Inhibition in Selective Memory Retrieval: Behavioral and Electrophysiological Insights

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Preface

In nowadays information society, successfully dealing with diverse information from multiple sources is essential. For instance, conducting an internet research on a specific topic will, in most cases, generate a vast number of results. Most of the common internet search engines generate these results in form of lists, leaving the user with the difficulty to choose the relevant information out of the bulk of relevant and irrelevant ones. Human memory faces a similar problem. Trying to remember a specific event from one's past, like the 2006 soccer world cup final, will activate a lot of related memories, relevant ones, like the teams that were playing in the final or the host country, and irrelevant ones, like details from the world cup final in 2010. Memory theory describes this every-day act as follows: A memory cue initiates the search in memory and activates various related memories, some of which may be relevant, and others irrelevant, inducing interference. Contrary to an internet search engine, human memory is capable of resolving the interference by inhibition and, most of the time, is able to retrieve a unique response that includes the relevant, sought-after information.

Of course, there has to be a downside to this extraordinary capability of human memory. Inhibition, resolving interference and thereby promoting retrieval of the target item on the one hand, causes forgetting of the interfering information on the other. These effects can be observed with the retrieval-practice paradigm (Anderson, Bjork & Bjork, 1994) which has inspired many studies investigating the conditions and constraints of the so called retrieval-induced forgetting. Still, there is an ongoing debate about the underlying cognitive and neural mechanisms and the functioning of inhibition. The scope of the present work is to contribute to the solving of this debate and to generate new insights into the functioning of the inhibitory mechanism.

In the retrieval-practice paradigm, subjects study categorized item lists and subsequently retrieve a subset of these items. Thereby, competing memories are activated by a common cue. This elicits interference which is resolved by suppression of the interfering items' memory representations (Anderson & Spellman, 1995). Typically, recall of the interfering items is impaired on a later test, a finding termed retrieval-induced forgetting. The central theme that guided the present work, the theoretical as well as the methodological approach, is the dynamic behavior underlying selective memory retrieval. The retrieval-practice paradigm provides two intriguing options for investigating this dynamic behavior: The retrieval-practice phase, when inhibition is assumed to resolve the interference, and the test phase, where the effects of inhibition can be observed.

Following the course of the retrieval-practice paradigm, the first part of the present thesis is concerned with the dynamics of inhibition "as it operates" in the neural system during the retrieval-practice phase. Electrophysiology, as measured with the EEG non-invasively, records neural signals in a millisecond range, and is thus well suited to disentangle the highly dynamic processes underlying memory retrieval. Analyzing brain oscillatory activity in electrophysiological data is an approach that inherently takes into account the idea of dynamic processes in neural systems. Communication in the human brain among distant brain areas as well as within local networks is believed to rely on the concurrent activation and reactivation of neural assemblies (see Fuster, 1997, for a review). In the growing field of cognitive neuroscience, the present work can contribute by investigating brain oscillatory correlates of inhibitory processes in human memory.

The second part of this work is concerned with insights into the effects of inhibition coming from behavioral experiments. In particular, the impact of inhibition on the absolute and relative strength of interfering information is investigated. To this end, a recognition test procedure and an analysis of the temporal dynamics of response latencies during free recall is employed in the retrieval-practice paradigm. Analyzing response latencies offers intriguing advantages compared to the more commonly used counting of “stable” numbers of recalled and forgotten words. Theoretically, the estimation of parameters based on the recall latencies gives information about the activated memory traces and the degree of competition among them - information that cannot be deduced from the mere number of recalled words.

Together, the two parts contribute to a better understanding of inhibitory processes during retrieval from long-term memory. Behavioral and neural evidence gained herein will elucidate the cognitive and neural mechanisms underlying inhibition in memory.

Contents

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Abstract

Selectively retrieving information from memory often induces interference from related memories. It is widely assumed that inhibition resolves this competition by suppressing the interfering items' memory representations. However, the exact nature of the inhibitory process is not yet understood. The present work provides insight into the functioning and the effects of inhibition in selective memory from two perspectives. In two electrophysiological experiments, the dynamics of inhibition as it operates in the neural system were investigated by analyzing brain oscillations across repeated cycles of selective retrieval. Theta oscillations reflected the dynamics of inhibition during selective retrieval from episodic memory and predicted later retrieval-induced forgetting (Experiment 1). During retrieval from semantic memory (Experiment 2), however, inhibition was not reflected by theta oscillations. Instead, alpha and beta oscillations were related to retrieval from semantic memory and theta oscillations were related to the formation of new episodic memory traces. Two further behavioral experiments gave insight into the effects of inhibition on the absolute and relative strength of previously interfering items. The absolute item strength was investigated by employing a recognition test procedure (Experiment 3). Retrieval-induced forgetting was found in the selective retrieval but not the reexposure condition, a result in line with the view that inhibition affects the interfering items' memory representation. The relative item strength was assessed by analyzing recall latencies during free recall (Experiment 4). No effect of inhibition on the previously interfering material was found. Together, the results elucidate the nature of inhibitory mechanisms during retrieval from long-term memory, revealing the neural dynamics of inhibition during selective retrieval, and the effects of inhibition on the representation of interfering memory information.

Part I

Background

Retrieval-Induced Forgetting

Searching for past episodes in memory activates both relevant and irrelevant memories. Once activated, these memories compete for being remembered, eliciting interference (Anderson & Neely, 1996). Cognitive research has devoted significant attention to this topic in many studies, starting with Müller and Pilzecker's (1900) discovery of retroactive interference that refers to the finding that the additional learning of new material diminishes the recall performance of the previously learned material. Closely related, proactive interference describes the impaired recall of recently learned material caused by previously learned material (Underwood, 1957). A crucial factor influencing the amount of memory impairment has been shown to be the similarity among competing items. The more similar the material, the more interference was induced (McGeoch & MacDonald, 1931). Interference through study of additional material has been shown in many studies, and research in this area has determined several constraints and conditions influencing interference effects (see Crowder, 1976, for a review), making a good case for the long-standing view that interference is a major source of forgetting. On the basis of these findings, influential theories and frameworks were developed that describe competition among multiple memory traces in the human memory system (e.g., McGeoch, 1942; Mensink & Raaijmakers, 1988). However, modern theories on forgetting emphasize that it may not be interference per se that leads to forgetting. Instead, they focus on how the need to overcome interference contributes to forgetting (see Anderson, 2003 or Bäuml, 2008, for reviews).

The Retrieval-Practice Paradigm

Over the past decades, cognitive research has devoted considerable effort on how interference can be overcome (see Anderson, 2003 or Bäuml, 2008, for reviews). In order to promote successful retrieval of a relevant target memory, interference by other, irrelevant memories needs to be resolved. The introduction of the so called retrieval-practice paradigm (Anderson, Bjork, & Bjork, 1994) has shed light on how this is accomplished. An outline of the typical experimental design of the retrieval-practice paradigm is depicted in Figure 1. Subjects first study categorized item lists (e.g., FRUIT-Orange, FRUIT-Banana, INSECT-Hornet). In a subsequent retrieval-practice phase, the to-be-practiced items, typically half of the items from half of the categories, are selectively retrieved in a word stem cued recall task (FRUIT-Or___). Usually, two or more subsequent cycles of such retrieval practice are conducted. During these retrieval attempts, interference is thought to arise, because other, unpracticed items (Banana) are activated by the common category cue.

Typically, in a later recall test, recall performance for practiced items (Orange) is increased as compared to control items (Cricket) originating from categories which were not part of the practice phase at all. The more intriguing finding, however, is that recall performance for unpracticed items (Banana) which were not practiced but belonged to a practiced category, is decreased as compared to control items. This behavioral memory impairment is called retrieval-induced forgetting.

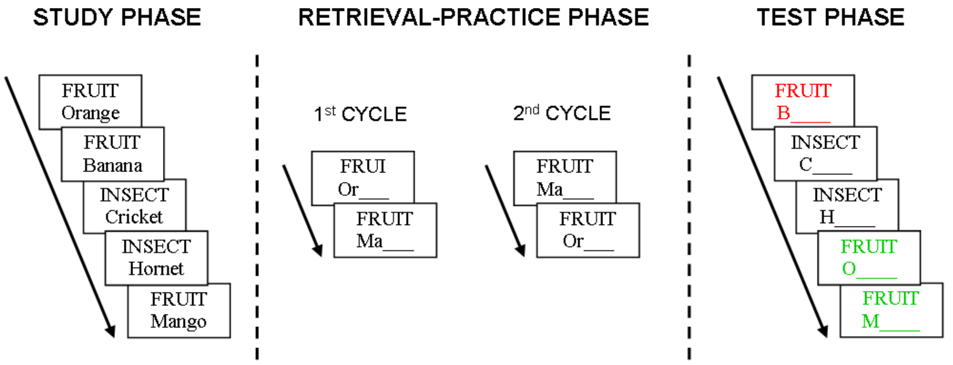


Figure 1. Schematic depiction of a typical experimental design as employed in the retrieval-practice paradigm. After studying categorized item material (study phase), subjects repeatedly retrieve a subset of items (retrieval-practice phase). This procedure creates three different types of items at test: practiced items (shown in green), unpracticed items (shown in red), and control items (shown in black). All of the studied items are subsequently tested (test phase).

Retrieval-induced forgetting is a rather general phenomenon. Besides the standard version of the paradigm with presentation of categorized verbal materials, a variety of experimental settings and various materials have been used to demonstrate retrieval-induced forgetting, such as visual (Ciranni & Shimamura, 1999), or autobiographical (Barnier, Hung, & Conway, 2004) material, eyewitness memory (Saunders & MacLeod, 2002; Shaw, Bjork, & Handal, 1995), false memories (Bäuml & Kuhbandner, 2003, Starns & Hicks, 2004), fact learning (Anderson & Bell, 2001), or social cognition (Dunn & Spellman, 2003) settings. Furthermore, retrieval practice is not restricted to episodic memory, but has also been shown in semantic memory (Blaxton & Neely, 1983; Brown, Zoccoli, & Leahy, 2005; Johnson & Anderson, 2004). Johnson and Anderson (2004) eliminated the episodic study phase in a retrieval-practice paradigm. Their experiment started with a so called semantic retrieval-practice phase, during which category labels and word stem cues were repeatedly presented to their subjects. Subjects were instructed to generate an item that matches both cues. Johnson and Anderson (2004) showed that memory performance for unpracticed items from practiced categories was impaired as compared to items from categories that were not presented during the semantic retrieval-practice phase.

Inhibition vs. Blocking

How is retrieval-induced forgetting explained? There is an ongoing debate about whether this retrieval-induced forgetting is inhibitory or non-inhibitory in nature (e.g., Anderson, 2003; Jakab & Raaijmakers, 2009). Most non-inhibitory accounts explain the observed forgetting by blocking (Roediger & Neely, 1982), which occurs due to strength-dependent competition during the final recall test. According to this view, the practiced items are strengthened during retrieval practice. During the final recall test, strengthened items are retrieved more easily and are recalled first, thus blocking subsequent recall of unpracticed items from the same category. Following this argument, enhancement and forgetting are interlinked, because the forgetting is explained as a by-product of the selective strengthening of target items, without the assumption of an additional (inhibitory) mechanism that causes the forgetting.

Strength-dependent competition has been shown in studies investigating the so-called list-strength effect, the finding that recall performance is dependent on the relative item strengths in a study list. Strengthening of the items is usually accomplished by repeated study, variations in study time, or a levels-of-processing manipulation. In such experiments, memory performance of pure-strength lists, consisting of items with equal strengths, is compared to that of mixed-strength lists, consisting of strong and weak items. Several studies showed that recall performance for strong items in mixed-strength lists is better than for items of the same strength that were studied in pure-strength lists, a so-called positive list strength effect (e.g., Malmberg & Shiffrin, 2005; Tulving & Hastie, 1972; Verde, 2009; Wixted, Ghadisha, & Vera, 1997; but see Ratcliff, Clark, & Shiffrin, 1990, for inconsistent findings in cued recall). This evidence has been criticized for confounding strengthening with the output position during recall. Bäuml (1997) found that when such a confound is prevented, no list strength effect occurs. Recently, Verde (2009) argued that strength-dependent competition and inhibitory mechanisms both contribute to the list-strength effect, at least if strength is varied via the number of study trials.

In opposition to the blocking account, the inhibitory account of retrieval-induced forgetting assumes a theoretical mechanism that accomplishes interference resolution during selective memory retrieval. According to this view, related, unpracticed items interfere during the retrieval-practice phase. To promote successful retrieval of target items, an inhibitory mechanism suppresses the interfering items' memory representations (Anderson & Spellman, 1995). The behavioral effect of this inhibition can be observed on the later memory test, when the previously interfering items are more likely to be forgotten.

Evidence for an Inhibitory Account of Retrieval-Induced Forgetting

Since its introduction, the retrieval-practice paradigm has produced considerable evidence in favor of the inhibitory account of retrieval-induced forgetting. Several studies showed that retrieval-induced forgetting is a retrieval-specific effect. Only if subjects engage in retrieving items during the retrieval-practice phase, substantial forgetting is found. Mere reexposure of the studied material, with the instruction to study the items again, does not cause forgetting, although practiced items are strengthened to a similar degree (Anderson, Bjork, & Bjork, 2000; Bäuml & Aslan, 2004; Ciranni & Shimamura, 1999, Wimber, Rutschmann, Greenlee, & Bäuml, 2009). These findings cannot be easily accounted for by blocking, because reexposure results in the same amount of enhancement for the practiced items but does not lead to forgetting. Recent studies demonstrated that the sheer attempt to retrieve some items from a category, even if not successful, is sufficient to cause retrieval-induced forgetting (Storm, Bjork, Bjork, & Nestojko, 2006; Storm & Nestojko, 2010). Again, this pattern cannot be explained by blocking theories, because forgetting is induced without the enhancement of other items in the category.

These findings are also in line with another feature of retrieval-induced forgetting, the so-called strength independence (Anderson, 2003). The amount of retrieval-induced forgetting has been shown to be independent of the level of strengthening of the to-be-practiced items. Rather than that, retrieval-induced forgetting has been shown to depend on the strength of the interfering items. Studies varying the taxonomic strength of the related, unpracticed items showed that strong competitors were inhibited, whereas weak ones were not (Anderson et al., 1994; Shivde & Anderson, 2001). Weak items do not induce severe interference during retrieval of the target items, and thus do not have to be suppressed by inhibition. This competition-dependency, together with the retrieval-specificity and the strength-independence, cannot easily be explained by non-inhibitory accounts of retrieval-induced forgetting. According to the blocking account of retrieval-induced forgetting, strengthening and forgetting are interlinked; blocking should occur independently of competition or retrieval during the retrieval-practice phase, as long as a subset of items in a given category is strengthened (but see Jakab & Raaijmakers, 2009).

Various other findings support the view that retrieval-induced forgetting is not bound to the strengthening of practiced items, thereby undermining the blocking account. Besides the finding that retrieval-induced enhancement and forgetting are not correlated (Hanslmayr, Staudigl, Aslan, & Bäuml, 2010), forgetting was repeatedly reported without enhancement and vice versa. Subjects in a negative emotional mood showed intact retrieval-induced enhancement for practiced items but no retrieval-induced forgetting (Bäuml & Kuhbandner, 2007). In a similar vain, Kössler, Engler, Riether, and Kissler (2009) found retrieval-induced enhancement but no forgetting in subjects under stress.

Inhibitory theory claims that interference is resolved by suppressing the interfering item's memory representation. To preclude that it is the association between item and cue that is affected by inhibition, studies used the so-called independent probe technique. By providing memory cues during the final test that had not been part of the study phase, these studies showed that retrieval-induced forgetting does not depend on an experimentally established association of the item to the retrieval cue (Anderson & Spellman, 1995; Aslan, Bäuml, & Pastötter, 2007, Saunders & MacLeod, 2006). However, other studies cast doubt on the validity of the independent probe technique or have failed to replicate the effect (Camp, Pecher, & Schmidt, 2007; Camp, Pecher, Schmidt, & Zeelenberg, 2009), thus strengthening opponents of the inhibitory account of retrieval-induced forgetting (see Perfect et al., 2004; Williams & Zacks, 2001).

Considering results from studies employing implicit test procedures in the retrieval-practice paradigm, a similar, mixed picture arises. Item-specific tests like lexical decision tasks can reduce or even eliminate strength-dependent competition that is crucial for a blocking account of retrieval-induced forgetting. Veling and van Knippenberg (2004) found retrieval-induced forgetting in such a task, whereas Racsmány and Conway (2006) failed to find an effect. Other authors claim that retrieval-induced forgetting in implicit tests is only found under specific circumstances, for example, in conceptual but not in perceptual implicit tests

(Perfect, Moulin, Conway, & Perry, 2002) or only if the subject is aware of the relationship between retrieval-practice and test phase (Camp, Pecher, & Schmidt, 2005). Contrarily, a recent study by Healey, Campbell, Hasher, and Ossher (2010) found retrieval-induced forgetting in an experimental setting where study, retrieval-practice, and test phase were implicit in nature, excluding subjects that were aware of the relationship between retrieval practice and test.

Another way to reduce the influence of strength-dependent competition is to use a recognition test procedure. In such tests, the item itself is provided as a retrieval cue, thereby rendering an influence of other items blocking its recall quite unlikely. Several studies reported retrieval-induced forgetting across a variety of recognition tasks (but see Koutstaal, Schacter, Johnson, & Gallucio, 1999, for a null effect on picture recognition). Hicks and Starns (2004) found that retrieval practice of a subset of studied items reduced the performance in an item recognition test. Verde (2004) showed that this also held true for word pairs in an associative recognition test, and Gómez-Ariza, Lechuga, Pelegrina, and Bacho (2005) expanded the evidence of retrieval-induced forgetting in recognition tests to episodically related sentences. Spitzer and Bäuml (2007) also found retrieval-induced forgetting in recognition memory. In their study, they compared the different predictions of a dual-process account (e.g., Yonelinas, 2002) and a single process account (e.g., Wixted, 2007) of recognition memory. Their conclusion that the observed retrieval-induced forgetting in recognition tests is due to a reduction in general memory strength fits nicely with the view that inhibition weakens the interfering items' memory representations. Together, the findings from studies using recognition tests strongly support an inhibitory account of retrieval-induced forgetting. Because of their item-specific nature, results from recognition tests speak against blocking accounts that assume strength-dependent competition to be responsible for retrieval-induced forgetting.

The results from recognition tests are well in line with the view that retrieval-induced forgetting affects the recovery stage of recall. According to two-stage models of recall (e.g., Raaijmakers & Shiffrin, 1981; Rohrer, 1996), after a search set has been established by a retrieval cue, items are sampled from this set during the sampling stage. The sampling process is described in terms of a ratio rule (see Rundus, 1973), a function of an item's strength to the sum of strengths of all of the items in the search set. After being sampled, the item is recovered at the recovery stage, but only if its absolute strength exceeds a given threshold. Because inhibition is assumed to weaken the unpracticed items' memory representation (Anderson, 2003), passing the recovery threshold should be impeded. Bäuml, Zellner, and Vilimek (2005) addressed this issue by measuring recall latencies during the test phase of a retrieval-practice paradigm. Recall latencies are assumed to reflect the sampling speed and the size of the search set at the sampling stage of recall (Rohrer, 1996). In their study, Bäuml et al. (2005) showed that recall totals, but not recall latencies differed for practiced, unpracticed, and control items. These results are well in line with the view that retrieval-induced forgetting is a recovery problem.

To summarize, convincing evidence has accumulated over the past decades that interference during selective memory retrieval is resolved by an inhibitory mechanism that weakens the representation of interfering memories (for reviews, see Anderson, 2003; or Bäuml, Pastötter, & Hanslmayr, 2010). Although retrieval-induced forgetting has been assumed to be a recovery problem, it remains unclear if the inhibitory mechanism also affects the sampling stage of recall.

Inhibition and Executive Control

Along with the vast amount of evidence underpinning that the mechanism underlying retrieval-induced is inhibitory in nature, several lines of evidence support the view that inhibition is an executive control process. Executive control processes are considered to be mediated by the prefrontal cortex, which exerts top-down control on the stream of information from other brain regions. A crucial feature of such an executive control mechanism is its limited capacity (see Miller & Cohen, 2001, for a review).

