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To gain or not to gain – the complex role of sleep for memory

Comment on Dumay (2015)

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1. Introduction

In the last decades several lines of research have consistently demonstrated the beneficial effect of sleep on memory consolidation (Rasch & Born, 2013; Walker & Stickgold, 2004). Generally, this enhancing effect of sleep on memory appears to be constituted mostly in less forgetting and in promoting memory stability (Diekelmann, 2014), for both procedural (Nettersheim, Hallschmid, Born, & Diekelmann, 2015; Rickard, Cai, Rieth, Jones, & Ard, 2008) as well as declarative memories (Gais, Lucas, & Born, 2006; Schönauer, Grätsch, & Gais, 2014). Still, there is an ongoing debate which processes are at the bottom of sleep's impact on memory processing: either a passive mechanism of protection from interference (Mednick, Cai, Shuman, Anagnostaras, & Wixted, 2011) or an active mechanism including information processing (Diekelmann & Born, 2010). Two recent studies (Dumay, 2015; Fenn & Hambrick, 2012) set out to shed light on this important issue and proposed a direct behavioral parameter, indicating either an active or passive memory mechanism during sleep: Behavioral memory gains vs. memory losses. Gained items are not remembered before, but only after the retention interval, whereas lost items are remembered before, but not after sleep and wakefulness. The conceptual idea is that gaining an item in memory during a retention interval can only be achieved via an active consolidation mechanism (e.g. memory reactivation etc.), which actively strengthens a memory trace above a retrieval threshold. Conversely, protection from losing a previously known item can be achieved by a passive "sheltering" mechanism. Consequently, Fenn & Hambrick (2012) and Dumay (2015) propose that differential effects of sleep vs. wakefulness on "gains" vs. "losses" can be directly attributed to one of the two different memory mechanisms. Remarkably, the results and conclusion of the two studies are quite different. Fenn &

Hambrick (2012) found the strongest effect of sleep with regards to maintained items, which led the authors to conclude that the memory function of sleep might rely for the most part on a "passive" protection from interference. In contrast, Dumay (2015) just found the opposite pattern of results with sleep showing a stronger effect on gained items as compared to maintained items. Dumay (2015) argued that the results obtained by Fenn & Hambrick (2012) might be flawed by a severe ceiling effect in memory performance after learning, preventing sleep to unfold its impact on gaining items and thereby reducing the validness of the results and interpretations. Thus, in opposition to Fenn & Hambrick (2012), the author concludes that sleep actively improves the accessibility of declarative memories, while protection against interference might play a subordinate role.

In this commentary, we intend to add further data and analyses to this important discussion. In particular, we re-analyzed three of our published datasets (Schreiner & Rasch, 2015a; Schreiner & Rasch, 2015b; Schreiner, Lehmann, & Rasch, 2015) in which participants learned foreign vocabularies, while subsets of the foreign words were replayed during the subsequent retention interval of sleep or wakefulness. As the experimental induction of memory reactivations by memory cues should primarily impact a consolidation mechanism that is considered "active" (i.e., memory reactivations), our data provide a unique opportunity to test the conceptual assumption raised by Dumay (2015). The author argues that if behavioral gains indeed reflect an active and losses a passive memory mechanism, then cueing during sleep should primarily impact behavioral gains without significant effects on memory losses. In contrast to the conclusion of Dumay (2015), here we show that cueing memories during sleep affects both memory gains and losses equally. In addition, sleep (vs. wakefulness) reduced behavioral losses rather than increasing gains in our data. We will discuss the results and potential pitfalls on the level of analysis of "gains" and "losses". Finally, we will argue that the general assumption (i.e., behavioral memory gains reflect an active and losses a passive consolidation mechanism) is problematic on a conceptual level.

2. Original methods

The data were taken from three previously published studies: study 1 (Schreiner & Rasch, 2015a;) study 2 (Schreiner & Rasch, 2015b) and study 3 (Schreiner, Lehmann, & Rasch, 2015). For detailed information about participants, stimuli, task and data acquisition see the original articles.

In short, study 1 comprised in total 64 subjects (31 female, mean age: 24.56 ± 0.51). Thirty of these subjects participated in two sleep groups and 34 subjects took part in two waking control groups. Another 32 subjects participated in study 2 (26 women, mean age 22.95 ± 0.36 years) again as waking controls. Finally, 43 subjects participated in study 3 (31 female, 22.72 ± 0.46), separated in three sleeping groups. Thus, overall data of 139 subjects entered the present re-analysis. All subjects were German-speaking without any prior knowledge of Dutch.

