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The effect of learning and post-learning practice on long-term episodic memories

PhD Thesis Booklet

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INTRODUCTION

Episodic memory, that is, the memory system in the service of storing the representations of events and experiences that are vivid in nature (Tulving, 1972), is known to be influenced by a number of factors. For instance, it has been shown to be modulated by encoding strategies as well as post-encoding practice strategies. One of the most widely known phenomena affecting long-term retention of episodic memories is retrieval-based learning, or the testing effect (Roediger & Karpicke, 2018). At a behavioral level, it has been demonstrated that repeated retrieval of the studied information aids memory performance to a better degree than repeatedly studying it (Roediger & Karpicke, 2006). Although the testing effect is very robust and holds under a variety of circumstances (e.g., Karpicke & Aue, 2015), some authors have questioned its robustness in specific conditions (Storm et al., 2014). Therefore, it is important to assess the essential conditions under which this effect can fulfill its potential and address potential methodological caveats for future research. At a neural level, perhaps the most important finding regarding repeated retrieval of memory items is that prefrontal cortical areas, such as the dorsolateral prefrontal cortex (DLPFC) shows a gradually decreasing activity as a result of repeated retrievals (e.g., Kuhl et al., 2007). It is well established that the communication between the frontal and hippocampal areas is crucial for forming episodic memories (Eichenbaum, 2017), but it remains to be characterized better how this communication, and the possible shift in its nature as a result of repeated memory encounters affects the retention of memories, and how the activity of the DLPFC influences this shift. Furthermore, it is an intriguing question what role the DLPFC plays when the reencounter takes place in the form of repeated study – in other words, it remains to be elucidated whether the activity decrease in the DLPFC during practice only affects retrieval-based learning, or if it has an effect on restudy practice as well, possibly pointing to a wider role of this region in repeated memory encounters and long-term retention. One possible way to experimentally alter the activity of certain brain regions is transcranial direct current stimulation, a promising non-invasive neurostimulation technique (Balconi, 2013; Bennabi et al., 2014). The role and function of cortical regions in retention is multi-faceted and can be investigated using numerous methods and be described in terms of multiple measures. Electroencephalography (EEG), among others, is a prominent method that can provide insight into the workings of memory functions. Previous results, for example, have consistently shown an association between long-term memory performance and EEG power in certain frequencies, such as alpha (8-12 Hz), beta (13-35 Hz) or slow (0.5-1 Hz) frequencies (Hanslmayr et al., 2016; Waldhauser et al., 2016). Interestingly, although both these changes in frequency power and the above-mentioned retrieval-based learning strategy seem to aid long-term retention, no study according to our knowledge assessed the potential interaction between these two factors, and thus it remains to be seen whether the effectiveness of retest or restudy strategies can be characterized by different EEG signatures. Apart from behavioral manipulations and cortical neural mechanisms, environmental factors such as contextual details can also have significant effects on episodic memory performance. Specifically, the reappearance of contextual details that were present at encoding seems to aid memory retrieval (Godden & Baddeley, 1975; Isarida & Isarida, 2007) as well as recognition memory performance (Smith & Vela, 2001), but it remains to be seen how the reappearance of a previous context affects the discrimination of similar, yet in fact, new memory items.

Here we present four studies in which we aimed to examine some of the factors outlined above, that is, at a behavioral level, the role of initial learning levels for the effectiveness of retrieval-based learning, the cortical mechanisms involved in effective long-term retention, and the role of previously encountered contexts in recognition and mnemonic discrimination. In the next section, we outline the main objectives and thesis points, and subsequently discuss our most important results and conclusions.