Results from neuropsychological studies are in line with the view that retrieval-induced forgetting is mediated by inhibitory executive control. Schizophrenics and ADHD patients show general deficits in executive functioning (see Schachar et al., 2007; Weisbrod, Kiefer, Marzanzik, & Spitzer, 2000). Both groups of patients also showed impaired retrieval-induced forgetting as compared to healthy controls (Soriano, Jiménez, Román, & Bajo, 2009; Storm & White, 2010, but see Racsmány et al., 2008, for inconsistent findings in schizophrenics). Román, Soriano, Gómez-Ariza, and Bajo (2009) directly manipulated executive control functioning by employing an additional, attention-consuming task during the practice phase of the retrieval-practice paradigm, thus overloading executive control resources at the point in time inhibition is assumed to suppress interfering items. Retrieval-induced forgetting was absent when subjects had to perform the additional task during retrieval practice.

Further support for the view that retrieval inhibition is an executive control process comes from studies investigating individual differences in working memory capacity. Working memory capacity has been assumed to be positively correlated with the ability to inhibit task-irrelevant information (for a review, see Redick, Heitz, & Engle, 2007). Aslan and Bäuml (in press) showed that the very relationship held true for the retrieval-practice paradigm. Subjects with a high individual working memory capacity showed more retrieval-induced forgetting compared to subjects who scored low on the working memory capacity task.

Developmental studies can also shed light on the underlying nature of inhibitory memory control. Executive control mechanisms are assumed to develop across life span. Due to a lack of resources, young children's performance on tasks involving inhibitory control is generally reduced (see Bjorklund & Harnishfeger, 1990, for a review). Concerning retrieval-induced forgetting, developmental research has shown that the efficiency of the inhibitory mechanism increases across childhood. Whereas kindergarteners showed impaired retrieval-induced forgetting, school children did not show this deficit (Aslan & Bäuml, 2010; Lechuga, Moreno, Pelegrina, Gómez-Ariza, & Bajo, 2006; Zellner & Bäuml, 2005). Older adults are also assumed to have a general inhibitory deficit (see Hasher & Zacks, 1988). This view is challenged by studies reporting intact retrieval-induced forgetting in older adults (Aslan et al., 2007; Moulin et al., 2002).

Critical to the finding of retrieval-induced forgetting in the context of executive processes seems to be the control of output interference. As some of the studies described above showed, intact retrieval-induced forgetting was found in cued recall tests not controlling for output interference, but not in recognition test that controlled for output interference (see Aslan & Bäuml, in press; Aslan & Bäuml, 2010; Soriano et al., 2009; Storm & White, 2010). This finding suggests that the intact forgetting effect found in groups of subjects suffering from impaired executive control could actually be due to an increased vulnerability to interference at test rather than to inhibition (e.g., Kane & Engle, 2000). In the next section, an overview on the neural correlates of retrieval-induced forgetting will provide further insight into the executive-control nature of inhibition in memory retrieval.

Neural Correlates of Retrieval-Induced Forgetting

The inhibitory account of retrieval-induced forgetting suggests an executive control mechanism which suppresses the interfering memories during selective retrieval. Executive control processes in cognition have been related to prefrontal cortex functioning in a wide range of tasks including memory control operations (for a review, see Mansouri, Tanaka, & Buckley, 2009). In particular, the anterior cingulate cortex (ACC) and the right lateral prefrontal cortex (LPFC) seem to play a crucial role when it comes to controlling behavior under conditions of interference. The ACC is assumed to be involved in the detection of conflict between competing responses (Botvinick, Cohen, & Carter, 2004), the right LPFC is assumed to assert the inhibitory control on task-irrelevant stimuli (Aron, Robbins, & Poldrack, 2004). An involvement of these areas in the suppression of interfering items in the retrieval-practice paradigm would clearly speak in favor of an executive-control account of retrieval-induced forgetting.

Several recent studies explored the neural correlates of retrieval-induced forgetting, both during the retrieval-practice phase and the final recall test. Because inhibition is assumed to operate during retrieval practice, investigating this particular phase can give insights into the inhibitory mechanism "as it operates".

The test phase, on the other hand, may deliver evidence for the effects of inhibition, that is, neural correlates of suppressed memory representations.

Neural Correlates of Inhibition during Retrieval Practice

Johansson, Aslan, Bäuml, Gäbel, and Mecklinger (2007) analyzed event-related potentials in the EEG during the retrieval-practice phase. They compared a selective retrieval (FRUIT-Or___) with a reexposure condition (FRUIT-Orange) and reported a stronger sustained positivity over frontal electrode sites during selective retrieval than reexposure. Because the frontal positivity predicted later retrieval-induced forgetting, the authors concluded that activation in the prefrontal cortex mediates inhibition during selective memory retrieval.

Hanslmayr et al. (2010) investigated brain oscillatory activity during the retrieval-practice phase. Instead of using a reexposure condition as a non-retrieval baseline, the authors compared a competitive retrieval condition (FRUIT - O___) with a noncompetitive retrieval condition (FRU___ - Orange). This idea was motivated by a study by Anderson et al. (2000) showing that retrieval-induced forgetting was found only in the competitive but not in the non-competitive condition. Using such a baseline condition, Hanslmayr et al. were able to control for general retrieval-related activity. Hanslmayr et al. found evoked oscillatory activity in the theta band (4-7 Hz) to be selectively increased in the competitive condition. The difference in evoked theta between the competitive and noncompetitive condition was negatively correlated with the amount of retrieval-induced forgetting and located over left parietal and frontal electrode sites. On the basis of previous findings suggesting that frontal theta is generated in the ACC (e.g., Gevins, Smith, McEvoy, & Yu, 1997; Ishii et al., 1999; Onton, Delorme, & Makeig, 2005), the results of are in line with the ERP findings described above.

In an fMRI study, Wimber et al. (2009) also compared a selective retrieval to a reexposure condition. Increased neural activity in left prefrontal and parietal areas was found during retrieval as compared to reexposure. An increase in BOLD signal in prefrontal cortex and anterior cingulate cortex (ACC) predicted later forgetting. Comparing reexposure and retrieval might not be optimal for isolating the inhibitory mechanism, though, because the two conditions differ in several other aspects, for example, the presence of general retrieval-related activity.

An fMRI study by Kuhl, Dudukovic, Kahn, and Wagner (2007) used a slightly different approach to investigate the retrieval-practice phase. They compared brain activity across repeated cycles of selective retrieval practice. This procedure also controls for general retrieval-related activity. Kuhl et al. (2007) showed that neural activity in lateral prefrontal areas and the ACC decreased with increasing number of retrieval cycles. Again, the BOLD signal decrease in these prefrontal brain regions predicted the amount of retrieval-induced forgetting. The authors thus concluded that the decreased engagement of the prefrontal cortex with repeated practice reflects the beneficial effects of inhibiting competing memories during the retrieval practice of target items.

Together, the studies investigating neural mechanisms of interference resolution during retrieval practice converge on the view that interference resolution by inhibition is mediated by prefrontal processes, thereby supporting the notion of inhibition as an executive-control mechanism.

Neural Correlates of the Effects of Inhibition in the Test Phase

The effects of inhibition, that is, the impairment of memory representations due to suppression become manifest during the test phase of the retrieval-practice paradigm. By using fMRI and EEG, the neural correlates of these effects can be explored. Spitzer, Hanslmayr, Opitz, Mecklinger, and Bäuml (2009) analyzed electrophysiological activity during a recognition test that was employed in a retrieval-practice paradigm and found that forgetting and enhancement were reflected by distinct components in the ERP. Unpracticed, suppressed items showed reduced early positivity over frontal electrode sites as compared to control items; practiced, enhanced items showed a larger late positivity over parietal electrode sites than control items.

Moreover, the authors compared oscillatory activity elicited by control items with oscillatory activity elicited by unpracticed items and practiced items. Again, distinct neural substrates were found for retrieval-induced forgetting (control vs. unpracticed items) and enhancement (control vs. practiced items). A stronger decrease in alpha power (8-13 Hz) reflected enhancement, whereas oscillatory activity in the theta (4-7 Hz) and gamma (65-80 Hz) band was specifically related to retrieval-induced forgetting. In particular, fronto-central theta power and occipital gamma power decreased for unpracticed items as compared to control items. The decrease in theta power predicted the inter-individual differences of retrieval-induced forgetting. Spitzer et al. (2009) concluded that the reduced synchronization in the theta band, together with the reduced early ERP component, reflect the activation of the (weak) unpracticed items' memory traces during the recognition test, which were inhibited in the previous retrieval-practice phase. This view is consistent with previous work showing that the activation of weak as compared to strong episodic memory traces during recognition is related to a decrease in theta power (Klimesch et al., 2006).

In an fMRI study, Wimber et al. (2008) contrasted the activation of unpracticed, suppressed items with practiced, enhanced items during a cued recall test. They found distinct neural correlates for retrieval-induced enhancement and forgetting, thus providing evidence against a blocking account of retrieval-induced forgetting. Particularly, left ventrolateral prefrontal activity was specifically related to the recall of unpracticed items and predicted the amount of retrieval-induced forgetting (but see Kuhl, Kahn, Dudukovic, & Wagner, 2008). Because activation in the ventrolateral prefrontal cortex has been assumed to reflect retrieval of weak memory representations (Badre & Wagner, 2007), the findings by Wimber et al. (2008) strongly support the inhibitory view of retrieval-induced forgetting.

Together, the results from fMRI and EEG studies investigating the neural correlates of the effects of inhibition during the test phase suggest that retrieval-induced forgetting arises due to a weakening of the unpracticed items' memory representations, thus supporting an inhibitory account of retrieval-induced forgetting. Moreover, the studies by Spitzer et al. (2009) and Wimber et al. (2008) revealed distinct neural markers for retrieval-induced forgetting and retrieval-induced enhancement during test. This finding speaks against a blocking account of retrieval-induced forgetting that assumes interdependency of enhancement and forgetting.

In sum, these studies paint a coherent picture of how retrieval-induced forgetting is mediated in the brain and are well in line with previous behavioral work. Inhibition, operating during the retrieval practice phase, is mediated by prefrontal areas, like the ACC and the LPFC, suppressing the interfering items' memory representations. Prefrontal activation predicted later retrieval-induced forgetting, thereby directly linking neural correlates with behavior. The inhibitory effects of the retrieval-practice phase can be observed during the subsequent test phase. Neural substrates were found that indicated the weakening of unpracticed items by inhibition and were correlated with the inter-individual level of forgetting. The involvement of the prefrontal cortex throughout the studies supports the view that inhibition in selective memory retrieval is an executive control mechanism.

Scope of the Present Work

Retrieval from episodic memory induces interference from related, irrelevant information. Human memory is capable of resolving such interference. The question of how the human cognitive system achieves this has been intensively investigated using the retrieval-practice paradigm (Anderson et al., 1994). Considerable evidence has been produced in favor of an inhibitory account of retrieval-induced forgetting.

One major goal of the present thesis was to investigate the inhibitory mechanism “as it operates” in the neural system. For this purpose, two electrophysiological experiments were conducted (Experiment 1 and 2) to examine oscillatory correlates of inhibition during selective memory retrieval. Because of its very high temporal resolution, analyzing electrophysiological activity during the retrieval-practice phase is capable of providing insights into the highly dynamic processes underlying inhibition in selective memory retrieval. The present work accounts for the dynamic nature of these cognitive processes by analyzing brain oscillatory activity in the EEG. Brain oscillations are assumed to reflect the concurrent activation and reactivation of neural assemblies, thereby mediating communication within local networks as well as among distant brain areas (see Fuster, 1997, for a review). The dynamics of inhibition were disentangled by comparing repeated cycles of selective retrieval, assuming that the engagement of inhibition is reduced across retrieval cycles (see Kuhl et al., 2007), thereby isolating the inhibitory mechanism and simultaneously controlling for effects of general retrieval-related activity or repetition priming.

A second major goal was to test whether an oscillatory correlate of inhibition generalizes across retrieval from episodic (Experiment 1) and retrieval from semantic memory (Experiment 2). All of the previous studies on neural correlates of inhibitory processes during selective memory retrieval investigated episodic memory, none of them semantic memory. However, retrieval-induced forgetting has been shown to occur also in semantic memory (Blaxton & Neely, 1983; Brown et al., 2005; Johnson & Anderson, 2004). To this end, Experiment 2 was designed to investigate oscillatory correlates of inhibition during retrieval from semantic memory. The design and procedure of Experiment 2 were based on Experiment 1, but adjusted such that inhibition was triggered due to interference in semantic, not episodic memory. The results of Experiment 2 will provide first evidence about the nature of the neural mechanisms of inhibition in semantic memory retrieval and advance the understanding of inhibitory functioning in memory retrieval on a neural level. Moreover, by matching the procedures of Experiment 1 and 2, intriguing insights into the similarities and differences between semantic and episodic memory retrieval on a neural basis can be gained.

Another major scope of the present work was to advance the understanding of the effects of inhibition on a theoretical level. Inhibitory theory claims that interference is resolved by weakening the interfering items' memory representations. How exactly inhibition affects the representation of a memory item is yet not well understood. In the present work, the impact of inhibition on the absolute and the relative strength of interfering items was investigated in two behavioral experiments.

In order to test the impact of inhibition on the absolute item strength, a recognition test procedure was employed in the retrieval-practice paradigm (Experiment 3). Using a reexposure condition as a baseline that does not induce interference from unpracticed material, inhibition-specific effects were isolated. The aim of Experiment 3 was to show that the absolute item strength of unpracticed material is impaired in the selective retrieval condition, but not in the reexposure condition.

The impact of inhibition on the relative strength of an item within a memory search set was investigated by analyzing recall latencies during free recall (Experiment 4). On the basis of two-stage models of recall (e.g., Raaijmakers & Shiffrin, 1981; Rohrer, 1996), which suggest that the sampling of an item depends on its relative strength within a memory search set, parameters characterizing the sampling probabilities of items were estimated (Rohrer & Wixted, 1994). If inhibition weakened the memory representations of interfering items during selective retrieval, the relative strength of such items within a search set should be affected. By comparing recall latencies during free recall in a selective retrieval and a reexposure condition, the effects of inhibition on the sampling stage of recall were isolated.

Part II

Oscillatory Correlates of Inhibition

Brain Oscillations

In the present thesis, electroencephalography (EEG) is used to investigate the dynamics of inhibition in selective memory retrieval. EEG is especially capable of revealing such dynamic processes, because it can track neural signals at very high temporal resolution. The EEG noninvasively measures electric potentials by means of electrodes at the head surface. The changes in voltage are due to summated excitatory post-synaptic potentials. The electrical activities of populations of neurons, representing a current dipole, are picked up by the EEG (see Lopes da Silva, 2010, for a review).

Starting with Hans Berger in the 1920s, the use of EEG has become common to cognitive neuroscientists today. A large portion of EEG research has focused on event-related potentials (ERPs), a method that basically averages the raw signal in the time domain, typically the moment when a stimulus (event) is presented. The present work focuses on a different way of analyzing the EEG, brain oscillations. A raw EEG signal can be decomposed into different brain oscillations by the means of a Fourier transform (or related analyses, like FFT or wavelet transforms). Today, brain oscillations are interpreted as a representation of the communication in the brain. This communication among distant brain areas as well as within local networks is believed to rely on the concurrent activation and reactivation of neural assemblies which is picked up by oscillations (see Fuster, 1997, for a review).

Every oscillation can be characterized by three parameters: frequency, phase, and amplitude. These parameters can be used to describe different patterns of neural activity and relate them to cognitive functioning. In the frequency domain, different frequency bands are defined. It is assumed that different networks in the brain oscillate in distinct frequency bands. Buzsáki (2006) proposed an inverse relationship between the size of network and the frequency they oscillate in. Small networks oscillate in high frequencies, for example, in the gamma range (frequencies > 30 Hz), and large networks oscillate in slower frequencies, for example, the alpha (~8-13 Hz) or the theta (~4-8 Hz) range.

Amplitude and phase of an oscillation are often used to characterize different forms of communication in the brain (see Varela, Lachaux, Rodriguez, & Martinerie 2001, for a review). Communication in local networks can be characterized by the amplitude of an oscillation. The amplitude is a measure of the local synchrony of cell assemblies in this particular network. Whereas the amplitude is known to fluctuate in spontaneous EEG (e.g., higher alpha amplitudes with eyes closed than eyes open), it is also known to be stimulus driven. Typically, after the presentation of a sensory stimulus, amplitudes in the theta and gamma band are increasing (synchronization), amplitudes in the alpha band are decreasing (desynchronization).

The phase of an oscillation can be used to estimate the communication between distant networks in the brain. The stability of the difference in phase between two (or more) different electrodes is assumed to reflect the long-range wiring of neural cell assemblies (Fries, 2005). Thus, a constant phase coupling across trials of an experiment can be interpreted as neural communication between distant brain regions, for example, between frontal and parietal networks in the brain. Besides the characterization of global synchronization, phase information can also be informative on a local level. The phase of an oscillation is assumed to trigger excitation and inhibition of neurons. Thus, the difference in phase across trials at a single electrode is a measure of the precise timing of the local neural assemblies picked up at that particular electrode site. The present work focuses on local synchronization by analyzing amplitudes of oscillatory activity.

Additionally, spatial information from multiple electrode sites can be used to characterize oscillations. Interpretation of the spatial distribution of electric activity on the scalp level has to be approached with caution, because the number and direction of the dipoles generating the particular pattern are unknown. Despite the presence of the inverse problem (deduction of the source current underlying to the measured activity at the scalp), advanced methods allow for localizing EEG activity (e.g., Beamformer) and add spatial information to its otherwise sparse spatial resolution. Thereby, source localization facilitates relating EEG results to other neuroimaging techniques like fMRI. The present work incorporated such a technique.

Experiment 1

The goal of Experiment 1 was to investigate brain oscillatory correlates of inhibition within the retrieval-practice paradigm "as it operates" in the neural system. Several recent studies investigated the neural correlates of retrieval-induced forgetting. FMRI findings suggest that inhibition in selective memory retrieval is related to initial activation and subsequent down-regulation of activation in anterior cingulate cortex (ACC) and lateral prefrontal areas (Kuhl et al., 2007, 2008; Wimber et al., 2008, 2009). Concerning brain oscillations, Hanslmayr et al. (2010) compared a competitive retrieval condition (FRUIT - O___) with a noncompetitive retrieval condition (FRU___ - Orange). This comparison is well suited to control for retrieval-related activity, but is not capable of controlling for effects of task difficulty or repetition priming.

In an effort to control for these confounds, the retrieval-practice paradigm was modified in Experiment 1, such that repeated cycles of selective retrieval and reexposure were employed. Because retrieval, but not reexposure, of previously studied material triggers inhibition in episodic memory (Anderson et al., 2000; Bäuml & Aslan, 2004), it was examined whether selective retrieval, but not reexposure, would be selectively associated with oscillatory activity. Examining the dynamics of inhibition, oscillatory activity was analyzed across repeated practice cycles of selective retrieval, expecting that inhibitory engagement would be reduced in the second as compared to the first cycle (Kuhl et al., 2007). A brain oscillatory correlate of inhibition should be largely unaffected across reexposure cycles. Moreover, measuring oscillatory activity across repeated cycles of reexposure controlled for effects of repetition priming.

Following the results of Hanslmayr et al. (2010), a prominent candidate for an oscillatory correlate of inhibition in memory retrieval could be theta oscillatory activity. Hanslmayr et al. (2010) found the difference in theta power between the competitive and non-competitive condition to be predictive of the amount of retrieval-induced forgetting, although, somewhat puzzling, the correlation was negative. A priori, one would have expected a positive relationship reflecting active inhibition being related to retrieval-induced forgetting. Another prominent candidate for reflecting inhibition was oscillatory activity in the alpha band. Alpha oscillations have been repeatedly related to top-down inhibition (see Klimesch, Sauseng, & Hanslmayr, 2007, for a review). Evidence from a directed forgetting study (Bäuml, Hanslmayr, Pastötter, & Klimesch, 2008) suggests that alpha oscillations selectively mediate the intentional suppression of previously studied information. If inhibition is a domain-general executive control mechanism, (see Anderson, 2003), alpha oscillations should also reflect unintentional inhibition in the retrieval-practice paradigm.

Experiment 1 investigates oscillatory correlates of inhibition during selective memory retrieval. Because retrieval, but not reexposure, of previously studied material triggers inhibition (Anderson et al., 2000; Bäuml & Aslan, 2004), the oscillatory correlate of inhibition was expected to be active during selective retrieval as compared to reexposure. Examining the dynamics of inhibition, selective retrieval and reexposure were analyzed across repeated practice cycles, expecting that an oscillatory correlate of inhibition would be reduced across retrieval cycles (Kuhl et al., 2007), but largely unaffected across reexposure cycles. Particularly, it was hypothesized that the sources of such an oscillatory correlate of inhibition are localized in the ACC. Finally, brain-behavior correlations were conducted to clarify the relationship between brain oscillatory activity and retrieval-induced forgetting. By grouping participants according to their behavioral suppression effect, that is, the amount of retrieval-induced forgetting, differences in oscillatory activity between participants were expected to reflect the different degrees of retrieval-induced forgetting.