Participants of all three studies performed a vocabulary-learning task. The task consisted of 120 Dutch words and their German translation, randomly presented in three learning rounds. Memory performance was tested in the third learning round using a cued recall procedure, without any feedback. Recall performance of this third round was taken as pre-retention learning performance.

The learning task started at 10 pm for subjects of studies 1 and 3, while in study 2 the beginning of the learning phase was distributed over the entire day (9 a.m.–3 p.m.). The learning phase was followed by a 3 hours retention interval either of sleep or wakefulness, depending on the experimental group. After the retention interval recall of the vocabulary was tested again using a cued recall procedure. In all but one experimental groups, subsets of the Dutch words learned before the retention interval were repeatedly replayed during 90 minutes of the retention interval via loudspeaker. In study 1, 30 Dutch words, which were remembered before the retention interval and 30 Dutch words which were not remembered before, were replayed during Non-REM sleep in one of the two sleeping groups. In the control sleep group no words were replayed. The same procedure was administered to the waking control groups. In the active waking group, cueing of Dutch words occurred during performance on a computerized n-back task, while participants of the waking control groups were not distracted while hearing the Dutch words. The two waking groups of study 2 resembled those just described. The only difference was that cueing of foreign vocabulary was performed during daytime wakefulness, as control participants of study 1 stayed awake during nighttime in order to keep circadian influences stable. In two of the three sleep groups of study 3, 40 of the prior learned Dutch words were replayed as single cues (only the Dutch words), 40 as word pair cues (Dutch and German words) and 40 were not replayed at all. In the third sleep group, 40 of the prior learned Dutch words were again not replayed at all, 40 were replayed as delayed word pair cues (i.e., with a longer inter-stimulus interval between the Dutch and German words of each word pair) and 40 were replayed as single cues (only Dutch words) which were directly followed by a pure tone. As cueing Dutch words during sleep only showed beneficial effects on memory performance either if single Dutch words were replayed during sleep or in the case of word pairs with a long inter-stimulus interval ('delayed word pairs'), we solely concentrated on these categories in our analysis concerning the impact of cueing memories on the fate of an item (for details concerning the behavioral effects of cueing see Schreiner, Lehmann, & Rasch, 2015).

3. Results

Following the analysis of Dumay (2015) we first computed a correlation between the pre-retention test scores and the amount of forgetting at retest. No significant correlation was present for both the overall sleep and wake groups ($p > 0.5$), excluding floor or ceiling effects. Thus, we used the entire sample for this re-analysis without selecting only the best participants (see Dumay, 2015). Importantly, wake and sleep groups did not differ in their pre-retention test scores (50.79 ± 1.35% remembered for wake vs. 50.29 ± 0.99%

remembered for sleep, $P = 0.79$), excluding any baseline differences.

In our main analysis of the entire sample, we observed a highly robust memory benefit after a retention interval filled with sleep as compared to wakefulness: Participants in the sleep groups (n = 73) remembered 94.51 ± 0.86% after the retention interval, whereas participants in the wake groups (n = 68) remembered only 84.50 ± 1.19% ($F_{(1,139)} = 43.15$, $P < 0.001$, $\eta^2 = 0.23$, with learning performance set to 100%). In contrast to the general results in Dumay (2015) where sleep led to improved performance, this pattern of result already suggests that the beneficial effects of sleep on memory in our paradigm expressed mainly in a relatively diminished forgetting in the sleep group (-5.49 ± 0.86%) as compared to the wake group (-15.5 ± 1.19%).

3.1 "Item fate" analysis

For an in depth analysis, we further followed the rational as exerted by Dumay (2015) and Fenn & Hambrick (2012) and assigned each item (both, cued and uncued items) to one of the following categories: (1) "maintained" (i.e., items recalled at both the pre-retention test and the final test); (2) "gained" (i.e., items not recalled at the pre-retention test, but recalled at the final test); (3) "lost" (i.e., items recalled at the pre-retention test, but not at the final test), (4) "never recalled". Items corresponding to the "never recalled" category were discarded, as they did not benefit our analyses. In addition, we accounted for the probability of the amount of items that theoretically could be maintained, gained and lost between the pre-retention and the final test for each subject (see Dumay 2015, for details):