MAIN OBJECTIVES AND THESIS POINTS

Thesis 1. – Sufficient level of initial learning is key for the long-term effectiveness of retrieval-based learning

The long-term effectiveness of retrieval-based learning is a well-established phenomenon (Roediger & Karpicke, 2018), and this effect, termed the testing effect, is considered one of the most robust effects in memory literature (Roediger & Karpicke, 2006). The advantage of practicing previously studied materials by repeatedly retrieving the studied items in contrast to simply repeatedly studying them has been demonstrated using a wide range of materials (Karpicke & Aue, 2015). However, a recent study has challenged the robustness of the effect by suggesting that in some circumstances (when the initial learning levels are extremely low and repetitive feedback at final tests is given), repeated studying in fact proves to be a more effective strategy (Storm et al., 2014). The authors interpret their results in the framework of the bifurcation account of the testing effect. In Study 1, in three experiments, we aimed to investigate if the effect of feedback on (and by extension the reversal of) the testing effect is modulated by the level of retrieval success during practice, by manipulating the level of initial learning. To do this, we used a classic experimental paradigm used to study the testing effect, replicating the design of Storm and colleagues' (2014) Experiment 1, but manipulating the number of initial learning cycles. In our first experiment ($n = 29$), replicating the design of the original Experiment 1, we used one initial learning cycle where participants were instructed to study 36 Hungarian- Swahili word pairs. In a subsequent practice phase subjects practiced one third of the pairs by repeated studying, one third by cued retrieval practice and they did not practice one third of the pairs, serving as baseline. The final test phase of the experiment took place one week after practice and consisted of six final test sessions, where all word pairs were tested by cued recall. Participants received feedback after each test trial, regardless of the success of recall, in the form of the correct word being presented to them. Our Experiment 2 (n = 30) and Experiment 3 (n = 24) were identical in design to our Experiment 1, except the number of initial learning cycles was 3 and 6, respectively.

In Experiment 1, we replicated the previous finding of a reversed testing effect in the final test sessions 2 to 6. However, in Experiment 2 and 3, no such reversal was observed, in fact, the increase of initial learning from 3 to 6 cycles produced an even stronger testing effect, lasting until the fourth final test session, after which performance reached ceiling levels in all three conditions. To summarize, as expected, the increase in initial learning (and by virtue, increase in successful recall at practice), "protected" the testing effect even when additional study opportunities for all items in the form of feedback at final tests were given.

Findings regarding Thesis 1:

1.1 Effectiveness of retrieval-based learning is reliant on sufficient levels of initial learning

1.2 Increasing the initial recall rate of test practice results in progressively robust testing effect

Thesis 2. – Maintaining activity in the dorsolateral prefrontal cortex during reencounters decreases long-term memory performance

Interactions via bidirectional connections between the hippocampus and the prefrontal cortex have been shown to be crucial for memory encoding as well as retrieval (Eichenbaum, 2017; Fletcher, 2001). Numerous studies have investigated the role of these areas in retrieval-based learning and found that the repeated retrieval (practice in the form of repeated testing) of items is commonly associated with a decrease in prefrontal activity that is traditionally linked to executive functions such as attention and monitoring, or in the framework of memory research, functions such as cue specification, search initiation and monitoring the output of retrieval (Balconi, 2013; Friedman & Robbins, 2022; Kuhl et al., 2007; Ranganath et al., 2003). Proposed explanations to this pattern of activity are the reduction of search set size (that is, with repeated retrieval, the set of potential target items that is activated by a retrieval cue decreases, and thus search becomes less effortful), and the automatization of cue-target associations (leading to a procedural, skill-like retrieval mechanism that is initiated by the perception of the cue [Racsmány et al., 2018]). In Study 2, we carried out two experiments to investigate whether hindering this normally occurring prefrontal activity decrease affects memory performance in the long term, we devised a paradigm where after learning, the practice of to-be-memorized material was preceded by excitatory direct-current stimulation of the right PFC, exerting its effects during the practice phase. In addition to retrieval-based practice, we included a condition where items were practiced by repeated studying to uncover any potential difference in how excitatory stimulation of the PFC during restudy or retest practice affects retention of practiced memory items.