Methods

Subjects

Twenty-seven adults participated in the experiment on a voluntary basis. Three of them were excluded from data analysis, because their EEG was heavily contaminated by movement artifacts. The remaining 24 subjects (19-33 years old, 21 women, three men) had normal or corrected to normal vision, had German as their native language, and reported no history of neurological disease. Subjects received course credit or 25 € for participation.

Materials

Stimuli were 216 German nouns from 36 semantic categories, drawn from several published norms (Mannhaupt, 1983; Scheithe & Bäuml, 1995). Each category consisted of six items with unique first letters with respect to their category. In each category, four items were low-frequency exemplars within their category (mean rank = 25.1, *SD* = 7.2); those items were practiced in the intermediate phase of the reexposure and the selective retrieval condition, and are referred to as “to-be-practiced items”. Two items in each category were high-frequency exemplars within their category (mean rank = 7.8, *SD* = 1.5); these items were not practiced, and are referred to as “unpracticed items”. Previous work has shown that high-frequency items of a category are more likely than low-frequency items to interfere during retrieval, and are therefore more likely to be subject to retrieval-induced forgetting (Anderson et al., 1994; Bäuml, 1998).

Design

An outline of the experimental design can be seen in Figure 2. The experiment consisted of three blocks (within-subjects design), each of which comprised a study phase, an intermediate phase, and a test phase. Blocks differed in the list that was provided and the type of CONDITION (selective retrieval vs. reexposure vs. control) conducted during the intermediate phase. In the selective retrieval condition, category labels and word stems of the four to-be-practiced (low-frequency) items (FRUIT - Man___) of each category were presented, and subjects were instructed to retrieve the corresponding items. In the reexposure condition, category labels together with the categories' four to-be-practiced (low-frequency) items (FRUIT - Mango) were presented intact, and subjects were instructed to restudy the items to enhance their performance on the upcoming test (e.g., Bäuml & Aslan, 2004). Both practice procedures were repeated once in the intermediate phase, resulting in a first ("SR1") and second ("SR2") practice cycle in the selective retrieval condition and a first ("RE1") and second ("RE2") practice cycle in the reexposure condition. In the control condition, no practice of studied items took place, and subjects performed a distracter task instead.

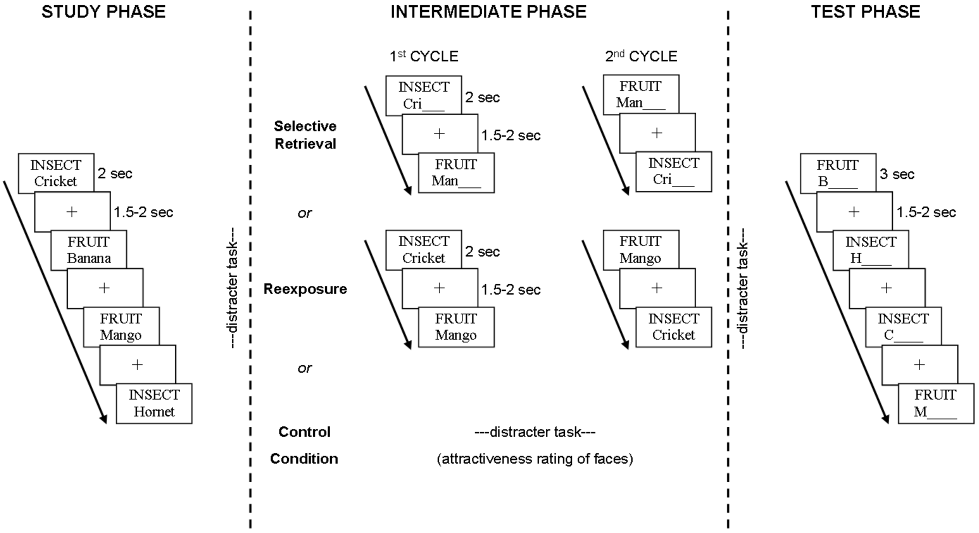


Figure 2. The experimental procedure as employed in Experiment 3. The experiment consisted of three blocks, each block comprising a study phase, an intermediate phase, and a test phase. In the study phase of each block, items were studied together with their category cue. In the test phase of each block, all of the items were tested using a cued recall test. The intermediate phase varied with condition: in the selective retrieval condition, a subset of the previously studied items was retrieved on two consecutive cycles; in the reexposure condition, the same subset of items was restudied on two consecutive cycles; in the control condition, no practice took place, and subjects conducted a distracter task instead. EEG was recorded during the intermediate phase of the selective retrieval and the reexposure block.

This design created practiced (low frequency) and unpracticed (high frequency) items for both the selective retrieval and the reexposure condition. Although there was no practice in the control condition, control items were split according to their normative frequency within the category to match practiced and unpracticed items. Accordingly, the beneficial effect (enhancement) of practice was defined as the difference in recall performance between low-frequency items in the control condition and practiced (low-frequency) items in either the selective retrieval or the reexposure condition. The detrimental effect (forgetting) was defined as the difference in recall performance between high-frequency control items and unpracticed (high-frequency) items in either the selective retrieval or the reexposure condition. The assignment of list to condition was counterbalanced across subjects, and the order of blocks was randomized.

Procedure

Subjects were tested individually in a quiet surrounding, seated in front of a 15-inch computer screen (70 Hz refresh rate).

Study Phase

Each of the three conditions started with a study phase, in which one list, consisting of 72 items from twelve different categories (e.g., FRUIT-Mango), was presented. The items of a list were presented sequentially in random order. A trial in the study phase started with a fixation cross with variable duration (1500-2000 msec). Thereafter, the stimulus word together with its category label was presented for 2000 msec. After the study phase, the subjects performed a distracter task for 30 sec, during which they were asked to rate pictures of famous and non-famous persons according to their attractiveness.

Intermediate Phase.

In the selective retrieval condition, subjects were asked to retrieve the respective memory item, which was cued by its category label and its unique word stem. Following the procedure of Johansson et al. (2007), subjects were asked to covertly retrieve the to-be-practiced items during selective retrieval, in order to avoid EEG artifacts elicited by speech. In the reexposure condition, to-be-practiced items were presented intact together with their category label. Subjects were asked to (quietly) restudy the items for the final recall test. In both the retrieval and the reexposure condition, a trial consisted of a fixation cross of variable duration (1500-2000 msec). Thereafter, the memory item (reexposure condition) or the item's word stem (retrieval condition) was presented for 2000 msec together with the item's category label. Items order in the intermediate phase was block randomized dividing the intermediate phase into four blocks that each contained one low frequency item from each of the list's categories. Both practice procedures were repeated once in the intermediate phase, and ended by another distracter task (attractiveness rating) of 30 sec. In the control condition, subjects performed a distracter task (attractiveness rating) rather than retrieving or relearning any items. Duration of the intermediate phase was held constant across conditions.

Test Phase

After the intermediate phase, a cued recall test was carried out in which all items were tested. A fixation cross with variable duration (1500-2000 msec) was presented prior to the memory item's cue. The memory cue consisted of the category name together with the first letter of the item, and was shown for 3000 msec. After cue presentation, participants were asked to respond orally with the corresponding item of the study list. Unpracticed (high-frequency) items of a category were tested first, followed by the practiced (low-frequency) items of the category. Order of categories was held constant across subjects, except for being reversed after half of the subjects, such that across subjects, each category had the same mean position. Mean recall frequency was used as dependent variable.

EEG Recording

During the intermediate phase in the selective retrieval and the reexposure conditions, the EEG was recorded from 62 Ag/AgCl scalp electrodes positioned according to the extended 10–20-system. EEGs were recorded against a reference electrode placed at FCz, and were later rereferenced against a common average reference. The vertical and the horizontal electrooculogram (EOG) were recorded from two additional channels to control for eye movements and blinks. Impedances were kept below 20 kΩ. A Brainamp MR+ amplifier (Megis, BrainVision, Gilching, Germany) was used for data acquisition. Sampling rate was 500 Hz.

Frequencies between 0.3 and 70 Hz were recorded, with a Notch-filter at 50 Hz. Prior to data analysis, EEG-data were corrected for EOG artifacts using calibration data to generate individual artifact coefficients and the algorithm implemented in the software package BESA (MEGIS Software BESA v5.1.8, see Ille, Berg & Scherg, 2002, for details). Remaining artifacts, due to muscle activity or poor EOG correction, were excluded by visual inspection.

Event-Related Potentials

In order to relate the present results in theta band activity to earlier electrophysiological findings in a similar experimental setting by Johansson et al. (2007), event-related potentials (ERPs) were investigated. For reasons of comparability, the EEG was digitally rereferenced against the mean of the left and the right mastoids. To analyze ERP waveforms, BESA (MEGIS Software BESA v.5.1.8) software and self-written Matlab codes (The Mathworks Inc.) were used. The data were epoched from -200 to 2000 msec. Before statistical comparison, the ERP waveforms were baseline corrected with respect to a prestimulus interval of -200 to 0 msec and low pass filtered at 15Hz (48db/oc, zero phase). Separately for the two practice cycles, paired comparisons across conditions (SR1 vs. RE1; SR2 vs. RE2) were conducted using Wilcoxon sign-rank tests (two-tailed). A randomization test (see Statistical Analyses) was used to check for significance of the effects.

Analysis of Oscillatory Amplitude

Time–frequency analyses were conducted using the BESA (MEGIS Software BESA v5.1.8) software package and self-written Matlab codes (The Mathworks Inc.). The EEG data were segmented into 2000 msec epochs (ranging from 500 ms preceding stimulus onset to 1500 ms after stimulus onset). To avoid filter artifacts at the edges of the epochs, the data was filtered in a slightly bigger time interval, but analysis was restricted to the 2000 msec time window. For analysis of low-frequency oscillatory amplitude, data was filtered in a frequency range of 4 to 20

Hz using BESA's time–frequency analysis module, with time–frequency resolution set to 111 msec and 1.99 Hz (full width half maximum), corresponding to a time-frequency sampling of 50 msec and 1 Hz. For analysis of high-frequency oscillatory amplitude, data was filtered in a frequency range of 20 to 70 Hz using BESA's time–frequency analysis module, with time–frequency resolution set to 22.2 msec and 9.93 Hz (full width half maximum), corresponding to a time-frequency sampling of 10 msec and 5 Hz.

To analyze event-related amplitude changes, the percentage of amplitude change in relation to a prestimulus baseline (set to 500-0 msec prior stimulus onset) was calculated. For statistical comparisons, the data were collapsed in order to obtain six frequency bands, theta (5-9 Hz), alpha (9-13 Hz), beta1 (13-20 Hz), beta2, (20-30 Hz), gamma1 (35-45 Hz) and gamma2 (55-70 Hz), and to obtain three consecutive time windows: T1 (0-500 msec); T2 (500-1000 msec); and T3 (1000-1500 msec).

Statistical Analyses

In order to investigate whether the difference between SR1 and SR2 is reliably bigger or smaller than the difference between RE1 and RE2, a CONDITION by CYCLE interaction was tested first. For those frequency bands which exhibited a significant interaction, pair-wise comparisons (Wilcoxon sign-rank tests, two-tailed) across conditions in the first cycle (SR1 vs. RE1) and between the first and the second cycle for each condition (SR1 vs. SR2; RE1 vs. RE2) were conducted. Time windows exhibiting significant effects were identified for each electrode position. The number of electrodes showing significant effects ($p < .05$) was then checked for significance by a randomization test using 2000 permutation runs. In this procedure, the two conditions were interchanged randomly for each subject and each randomization run, thereby eliminating any systematic difference between the conditions. After each randomization run, Wilcoxon sign-rank tests were calculated, returning the number of electrodes showing a significant difference between the two conditions. After 2000 permutation runs, a random distribution of the number of electrodes showing significant effects by chance is generated. This distribution is used to determine the p-level of an experimental effect, reflecting how many times a given number of significant electrodes (e.g., 8) was exceeded during the permutation runs (values higher than 8). Thus, the p-level reflects the probability that a given number of electrodes exhibiting a significant difference between two conditions is found by chance. This method is based on the algorithm described by Blair & Karniski (1993) and was already applied in several published studies (Hanslmayr et al., 2007, Hanslmayr, Spitzer, & Bäuml, 2009).

Brain-Behavior Correlations

Following Kuhl et al. (2007), brain-behavior correlations were calculated based on suppression scores, which depict an individual measure of retrieval-induced forgetting relative to recall performance in the control condition,

$$\text{suppression score} = \frac{C^{-} - SR^{-}}{C^{-}},$$

where C^{-} equals the number of remembered high-frequency items from the control condition and SR^{-} equals the number of remembered unpracticed, high-frequency items from the selective retrieval condition.

In the same manner, an enhancement score was established, which depicts individual retrieval-induced enhancement relative to recall performance in the control condition,

$$\text{enhancement score} = \frac{SR^{+} - C^{+}}{C^{+}},$$

where SR^{+} equals the number of remembered practiced, low-frequency items from the selective retrieval condition and C^{+} equals the number of remembered low-frequency items from the control condition. As electrophysiological measures, differences in amplitude across cycles in the selective retrieval condition were used, but only for those frequency bands and time windows which showed a significant effect in the interaction analysis. These particular time-windows and frequency bands are supposed to reflect neural activity due to inhibition.

Source Localization

To localize the sources of oscillatory activity, the Multiple-Source Beamformer approach was used as implemented in BESA. This method is a modified version of the linearly constrained minimum variance vector Beamformer (Gross et al., 2001). This algorithm allows imaging evoked and induced oscillatory activity in a user-defined time-frequency domain. Note that in contrast to other source analysis methods, like dipole fitting techniques, this approach does not require a priori knowledge of the number or location of sources. The Beamformer computes the changes of power in a poststimulus interval relative to a prestimulus baseline (set to 500-0 ms prior stimulus onset), transforming data into standard MNI space (Montreal Neurological Institute, Montreal, Quebec, Canada). Beamformer source analysis was carried out for each cycle in the selective retrieval condition separately (SR1 and SR2), but only for those time - frequency windows which exhibited significant effects in the interaction analysis on the scalp electrode level and showed a significant correlation with behavioural measures. Differences in power in the theta band (5-9 Hz) between SR1 and SR2 were examined by Wilcoxon tests. Analysis and plotting of the results was done using the Matlab toolbox Fieldtrip (can be downloaded at http://www.ru.nl/fcdonders/fieldtrip) and self-written Matlab codes.

Results

Behavioral Results

The behavioral results are depicted in Figure 3.

Forgetting

Mean recall performance for unpracticed items was 35.6 % (*SE* = 3.6 %) in the selective retrieval condition, 45.3 % (*SE* = 2.6 %) in the reexposure condition, and 47.8 % (*SE* = 3.3 %) in the control condition (Fig. 3). A one-way ANOVA for the unpracticed items yielded a significant main effect of CONDITION (selective retrieval, reexposure, control), [$F_{2,46} = 4.94$, $p < .05$]. Recall performance for unpracticed items in the selective retrieval condition differed significantly from the control condition [$t_{23} = 3.04$, $p < .01$] and the reexposure condition [$t_{23} = 2.55$, $p < .05$]. In the reexposure condition, subjects did not recall significantly less unpracticed items than in the control condition [$t_{23} = .54$, $p = .59$].

Enhancement

Mean recall performance for practiced items was 70.0 % (*SE* = 3.0 %) in the selective retrieval condition, 67.1 % (*SE* = 3.3 %) in the reexposure condition, and 42.8 % (*SE* = 3.1 %) for corresponding low-frequency items in the control condition (Fig. 3). A one-way ANOVA for the practiced items yielded a significant main effect of CONDITION (selective retrieval, reexposure, control), [$F_{2,46} = 95.2$, $p < .001$]. Recall rates for practiced items in the selective retrieval condition and the reexposure condition did not differ [$t_{23} = 1.45$, $p = .16$], but in both conditions, practice led to higher recall levels compared with the control condition [$t_{23} > 9.5$, $p < .001$, for both paired comparisons]. Enhancement was not significantly correlated with forgetting [$r = -.15$, $p = .49$].

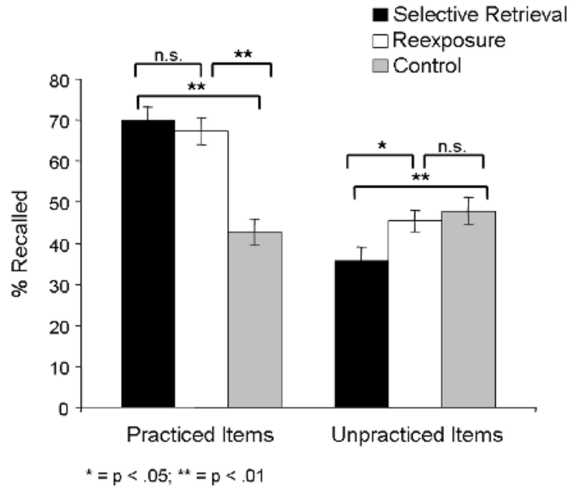


Figure 3. Behavioral results. Forgetting, as indicated by the difference in recall rates between unpracticed (high-frequency) items and high-frequency control items, is depicted on the right (error bars indicate S.E.). Whereas recall of unpracticed items in the reexposure condition did not differ from recall in the control condition, less unpracticed items were recalled in the selective retrieval condition than in the reexposure and the control condition. On the left, enhancement, as indicated by the difference in recall rates between practiced (low-frequency) items and low-frequency control items, is depicted. Recall rates of practiced items did not differ between the selective retrieval and the reexposure condition, but in both conditions more practiced items were recalled than in the control condition.

EEG-Results

Event-Related Potentials

For the first practice cycle, the ERP waveforms for SR1 and RE1 are shown for nine electrodes covering frontal, central, and parietal regions of the scalp (Fig. 4a). An effect in a large time window (750 - 1500 msec, $p_{\text{corr}} < .01$) was found, with frontal electrodes showing larger positive-going amplitudes during SR1 than RE1 (Fig. 4b). This effect replicates the findings by Johansson et al. (2007), who used only one practice cycle, in showing that selective retrieval induces larger sustained positivity over frontal electrode sites than reexposure. While for the first practice cycle, 27 electrodes were identified showing more positive-going amplitudes during SR1 than RE1, for the second practice cycle only 9 electrodes showed this effect. The difference in the second cycle turned out to be only marginally significant ($p < .10$), although statistically it did not differ in size from the effect in the first practice cycle ($p > .11$). Note that the present results are somewhat less sustained than those reported by Johansson et al. (2007). This might be due to the fact that the EEG was recorded with a low-cutoff filter at 0.3 Hz, which decreases the contribution of slow potentials to the ERP waveforms.

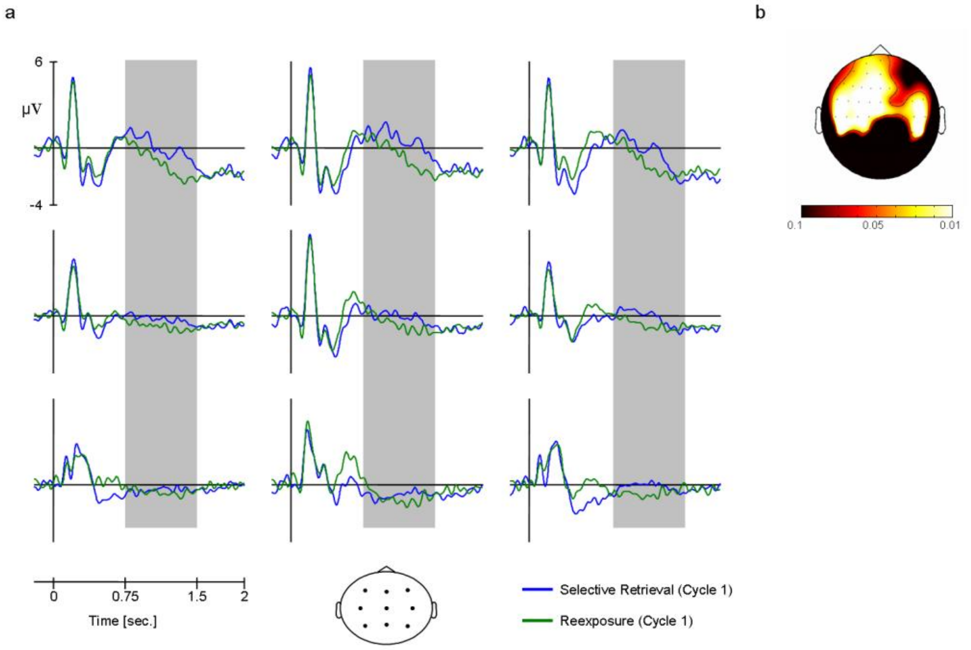


Figure 4. (a) The ERP waveforms of the selective retrieval condition (SR1) and the reexposure condition (RE1) are depicted for nine electrodes covering the frontal, central, and parietal regions of the scalp. (b) Significant electrode sites, obtained by the Wilcoxon sign-rank tests, are shown.

