewar 2018; Craig et al. 2019; Dewar et al. 2014).

Memories are not destined to remain fixed and unmodifiable once consolidated. An increasing body of evidence suggests that the cueing or retrieval of consolidated memories, e.g. via internally or externally generated exposure to learned materials (Wichert et al. 2011; Agren 2014), can return such memories into a labile state (Schwabe et al. 2014; McKenzie and Eichenbaum 2011; Dudai and Eisenberg 2004). These re-labilized memories are thought to require a process of 'reconsolidation' (Rodriguez et al. 1993; Przybyslawski and Sara 1997) in order to re-stabilise and persist. Evidence for reconsolidation in humans comes from research demonstrating that memories can be disrupted and/or updated by the application of treatments shortly following their retrieval. This includes (i) the disruption and modification of episodic memories via the presentation of similar/related materials (Hupbach et al. 2007; Loftus 2005), (ii) a reduction in the number of traumatic memory intrusions following post-retrieval engagement in visuospatial tasks (James et al. 2015; Deeproose et al. 2012; Hagensars et al. 2017), and (iii) the extinction of fear memories and increased forgetting of emotional memories via the administration of pharmaceuticals and electrophysiological stimulation (Debiec and Ledoux 2004; Cahill et al. 1994; Kroes et al. 2014). In all cases, the effect of post-retrieval treatment is seen only for memories that are *retrieved* (e.g. via a memory test or cue) prior to the treatment. Memories that were *not retrieved* (i.e. controls) are unaffected, indicating that the treatment hampered reconsolidation specifically.

Episodic memory reconsolidation can also be enhanced. Of particular interest to our paper is the finding that reconsolidation, like consolidation, benefits from sleep. If recently or remotely-encoded episodic memories are reactivated before an extended period of sleep, the reactivated memories are protected against further forgetting (for reviews see: Dudai, 2012; Spiers & Bendor, 2014; Stickgold & Walker, 2007). Moreover, even naps benefit reconsolidation. It has been shown that a short 40-minute nap period facilitated the reconsolidation of remote memories, whereas recently encoded memories did not benefit at all (Klinzing et al. 2016). It is possible that, as is the case for consolidation, sleep is conducive to reconsolidation because it provides a *state of reduced cognitive engagement and sensory input* (Mednick et al. 2011; Wixted 2004; Hasselmo 1999; Dewar et al. 2012). If so, awake quiescence, which has this in common with sleep, should also be conducive to reconsolidation.

In the study reported here, we examined whether a period of awake quiescence following retrieval protects episodic memories from further forgetting by facilitating their reconsolidation. To this end, we combined a computerised item-location memory test with a modified version of our established consolidation paradigm, which compares between-subject effects of post-encoding rest vs. task engagement on recently encoded memories (e.g., Dewar et al., 2012). Item-location memory tests have previously been sensitive to the effects of post-retrieval (reconsolidation) manipulations, including sleep (e.g. Klinzing et al., 2016) hence, subtle differences in memory scores can be recorded. Figure 1 provides an overview of the procedure. Sixty young adults (mean age = 21.47 years, SD = 1.79 years; 26M:34F) were sequentially presented photos of 60 everyday items in unique locations on a 22-inch touchscreen computer monitor. Immediately after each object's presentation, participants were asked to recall the object's location via a touchscreen response as part of a 'short-term spatial memory test' (encoding). They were unaware that they would perform subsequent long-term memory tests pertaining to the locations of these items. Location memory for half (N = 30) of the encoded items ('retrieved items') was probed in a *first delayed recall test* that occurred after a 10-minute delay filled with a visual spot-the-difference game (Dewar et al. 2012). There was no overlap between encoded photos and spot-the-difference game stimuli. The first delayed recall test was followed by