- Maintained: Number of maintained items relative to the number of items recalled at the pre-retention test
- Gained: Number of gained items relative to the total number of items ***not*** recalled at the pre-retention test (i.e., total number of items (120) minus recalled items)
- Lost: Number of lost items relative to the number of items recalled at the pre-retention test (not reported by Dumay (2015))

On average in our entire sample, the probability of gaining an item (9.63 ± 0.45%) was much lower than maintaining an item (80.19 ± 0.77%). Conversely, the likelihood for losing an item was 19.81 ± 0.77%. To examine sleep benefits on memory, we first calculated these parameters separately for sleep and wake groups and computed sleep-to-wake ratios. In accordance with Dumay (2015), the sleep-to-wake ratio for gained items (1.17; sleep 10.34 ± 0.71%, wake: 8.85 ± 0.52%, gained items, respectively) was descriptively higher than the sleep-to-wake ratio for maintained items (1.10, sleep: 83.89 ± 0.84%, wake: 76.20 ± 1.15%, respectively). Most importantly (and not at all "complementary" to maintained items as argued by Dumay (2015)), the wake-to-sleep ratio was highest for lost items (1.47, wake: 23.79 ± 1.15% vs. sleep: 16.11 ± 0.84%, please note that the ratio for lost items was flipped to obtain a comparable direction to gained and maintained items).

For the statistical analysis, the proportions of the maintained, gained and lost items were rescaled to account for their differing probabilities by applying a normalization-by-the-mean (i.e. the subject's proportion of gained, lost and maintained items were divided by their respective overall means). To account for the fact that consolidation processes affect gained and lost items in opposite directions (i.e., consolidation should reduce the number of lost, but enhance the number of gained memories, which might lead to trivial interaction effects) we computed an inverse measure for lost items to enable comparability between categories. The inverse measure for lost items was computed as follows: $p_{Inv}(loss) = 1 - (p(loss) - 1)$, with p(loss) being the rescaled proportions of lost items. Please note that the mean, as well as the standard error of the mean are identical for both the original and the inverse measure of lost items computed over all participants (mean: 1; SEM: 0.039), indicating their dependency. Afterwards, an ANOVA was performed using the between subject factor sleep vs. wake and the within-subject factor item condition (i.e. gained vs. maintained vs. lost.

We observed a significant interaction ($F_{(1,278)} = 6.34$, $P = 0.002$, $\eta_p^2 = 0.04$), indicating that the item conditions differed significantly according to whether the retention interval was filled with sleep or wakefulness. Afterwards, specific ANOVAs were performed using the between subject factor sleep vs. wake and either the within-subject factor gained vs.

maintained or gained vs. lost in order to depict specific differences between gained and lost or maintained items, respectively.

While we observed a significant interaction also in the first analysis ($F_{(1,139)} = 6.51$, $P = 0.01$, $\eta_p^2 = 0.04$), the interaction effect was even stronger when analyzing gained vs. lost items ($F_{(1,139)} = 20.37$, $p < 0.001$, $\eta_p^2 = 0.12$). Post-hoc pair-wise comparisons further revealed that the largest sleep effects were observable for lost and maintained items (both $t = - 5.41$, $P < 0.001$, $\eta_p^2 = 0.17$), while we observed only a marginal trend for gained items ($t = - 1.67$, $P = 0.09$, $\eta_p^2 = 0. 019$). Thus, while the results reported by Dumay (2015) indicate that sleep had the most substantial influence on gaining an item when compared with maintained items, our data suggest that sleep mainly reduces lost items and protects maintained items (see Fig. 1a). In particular, taking lost items into account changes the overall picture and ignoring this behavioral category may lead to misleading conclusions.

3.2 The impact of cueing memories on the fate of an item

In an additional analysis protocol we took advantage of the fact that in eight of the nine experimental groups used in this re-analysis, subsets of the prior learned Dutch words were cued using single cues during the retention interval (either during wakefulness or sleep, depending on the experimental group, see (Schreiner & Rasch, 2015a; Schreiner & Rasch, 2015b, Schreiner, Lehmann, & Rasch, 2015)). In theses studies we could repeatedly show that presenting single word cues during sleep after word-pair learning improves cued recall of the associated second word. We encountered the same beneficial effect of cueing with regards to word pairs comprising a long inter-stimulus interval. In contrast, presentation of word-pairs with short interstimulus interval during sleep did not result in memory benefits, therefore we excluded this data from the re-analysis. Thus, the wake group comprised again of 68 subjects, while the sleep group contained 58 subjects.