Interaction Analysis

An interaction analysis with the factors CONDITION (selective retrieval vs. reexposure) and CYCLE (first vs. second cycle) was conducted (an overview of the results is shown in Table 1).

Table 1. Number of electrodes showing significant differences in the interaction analysis in each of the time windows (T1 = 0-500 msec, T2 = 500-1000 msec, T3 = 1000-1500 msec).

	[SR1-SR2] > [RE1-RE2]			[SR1-SR2] < [RE1-RE2]		
	T1	T2	T3	T1	T2	T3
Theta(5-9)	7	11*	1	0	0	1
Alpha(9-13)	0	0	0	5	2	7*
Beta1(13-20)	0	0	0	1	5	22**
Beta2(20-30)	0	1	0	2	3	11*
Gamma1(30-45)	1	3	2	3	1	1
Gamma2(55-70)	0	2	5	0	0	0

*= $p_{\text{corr}} < .05$; ** = $p_{\text{corr}} < .01$

Theta Band. A significant interaction effect in the theta band (5-9 Hz) was revealed in the second time window (500-1000 msec, $p_{\text{corr}} < .05$), which was located over mid-frontal electrode positions. This effect was due to a pronounced power decrease across cycles in the selective retrieval condition, which was not evident in the reexposure condition (see Fig. 5a).

Alpha Band. In the alpha band (9-13 Hz), a significant interaction effect was found in the third time window (1000-1500 msec, $p_{\text{corr}} < .05$). It was located over occipital and central electrode positions, due to a larger decrease in alpha amplitude in the selective retrieval than in the reexposure condition in the third time window (see Fig. 5b).

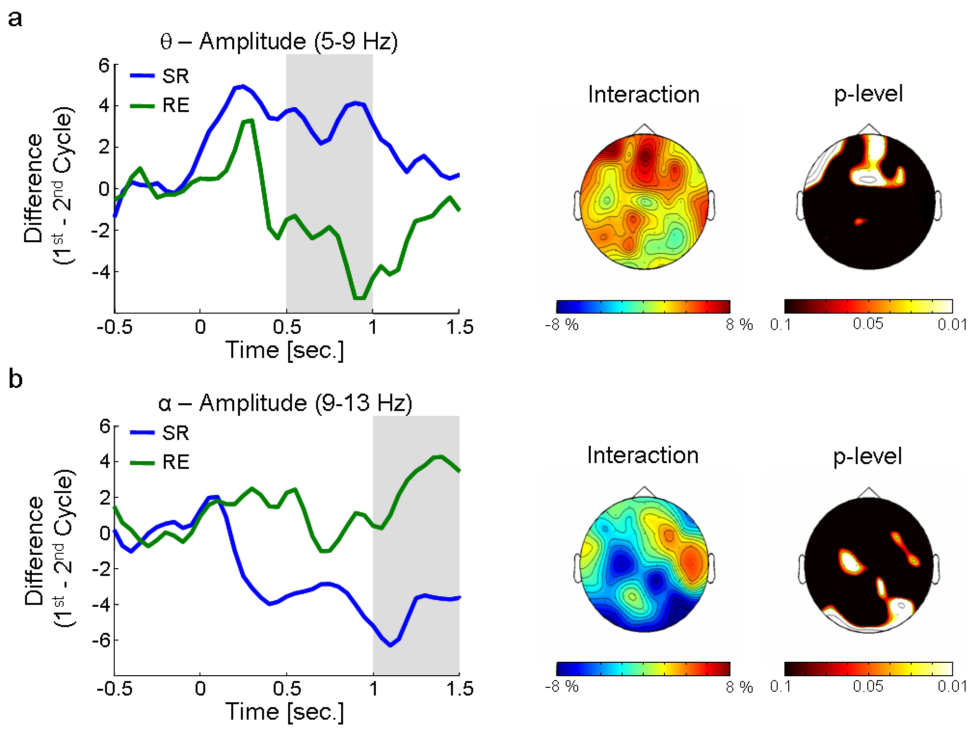


Figure 5. Interaction analysis (CONDITION x CYCLE). Left column: The time course of the difference in amplitude across cycles (1^{st} - 2^{nd} Cycle) in the selective retrieval (SR) condition and across cycles in the reexposure condition (RE), averaged over those electrode positions showing a significant effect, is depicted. Time windows corresponding to adjacent topographies are colored gray. Right column: Topographies of the interaction (left) and significant electrodes obtained by Wilcoxon sign-rank tests (right) is depicted. (a) In the theta band, a significant effect was found in the second time window (0-500 msec), located over mid-frontal and electrode positions. (b) In the alpha band, the third time window (1000-1500 msec) showed a significant effect, most pronounced over occipital and central electrode positions.

Beta1 Band. In the beta1 band (13-20 Hz), the interaction analysis yielded a significant effect in the third time window (1000-1500 msec, $p_{corr} < .01$), located over occipital and left central electrode positions. This effect was due to a large decrease in beta1 amplitude across cycles during selective retrieval in the third time window, which was reversed in the reexposure condition (see Fig. 6a).

Beta2 Band. A significant interaction effect in the beta2 band (20-30 Hz), was found in the third time window, ($p_{corr} < .05$), located over occipital and central electrode positions, due to a larger decrease in alpha amplitude in the selective retrieval than in the reexposure condition in the third time window (see Fig. 6b).

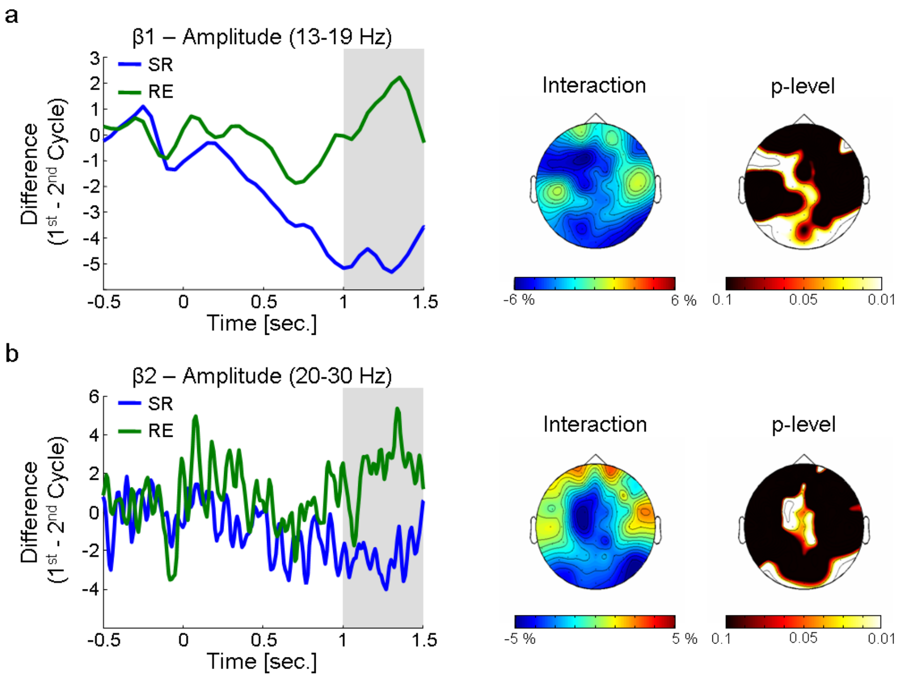


Figure 6. Interaction analysis (CONDITION x CYCLE). Left column: The time course of the difference in amplitude across cycles (1^{st} - 2^{nd} Cycle) in the selective retrieval (SR) condition and across cycles in the reexposure condition (RE), averaged over those electrode positions showing a significant effect, is depicted. Time windows corresponding to adjacent topographies are colored gray. Right column: Topographies of the interaction (left) and significant electrodes obtained by Wilcoxon sign-rank tests (right) is depicted. (a) In the beta1 band, a significant effect was found in the third time window (1000-1500 msec), most pronounced over left-central and occipito-parietal electrode positions. (b) In the beta2 band, the third time window (1000-1500 msec) showed a significant effect, located over central and occipital electrode positions.

No interaction effects were found in the gamma1 or the gamma 2 band (30-45 Hz, and 55-70 Hz, respectively).

Based on the results of the interaction analysis, all subsequent analysis of oscillatory activity were restricted to those frequency bands showing a significant interaction effect (theta, alpha, beta1, and beta2 band).

Selective Retrieval vs. Reexposure

An overview of the results of the comparison of the first cycles across conditions (SR1 vs. RE1) is shown in Table 2.

Table 2. Number of electrodes showing significant differences in the comparison between the first cycle of the selective retrieval and the reexposure condition (SR1 > RE1 / SR1 < RE1) in each of the three time windows (T1 = 0-500 msec, T2 = 500-1000 msec, T3 = 1000-1500 msec).

	SR1 > RE1			SR1 < RE1		
	T1	T2	T3	T1	T2	T3
Theta(5-9)	12**	1	0	0	0	9*
Alpha(9-13)	0	0	0	6	24**	15*
Beta1(13-20)	0	0	0	1	25**	35**
Beta2(20-30)	0	1	2	9*	24**	23**

*= $p_{\text{corr}} < .05$; ** = $p_{\text{corr}} < .01$

Theta Band. Comparing the first cycle of the selective retrieval (SR1) with the first cycle of the reexposure (RE1) condition, statistical analyses revealed a difference in the first time window in the theta band (5-9 Hz, 0-500 msec, $p_{\text{corr}} < .01$). Figure 7a shows the larger increase in theta amplitude in SR1 than RE1. The difference was mainly located over mid- and right-frontal and left parietal electrode sites. Whereas there was no difference between conditions in the second time window (500-1000 msec), a significant effect was observed in the third time window (1000-1500 msec), where theta amplitude over central and right parietal electrodes was significantly lower in SR1 than RE1 ($p_{\text{corr}} < .05$; Fig. 7b).

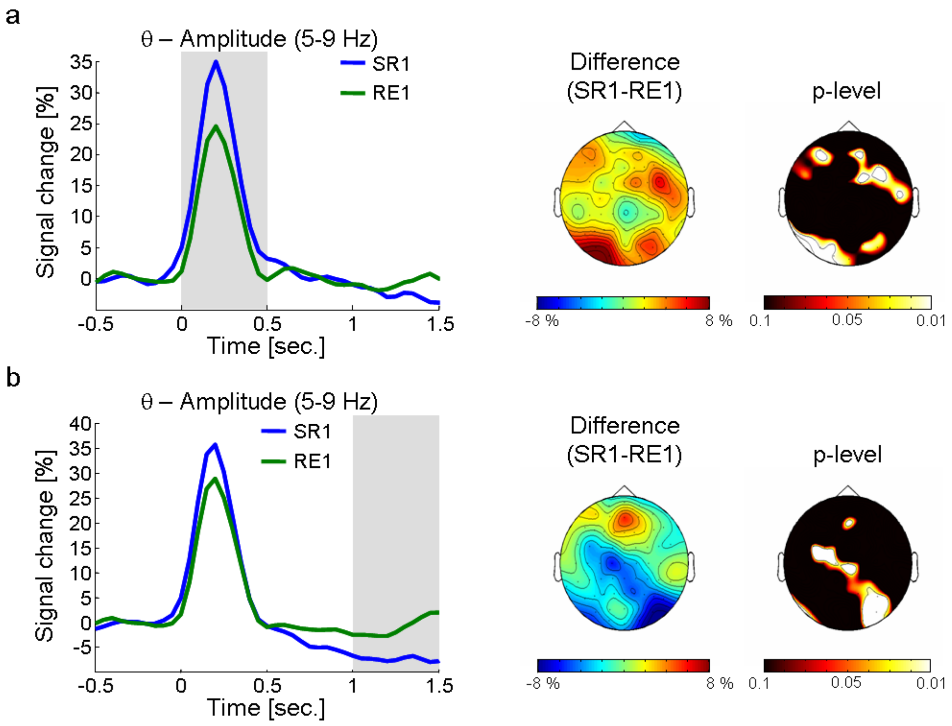


Figure 7. Selective Retrieval (Cycle 1) vs. Reexposure (Cycle 1). Left column: Time course of amplitude, averaged over those electrode positions showing a significant effect. Time windows corresponding to adjacent topographies are colored gray. Right column: Topographies of the difference in amplitude (left) and significant electrodes obtained by Wilcoxon sign-rank tests (right) is depicted. In the theta band, significant effect was found (a) in the first time window (0-500 msec), located over right-frontal and occipital electrode positions and in the (b) third time window (1000-1500 msec), located over right parieto-occipital including central electrode positions.

Alpha Band. In the alpha band (9-13 Hz), statistical analyses revealed a greater decrease in the selective retrieval (SR1) than in the reexposure (RE1) condition, in the second (500-1000 msec, $p_{\text{corr}} < .01$) and third time window (1000-1500 msec, $p_{\text{corr}} < .05$). Figure 8a shows a larger decrease in alpha amplitude during SR1 than RE1. The difference was most pronounced over parieto-occipital, including central electrode positions.

Beta1 Band. A similar pattern to that obtained in the alpha band was found in the beta1 band (13-20Hz). Figure 8b shows a larger decrease in beta1 amplitude in SR1 than RE1 in the second (500-1000 msec, $p_{\text{corr}} < .01$) and third time window

(1000-1500 msec, $p_{\text{corr}} < .01$). The difference was located over occipital, parietal and central electrode sites.

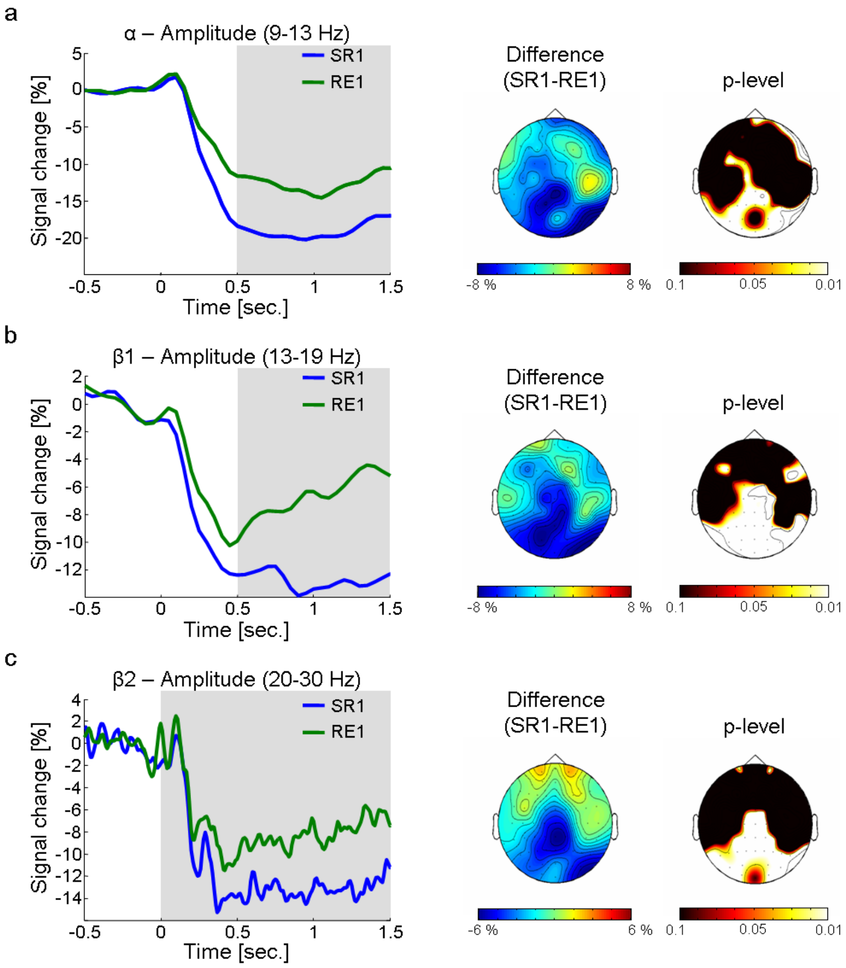


Figure 8. Selective Retrieval (Cycle 1) vs. Reexposure (Cycle 1). Left column: Time course of amplitude, averaged over those electrode positions showing a significant effect. Time windows corresponding to adjacent topographies are colored gray. Right column: Topographies of the difference in amplitude (left) and significant electrodes obtained by Wilcoxon sign-rank tests (right) is depicted. A significant effect was found (a) in the alpha band in the second and third time window (500-1500 msec), located over parieto-occipital and central electrode positions and in the (b) beta1 band in the second and third time window (500-1500 msec), also over parieto-occipital and central electrode positions. (c) In the beta2 band, the difference was significant in all of the three time windows (0-1500 msec), again located over parieto-occipital and central electrode positions.

Beta2 Band. In the beta2 band (30-45 Hz), the decrease was significantly larger in SR1 than RE1 during all of the three time windows (0-500 msec, $p_{\text{corr}} < .05$; 500-1000 msec, $p_{\text{corr}} < .01$; 1000-1500 msec, $p_{\text{corr}} < .01$). Again, the difference was located over parieto-occipital and central electrode positions (see Fig. 8c).

Selective Retrieval – First vs. Second Cycle

An overview of the results of the comparison of the first and the second cycle in the selective retrieval condition (SR1 vs. RE1) is shown in Table 3.

Table 3. Number of electrodes showing significant differences in the comparison between the first and the second cycle of the selective retrieval condition in each of the three time windows (T1 = 0-500 msec, T2 = 500-1000 msec, T3 = 1000-1500 msec)

	SR1 > SR2			SR1 < SR2		
	T1	T2	T3	T1	T2	T3
Theta(5-9)	20**	9*	0	0	0	2
Alpha(9-13)	0	0	0	9*	16**	13*
Beta1(13-20)	0	0	0	4	19**	30**
Beta2(20-30)	0	1	0	5	10*	10*

*= $p_{\text{corr}} < .05$; ** = $p_{\text{corr}} < .01$

Theta Band. Statistical analyses revealed that SR1 differed from SR2 in the theta band (5-9 Hz) in the first (0-500 msec, $p_{\text{corr}} < .01$) and second time window (500-1000 msec, $p_{\text{corr}} < .05$) time window. Figure 9a shows a decrease in theta amplitude from the first to the second cycle. The effect was mainly located over mid-frontal and left parietal electrodes.

Alpha Band. In the alpha band (9-13 Hz), a significantly larger decrease in the first than in the second cycle was found in all of the three time windows (0-500 msec, $p_{\text{corr}} < .05$; 500-1000 msec, $p_{\text{corr}} < .01$; 1000-1500 msec, $p_{\text{corr}} < .01$). Figure 9b shows a relative increase in alpha amplitude from the first to the second cycle. The difference was located over parieto-occipital electrode sites (see Fig. 9b).