By artificially maintaining activity during practice, we expected a diminished memory performance on a later criterion test. Both experiments consisted of a traditional testing effect paradigm, allowing us to examine the effects of stimulation not only during retrieval-based practice, but restudy as well (collectively referred to as reencounters). In both experiments, the first phase was an initial learning phase where subjects were instructed to memorize 40 Swahili-Hungarian word pairs in 5 learning cycles. Next, in the reencounter phase, half of these word-pairs were reencountered in the form of repeated studying, and half in the form of repeated testing in five consecutive cycles. The final criterion test took place after a 7-day delay in the form of cued recall. In Experiment 1 (n = 67), transcranial direct current stimulation was applied immediately before the reencounter phase for 15 minutes. Half of subjects received real anodal excitatory stimulation (2 mA current intensity) over the right DLPFC, and half of them received sham stimulation. Experiment 2 (n = 53), serving as control experiment, was methodologically identical, except the stimulation followed the reencounter phase instead of preceding it.

We found a reliable testing effect in both experiments, that is, at a behavioral level, testing was the more beneficial reencounter type. In terms of stimulation, when it preceded the reencounter phase, anodal stimulation resulted in diminished long-term memory performance as compared to sham stimulation, independent of reencounter type. However, when stimulation followed the reencounter phase, no such effect of stimulation was observable. This suggests that excitatory stimulation exerting its effect over the right DLPFC during reencounters with previously encoded items hinders the beneficial processes that normally occur as a result of either type of reencounter. The finding that stimulation after reencounters did not have such detrimental effects suggests that a decreased activity in the DLPFC is not a key factor in consolidation processes immediately following memory reencounters.

Findings regarding Thesis 2:

2.1 Excitatory stimulation of DLPFC during memory reencounters decreases long- term memory performance

2.2 The decrease in DLPFC activity might be crucial during not only repeated retrieval practice, but also for repeated study practice for maximum effectiveness

2.3 Activity decrease in the DLPFC might not be a key factor in consolidation occurring immediately memory reencounters

Thesis 3. – Changes in cortical oscillation during learning combined with reencounters predict long-term memory performance

Bidirectional connections and interactions between the neocortex and hippocampal and parahippocampal areas in the service of memory formation are proposedly prominent during learning, practice, and also rest following learning, although the role and pattern of cortical activity for successful encoding and practice in such processes is not entirely understood. At the behavioral level, long-term episodic retention has been shown to be aided by different types of memory reencounters, such as repeated retrieval and repeated study. At an electrophysiological level, decrease in alpha (and beta) frequency EEG power has been established as a marker of not only successful memory encoding, but retrieval. In Study 3, using electroencephalography, we investigated the electrophysiological predictors of long- term memory success in situations where reencounters in the form of repeated study or retrieval occurred after learning. The experiment (n = 68), in terms of design, was again based on the traditional testing effect experiments, and as a result we were able to study potential differences in cortical signatures between two reencounter types (retrieval or re-presentation). In the first session, subjects took part in the initial learning phase (involving 5 encoding cycles of 36 word-pairs to be memorized) and the reencounter phase (as a between subject design, with 30 subjects in the retest and 31 subjects the restudy groups). A final criterion test was administered after a 7-day long retention interval, involving the cued recall of all 36 word-pairs. Electrophysiological data was recorded during 15-minute resting periods before the initial learning phase (serving as baseline measure), and also immediately after the reencounter phase. As a measure of cortical activity, we examined power change measures from the pre-learning resting period to the post-reencounter resting state period.

Behaviorally, the advantage of repeated retrieval as a practice strategy was observed.

However, from baseline to post-reencounter rest, alpha and beta change values were shown to be negatively, while slow frequency power change was found to be positively associated with long-term memory performance, regardless of reencounter type. These results extend previously observed patterns of cortical activity during memory formation to situations where memory reencounters occur after learning.

Findings regarding Thesis 3.

