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Testing alters brain activity during subsequent restudy: Evidence for test-potentiated encoding

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ABSTRACT

Mixed testing/studying lead to better memory retention compared to repeated study only. A potentiating influence of tests on encoding, particularly during restudy of non-retrieved items, may contribute to this effect. This study investigated whether and how testing affects brain activity during subsequent restudy of Swahili–Swedish word pairs after a cued-recall test. Item-events during fMRI were categorized according to history (tested/studied only) and recall outcome at prescan and postscan tests. Activity was higher for tested compared to studied-only items in anterior insula, orbital parts of inferior frontal gyrus and hippocampus, and lower in regions implicated in the default network, such as precuneus, supramarginal gyrus and the posterior middle cingulate. Findings are discussed in terms of top-down biasing of attention to tested items with concomitant deactivation of regions in the default network. Increased/focused attention to tested items during restudy may lead to test-potentiated encoding via deeper semantic processing and increased associative binding.

1. Introduction

The benefits of testing for learning and memory are well documented for various types of tests and materials (for reviews, see e.g., [50,51]). Repeated testing (after initial study) and mixed testing/studying generally lead to better memory retention compared to only repeated study (e.g., [13,30,74]). The theoretical explanations for such *testing effects* have mainly focused on retrieval processes engaged during testing for already acquired material, termed *direct, or unmediated effects of testing* [51], and more precisely defined as the *beneficial effect of successful retrieval on retention*. Recently, Arnold and McDermott [2] stressed the importance of distinguishing these direct effects from other *indirect, or mediated effects of testing* (also see [51]) when research paradigms include restudy opportunities and/or feedback that re-presents the material. This is particularly important as it is under such conditions that the greatest effects of testing on memory performance typically are observed (see e.g., [29]), suggesting that retrieval–encoding interactions during study-test-study sequences contribute to the beneficial effects of testing.

A particularly noteworthy mediated effect, *test-potentiated encoding* (TPE; formulated as potentiation of the effectiveness of subsequent reinforcements or acquisition) was suggested based on a series of experiments with paired associates by Izawa (e.g., [27]). The author concluded that learning does not occur on tests per se (as measured by increased correct-response probability over successive tests without intervening study), but that testing prevents forgetting and increases the effectiveness of encoding at subsequent restudy (for a recent replication of the results, see [2]). Observations of testing effects when there are no opportunities for restudy or feedback naturally lend themselves to theoretical explanations with a focus on successful retrieval and thus retrieval processes (but see [65]). TPE on the other hand highlights a potential role for previous *unsuccessful* retrieval attempts and encoding processes. The possibility that testing not only benefits retention but also encoding has clear implications for educational practice. This could encourage students to take regular tests, knowing that they, even if failing, have benefits for future learning. Furthermore, investigations of retrieval–encoding interactions contribute to our basic understanding of memory processes, with applicability to many other disciplines.

Izawa [27] was one of the first to address a possible role of testing for encoding during restudy, but more recent studies have also found evidence that unsuccessful retrieval attempts enhance memory [20,49], provided that they are followed by restudy. However, whereas the effects of successful retrieval on future retrieval and retention are relatively straightforward to investigate with behavioral paradigms, effects of testing on subsequent encoding are more complicated to uncover. The foremost challenge is one of disambiguating the contributions of successful encoding and successful retrieval to memory performance (for a similar argument,

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see e.g., [25]). In research on testing effects this issue can be formulated in terms of disambiguating the contributions of indirect and direct effects of testing. In this study, we used fMRI as a window for studying the encoding process in a more direct manner.

In the following section we will briefly review hypotheses and explanations for TPE based on behavioral findings.

1.1. Hypotheses and explanations for test-potentiated encoding

Previously unsuccessfully retrieved items have been the prime candidates for a subsequent TPE effect in behavior-based studies (see e.g., [20,47]). However, an overall TPE effect on subsequent encoding, regardless of whether the previous retrieval attempt was successful or not is also a theoretical possibility (see [22]). This hypothesis is implicit in the *test-trial potentiating model* of Izawa [27], with the reservation that she considered learning as an increase in correct response probability (that logically could only occur if previously non-retrieved items are retrieved). An overall TPE effect has generally not been supported by conclusions from behavioral findings (e.g., [22,29]; but see [28]).

A second alternative is that TPE is confined to previously unsuccessfully retrieved items [19,22], whereas successfully retrieved items are unaffected (and thereby possibly equivalent to repeated study). Finally, it is possible that there are opposite effects, that is, whereas the encoding of previously unsuccessfully retrieved items is potentiated, the encoding of successfully retrieved items is actually suppressed, that is, less encoding than that for repeated study (learned items can be ignored; [52]).