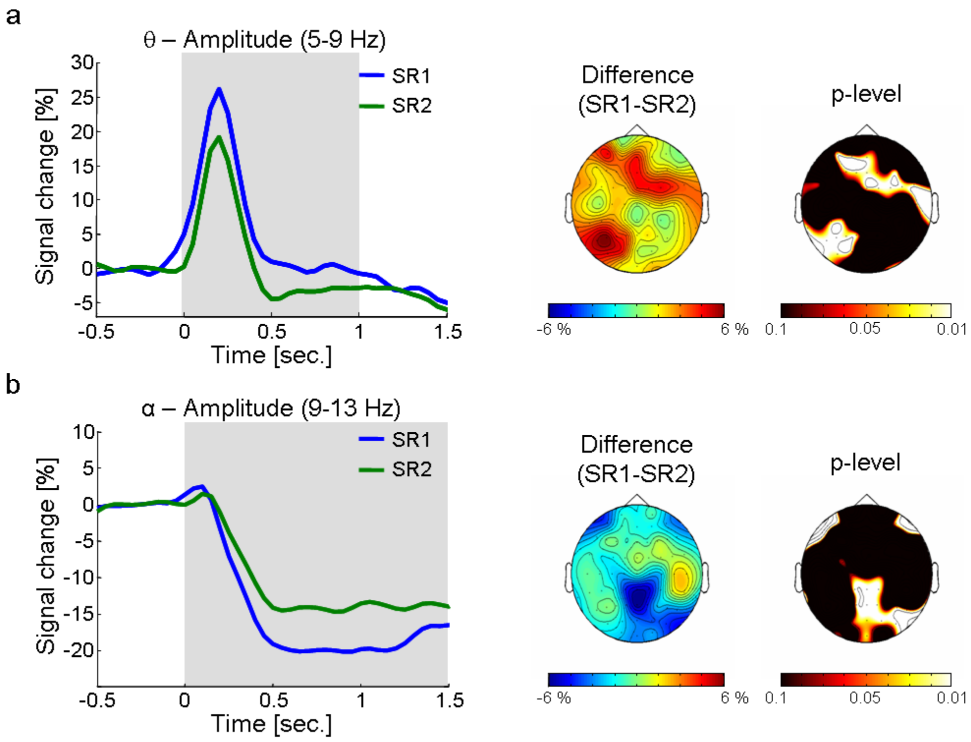


Figure 9. Selective Retrieval, Cycle 1 (SR1) vs. Cycle 2 (SR2). Left column: Time course of amplitude, averaged over those electrode positions showing a significant effect. Time windows corresponding to adjacent topographies are colored gray. Right column: Topographies of the difference in amplitude (left) and significant electrodes obtained by Wilcoxon sign-rank tests (right) is depicted. A significant effect was found (a) in the theta band in the first and second time window (0-1000 msec), located over mid-frontal and left parietal electrode positions. (b) In the alpha band, a significant effect was found in all three time window (0-1500 msec). The difference was located over parieto-occipital electrode positions.

Beta1 Band. In the second (500-1000 msec, $p_{corr} < .01$) and third time window (1000-1500 msec, $p_{corr} < .01$), significant differences were found in the beta1 band (13-20 Hz). A larger desynchronization during the first than the second cycle of selective retrieval was found. The difference was located over parieto-occipital and bilateral frontal electrode sites (see Fig. 10a).

Beta2 Band. The results of the beta2 band (20-30 Hz) were similar to those obtained in the beta1 band. A larger decrease in amplitude during the first than the second cycle of selective retrieval was found in the second (500-1000 msec, p_{corr} <

.05) and the third time window (1000-1500 msec, $p_{corr} < .05$), located over parieto-occipital electrode positions (see Fig. 10b).

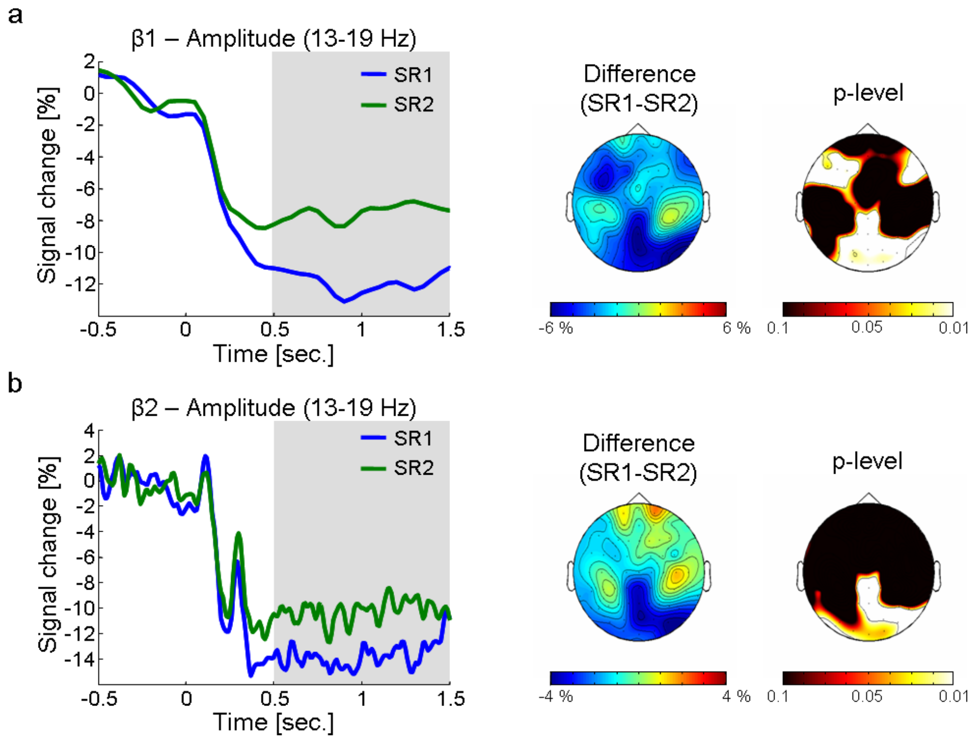


Figure 10. Selective Retrieval, Cycle 1 (SR1) vs. Cycle 2 (SR2). Left column: Time course of amplitude, averaged over those electrode positions showing a significant effect. Time windows corresponding to adjacent topographies are colored gray. Right column: Topographies of the difference in amplitude (left) and significant electrodes obtained by Wilcoxon sign-rank tests (right) is depicted. (a) A significant effect was found in the beta1 band in the second and third time window (500-1500 msec), located over parieto-occipital and bilateral frontal electrode positions. (b) In the second and third time window (500-1500 msec), a significant effect was found in the beta2 band, located over parieto-occipital electrode positions.

Reexposure – First vs. Second Cycle

Comparing the first with the second cycle of the reexposure condition, only one significant effect emerged. In the beta2 band, a larger decrease in the second than in the first cycle was found in the third time window over seven electrodes (1000-

1500 msec, $p_{corr} < .05$).The difference was mainly located over fronto-central electrode positions (see Fig. 11).

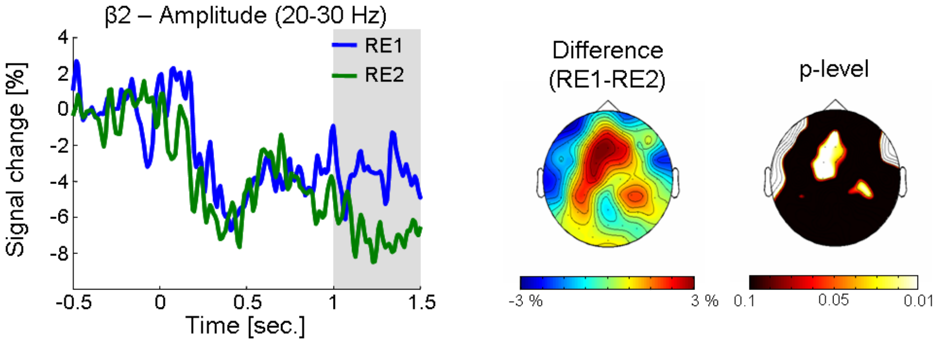


Figure 11. Reexposure, Cycle 1 (RE1) vs. Cycle 2 (RE2). Left column: The time course of the beta2 amplitude, averaged over those electrode positions showing a significant effect, is shown on the left. A significant effect was found in the beta1 band in third time window (1000-1500 msec). Time windows corresponding to adjacent topographies are colored gray. Right column: Topographies of the difference in beta2 amplitude (left) and significant electrodes obtained by Wilcoxon sign-rank tests (right) is depicted. The difference in the beta2 band was mainly located over fronto-central electrode positions.

Brain-Behavior Relationships

In the theta band, amplitude across cycles in the second time window (500-1000 msec) of the selective retrieval condition from each participant was used. As suggested by the topographies in Figure 12a, electrodes were split into a frontal and a parietal pool. Non-parametric correlations showed that the reduction in theta band amplitude over the frontal pool predicted later forgetting [$r = .42$, $p < .05$], whereas the reduction over the parietal pool did not [$r = .06$, $p = .77$]. Enhancement score was not significantly correlated with the decrease in theta amplitude, neither over the frontal pool nor the parietal pool ($p > .10$, in both tests). No significant correlations with behavior (suppression and enhancement score) arose in any of the other frequency bands (all *p*'s > .10).

To further investigate the brain-behavior relationship in the theta band, the subject sample was split into a high and a low forgetting group, based on the median in individual suppression scores. Theta band amplitude across cycles in the selective retrieval condition, pooled over frontal electrodes, was then compared separately in high and low forgetters. A 2 x 2 ANOVA with the factors GROUP (high vs. low forgetters) and CYCLE (SR1 vs. SR2) revealed a significant GROUP x CYCLE interaction [$F_{1,22}$=4.99; $p < .05$], showing that the decrease in theta amplitude from the first to the second cycle during selective retrieval was larger for the high forgetters than the low forgetters (Fig. 12b). In the low forgetting group, no reliable difference in theta amplitude between SR1 and SR2 was found [t_{11} = .80; p = .44]. No GROUP by CYCLE interaction was found in the reexposure condition [$F_{1,22}$ = .79; p = .38]. For the split into high and low enhancers, based on the individual enhancement score, a two-way ANOVA with factors GROUP (high vs. low enhancers) and CYCLE (SR1 vs. SR2) did not reveal a significant interaction [$F_{1,22}$ = 1.49; p = .23].

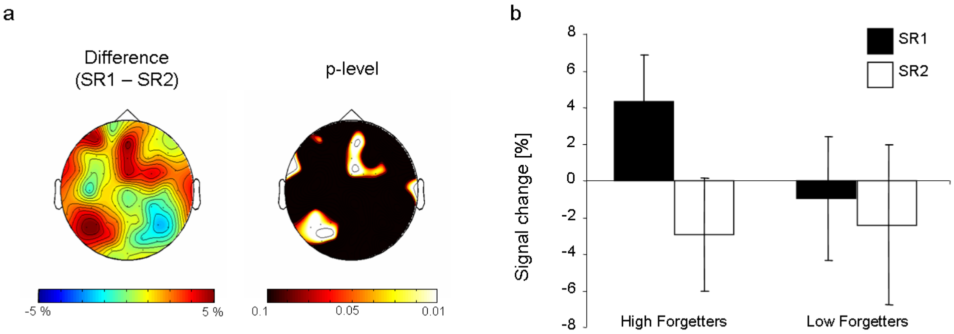


Figure 12. Brain-behavior relationships. (a) The topography of the difference in theta amplitude (SR1 vs. SR2) in the second time window (500-1000 msec) is shown. The right plot shows significant electrode sites, obtained by non-parametric Wilcoxon sign-rank tests. (b) Theta amplitudes for high and low forgetters in the first (SR1) and second (SR2) cycle of the selective retrieval condition are shown. Amplitudes were collapsed over frontal electrode sites exhibiting significant differences in the second time window (500-1000 msec).

Source Localization

The Beamformer analysis revealed that the decrease in theta amplitude across cycles in the selective retrieval condition was localized to the left anterior cingulate cortex (MNI-coordinates: -2 40 24; ~ BA 9 / BA 32; Fig. 13a) and the right parieto-occipital cortex (MNI-coordinates: 15 -70 5; ~ BA 30 / BA 23 / BA 17; Fig. 13b).

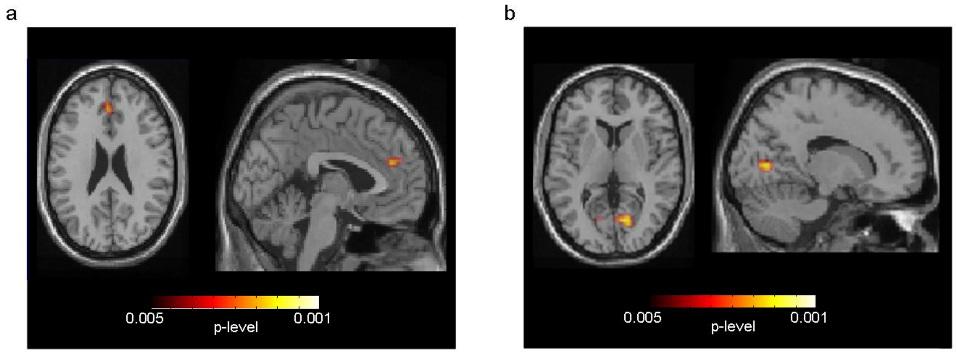


Figure 13. Source localization (Beamformer) of the difference in theta amplitude between the first and second cycle of selective retrieval (500-1000 msec) to the (a) anterior cingulate cortex and the (b) the right parieto-occipital cortex is depicted. Differences for each voxel are plotted by means of p-values, obtained by non-parametric Wilcoxon tests.

Discussion

On a behavioral level, the results of Experiment 1 replicate prior work (Anderson et al., 2000; Bäuml & Aslan, 2004; Ciranni & Shimamura, 1999), by showing that selective retrieval, but not reexposure, of a subset of studied items leads to retrieval-induced forgetting of related, unpracticed items. Unlike reexposure, attempting to selectively retrieve a target item creates interference from related items; this interference is resolved by inhibition which suppresses the items' memory representations and leads to later forgetting of the interfering information (Anderson & Spellman, 1995; Spitzer & Bäuml, 2007). As a corollary, the results thus confirm that reexposure can be used as a neural baseline for selective retrieval to isolate interference and inhibition (Johansson et al., 2007; Wimber et al., 2009).

In Experiment 1, a modification of the retrieval-practice paradigm (Anderson et al., 1994) with repeated cycles of practice in both the selective retrieval and the reexposure condition was used to modify the level of inhibition within and across conditions. In the selective retrieval condition, a high initial level of interference was assumed to be present, triggering inhibition. Inhibition supposedly resolved (at least partly) the interference during the first retrieval cycle, resulting in a lower level of interference in the second cycle. Therefore, less inhibition was needed in the second cycle of selective retrieval. In the reexposure condition, no inhibition was triggered in the first cycle (because of the retrieval-specificity, see Background section). This status should not differ between repeated cycles of reexposure.

Comparing event-related potentials between the first cycles of selective retrieval and reexposure, the results of a previous ERP study were replicated. Johansson et al. (2007) found stronger sustained positivity over frontal electrode sites during selective retrieval than reexposure. Similarly, in the ERP analysis of Experiment 1, an enhanced positive slow wave was found over frontal electrode sites in the first cycle of the selective retrieval condition compared to the first cycle of the reexposure condition. Comparing the second cycles across conditions, the effect was attenuated, although not significantly different from the comparison of the first cycles. This pattern likely reflects the decreasing engagement of inhibition across cycles.

Theta Synchronization and Inhibition

Selective retrieval induced a higher level of theta activity compared to the reexposure condition in the first cycle. Across cycles of selective retrieval, a decrease in theta amplitude from the first to the second cycle in the selective retrieval condition was found that was not present in the reexposure condition. This reduction in theta amplitude predicted the amount of retrieval-induced forgetting. Thus, the theta oscillatory activity followed exactly the dynamics that were hypothesized to reflect inhibition in the experimental manipulation. The results indicate that theta oscillations reflect the engagement of the inhibitory mechanism during selective memory retrieval as predicted by cognitive models, thus providing a link between brain oscillations and cognitive theory.

The results from the selective retrieval condition are in line with the findings of Kuhl et al. (2007), who found a reduction in BOLD signal in prefrontal areas across repeated cycles of selective retrieval, indicating that less inhibitory control is necessary when interference has been resolved during initial selective retrieval. Consistent with fMRI studies in which parietal and frontal areas were found to be specifically involved in selective memory retrieval (Kuhl et al., 2007; Wimber et al., 2009), the effects in the theta band were located over frontal and parietal electrode sites. Locating the sources of theta oscillations, the difference between the first and second cycle in the selective retrieval condition could be localized to the ACC. This finding is in line with fMRI results showing that BOLD signal changes in the ACC predict retrieval-induced forgetting (Kuhl et al., 2007; Wimber et al., 2009), and is consistent with studies showing a strong contribution of the ACC to frontal theta oscillations (Ishii et al., 1999; Onton et al., 2005). Our results, therefore, link brain oscillations to fMRI findings and suggest that the electrophysiological mechanism underlying activation of ACC during selective memory retrieval may be synchronization of local cell assemblies in the theta rhythm.

Consistent with the interpretation that the differences in theta amplitude between the selective retrieval and the reexposure condition reflect the dynamics of inhibition, brain-behavior correlations revealed that the reduction in theta activity over frontal electrodes across retrieval cycles predicted retrieval-induced forgetting. The larger the decrease from the first to the second cycle in the selective retrieval condition, the more likely the interfering items were forgotten on the later test. This pattern was evident in the correlation as well as in the behavior-based split of the subject sample. Typically, the finding of no retrieval-induced forgetting on the final recall test is interpreted as the failure to successfully inhibit interfering items in selective memory retrieval, and is attributed to a deficit in inhibitory function (e.g., Anderson, 2003). The data of the present experiment support this view. High forgetters showed high theta amplitudes during the first cycle of selective retrieval, indexing the engagement of inhibition. Because interference supposedly was successfully resolved by these subjects, lower theta amplitudes in the second cycle index less engagement of inhibition. In low forgetters, low theta amplitudes during both cycles of selective retrieval reflect the lack of inhibition in these subjects. Consequently, these subjects show minor (if not zero) retrieval-induced forgetting.

Hanslmayr et al. (2010) found similar results comparing oscillatory activity during competitive and non-competitive retrieval practice. In their study, higher evoked theta activity in the competitive condition predicted inter-individual differences in retrieval-induced forgetting. Experiment 1 replicated and extended these findings. By comparing oscillatory activity across retrieval cycles, the dynamics of inhibition were disentangled, an instance that was not possible in the study by Hanslmayr et al. (2010). On the basis of the present results, the puzzling negative relationship between retrieval-induced forgetting and theta oscillations found by Hanslmayr et al. (2010) can be explained as reflecting the effects of inhibition rather than the inhibitory process itself.

Alternative Interpretations of Theta Synchronization

Whereas in Experiment 1 the difference in theta amplitude between the selective retrieval and the reexposure condition can be attributed to inhibition, a priori alternative interpretations of the effect may arise. For instance, the theta effect may be due to the presence (as during retrieval) versus absence (as during reexposure) of retrieval processing itself. The fact that theta amplitude also decreases across retrieval cycles, however, speaks against such an interpretation.

The theta effect might also reflect mental effort, as (actively) retrieving an item from episodic memory might be more effortful than (passively) studying the item again. According to this view, one would expect a correlation between the reduction in theta amplitude and the enhancement of practiced items; enhancing some items should make other (unpracticed) items relatively less competitive, thereby reducing the effort required to retrieve the practiced items on the next practice cycle. Because high enhancers did not show a larger decrease in theta amplitude than low enhancers, the results speak against such an effort view. In a similar vein, the repeated cycles of retrieval practice might be contaminated by effects of repetition priming (Grill-Spector, Henson, & Martin, 2006). However, such an effect can be excluded by establishing the reexposure condition as a neural baseline for selective retrieval in the present experiment. Indeed, the finding of no difference in the theta band between the first and the second cycle of the reexposure condition renders an explanation in terms of repetition priming quite unlikely.

Alpha / Beta Desynchronization and Inhibition

Compared to the reexposure condition, selective retrieval induced greater alpha and beta desynchronization in the first cycle. Across cycles of selective retrieval, a relative increase in alpha and beta amplitude from the first to the second cycle in the selective retrieval condition was found. In the reexposure condition, only the beta2 band showed a significant effect, with stronger desynchronization in the second than in the first cycle. Because of similar temporal dynamics and similar topographies, the results from alpha and beta bands are discussed together.

Parallel to synchronization in the theta band, alpha / beta desynchronization could reflect the dynamics of inhibition in the retrieval-practice paradigm. However, alpha / beta desynchronization was not correlated with retrieval-induced forgetting. Moreover, previous work related relative synchronization - rather than desynchronization - of alpha oscillatory activity to inhibition (Klimesch et al., 2007). Therefore, the decrease in alpha / beta desynchronization across cycles of selective retrieval found in Experiment 1 is theoretically unlikely to reflect inhibition in selective memory retrieval.

Beta2 Desynchronization

Comparing the first with the second cycle of reexposure, a decrease in beta2 amplitude was found. This decrease could reflect the effects of repeated stimulus presentation, that is, repetition priming. It has been repeatedly shown that when stimuli are repeatedly presented, the neural response to this stimulus decreases across repetitions (see Schacter, Wig, & Stevens, 2007, for a review). Concerning brain oscillations, pervious studies showed that repetition priming was reflected by a decrease in gamma oscillatory synchronization (Gruber & Müller, 2002;

Moldakarimov, Bazhenov, & Sejnowski, 2010). Some authors included the frequency range (20-30 Hz) of the present effect in the gamma frequency range (e.g., Gruber & Müller, 2005), such that the present effect could be argued to be a replication of previous results in the gamma band. However, with its (fronto-central) topography and latency (1000 msec after stimulus onset), the present effect shows different characteristics than previous effects of repetition priming (parieto-occipital topography, ~200-400 msec after stimulus onset).