3.1 Decrease in alpha and beta oscillation power from pre-to post-learning rest periods is associated with better long-term memory performance

3.2 Increase in slow oscillation power from pre-to post-learning rest periods is associated with better long-term memory performance

3.3 Changes in alpha, beta and slow frequency bands predict memory performance regardless of post-learning reencounter type

Thesis 4. – Reinstatement of unattended encoding context at test aids recognition but decreases discrimination

It is well established that the reoccurrence of environmental context that was present at initial encoding aids episodic recall of focal items. Although this observation is indeed quite ubiquitous in case of tests involving recall, some more controversial results were found when recognition test were applied. A large volume of research indicates that recognition is also affected by the re-presentation of encoding context, but there are numerous exceptions. Also, previous research mostly focused on intentional initial learning situations, while incidental learning is largely neglected. The objective of Study 4 was to investigate how the reinstatement of encoding context at recognition influences not only correct recognition of focal items, but false alarm rates as well. Altogether, we expected to gain insight into how the reappearance of irrelevant, unattended context influences memory discrimination processes needed for mnemonic pattern separation. We carried out two experiments, Experiment 2 serving as control to Experiment 1. In Experiment 1 (n = 28) experiments subjects made indoor/outdoor judgements about 60 images of everyday objects on a scenic image background. Later, in a surprise recognition memory task, the original target objects were presented together with similar lure objects and completely new foils with 30 images in each condition. Each target and lure object was presented either on the same or on a new background context as at encoding. Participants were instructed to make "old"/"similar"/"new" decisions. In Experiment 2 (n = 40), the sole difference in comparison to Experiment 1 was that at the surprise recognition test, participants were explicitly instructed to make their judgements based on the object, whereas in Experiment 1, no such instruction was given.

Our key finding is that although the reappearance of context did increase the hit rate for target objects, it also decreased mnemonic discrimination and false alarms to lure items, even when participants were explicitly instructed to neglect the context scene while making recognition judgements. Altogether these results provide evidence that the re-presentation of a previously encountered context increases recognition hits, but also increase false recognition and diminished discriminability for similar novel information, suggesting an overall bias towards „old" responses and a sense of familiarity.

Findings regarding Thesis 4:

4.1 Reinstatement of unattended encoding context of incidentally encoded focal items increases recognition of target items

4.2 Reinstatement of unattended encoding context of incidentally encoded focal items increases false recognition of non-target, new items

SUMMARY AND GENERAL DISCUSSION

In the presented thesis we investigated several key factors of long-term memory encoding and practice. First, we showed that although some studies (Storm et al., 2014) have found that the beneficial effect of retrieval over restudy as a practice strategy is limited and can be diminished by applying feedback at various stages of testing, this was only observed due to insufficient levels of initial learning. When sufficient levels of learning are achieved, the effect of testing remains robust, which is a reassuring finding that is useful from both a methodological and a practical, educational point of view. Next, we investigated possible cortical mechanisms of these reencounter practice types (re-presentation or retrieval of the previously studied material). By introducing excitatory stimulation to the right DLPFC before the reencounter practice, we found that long-term retention of reencountered memories was negatively affected, regardless of reencounter type. These results are in line with previous findings demonstrating the decrease of prefrontal activity during repeated retrieval (e.g., Kuhl et al., 2007). We can assume that a naturally occurring decrease in frontal areas upon repeated retrieval events of the same material implies the reduced need for these control processes, and artificially maintaining activity in executive-control-related areas might hinder the communicational shift between frontal and hippocampal communication that is key for successful memory formation (Eichenbaum, 2017). The result that long-term retention of repeatedly studied items also suffered as a result of preceding excitatory stimulation highlights a broader role of prefrontal activity decrease (and possibly the resulting change in fronto-hippocampal communication [Bilek et al., 2013]) at memory reencounters. We can speculate that the maintenance of DLPFC activity in our experiment produced an overstimulation in the hippocampus, thereby causing less efficient memory formation. In the next study, by means of electroencephalography, we examined cortical markers of successful memory formation. Our results indicate that long-term memory performance is negatively related to alpha and beta, and positively related to slow EEG frequency power change during learning, in line with earlier findings (Hanslmayr et al., 2016). Importantly, again, we highlight that retrieval-practice is, a highly effective learning strategy, whose effectiveness seems to be independent from the EEG signatures of successful memory consolidation, as these two factors do not seem to interact. Lastly, we shifted focus to the effect of contextual details on incidentally encoded information and its discriminability from future overlapping stimuli. Our results suggest that reinstating the original, unattended environmental context of incidental encoding at recognition test increases correct recognition of previously encountered items, but it is detrimental for the discrimination of highly similar new items, suggesting that upon perception of only part of the whole encoded item-and-context ensemble, the whole representation is reactivated, causing a general bias towards categorizing the episode and the focal memory items as old. We highlight that context is embedded into the memory trace representing an event, and that even the reappearance of irrelevant, unattended contextual details can alter the perception/recognition of stimuli we encounter daily.