Overall, participants in the sleep group correctly recalled 99.78 ± 1.36% of the cued words, whereas only 91.19 ± 1.23% of the uncued words were correctly recalled after sleep ($F = 36{,}83$, $P < 0.001$, $\eta_p^2 = 0.39$, with learning performance set to 100%). Cueing did not have any effect on memory performance when applied during wake (cued: 85.85 ± 1.68%; uncued: 84.73 ± 1.34% correctly recalled, respectively (*P* > 0.6)).

For the item fate analyses, we followed at large the same procedure as described above but further divided the data set with respect to the factor cued vs. uncued (see Table 1 for the likelihoods of the different categories). When comparing sleep-to-wake ratios for cued and uncued items on a descriptive level, it becomes evident that the additional benefit of cueing was present for all three category items: While we observed a (flipped) sleep-to-wake ratio of 1.71 for cued lost items (sleep: 13.77 ± 1.26% vs. wake: 23.51 ± 1.41%), the ratio was only 1.33 for uncued lost items (sleep: 18.03 ± 1.28% vs. wake: 24.00 ± 1.24%). The ratio was also higher for cued gained items (1.37, sleep: 12.85 ± 0.96% vs. wake: 9.39 ± 0.72%) as compared to uncued gained items (1.13, sleep: 9.12 ± 0.87% vs. wake: 8.07 ± 0.59%), and finally for maintained items (1.12 sleep: 86.22 ± 1.26% vs. wake: 76.48 ± 1.41%) as compared to uncued maintained items (1.07; sleep: 81.96 ± 1.28% vs. wake: 75.99 ± 1.24%).

In the final analyses we ran ANOVA was performed using the between subject factor sleep vs. wake and the within-subject factor item condition (i.e. gained vs. maintained vs. lost) and the within subject factor cued vs. uncued. We tested again for possible interaction effects and rescaled the proportions of the cued and uncued gained, lost and maintained items to account for their differing probabilities. Here, we rescaled the respective values with regards to the sleep/wake condition, as differences between cued/uncued items were only observable after sleep. Thus, scores of participants of the sleep groups were divided by the total mean of all sleep group subjects, while the same procedure was administered to the waking group subjects.

We observed a significant interaction between the factors sleep vs. wake and cued vs. uncued ($F_{(1,124)} = 9.07$, $P = 0.003$, $\eta_p^2 = 0.06$) and a significant interaction between item conditions (gained vs. lost vs. maintained) and cued vs. uncued ($F_{(1,124)} = 6.12$, $P = 0.003$, $\eta_p^2 = 0.04$). Post hoc comparison confirmed significant differences between cued and uncued items for both gained items ($t = 4.19$, $P < 0.001$, $\eta_p^2 = 0.12$) and lost items as well as maintained items during sleep (both $t = 2.91$, $P = 0.005$, $\eta_p^2 = 0.06$), but not during wakefulness (all $P > 0.15$, see Fig. 1b). This results pattern indicates that cueing equally benefits gained as well as lost and maintained items during sleep, with the strongest impact on gained items.

4. Discussion

The question whether sleep actively or passively supports memory formation is highly important. Here we show that, compared with wakefulness, the beneficial effect of sleep on the consolidation of newly learned foreign vocabulary appears mostly on maintaining previously learned items and on counteracting forgetting. Furthermore, cueing vocabulary during sleep (but not during wakefulness) resulted in increased memory gains, but simultaneously also in reduced memory losses. Overall, our data are in line with the notion that sleep mainly benefits maintaining memories (Fenn& Hamrick, 2012), and contradict the conclusion that sleep might mainly serve the gaining of memories, put forward by Dumay (2015).

Several reasons might have contributed to these inconsistent results. First, in the data reported by Dumay (2015), performance levels after sleep generally exceeded those observed before sleep already in the overall analysis, which was not the case in our data. For declarative memory paradigms, such strong gains are generally an uncommon finding, particularly if feedback after the last learning round is omitted before sleep (please note that in the study conducted by Fenn & Hambrick (2012) feedback was given during recall testing before sleep, which was not the case with regards to Dumay (2015)) (Diekelmann, 2014; Marshall & Born, 2007). Thus, the characteristics of the specific learning paradigm and stimuli, the pre-sleep performance level, individual learning ability of the participants as well as the specifications of retrieval testing (cued vs. free recall vs. recognition) might strongly influence the general performance level, and thereby also significantly alter the item fate analysis. Second, the calculation of sleep-wake ratios done by Dumay (2015) might have led to misleading conclusions, particularly as the “lost” category was not included in the analyses. While the proportion of “maintained” and “lost” items are indeed complementary in the overall analysis steps, they strongly differ when ratios are calculated. A rough recalculation of the data by Dumay (2015) revealed a (flipped) sleep-wake ratio for losses of 1.71, which is larger than the sleep-wake ratio for maintained items (1.49). Thus, by including lost items, the conclusion of the preferential benefit of sleep for gained items would have at least been weaker also in the data reported by Dumay (2015).