Evidence pro Inhibition

Concerning the ongoing debate on whether retrieval-induced forgetting is inhibitory or non-inhibitory in nature (e.g., Anderson, 2003; Jakab & Raaijmakers, 2009), the present results speak in favor of the inhibitory account. Non-inhibitory accounts of retrieval-induced forgetting mostly explain forgetting by assuming that practiced (strengthened) items block access to the unpracticed (and thus only relatively weaker) items at test, thus suggesting a correlation between enhancement and forgetting. Both on a behavioral and a neural level, the present results challenge such a view. In Experiment 1, enhancement was not correlated with forgetting, and the theta effect was predictive for forgetting but not for enhancement.

Conclusion

Replicating and extending previous EEG studies, the present results support the view that theta oscillatory activity reflects inhibition during selective memory retrieval. Theta oscillations followed the dynamics of inhibition as theoretically hypothesized in the retrieval-practice paradigm and predicted the amount of retrieval-induced forgetting. The sources of the reduction in the theta band were localized to the ACC, a result that nicely fits with previous fMRI studies showing a crucial involvement of the prefrontal cortex in mediating retrieval-induced forgetting.

Experiment 2

The results of Experiment 1 indicated that theta oscillations reflect inhibitory processes in episodic memory retrieval. The goal of Experiment 2 was to test whether theta oscillations also reflect inhibition, if such inhibition is triggered by interference during retrieval from semantic memory – as compared to episodic memory in Experiment 1. To this end, brain oscillatory correlates of inhibition during retrieval from semantic memory were investigated.

Typically, the retrieval-practice paradigm is conducted to assess interference resolution in episodic memory (e.g., Anderson et al., 1994), as defined by the encoding of item material in a study phase. However, retrieval-induced forgetting has been demonstrated without such an episodic study phase, indicating that retrieval-induced forgetting can also occur in semantic memory (Blaxton & Neely, 1983; Brow et al., 2005; Campbell & Phenix, 2009; Johnson & Anderson, 2004). Johnson and Anderson (2004) conducted a retrieval-induced forgetting experiment without prior learning. Instead, they repeatedly presented category labels and word stem cues (e.g., SEASONING - Nu___) to their subjects, instructing them to generate an item that matches both cues. During this so called semantic retrieval-practice phase, semantically related items (i.e., items from the same category) are assumed to interfere and in turn to be suppressed by inhibition. Johnson and Anderson (2004) showed that in an independent probe test, memory performance for previously interfering items was impaired as compared to items from categories that were not presented during the semantic retrieval-practice phase.

The design and procedure of Experiment 2 paralleled the one used in Experiment 1, except that the episodic study phase and the reexposure condition were removed in Experiment 2. During semantic retrieval-practice, category labels were presented together with word stems, and subjects had to generate exemplars matching both cues. Four cycles of such selective semantic retrieval-practice were conducted. The final semantic retrieval test assessed whether previous semantic retrieval of some items from a category impaired the semantic retrieval of category exemplars that were not generated before. In the test phase, subcategory labels and word stems were presented as cues. Similar to the independent probe technique, subcategory labels were not presented in the experiment until the test phase, thus minimizing the possibility of blocking.

Experiment 2 is the first study to investigate brain oscillatory correlates of inhibition during retrieval from semantic memory. Previous studies, focusing on neural correlates of retrieval processes in general, found distinct correlates for retrieval from semantic and retrieval from episodic memory (see Klimesch, Freudenberger, & Sauseng, 2010, for a review). Whereas theta oscillations are involved in retrieval from episodic memory, alpha (10-12 Hz) phase synchronization is thought to reflect retrieval from semantic long-term memory. A recent single-subject intracranial EEG study compared an autobiographical condition with semantic memory conditions, and found enhanced theta activity in the enthorhinal cortex to be selective for autobiographical (episodic) memory (Steinvorth, Wang, Ulbert, Schomer, & Halgren, 2010). Contrary to this view of a selective involvement of theta in episodic memory retrieval, however, studies investigating lexical-semantic retrieval operations have sometimes shown an involvement of theta oscillations in semantic memory retrieval (Bastiaansen, Oostenfeld, Jensen, & Hagoort, 2008; Bastiaansen, van der Linden, Ter Keurs, Dijkstra, & Hagoort, 2005).

A general difference between retrieval from semantic and episodic memory is the involvement of the medial-temporal lobe, including the hippocampal complex (see Moscovitch, Nadel, Winocur, Gilboa, & Rosenbaum, 2006, or Squire & Bayley, 2007, for reviews). Whereas retrieval from episodic memory is hippocampus-dependent, semantic retrieval is assumed to rely on a widespread distributed network in the brain, rather than being dependent on one particular structure (e.g., Thompson-Schill, 2003, for a review). Together with numerous studies showing that theta oscillations are predominant in the hippocampal complex (for reviews, see Buzsáki, 2006; Düzel, Penny, & Burgess, 2010), these findings could indicate that theta oscillations do not play a crucial role when retrieving information from semantic memory. Whether or not these differences in neural correlates of retrieval processes might influence the oscillatory correlates of inhibition during retrieval from semantic memory remains to be clarified.

The results of Experiment 1 suggested that theta oscillations reflect inhibition during selective retrieval from episodic memory. If inhibition is a domain-general executive control process (see Anderson, 2003) that resolves interference in both episodic and semantic memory, it could be expected that theta oscillations also reflect the dynamics of inhibition during selective retrieval from semantic memory. Therefore, it was hypothesized that theta oscillations would be reduced across repeated cycles of retrieval from semantic memory. The decrease was expected to predict the inter-individual amount of retrieval-induced forgetting.

Methods

Subjects

Thirty-seven adults participated voluntarily in the experiment. Five of them were excluded from data analysis, because their EEG was contaminated by movement artifacts. The remaining 32 subjects (19-30 years old, 26 women, six men) had normal or corrected to normal vision, had German as their native language, and reported no history of neurological disease. Subjects received course credit or 25 € for participation.

Materials

Stimuli were 140 German nouns from 14 semantic categories, drawn from several published norms (Mannhaupt, 1983; Scheithe & Bäuml, 1995). Each category consisted of ten items, with the two initial letters of each item being unique with respect to that item's category. Within a category, four of the ten items belonged to a specific semantic subcategory; those items were not generated during the semantic retrieval-practice phase, and are referred to as “competitor items”. The remaining six items of a category did not belong to this particular subcategory.

Those items had to be generated during the semantic retrieval-practice phase, and are referred to as “to-be-generated” items. Within the category “profession”, for instance, the four competitor items belonged to the subcategory “craftsman”, whereas the six to-be-generated items were professions other than craftsman. Compared to competitor items (mean rank = 22.0, *SD* = 13.7), to-be-generated items (mean rank = 33.6, *SD* = 17.5) were low frequency exemplars within their category. Previous work has shown that strongly associated items of a category are more likely to interfere during retrieval, and thus to be more subject to retrieval-induced forgetting than weakly associated items (Anderson et al., 1994; Bäuml, 1998).

Design

An outline of the experimental design can be seen in Figure 14. The experimental design was very similar to the selective retrieval condition of Experiment 1, with the difference that the study phase was removed. As a consequence, subjects had to generate items from semantic memory, rather than retrieving previously studied items. The experiment consisted of seven blocks, each comprising a semantic retrieval-practice phase (the equivalent to the intermediate phase in Experiment 1) and a final semantic retrieval phase (the equivalent to the test phase in Experiment 1). For each block, an item list was constructed consisting of two categories. Within a list, one category was assigned to the semantic practice condition, the other one to the control condition. Assignment of category to condition was counterbalanced across subjects. After 16 subjects, assignment of categories to the item lists was changed for the remaining subjects.

During semantic retrieval-practice, category labels and word stems of the six to-be-generated items (PROFESSION - Mu___) of the semantic practice condition were presented in four consecutive cycles. Subjects were instructed to generate an adequate item matching each cue. During final semantic retrieval, word stems and subcategory labels of the four competitor items from the semantic practice condition (CRAFTSMAN – Ro___) and from the control condition (DECIDUOUS TREE – Al___) were presented. Accordingly, the detrimental effect (forgetting) was defined as the difference between competitor items from the semantic practice condition and corresponding items from the control condition.

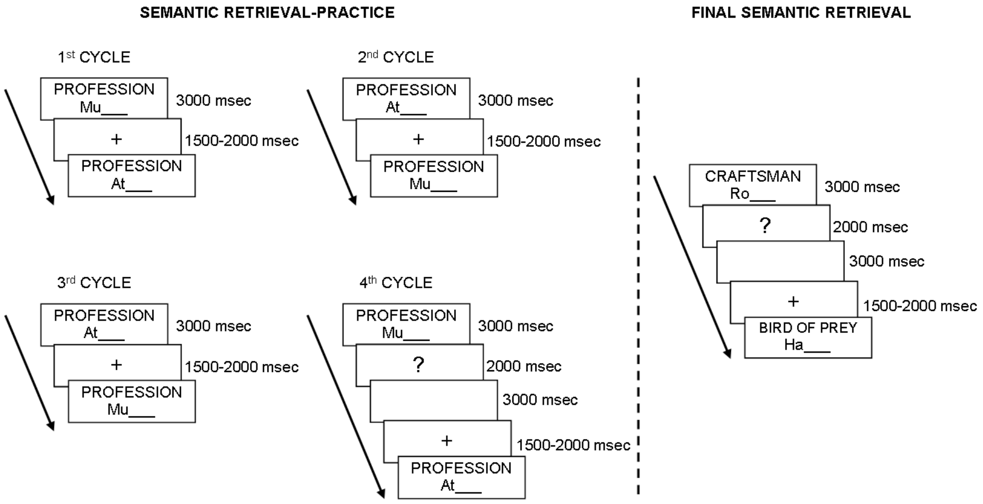


Figure 14. The experimental procedure as employed in Experiment 2. The experiment consisted of seven blocks, each block comprising a semantic retrieval-practice phase and a final semantic retrieval phase. In the semantic retrieval-practice phase, subjects had to retrieve to-be-generated items from semantic memory by using category labels and word stems as cues. Each semantic retrieval-practice phase comprised four consecutive cycles, with oral responses given in the fourth cycle only. In the final semantic retrieval phase, competitor items had to be retrieved by using word stems and subcategory labels as cues. EEG was recorded during the semantic retrieval-practice phase.

Procedure

Subjects were tested individually in a quiet surrounding in front of a 15-inch computer screen (70 Hz refresh rate). The seven blocks were conducted successively, with a brake of approximately 3 minutes after four blocks.

Semantic Retrieval-Practice Phase

Subjects were instructed to generate an item matching the word-stem and the respective category label of six to-be-generated items during four consecutive cycles. Following the procedure of Experiment 1, subjects were asked to covertly generate the to-be-generated items during the first three cycles, in order to avoid EEG artifacts elicited by speech. A trial consisted of a fixation cross of variable duration (1500-2000 msec), followed by the item's word stem which was presented for 3000 msec together with its category label. During the fourth cycle, subjects were instructed to respond with an adequate item. For trials in the fourth cycle, a question mark, which prompted the subjects to overtly respond with an adequate item, was presented for 2000 msec after the item's word stem, followed by a blank screen for another 3000 msec. Order of items was randomized within each cycle, with the constraint that no two identical items succeeded each other at cycle borders.

Final Semantic Retrieval Phase.

After the four repetitions of the semantic retrieval-practice phase, competitor items from the semantic practice and the corresponding items from the control condition were presented in consecutive blocks. Subjects were instructed to overtly respond with an adequate item. A trial consisted of a fixation cross with variable duration (1500-2000 msec), followed by the item's word stem that was presented together with its subcategory label for 3000 msec. Thereafter, a question mark (2000 msec) prompted the subject's response, followed by a blank screen (3000 msec). Order of items was randomized within each condition. Order of conditions was balanced across subjects.

EEG Recording

The EEG was recorded from 61 equidistant electrodes (Easy Cap Montage No. 10; http://www.easycap.de) during the semantic retrieval-practice. Apart from this different electrode setting, EEG recording was identical to Experiment 1.

Analysis of Oscillatory Amplitude

Time–frequency analyses were conducted using the BESA (MEGIS Software BESA v5.1.8) software package and self-written Matlab codes (The Mathworks Inc.). The EEG data were segmented into 2000 msec epochs (ranging from 500 ms preceding stimulus onset to 1500 ms after stimulus onset). To avoid filter artifacts at the edges of the epochs, the data was filtered in a slightly bigger time interval, but analysis was restricted to the 2000 msec time window. For analysis of low-frequency oscillatory amplitude, data was filtered in a frequency range of 4 to 20 Hz using BESA's time–frequency analysis module, with time–frequency resolution set to 111 msec and 1.99 Hz (full width half maximum), corresponding to a time-frequency sampling of 50 msec and 1 Hz. For analysis of high-frequency oscillatory power (20-70 Hz), time–frequency resolution was set to 22.2 msec and 9.93 Hz (full width half maximum), corresponding to a time-frequency sampling of 10 msec and 5 Hz.

To control for filtering artifacts due to smearing in the frequency domain, an *additional analysis* of low-frequency oscillatory amplitude (4-20 Hz) was conducted with a higher frequency resolution (at the expense of lower temporal resolution). For the additional analysis, the time–frequency resolution was set to 554 msec and 0.397 Hz (full width half maximum), corresponding to a time-frequency sampling of 250 msec and 0.2 Hz.

To analyze event-related amplitude changes, the percentage of amplitude change in relation to a prestimulus baseline (set to 500-0 msec prior to stimulus onset) was calculated. For statistical comparisons, the data were collapsed into six frequency bands: Theta (5–9 Hz); Alpha (9–13 Hz); Beta1 (13–20 Hz); Beta2 (20–30 Hz); Gamma1 (30–45 Hz); and Gamma2 (55–70 Hz); and three consecutive time windows: T1 (0-500 msec), T2 (500-1000 msec), and T3 (1000-1500 msec).

Pair-wise comparisons (Wilcoxon sign-rank tests, two-tailed) between the first and the third cycle (Cy1 vs. Cy3) of the semantic retrieval-practice phase were conducted. Frequency bands and time windows exhibiting significant effects were identified for each electrode position. The number of electrodes showing significant effects ($p < .05$) was then checked for significance by a randomization test (see Experiment 1, for a detailed description of the randomization procedure). Based on those electrodes positions exhibiting a significant difference between the first and third cycle, amplitudes were entered into a one-way analysis of variance with the within-subjects factor of CYCLE (Cy1, Cy2, Cy3). Post-hoc t-tests were conducted to reveal significant differences between the individual cycles.

Brain-Behavior Correlations

Brain-behavior correlations were calculated based on suppression scores, which depict an individual measure of retrieval-induced forgetting relative to recall performance in the control condition (see Experiment 1, for details).

Results

Behavioral Results

Mean generation performance for to-be-generated items was 66.2 % (*SE* = 1.9 %). Mean generation performance for competitor items was 63.3 % (*SE* =1.9 %) in the semantic practice, and 66.8 % (*SE* = 1.6 %) for corresponding items in the control condition (Fig. 15). The forgetting effect (3.5 %) was significant [t_{31} = 2.16, $p <$ .05]. Enhancement was not reported because the to-be-generated items were not part of the final semantic retrieval phase.

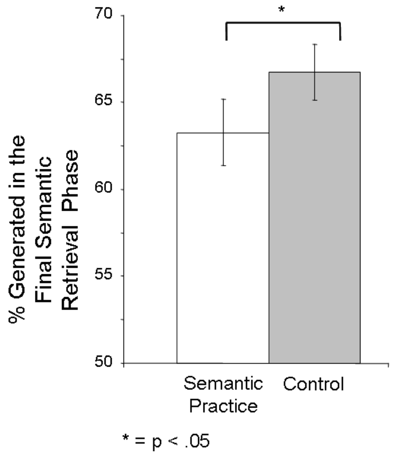


Figure 15. Behavioral results. Mean generation performance of competitor items in the semantic practice and the control condition (error bars indicate S.E.). Significant forgetting was found.

EEG-Results

An overview of the statistical results of the comparison between Cycle 1 and Cycle 3 in the different frequency bands and time windows is shown in Table 4.

Table 4. Number of electrodes showing significant differences between the first and the third cycle of the semantic retrieval-practice phase in the different frequency bands and time windows.

	Cycle 1 > Cycle 3			Cycle 1 < Cycle 3		
	T1	T2	T3	T1	T2	T3
Theta(5-9)	0	0	0	3	21**	16**
Alpha(9-13)	0	0	0	10*	58**	45**
Beta1(13-20)	0	0	0	7*	49**	49**
Beta2(20-30)	1	0	0	3	42**	35**
Gamma1(30-45)	2	2	1	0	12*	7*
Gamma2(55-70)	1	2	2	1	1	2

*= $p_{\mathrm{corr}} < .05$; ** = $p_{\mathrm{corr}} < .01$

Theta Band. In the theta band (5-9 Hz), the first and the third cycle differed in the second (500-1000 msec, $p_{\mathrm{corr}} < .01$) and the third (1000-1500 msec, $p_{\mathrm{corr}} < .01$) time window. Figure 16a shows a larger increase in theta amplitude in the third than in the first cycle. The difference was located over frontal, central, and parietal electrode positions. Based on those electrodes exhibiting a significant difference between the first and third cycle, amplitudes were entered into a one-way ANOVA with the within-subjects factor of CYCLE (Cy1, Cy2, Cy3), which yielded a significant effect [$F_{2,62} = 12.8$, $p < .0001$]. The third cycle differed significantly from the first [$t_{31} = 4.45$, $p < .001$] and the second [$t_{31} = 3.76$, $p < .001$] cycle. The difference between the first and the second cycle was not significant [$t_{31} = -1.49$, $p = .15$; see Fig. 18].

Alpha Band. Statistical analyses revealed significant differences between the first and the third cycle of the semantic retrieval-practice phase in the alpha band (9-13 Hz) in the first (0-500 msec, $p_{\text{corr}} < .05$), second (500-1000 msec, $p_{\text{corr}} < .01$) and third (1000-1500 msec, $p_{\text{corr}} < .01$) time window. Figure 16b shows a larger decrease in alpha amplitude during the first than the third cycle. The difference was located over widespread electrode positions and was most pronounced over parieto-occipital electrode sites. A one-way ANOVA with the within-subjects factor of CYCLE (Cy1, Cy2, Cy3) yielded a significant effect [$F_{2,62} = 17.5$, $p < .0001$]. The third cycle differed significantly from the first [$t_{31} = 5.6$, $p < .001$] and the second [$t_{31} = 4.09$, $p < .001$] cycle. The difference between the first and the second cycle was only marginally significant [$t_{31} = -1.95$, $p = .06$; see Fig. 18].

Beta1 Band. In the beta1 (13-20 Hz) band, significant differences were found in the first (0-500 msec, $p_{\text{corr}} < .05$), second (500-1000 msec, $p_{\text{corr}} < .01$) and third (1000-1500 msec, $p_{\text{corr}} < .01$) time window. Figure 16c shows a larger amplitude decrease in the first cycle than in the third cycle. The difference was located over widespread electrode positions, but was most pronounced over parieto-occipital electrode sites. Amplitudes were entered into a one-way ANOVA with the within-subjects factor of CYCLE (Cy1, Cy2, Cy3) which yielded a significant effect [$F_{2,62} = 22.9$, $p < .0001$]. The first cycle differed significantly from the second [$t_{31} = -3.69$, $p < .001$] and the third [$t_{31} = -6.66$, $p < .001$] cycle. The difference between the second and the third cycle was also significant [$t_{31} = -3.15$, $p < .005$; see Fig. 18].