To conclude, in four studies, spanning eight experiments, we have investigated some of the key factors influencing the long-term retention and the discriminability of memory traces. Our results provide important insight into the mechanisms of cortical processes underlying the behavioral observation that memory reencounters (in most circumstances) aid long-term retention. We also showed how the reappearance of the original encoding context at retrieval can alter the recognition of old and novel stimuli, causing increased familiarity and a bias towards pattern completion.

The dissertation is based on the following works:

(1) Racsmány, M., Szőllősi, Á., & **Marián, M.** (2020). Reversing the testing effect by feedback is a matter of performance criterion at practice. *Memory & Cognition*, *48*(7), 1161– 1170. https://doi.org/10.3758/s13421-020-01041-5 - **Thesis 1**

(2) **Marián, M.,** Szőllősi, Á., & Racsmány, M. (2018). Anodal transcranial direct current stimulation of the right dorsolateral prefrontal cortex impairs long-term retention of reencountered memories. *Cortex*, *108*, 80–91. https://doi.org/10.1016/j.cortex.2018.07.012 - **Thesis 2**

(3) Bencze, D., **Marián, M.,** Szőllősi, Á., Simor, P., & Racsmány, M. *Resting-dependent changes of post-learning oscillatory power predict long-term memory success.* [Manuscript in preparation]. Department of Cognitive Science, Budapest University of Technology and Economics. - **Thesis 3**

(4) Racsmány, M., Bencze, D., Pajkossy, P., Szőllősi, Á., & **Marián, M.** (2021). Irrelevant background context decreases mnemonic discrimination and increases false memory. *Scientific Reports*, *11*(1), 6204. https://doi.org/10.1038/s41598-021-85627-2 -**Thesis 4**

REFERENCES

Balconi, M. (2013). Dorsolateral prefrontal cortex, working memory and episodic memory processes: Insight through transcranial magnetic stimulation techniques. *Neuroscience Bulletin*, *29*(3), 381–389. https://doi.org/10.1007/s12264-013-1309-z

Bennabi, D., Pedron, S., Haffen, E., Monnin, J., Peterschmitt, Y., & Van Waes, V. (2014). Transcranial direct current stimulation for memory enhancement: From clinical research to animal models. *Frontiers in Systems Neuroscience*, *8*. https://doi.org/10.3389/fnsys.2014.00159

Bilek, E., Schäfer, A., Ochs, E., Esslinger, C., Zangl, M., Plichta, M. M., Braun, U., Kirsch, P., Schulze, T. G., Rietschel, M., Meyer-Lindenberg, A., & Tost, H. (2013). Application of

High-Frequency Repetitive Transcranial Magnetic Stimulation to the DLPFC Alters Human Prefrontal–Hippocampal Functional Interaction. *Journal of Neuroscience*, *33*(16), 7050–7056. https://doi.org/10.1523/JNEUROSCI.3081-12.2013