Third, the cueing approach might be a more appropriate method to answer the question of a passive vs. active role of sleep for memory than the simple sleep/wake comparison. It seems undoubted that memory reactivations during sleep represent active processes operating during sleep, and several studies have demonstrated that those processes can be triggered by cueing procedures (Bendor & Wilson, 2012; Diekelmann, Büchel, Born, & Rasch, 2011; Fuentemilla et al., 2013; Schönauer, Geisler, & Gais, 2013; Schreiner & Rasch, 2016). Thus, if the influence of sleep counteracting forgetting solely reflects passive processes, while active processing is only mirrored in the effect on gaining items, cueing memories during sleep should only affect the chance to gain items. This assumption was likewise put forward by Dumay in his work (2015). Our results that cueing memories during sleep as compared to wakefulness affected both categories, by reducing the chance to loose an item and enhancing the probability to gain an item, clearly show that the simple allocation of those categories to passive and active processes oversimplifies this issue.

In conclusion, we would like to question the assumption that losses are solely indicative for a passive mechanism. We know from memory studies in *Aplysia* that maintaining a simple memory as the syphon reflex requires a complex cascade of molecular processes and plastic changes also after its acquisition (Cai, Pearce, Chen, & Glanzman, 2011). Similarly, maintenance of conditioned responses in rodents requires several waves of (active) consolidation processes including transcriptional factors, protein synthesis etc. (McGaugh, 2000). At its very core, memory is conceptually defined as the maintenance of newly acquired information over time, and without plastic processes, this information is lost and forgotten. Generally, keeping an ordered state in biological (and therefore mostly fluid) systems requires energy, so the process of memory maintenance itself requires active plastic processes.

Of course, losses in memory can occur due to passive processes like memory trace decay or interference (Wixted, 2004). However, also active plastic processes can reduce loss of memory i.e., the stabilization and consolidation of memory traces leading to reduced forgetting. Conversely, reasons for maintaining an item can both be due to passive processes (no decay, no interference) as well as active processes (stabilization, reactivation etc.). Thus, behaviorally maintaining or losing an item can be indicative of both active and passive memory mechanisms, and should not be taken as indicator for solely passive memory mechanisms.

Are behavioral gains indicative for active consolidation processes? The advantage of memory gains is that they mostly require a strengthening of the memory trace to reach a certain retrieval threshold, which was not reached before the retention interval. Thus, on average, gained items are probably actively consolidated items. However, at least some gains can also be achieved by other factors: For example, previous retrieval attempts might have failed in spite of a sufficiently strong memory trace due to distraction, incomplete search, reduced attentional resources etc. Furthermore, simply repeating retrieval attempts without any retention interval leads to increases in recall success and can produce memory gains, a phenomenon known as “hypermnesia” (Mulligan, 2005; Roediger & Payne, 1982). And finally, if we assume that retrieval is a probability process depending on the strength of the memory trace, some gains will always occur by chance.

To summarize, our data indicate that sleep mainly benefits the maintenance of newly acquired memory, which can be due to both active and passive memory processes. Furthermore, actively reactivating memories during sleep by cueing also reduces memory losses in addition to increased gains, suggesting that spontaneous reactivation processes assumed to act during sleep likewise improve memory maintenance. While separately analyzing gains and losses in sleep and memory studies is an interesting suggestion, we conclude that this analysis is not sufficient to answer the important question whether the benefit of sleep on memory is due to active or passive memory mechanisms.

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Figure Legend

Fig.1

(a) Normalized proportions of "maintained", "gained" and "lost" items for the sleep and wake groups. (b) Normalized proportions of cued vs. uncued "maintained", "gained" and "lost" items for the sleep and wake groups. Values are mean ± s.e.m. $+P \leq 0.1$, $*P \leq 0.05$, $**P \leq 0.01$.

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