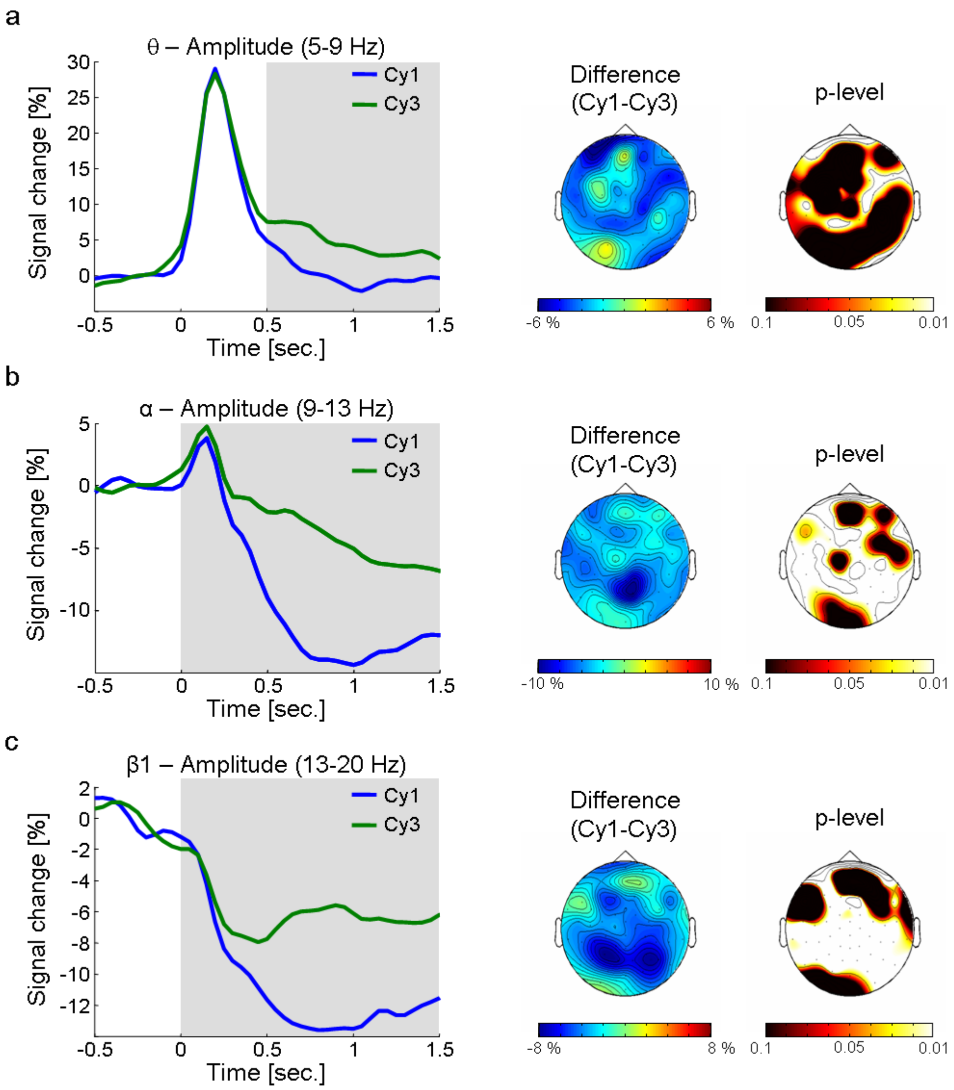


Figure 16. Cycle 1 vs. Cycle 3. Left column: Time course of amplitude, averaged over those electrode positions showing a significant effect. Time windows corresponding to adjacent topographies are colored gray. Right column: Topographies of the difference in amplitude (left) and significant electrodes obtained by Wilcoxon sign-rank tests (right) is depicted. (a) In the theta band, the second and third time window (500-1500 msec) showed a significant effect. (b) In the alpha band, all three time windows (0-1500 msec) differed significantly. (c) In the beta1 band, all three windows (0-1500 msec) showed a significant effect.

Beta2 Band. In the beta2 band (20-30 Hz), significant differences between the first and third cycle were found in the second (500-1000 msec, $p_{\text{corr}} < .01$) and the third (1000-1500 msec, $p_{\text{corr}} < .01$) time window. Figure 17a shows a larger amplitude decrease in the first than in the third cycle. The difference was mainly located over central and parieto-occipital electrode sites. A one-way ANOVA with the within-subjects factor of CYCLE (Cy1, Cy2, Cy3) yielded a significant effect [$F_{2,62} = 28.9$, $p < .0001$]. The first cycle differed significantly from the second [$t_{31} = -2.73$, $p < .05$] and the third [$t_{31} = -7.32$, $p < .001$] cycle. The difference between the second and the third cycle was also significant [$t_{31} = -4.77$, $p < .001$; see Fig. 18].

Gamma1 Band. In the gamma1 band (30-45 Hz), significant differences were found in the second (500-1000 msec, $p_{\text{corr}} < .05$) and the third (1000-1500 msec, $p_{\text{corr}} < .05$) time window. Figure 17b shows a larger decrease in gamma amplitude during the first than the third cycle. The difference was located over central and parietal electrode sites. Amplitudes were entered into a one-way ANOVA with the within-subjects factor of CYCLE (Cy1, Cy2, Cy3) which yielded a significant effect [$F_{2,62} = 14.9$, $p < .0001$]. The third cycle differed significantly from the first [$t_{31} = 5.31$, $p < .001$] and the second [$t_{31} = 3.64$, $p < .001$] cycle. The difference between the first and the second cycle was only marginally significant [$t_{31} = -1.77$, $p = .09$; see Fig. 18].

No differences were found in the *gamma2* band (55-70 Hz).

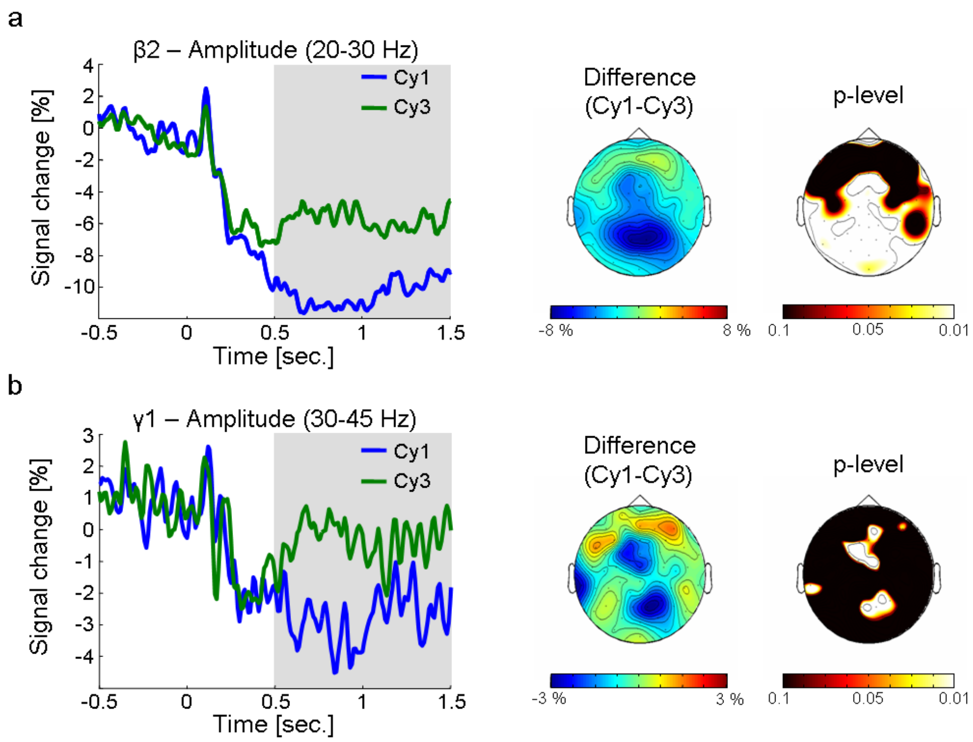
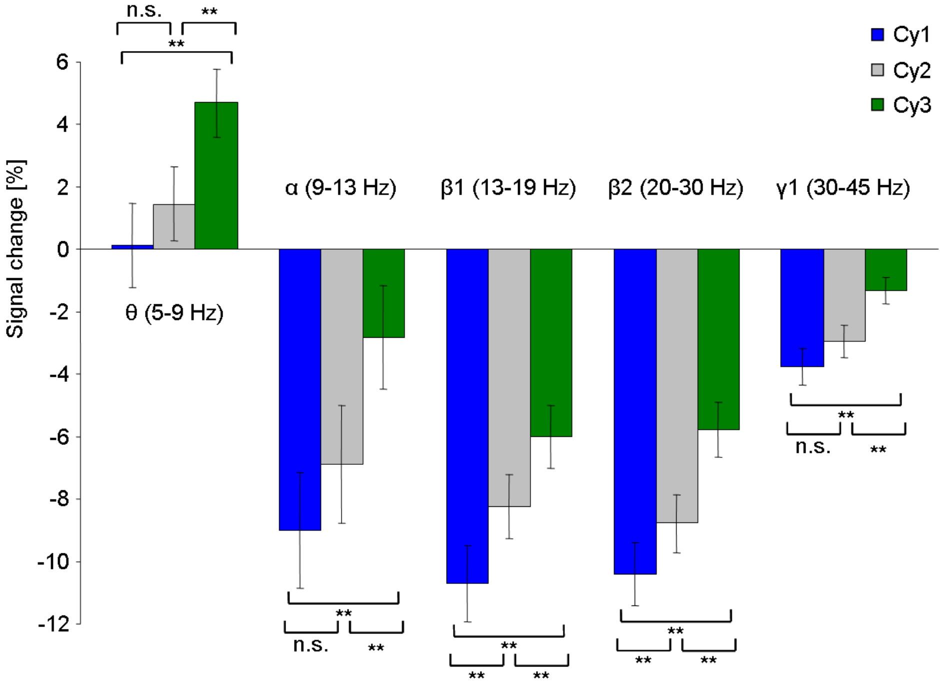


Figure 17. Cycle 1 vs. Cycle 3. Left column: Time course of amplitude, averaged over those electrode positions showing a significant effect. Time windows corresponding to adjacent topographies are colored gray. Right column: Topographies of the difference in amplitude (left) and significant electrodes obtained by Wilcoxon sign-rank tests (right) is depicted. (a) The amplitude in the beta2 band differed significantly in the second and third time window (500-1500 msec). (b) In the gamma1 band, the second and the third time windows (500-1500 msec) showed a significant effect.

Additional Analysis - High Frequency Resolution

In the *theta band (5-9 Hz)*, Cycle 3 showed significantly higher theta amplitudes than Cycle 1 in all of the three time windows (0-500 msec, $p_{\text{corr}} < .05$; 500-1000 msec, $p_{\text{corr}} < .01$; 1000-1500 msec $p_{\text{corr}} < .01$). In the *alpha band (9-12 Hz)*, significant differences were found in all three time windows (0-1500 msec, all p_{corr}'s $< .01$), with a larger decrease in alpha amplitude during the first than the third cycle. In the *beta1 band (13-20 Hz)*, significant differences were also found in all three time windows (all p_{corr}'s $< .01$), with a larger decreases in beta1 amplitude during the first than the third cycle.



* = p < .05; ** = p < .01

Figure 18. Amplitude dynamics from the first to the third cycle, depicted separately for each frequency band of interest. Amplitudes are base on those electrode positions which showed a significant effect in the comparison between the first and the third cycle.

Brain-Behavior Relationships

As in Experiment 1, the individual suppression score was used as a behavioral measure for the brain-behavior correlations. Because to-be-practiced items were not part of the final semantic retrieval phase, an enhancement score could not be computed. As electrophysiological measures the time windows and frequency bands that showed significant differences in the comparisons across cycles (Cy1 vs. Cy3) were used. Non-parametric correlations did not reveal any significant correlations between EEG measures and the suppression score.

To further investigate brain-behavior relationships, the subject sample was split into a high and a low forgetting group, based on the median in individual suppression scores. 2 x 3 ANOVAs with the between factor of GROUP (high vs.

low forgetters) and the within factor of CYCLE (Cy1, Cy2, Cy2) revealed no significant interactions for all frequency bands of interest (all *p*'s > .30).

Discussion

The behavioral results replicate previous studies (Blaxton & Neely, 1983; Brown et al., 2005; Campbell & Phenix, 2009; Johnson & Anderson, 2004), showing that retrieval-induced forgetting can be found in semantic memory. By eliminating the study phase of a standard retrieval-practice paradigm, subjects had to retrieve items from semantic rather than episodic memory during the practice phase. During repeated selective retrieval of some category exemplars, other members of that category are thought to interfere. Inhibition supposedly resolves the interference by suppressing the interfering items' memory representations. The behavioral data of Experiment 2 are consistent with this view. Generation performance for items that shared a common category with practiced items was impaired as compared to generation performance for items from categories that were not part of the semantic retrieval-practice phase.

Following the logic of Experiment 1, repeated cycles of semantic retrieval-practice were used to induce varying degrees of inhibition in Experiment 2. During the first cycle of semantic retrieval-practice, high competition among category exemplars is assumed to trigger high levels of inhibition. If inhibition resolves interference during the first cycle, less inhibitory control should be required in the second and the third cycle of semantic retrieval-practice compared with the first cycle. However, theta oscillations did not reflect the theoretically assumed dynamics of inhibition across semantic retrieval cycles. Contrary to the findings of Experiment 1, theta amplitude did not show the hypothesized decrease across semantic retrieval cycles.

There are several reasons why no reduction in theta amplitude was found across cycles in Experiment 2. Reconsidering the behavioral results, it appears that the forgetting effect was rather small. Possibly, not enough interference was elicited among members of the same category during retrieval from semantic memory. If so, the level of inhibition triggered to overcome interference was already low during the first cycle of semantic retrieval-practice. Therefore, it may well be that the difference in inhibition across cycles in Experiment 2 was too small to be captured by oscillatory activity in the EEG.

Another explanation why the expected decrease across cycles was not found could be that it was superimposed by the very strong effects in the alpha and beta1 band (discussed later in this section). Therefore, an additional time-frequency analysis was performed, with higher resolution in the frequency domain (and, consequently, lower resolution in the time domain) in order to prevent superimposition smearing in the frequency domain that could have concealed effects in the theta band. However, the results of the high frequency resolution analysis confirmed that theta amplitude was not reduced across cycles of semantic retrieval-practice.

Alternatively, one cannot rule out the possibility that inhibition in semantic memory and inhibition in episodic memory are reflected by distinct brain oscillatory correlates. Although there is no experimental evidence that inhibition triggered by interference during episodic memory retrieval is different from inhibition triggered by interference during semantic retrieval, neuronal evidence shows that cognitive processes, in general, vary across both memory systems (see Klimesch, Freudenberger, & Sauseng, 2010, for a review) and that episodic and semantic memory rely on different cortical networks (e.g., Squire & Bayley, 2007; Thompson-Schill, 2003, for reviews).

Theta Synchronization and Episodic Processes

The analysis of theta oscillatory activity across the three consecutive cycles yielded a continuous increase in amplitude. Whereas the theta amplitude in the first cycle was at zero, a rise in theta synchronization was found in the second and the third cycle. Semantic retrieval initiates the formation of an episodic memory trace (e.g., Habib, Nyberg, & Tulving, 2003; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994) and can lead to enhanced recall rates compared to other encoding instructions (the generation effect, Slamecka & Graf, 1978). Thus, the generation of an item during semantic retrieval-practice can act as an encoding event, creating an episodic memory trace of this item. Across cycles of semantic retrieval-practice, more and more episodic memory traces are established. The increase in theta amplitude across cycles could thus reflect the increasing amount of episodically stored items. This interpretation would be in line with a recent study demonstrating a positive relation between the amount of episodic memory traces connected to a cue and theta oscillations (Khader & Rösler, 2010).

Contrary to Experiment 1, in Experiment 2 the generated and, thereby, episodically stored items are not subject to inhibition. In the standard retrieval-practice paradigm, only a subset of items is being selectively retrieved. Unpracticed items interfere and get suppressed, which in turn reduces interference. The decrease in theta synchronization might then indicate successful interference resolution by inhibition (see Experiment 1). In Experiment 2, however, an episodic memory trace is only being established for those items that are repeatedly being generated. This repeated generation protects those items from being suppressed by inhibition, and could be the reason why no reduction in theta amplitude is found from the second to the third cycle.

Alpha / Beta Desynchronization

Paralleling the increase found in the theta band across cycles, a relative increase in alpha and beta amplitude was found across cycles of semantic retrieval-practice over widespread electrode positions. The desynchronization in the alpha and beta band (relative to the prestimulus baseline) was strongest in the first cycle of the semantic retrieval-practice phase, and continuously decreased across cycles. Because of similar temporal dynamics and similar topographies, the results from alpha and beta bands are discussed together. As shown by brain-behavior correlations, alpha and beta band desynchronization did not predict inter-individual differences in retrieval-induced forgetting. Thus, inhibition during retrieval from semantic memory is unlikely to be reflected by amplitude modulations of the alpha / beta band.

Previous studies have associated alpha desynchronization with semantic memory processes (see Klimesch et al., 2010, for a review). In particular, desynchronization in the upper alpha band (10-12 Hz) has been suggested to reflect retrieval from semantic long-term memory (Klimesch, 1999). Studies investigating the subsequent memory effect have found that the level of alpha desynchronization was predictive of whether the items were remembered or not in a later memory test (Klimesch et al., 1996; Weiss & Rappelsberger, 2000). Similar results were reported for beta oscillations. The more desynchronization in the beta band occurred during encoding, the more likely an item was remembered on a later memory test (Sederberg, Kahana, Howard, Donner, & Madsen, 2003; Sederberg et al., 2007). In a recent study, Hanslmayr et al. (2009) dissociated these subsequent memory findings by comparing a non-semantic and a semantic encoding task. Intriguingly, beta desynchronization was specifically related to successful semantic encoding, whereas theta synchronization was related to non-semantic encoding. Thus, alpha and beta desynchronization can be interpreted as reflecting the engagement of semantic memory processes.

On the basis of these previous findings, the reduction of alpha and beta desynchronization across cycles may reflect the decrease in the engagement of semantic memory processes across cycles. As discussed before, with increasing number of cycles, episodic memory processes become dominant, rendering retrieval from semantic memory more and more unnecessary. Desynchronization in the alpha and beta bands was strongest during the first cycle of semantic retrieval-practice, when subjects had to rely solely on semantic memory. The widespread topographies on numerous electrode positions reported here fit with the notion that semantic memory is a distributed network in the brain, incorporating many different brain regions (see Binder, Desai, Graves, & Conant, 2009, for a review).

Gamma Band

In the gamma1 band, a difference was found between the second and the third cycle of semantic retrieval-practice. In both cycles, gamma band activity showed a somewhat untypical desynchronization. In general, gamma band activity is synchronized in response to a stimulus (see Tallon-Baudry, 2009, for a review). Therefore, a desynchronization in the gamma band, as found in the present experiment, is puzzling. Rather than being of functional significance, the effect found in the gamma band could be due to superimposition from other frequency bands. The large-scale and widespread decrease in alpha and beta bands could have covered possible gamma band effects. The similarity in topographies and time courses between the alpha / beta effect and the gamma effect also speak in favor of such an interpretation.

Conclusion

Behaviorally, Experiment 2 replicated previous findings in showing that retrieval-induced forgetting can be found in semantic memory. However, theta oscillations did not reflect the dynamics of inhibition in semantic memory retrieval. Because of the rather small retrieval-induced forgetting effect in Experiment 2, it may well be that changes in inhibitory engagement across cycles of semantic retrieval were not captured in the EEG. Therefore, the question whether theta oscillations also reflect inhibition during retrieval from semantic memory – as hypothesized on the basis of the results of Experiment 1 – remains open to future research.

In Experiment 2, an increase in theta synchronization across cycles was found, possibly reflecting the formation of an episodic memory trace via item generation. Desynchronization in the alpha and beta band, on the other hand, could reflect the decreasing recruitment of semantic memory retrieval processes in the course of the semantic retrieval-practice phase. This interpretation would be in line with several other previous studies, showing that theta reflects episodic memory processes (Klimesch et al., 1996; Sederberg et al., 2003; Steinvorth et al., 2010) and alpha / beta reflect semantic memory processes (Hanslmayr et al., 2009; Klimesch et al., 2010). However, no relation between inhibition and the effects in the alpha and beta band was found.

Interim Summary

In the first part of the present work, two electrophysiological experiments were conducted to investigate the oscillatory correlates of inhibition during selective memory retrieval. In Experiment 1, retrieval of previously studied material was supposed to elicit interference among episodic memory traces, whereas in Experiment 2, retrieval from semantic memory was supposed to trigger interference among category members stored in semantic memory. In both experiments, retrieval-induced forgetting was found, suggesting that inhibition was triggered by interference during episodic as well as semantic memory retrieval.