Eichenbaum, H. (2017). Prefrontal–hippocampal interactions in episodic memory. *Nature Reviews Neuroscience*, *18*(9), Article 9. https://doi.org/10.1038/nrn.2017.74

Fletcher, P. C. (2001). Frontal lobes and human memory: Insights from functional neuroimaging. *Brain*, *124*(5), 849–881. https://doi.org/10.1093/brain/124.5.849

Friedman, N. P., & Robbins, T. W. (2022). The role of prefrontal cortex in cognitive control and executive function. *Neuropsychopharmacology*, *47*(1), Article 1. https://doi.org/10.1038/s41386-021-01132-0

Godden, D. R., & Baddeley, A. D. (1975). Context-Dependent Memory in Two Natural Environments: On Land and Underwater. *British Journal of Psychology*, *66*(3), 325–331. https://doi.org/10.1111/j.2044-8295.1975.tb01468.x

Hanslmayr, S., Staresina, B. P., & Bowman, H. (2016). Oscillations and Episodic Memory: Addressing the Synchronization/Desynchronization Conundrum. *Trends in Neurosciences*, *39*(1), 16–25. https://doi.org/10.1016/j.tins.2015.11.004

Isarida, T., & Isarida, T. K. (2007). Environmental context effects of background color in free recall. *Memory & Cognition*, *35*(7), 1620–1629. https://doi.org/10.3758/BF03193496

Karpicke, J. D., & Aue, W. R. (2015). The Testing Effect Is Alive and Well with Complex Materials. *Educational Psychology Review*, *27*(2), 317–326. https://doi.org/10.1007/s10648-015-9309-3

Kuhl, B. A., Dudukovic, N. M., Kahn, I., & Wagner, A. D. (2007). Decreased demands on cognitive control reveal the neural processing benefits of forgetting. *Nature Neuroscience*, *10*(7), Article 7. https://doi.org/10.1038/nn1918

Racsmány, M., Szőllősi, Á., & Bencze, D. (20170629). Retrieval practice makes procedure from remembering: An automatization account of the testing effect. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *44*(1), 157. https://doi.org/10.1037/xlm0000423

Ranganath, C., Johnson, M. K., & D'Esposito, M. (2003). Prefrontal activity associated with working memory and episodic long-term memory. *Neuropsychologia, 41*(3), 378–389. https://doi.org/10.1016/S0028-3932(02)00169-0

Roediger, H. L., & Karpicke, J. D. (2006). Test-enhanced learning: Taking memory tests improves long-term retention. *Psychological Science*, *17*(3), 249–255. https://doi.org/10.1111/j.1467-9280.2006.01693.x

Roediger, H. L., & Karpicke, J. D. (2018). Reflections on the Resurgence of Interest in the Testing Effect. *Perspectives on Psychological Science*, *13*(2), 236–241. https://doi.org/10.1177/1745691617718873

Smith, S. M., & Vela, E. (2001). Environmental context-dependent memory: A review and meta-analysis. *Psychonomic Bulletin & Review*, *8*(2), 203–220. https://doi.org/10.3758/BF03196157

Storm, B. C., Friedman, M. C., Murayama, K., & Bjork, R. A. (2014). On the transfer of prior tests or study events to subsequent study. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *40*, 115–124. https://doi.org/10.1037/a0034252

Tulving, E. (1972). Episodic and semantic memory. In *Organization of memory* (pp. xiii, 423–xiii, 423). Academic Press.

Waldhauser, G. T., Braun, V., & Hanslmayr, S. (2016). Episodic Memory Retrieval Functionally Relies on Very Rapid Reactivation of Sensory Information. *Journal of Neuroscience, 36*(1), 251–260. https://doi.org/10.1523/JNEUROSCI.2101-15.2016