one of two post-retrieval 10-minute delay periods: (i) awake quiescence (quiet resting under strict conditions of minimal sensory input in a dimly lit room) (N = 30 participants), or (ii) a further filler task (a spot-the difference game comprising different stimuli to earlier, Dewar et al., 2012) (N = 30 participants). Memory for the location of all 60 encoded items was then probed via a *second delayed recall test*. This test included the 30 items that were probed during the first delayed recall test (retrieved items) and the 30 control items that were not probed during the first delayed recall test (non-retrieved items). Our key measure was the distance of error (cm) between the initially presented locations of the everyday objects during encoding, and the recalled location during the first and second delayed recall tests. We also recorded the time that participants took to respond as well as confidence ratings during encoding and the first and second delayed recall tests. Analyses were performed using SPSS 19 using ANOVAs, RM ANOVAs and follow up t-tests that were employed to investigate possible between-group differences. See Supplementary Materials for detailed methods.

Given that our manipulation occurred during the post-retrieval delay, we expected groups to be matched in their encoding, post-encoding delay task, and first delayed memory test. Crucially, if post-retrieval awake quiescence is conducive to episodic memory reconsolidation, then those who experience awake quiescence after the first delayed recall test should demonstrate less forgetting of 'retrieved' items (smaller distances of error scores) in the second delayed recall test relative to those who experience the filler task after the first delayed recall test. Given that 'control' items were not retrieved during the first delayed recall test immediately prior to our experimental manipulation (post-retrieval quiescence vs. task), we predicted that memory (distance of error scores) for control items should be matched between groups in the second delayed recall test.

<<INSERT FIGURE 1 ABOUT HERE>>

Data from two participants (perceptual task group) were lost due to technical issues. Thus, the following analyses report data from 58 participants (quiescence group: N = 30, perceptual task group: N = 28). The two groups were well matched in their backgrounds and performance of the post-

encoding delay task (spot-the-difference game) (see Supplementary Materials). Moreover, as expected, the two groups were well matched in all memory measures occurring *prior to* our experimental manipulation. Specifically, we found no significant main effect of group in the mean distance of error (cm) during (i) encoding of the items (quiescence: mean = 1.84 cm, SD = 0.57; perceptual task: mean = 2.00 cm, SD = 0.47; $F(1,56) = 1.303$, $p = .259$, $\eta^2 = .023$), (ii) the first delayed recall test of the 30 'retrieved' items (quiescence: mean = 13.36 cm, SD = 3.37; perceptual task: mean = 14.17 cm, SD = 3.67; $F(1,56) = 0.775$, $p = .383$, $\eta^2 = .014$), or (iii) the response times and confidence ratings in the first delayed recall test (see Supplementary Materials).

The second delayed recall test was completed immediately following our experimental manipulation, where participants experienced 10 minutes of either (i) awake quiescence (N = 30 participants), or (ii) ongoing sensory input and cognitive engagement via an unrelated perceptual task (a different spot-the-difference game; Dewar et al., 2012) (N = 30 participants). This delayed recall test included the 30 items that were probed during the first delayed recall test (retrieved items) and the 30 control items that were not probed during the first delayed recall test (non-retrieved items). A RM ANOVA comprising within-subject factor *item type* (retrieved vs. non-retrieved) and between-subject factor *group* (awake quiescence vs. perceptual task) revealed no significant main effect of group in distance of error scores (cm) ($F(1,56) = 0.686$, $p = .411$, $\eta^2 = .012$). We did however find a significant main effect of item type (retrieved vs. non-retrieved) ($F(1,56) = 14.138$, $p < .001$, $\eta^2 = .202$) because, overall, the distance of error (cm) was larger for non-retrieved (mean = 14.56 cm, SD = 3.49 cm) than retrieved (mean = 13.36 cm, SD = 3.38 cm) items. There was a significant interaction between group (awake quiescence vs. perceptual task) and item type (retrieved vs. non-retrieved) ($F(1,56) = 4.561$, $p = .037$, $\eta^2 = .075$).