TPE, and particularly the benefits of previous unsuccessful retrieval have been explained in metacognitive terms as the result of performance evaluation [22], knowledge of recallability [65], or mediator effectiveness evaluation [47] resulting in a shift in encoding strategies, encoding effort, or mediators for previously failed items. A related set of explanations involve attention to not-yet-mastered material or selective attention [34]. Attention is also a candidate process for an overall TPE effect when tests are inserted between repeated study sessions (e.g., [45]), or when only a subset of a previously studied material is subjected to testing and then followed by restudy of the complete material. Some additional support for this view comes from findings that pre-questions for a subsequently read text enhances memory and allocation of attention for related information [35,48].

Recently, elaborating on ideas by Kornell et al., Grimaldi and Karpicke [20] presented three possible explanations for why failed retrieval attempts may enhance subsequent encoding. The first, *search set theory*, proposes that a cue (word) on a test starts a search process that activates related candidates in a semantic network (search set). A failed retrieval attempt may thereby lead to enhanced encoding at subsequent study because of the relatedness of the target word to the activated search set (also see [27]). The search set theory does not preclude a TPE effect for previously successfully retrieved items, but it is possibly weaker as there should be less need for memory search for an item that has been successfully retrieved at least once. Regardless of outcome, a retrieval attempt should involve memory search to a greater extent than study.

The second explanation, *error correction theory*, proposes that any discrepancy between a produced response and the correct response at test leads to an error signal. An error correction mechanism then guides adjustment of the system in favor of the correct response alternative. The error correction theory predicts TPE for unsuccessfully retrieved, but not for successfully retrieved, items. The theory also necessitates some kind of memory for previous erroneous responses when there is a lag between the produced and correct responses. The error correction theory predicts suppressed encoding for previously successfully retrieved items (compared to studied-only) as the discrepancy between the produced and correct responses is minimal.

The third explanation, *additional cue theory*, proposes that an initial response at a failed retrieval attempt is encoded and then covertly recalled at a future retrieval attempt. The response then functions as an additional cue aiding retrieval of the target item. The theory predicts that the TPE effect should be confined to previously unsuccessfully retrieved items, and furthermore most pronounced for those items to which erroneous responses are actually produced rather than for those to which no response is produced.

1.2. Putative neurocognitive processes and brain regions involved in test-potentiated encoding

Only a limited number of previous fMRI studies have explicitly addressed testing effects (see e.g., [15,23,73,75]), and to the best of our knowledge there exists only one published fMRI study on TPE. Nelson and coauthors [41] found that regions in the parietal cortex were sensitive to retrieval practice, and were most active during a final study session for items that had been tested compared with those that had been restudied (and neither tested nor restudied). Furthermore they found a positive correlation between neural activity in the left posterior inferior parietal lobule/dorsal angular gyrus and an “index of new learning” that was calculated for each participant. The authors concluded that testing facilitates subsequent encoding by engagement of retrieval processes during the subsequent study phase.

Even though there is limited direct evidence on neurocognitive processes and brain areas involved in TPE, results from studies of related processes can be informative. In general, a consistent finding from imaging studies is that intentional and incidental episodic memory encoding is related to increased neural activity in the frontal lobes, specifically left prefrontal cortex for verbal materials (for reviews, see e.g., [6,9,58,72]), and medial temporal lobe regions, such as the parahippocampal gyrus and anterior parts of the hippocampus [31,53,58]. The ventrolateral prefrontal cortex (VLPFC) is believed to be involved in the selection of goal-relevant item information during encoding, whereas dorsolateral parts are involved in organizing information in working memory, thereby strengthening memory for associations among items in long-term memory [4].

Imaging studies have further implicated the anterior cingulate cortex (ACC) in error detection and performance monitoring (e.g., [10]) and evaluation of feedback (e.g., [1]), making it a potential key region for explanations focusing on TPE after unsuccessful retrieval.

The search set and additional cue theories presumably involve representations in an associative network. As such, one would expect large distributed networks across several brain areas to be involved, such as the anterior temporal cortex representing conceptual knowledge (for a review, see [64]). Working memory processes are likely also implicated, again suggesting a role for left prefrontal areas (for reviews, see e.g. [3,18]). Explanations for TPE in terms of increased or focused attention suggest involvement of the premotor- and posterior parietal cortex – regions that may support attention during memory encoding [31]. Related to this, the premotor and parietal cortices have been implicated in various types of switching of attention [71], and the dorsal posterior parietal cortex in particular has been suggested to mediate goal-directed attention during successful encoding [69].

1.3. The current study

An effect on final behavioral performance after repeated, mixed testing/restudying is likely the result of the cumulative contributions

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