Paired t-tests revealed that the above interaction emerged because, in the perceptual task group, the distance of error was significantly larger for non-retrieved (mean = 15.27, SD = 3.32 cm) than retrieved (mean = 13.37 cm, SD = 3.64 cm) items ($t(27) = -5.05$, $p < .001$; see Figure 2). This significant finding

survived Bonferroni correction for multiple comparisons (alpha level of .050 / four comparisons = corrected alpha level of .013). This was not the case in the quiescence group, where no significant item type difference was observed (retrieved: mean = 13.36 cm, SD = 3.49 cm; non-retrieved: mean = 13.89 cm, SD = 3.26 cm; $t(29) = -1.018$, $p = .317$). Independent t-tests revealed no effect of delay group in the distance of error for retrieved items (quiescence: mean = 13.36 cm, SD = 3.49 cm; task: mean = 13.37, SD = 3.33; $t(56) = -0.008$, $p = .994$) or non-retrieved items (quiescence: mean = 13.88 cm, SD = 3.26 cm; task: mean = 15.27 cm, SD = 3.64 cm; $t(56) = -1.530$, $p = .132$). The groups were matched in their second delayed recall test response times and confidence ratings (see Supplementary Materials).

<<INSERT FIGURE 2 ABOUT HERE>>

Our data reveal comparable delayed recall performance for recently retrieved photo locations in participants who rested quietly after retrieval and those who played a spot-the-difference game after retrieval (see 'retrieved' data in Figure 2). Although these findings could suggest that awake quiescence had no effect on the reconsolidation of photo-location memories, methodological shortfalls (discussed below) render this conclusion unlikely. However, we did find an unforeseen beneficial effect of quiescence for non-retrieved vs. retrieved photo locations: those who experienced the spot-the-difference game in the second delay phase demonstrated significant forgetting of non-retrieved items relative to retrieved items, whereas those who experienced awake quiescence in the second delay phase did not demonstrate such forgetting (see 'non-retrieved' data in Figure 2). We discuss these two key findings in turn.

Why did we not observe any effects of post-retrieval awake quiescence on reconsolidation in our study? One possibility is that, unlike sleep, awake quiescence simply does not benefit reconsolidation. A much more likely possibility is that methodological shortfalls mean that our study did not in fact probe reconsolidation. This may be true for a few reasons. First, sometimes, retrieval is not sufficient to reactivate memories and reintroduce them into a labile state (e.g. Cammarota et al., 2004; Forcato et al., 2009). In fact, the *protective* effect of retrieval against forgetting is well documented, even over

a delay of a few minutes (Karpicke and Roediger 2008; Roediger and Butler 2011), possibly because it provides a ‘fast route to consolidation’ of new memories (Antony et al. 2017). Notwithstanding the power of retrieval to boost memory, the research discussed earlier shows that memories reactivated via retrieval can (still) benefit from post-retrieval sleep. Do these studies differ from our own with regards to memory reactivation? Possibly. Reactivation in our study occurred after a short delay (10 minutes). It is possible that retrieval was so effective at protecting against forgetting in our study because it occurred shortly after encoding and during the initial consolidation of memory traces. Indeed, studies investigating the role of different treatments (e.g. sleep, pharmaceuticals) in reconsolidation typically require participants to retrieve previously encoded memories after a much longer delay period (several hours to days). After lengthy delays such as those, encoded memories would be expected to have completed initial consolidation, or at least be much further along in the consolidation process than in our study. The 10-minute delay in our study might simply have been too short for memories to consolidate sufficiently to be re-labilized again. As a result, retrieval might have simply strengthened memories against forgetting and did not sufficiently return them to a labile state. These methodological shortfalls mean that our study is unlikely to have probed reconsolidation effectively. Therefore, we cannot conclude whether post-retrieval awake quiescence benefits the reconsolidation of episodic memories.

How can we explain the unforeseen finding that ‘post-retrieval’ awake quiescence protected against subsequent forgetting for non-retrieved (control) items, which were not probed in the first delayed recall test? Our data reveal an effect of delayed rest that was on par with the overall beneficial effect of retrieval-mediated memory reactivation (i.e. the well-established effect of retrieval practice – see above). The findings suggest that in the task group, the lack of reactivation for non-retrieved items in the first delayed recall test negatively affected these memories. However, in the quiescence group, this lack of reactivation was offset by *delayed* rest, which seemingly had a similarly beneficial effect on non-retrieved memories. It is unlikely that this benefit of delayed rest can be explained by intentional rehearsal. The occurrence of quiet rest after a 10-minute filled delay, as opposed to

immediately after encoding, makes it unlikely that participants rehearsed the non-retrieved items during the rest period because they would require explicit knowledge that they had been tested on only half of the encoded items in the first delayed recall test and spend their time rehearsing what they could recall from the subset of items that were not tested. While this does not rule out rehearsal completely, our findings reinforce recent data (e.g., Dewar et al. 2014) showing that rest-related enhancements in memory cannot simply be explained by intentional rehearsal. A consolidation account can provide a more likely explanation.

Previous research on the beneficial effect of awake quiescence on memory has focused on *immediate* rest, i.e. rest periods occurring immediately following encoding (Craig and Dewar 2018; Craig et al. 2015, 2016; Dewar et al. 2012, 2007, 2014; Brokaw et al. 2016; Mercer 2015; Humiston and Wamsley 2018; Sacripante et al. 2019). The rationale for this focus has been that new memories are most labile upon their initial formation (Wixted and Cai 2013; Mednick et al. 2011), and thus, supportive or disruptive interventions applied during this time should be most effective. The findings of the current study suggest that the effect of awake quiescence is sufficiently powerful to influence new memories even 10 – 20 minutes after encoding, i.e. when memories have – presumably – benefited from some initial consolidation and are no longer highly labile. Moreover, they indicate that awake quiescence can support the consolidation of new memories even if the awake quiescence occurs after a period of task engagement rather than immediately after encoding. The latter hypothesis resonates with the view that consolidation is an opportunistic process (Mednick et al. 2011) and raises interesting questions about how late the onset of rest would need to be for rest to no longer facilitate the consolidation of new memories. This remains to be established, but we predict that the benefit of quiescence should diminish in accordance with increasing delay in the onset of the rest period as memories are increasingly stabilised through consolidation that occurs independently of that during intentional rest. Investigation of this question may provide insights into the initial timeline of episodic memory consolidation, which is characterised poorly. Thus, more work is required to establish if a

relationship exists between the precision of item location memory and the time lag between initial encoding and post encoding quiescence.

In summary, methodological shortfalls mean that we failed to probe the possible effect of awake quiescence on episodic memory reconsolidation. Nonetheless, we unexpectedly revealed that awake quiescence following encoding reduces forgetting, even when experienced at a delayed point in time and following a period of task engagement. This finding indicates that awake quiescence need not commence immediately following encoding to benefit memory consolidation, at least for object-location memories. Further investigation and independent replication of this effect are required to better understand the underlying mechanisms and implications of our unexpected finding.

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Figure legends

Figure 1. Experimental paradigm. Participants were presented 60 photos of unique everyday items from the Mnemonic Similarity Task (e.g. Stark et al. 2013) in unique locations on a computer screen. They then experienced 10 minutes of a post-encoding delay task (a spot-the-difference game). Memory for the location of half of the encoded items (N = 30) was then probed via a first delayed recall test (via touchscreen response), before participants completed one of two post-retrieval delay periods, each of which were 10 minutes in duration: **A**) awake quiescence (N = 30), or **B**) an engaging perceptual task (a further spot-the-difference game comprising different stimuli to the earlier one) (N=30). In the subsequent second delayed recall test, participants' memory for the location of *all* the retrieved and non-retrieved items was probed (N = 60) (via touchscreen response). The experimental procedure took place in a single session.

Figure 2. Memory performance in the second delayed recall test. Mean distance of error (cm) in the second delayed recall test for items that were and were not 'retrieved', i.e. probed, during the first delayed recall test. The data for both the quiescence and task groups are shown. Distance of error refers to the deviation in location from the initially presented location of each item. Error bars show the standard error of the mean. Full lines show between-group comparisons (quiescence vs. task) of distance of error (cm) scores, and dashed lines show within-subject comparisons (retrieved vs. non-retrieved).