However, only in Experiment 1, an oscillatory correlate of inhibition was found. Theta oscillations reflected the dynamics of inhibition across repeated cycles of retrieval-practice, showing higher amplitudes during the first cycle, when high levels of inhibition were supposed to be required to resolve interference, than during the second cycle, when less inhibition is necessary, because competition should have been already resolved during the first cycle. The reduction in theta amplitude across cycles predicted later retrieval-induced forgetting, supporting the conclusion that theta oscillations reflect the dynamics of inhibition in selective memory retrieval.

On the basis of the findings of Experiment 1, it was hypothesized that theta oscillations also reflect inhibition triggered by interference during retrieval from semantic memory. However, the expected reduction in theta amplitude was not found across cycles of semantic retrieval-practice in Experiment 2. Because the forgetting effect was rather small in Experiment 2, it may well be that the changes in inhibitory engagement across cycles of semantic retrieval-practice were too small to be captured by brain oscillatory analyses. The question whether the same oscillatory correlate could index inhibition during retrieval from episodic and semantic memory remains open to future research.

Part III

Effects of Inhibition on Absolute and Relative Item Strength

Absolute and Relative Item Strength

Inhibitory theory claims that interference during retrieval from long-term memory is resolved by suppressing the interfering items' memory representations, resulting in a persistent weakening of the suppressed item (see Anderson, 2003 or Bäuml, 2008, for reviews). However, how exactly such weakening affects an item's representation is still under debate. In an effort to clarify this question, the second part of the present work was concerned with the question whether inhibition affects an item's inherent memory strength (absolute strength), or its strength in relation to other items' strengths within a memory search set (relative strength), or both.

Absolute Strength

Experiment 3 examined the detrimental effects of inhibition on interfering items' absolute strengths by employing a recognition test procedure in the retrieval-practice paradigm. Signal-detection theory provides a useful framework for recognition tests (see Banks, 1970, for a review). According to this view, target (signal) and lure (noise) items can be ordered on a strength (or familiarity) dimension. Gaussian distributions represent the strength distributions of both item types on the strength continuum (the variances of these distributions can be unequal). The distributions may overlap to a certain extent, but, in general, the targets' mean strength is higher than the lures' mean strength, because target items gain memory strength during encoding. If the inherent strength of a target or a lure exceeds a criterion, it is judged old. A subject's individual criterion can either be liberal, producing relatively high hit and false alarm rates, or strict, producing lower hit and false alarm rates. D prime, calculated as the difference between the z-transformed hits and false alarms, provides a measure of a subject's ability to discriminate target and lure items. Thus, on the basis of the signal-detection theory, calculating d-prime in recognition tests can provide a suitable measure to assess the impact of inhibition on the absolute strength of interfering items (see Wixted, 2007, for further discussions on theories of recognition memory).

Relative Strength

Assessing an items' relative strength is possible by measuring response latencies during a free recall test, that is, the time elapsed since the beginning of the recall period. According to several theoretical models of memory, recall is a two-stage process (e.g., McGill, 1963; Raaijmakers & Shiffrin, 1981; Rohrer, 1996). These models state that, after retrieval is initiated, a retrieval cue delimits possible outcomes in a search set. Subsequently, the two-step retrieval process is set off. First, items are sampled from the search set. Second, an item is recovered, but only if its absolute strength exceeds a given threshold. The sampling process of an item is described in terms of a ratio rule (see Rundus, 1973). Basically, the probability of being sampled is a function of the item's strength relative to the sum of strengths of all the items belonging to the same search set [s_k / $\sum s_{i;}$; details of the computation of this ratio may vary across models]. Accordingly, an item's probability for being sampled depends on its relative strength within a search set.

An idea how to describe the sampling stage during recall can be gained when closely inspecting the time course of free recall. Typically, the output in a free recall test declines rapidly with time, a characteristic which has been shown to be nicely described by an exponential equation,

$$r(t) = \left(\frac{N}{\tau}\right) e^{\left(\frac{-t}{\tau}\right)},$$

where r(t) represents the number of items recalled at time t, N represents asymptotic recall (the number of items recalled if t was infinite) and τ represents the mean latency of those items, that is, the average of the response latency of each item (Bousfield & Sedgewick, 1944; McGill, 1963).

The exponential as a description of the time course of recall has been developed in the random-search model (McGill, 1963), a forerunner of relative-strength models. This two-stage model assumes equal strengths of all of the items in a search set. Sampling is accomplished randomly, one item at a time, at a constant rate. After the recovery stage, the item is replaced (sampling-withreplacement) and has an equal chance of being sampled again. As a consequence of the increase in resampling of already recalled, intruding, or not recoverable items over the recall period, the probability of recalling new items declines with proceeding recall. Although some of the assumptions of the random-search model might be over-simplified, a very useful prediction is derived from the model:

$$\tau(\mathit{mean\ latency}) = \mathit{sample\ size} \times \mathit{sampling\ speed}$$

The equation describes a linear relationship between mean latency on the one side and search set size and the time it takes to sample one item on the other. Assuming that sampling speed per item remains constant across a recall period, mean latency can be used as a direct measure for the size of the search set. Thus, if the search set size is doubled, mean latency should become doubled as well. Rohrer and Wixted (1994) manipulated the study list length, thereby manipulating the search set size, and showed that mean latency increased linearly with increasing list length. As can be seen from the equation, mean latency does not depend on the item's absolute strength. Rohrer and Wixted (1994) tested this prediction by manipulating item strength via presentation duration. Subjects studied items for one, two or four seconds. As predicted, mean latency did not vary with study time, whereas recall totals increased with increasing study time.

The independence of recall totals and mean latencies has been nicely demonstrated in a neuropsychological study. Rohrer et al. (1999) measured response latencies of patients suffering from Alzheimer's disease and patients suffering from Huntington's disease. Recall totals did not differ between the groups, but Alzheimer's patients showed smaller mean latencies and Huntington's patients showed greater mean latencies than a control group. The smaller mean latencies in Alzheimer's patients are in line with the hypothesis that Alzheimer impairs the storage of memory traces, thereby reducing the search set size during memory recall. Huntington's disease is assumed to slow the retrieval process, which is mirrored in the slower latencies. These and other studies (e.g., Bäuml et al., 2005; Rohrer, 1996, Rohrer, Salmon, Wixted, & Paulsen, 1999; Rohrer & Wixted, 1994; Rohrer, Wixted, Salmon, & Butters, 1995; Wixted et al., 1997;

Wixted & Rohrer, 1994) indicate that recall totals and recall latencies are independent measures of memory performance. This independency, in reverse, supports models that incorporate a two-stage process of retrieval (e.g., Raaijmakers & Shiffrin, 1981; Rohrer, 1996).

Important for the current purpose, the dependency of the mean response latency on the search set size can be expressed in terms of the relative strength rule. The recall latency of an item is inversely related to its recall probability during sampling, defined by the relative strength rule (see Wixted et al., 1997, for a derivation). Thus,

$$\tau = \frac{1}{p},$$

$$\text{with } p = \left[\frac{s_k}{\sum s_i} \right],$$

representing the item's strength relative to the sum of strengths of all of the items belonging to the search set. In other words, mean recall latencies can be used as a direct measure of an item's relative strength within a search set. They could, under certain circumstances, be sensitive to the effects of inhibition on interfering items.

Experiment 3

Experiment 3 investigates how inhibition affects the absolute strength of interfering items. For this purpose, a recognition test procedure was employed in the retrieval-practice paradigm. Previous findings of retrieval-induced forgetting in recognition tests (Gómez-Ariza et al., 2005, Hicks & Starns, 2004, Spitzer & Bäuml, 2007, Verde, 2004) support the view that inhibition affects the absolute item strengths. Inhibitory theory assumes that, within the retrieval-practice paradigm, an interfering items' memory representation is weakened (for reviews, see Anderson, 2003, or Bäuml et al., 2010). Spitzer and Bäuml (2007) compared different predictions of a dual-process account (e.g., Yonelinas, 2002) and a single process account (e.g., Wixted, 2007) of recognition memory in the retrieval-practice paradigm. They found retrieval-induced forgetting in recognition memory and found their results to be better accounted for by the single process account of recognition memory. Spitzer and Bäuml (2007) concluded that the observed retrieval-induced forgetting in recognition tests is due to a reduction in general memory strength by inhibition.

However, whether a forgetting effect in the retrieval-practice paradigm can be attributed solely to inhibition, or could also (at least partly) originate from strength-dependent competition, is still under debate. Recently, Verde (2009) demonstrated in a series of experiments and simulations that list-strength effects, induced by the selectively strengthening subsets of items, could be found in cued recall, while controlling for the contribution of retrieval inhibition. The author concluded that strength competition contributes to the forgetting of items, as well as retrieval inhibition. Such list-strength effects were also found in studies using recognition tests (Norman, 2002; Verde & Rotello, 2004). In order to control for effects of strength-dependent competition, a reexposure condition was included in Experiment 3.

Experiment 3 was designed to replicate and extend previous findings of retrieval-induced forgetting in recognition tests, using reexposure as a control condition. In both the selective retrieval and the reexposure condition, to-be-practiced items are strengthened during the practice phase. In contrast to selective retrieval, reexposure of a part of the previously studied material does not induce interference, and does therefore not trigger the inhibition of unpracticed items (Bäuml & Aslan, 2004). Thus, the absolute memory strength of unpracticed items in the reexposure condition should not be affected. Retrieval-induced forgetting in recognition memory is expected to be found in the selective retrieval, but not in the reexposure condition.

Methods

Subjects

Subjects were 96 students at the University of Regensburg (18-33 years old, 78 women, 18 men). All subjects had German as their native language and received course credit or 5 € for participation.

Materials

Stimuli were 216 German nouns from 18 semantic categories, drawn from published norms (Mannhaupt, 1983; Scheithe & Bäuml, 1995). Each category consisted of six items (mean rank = 9.5, *SD* = 2.6) with unique word-stems with respect to their category, that were used in the study phase of the experiment, and six items (mean rank = 9.8, *SD* = 5.8) that were used as lure items in the recognition memory test. The six items used in the study phase were divided into two sets practiced in the intermediate phase of the selective retrieval and the reexposure condition.

Design

The experiment consisted of three blocks (within-subjects design), each of which comprised a study phase, an intermediate phase, and a recognition phase. Blocks differed in the list that was provided and the type of CONDITITON (selective retrieval, reexposure, control) conducted during the intermediate phase. In the selective retrieval condition, category labels and word stems of the three to-be-practiced items (SPORT - Hoc___) in each category were presented. Subjects were instructed to retrieve the corresponding items. In the reexposure condition, category labels of one set of three intact to-be-practiced items (SPORT - Hockey) per category were presented; subjects were instructed to restudy the items to enhance their performance on the recall test (e.g., Bäuml & Aslan, 2004). Both practice procedures were repeated once in the intermediate phase (1st and 2nd cycle).

The practice procedure created two types of items in the selective retrieval and the reexposure condition, practiced and unpracticed items. Unpracticed items were always tested before practiced items during the subsequent recognition test. Although no practice procedure was conducted in the control condition, items in the control condition were also split into two sets, matching practiced and unpracticed items in terms of test order (first set, second set). During the test phase of each block, the 36 studied items were presented, intermixed with 36 lure items. Lure items were also split into two sets, according to their order of appearance during the recognition test (first set vs. second set). The detrimental effect (forgetting) of practice was defined as the difference between first set control items and unpracticed items in either the selective retrieval or the reexposure condition. The beneficial effect (enhancement) was defined as the difference between second set control items and practiced items from either the selective retrieval or the reexposure condition. The assignment of list to condition and of item set to item type (practiced vs. unpracticed) was counterbalanced across subjects; the order of blocks was randomized.

Procedure

Subjects were tested individually in a quiet surrounding, seated in front of a 15-inch computer screen.

Study Phase

After instructing the subjects and making them familiar with the experiment's requirements via a short demonstration run, each of the three conditions started with a study phase. The items of one list (36 items from six categories) were presented sequentially, together with their category, for 4000 msec each and in random order. After the study phase, subjects performed a distracter task for 60 sec, during which they had to count backwards. The distracter task was carried out to prevent subject from rehearsing the most recently studied items.

Intermediate Phase

In the selective retrieval condition, subjects were asked to retrieve the respective item cued by its category label and unique word stem. The experimenter noted the subject's response on a prepared data sheet. In the reexposure condition, subjects were asked to restudy the item for the final recall test. In both conditions, to-be-practiced items were presented for 3000 msec. The items' order in the intermediate phase was block randomized, with three blocks, each containing one practiced item from each of the lists categories. Both practice procedures were repeated once in the intermediate phase. In the control condition, subjects conducted a distracter task, during which they had to rate pictures of famous people according to their attractiveness rather than retrieving or relearning any items. The intermediate phase was ended by another distracter task (sequencing digits in ascending order) lasting 120 sec, to exclude short term memory effects. Duration of the intermediate phase was held constant across conditions.

Test phase

In the test phase, a recognition test was conducted. Items were presented sequentially without their category. Subjects were instructed to indicate via specified keys on the PC keyboard whether the presented item was old (presented during study phase) or new (not presented during study phase). The next item was presented after the subject's response, or after a maximum response time of 10 sec had elapsed. No response feedback was given. Unpracticed items and half of the lure items (randomly chosen out of all lure items) were tested first. Thereafter, the remaining practiced items were presented, intermixed with the remaining lure items. Order of studied and lure items was randomized with the constraint that neither of the three item types was presented more than four times in a row.

Results

Selective Retrieval Phase

In the selective retrieval condition, 87.1 % (*SE* = 1.0 %) of the to-be-practiced items were successfully completed, confirming that retrieval of practiced items was successful.

Recognition Performance

D-prime[1] was calculated as the difference between the z-transformed hit and false alarm rate (see Fig. 19).

Unpracticed Items

D-prime for unpracticed items was 1.68 (*SE* = .09) in the selective retrieval condition, 2.03 (*SE* = .11) in the reexposure condition, and 1.98 (*SE* = .09) in the control condition. T-tests revealed that the difference between the selective retrieval and the control condition [t_{47} =2.96, $p < .01$] was significant, as well as the difference between the selective retrieval and the reexposure condition [t_{47} = 3.03, $p < .01$]. The difference in d-prime between the reexposure and the control condition was not significant [$t_{47} < 1$].

The recognition hit rate for unpracticed items was .73 (SE= .02) in the selective retrieval condition, .76 (SE= .02) in the reexposure condition and .81 (SE= .02) in the control condition. T-tests revealed that the difference between the selective retrieval and the control condition was significant [t(47)=4.01, p<.001], as

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[1] To avoid undefined values in the computation of d-prime, the hit and false alarm rates were adjusted by adding 0.5 to the number of hits and false alarms and dividing them by the number of responses +1.0 (Snodgrass & Corwin, 1988).

well as the difference between the reexposure and the control condition [t(47)=2.29, p<.05]. The difference in recognition hits between the selective retrieval and the reexposure condition was not significant [t(47)=1, p=.32].

The false alarm rate for unpracticed items was .14 (SE= .02) in the selective retrieval condition, .11 (SE= .02) in the reexposure condition and .15 (SE= .02) in control condition. T-tests revealed that the difference between the selective retrieval and the reexposure condition [t(47)=2.47, p<.05] was significant, as well as the difference between the reexposure and the control condition [t(47)=2.57, p<.05]. The difference in false alarm rate between the selective retrieval and the control condition was not significant [t(47)<1].

Practiced Items

D-prime for practiced items was 2.38 (*SE* = .09) the selective retrieval condition, 2.43 (*SE* = .09) in the reexposure condition and 1.92 (*SE* = .11) in the control condition. T-tests revealed that the difference between the selective retrieval and the control condition [t_{47} = 4.76, $p < .001$] was significant, as well as the difference between the reexposure and the control condition [t_{47} = 5.17, $p < .001$]. The difference in d-prime between the selective retrieval and the reexposure condition was not significant [$t_{47} < 1$].

The recognition hit rate for practiced items was .91 (SE= .01) in the selective retrieval condition, .93 (SE= .01) in the reexposure condition and .78 (SE= .02) in control condition that did not involve practice. T-tests revealed that the difference between the selective retrieval and the control condition was significant [t(47)=5.78, p<.001], as well as the difference between the reexposure and the control condition [t(47)=6.75, p<.001]. The difference in recognition hits between the selective retrieval and the reexposure condition was not significant [t(47)=1.34, p=.19].

The false alarm rate for practiced items was .14 (SE= .02) in the selective retrieval condition, .15 (SE= .02) in the reexposure condition and .14 (SE= .02) in control condition. T-tests revealed no significant differences between the conditions [all t's(47)<1].

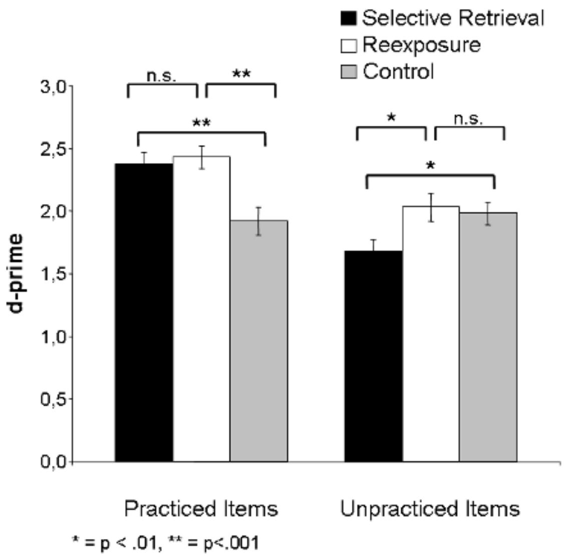

Figure 19. Recognition performance. Forgetting, as indicated by the difference in d-prime between unpracticed items and first set control items, is depicted on the right (error bars indicate S.E.). Whereas recognition performance in the reexposure condition did not differ from the control condition, d-prime was significantly lower in the selective retrieval condition than in the reexposure and the control condition. On the left, enhancement, as indicated by the difference in d-prime between practiced items and second set control items, is depicted. Recognition performance of practiced items did not differ between the selective retrieval and the reexposure condition, but in both conditions d-prime was higher in the control condition.

Discussion

Experiment 3 replicated previous findings in showing that retrieval-induced forgetting can be found in recognition tests (Gómez-Ariza et al., 2005, Hicks & Starns, 2004, Spitzer & Bäuml, 2007, Verde, 2004). Memory performance, as measured by d-prime, for unpracticed items was reduced in an old / new recognition test as compared to the control condition. Extending previous findings, Experiment 3 included a reexposure condition as an additional control condition. Restudying a subset of items does not lead to forgetting of unpracticed items in cued recall tests (Bäuml & Aslan, 2004). Experiment 3 showed that this holds true using a recognition test procedure. Memory performance for unpracticed items in the reexposure condition matched the memory performance in the control condition. In contrast, both selective retrieval and reexposure induced significant enhancement of the practiced items, compared to the control condition in which no items were practiced between study and the recognition test.

The present results clearly support an inhibitory account of retrieval-induced forgetting (for reviews, see Anderson, 2003, or Bäuml et al., 2010). This account states that during retrieval of a subset of previously studied items, the interfering items' memory representations are being suppressed. Absolute item strength, as measured by recognition performance, of unpracticed items in the selective retrieval was impaired as compared to absolute strength of unpracticed items from in the reexposure condition. Non-inhibitory blocking accounts have difficulties explaining the present results. A recognition test directly accesses the absolute strength of an item. Thus, interference by other, strong competitors that could block the recall of unpracticed items is circumvented. Moreover, if strength-dependent competition contributed equally to forgetting, as a study on the list-strength effect suggested (Verde, 2009), forgetting of unpracticed items as compared to control items should have been found in the reexposure condition, which was not the case.

Prior studies using cued recall at the final test have found that retrieval-induced forgetting is retrieval-specific (see Anderson, 2003, or Bäuml et al., 2010). The current results expand those previous findings, showing that the detrimental effect of retrieval practice on the recognition of previous competitors is also retrieval-specific. No similar impairment was found in the reexposure condition, which involves strengthening of some items, but no interference by unpracticed items, and thus no inhibition of the unpracticed items. Consistently, the recognition performance of unpracticed items was not impaired in the reexposure condition.

Whereas the results from the recognition performance analysis (d-primes) clearly speak in favour of an impairment of interfering items by inhibition in the selective retrieval condition, the hit and false alarm rates need closer examination. Hit rates did not differ between the selective retrieval and reexposure condition, but, subjects showed higher false alarm rates in the selective retrieval than in the reexposure condition. This pattern can be explained by assuming that the subjects shifted their criterion across conditions, based on the strength of the items in these conditions. Such strength-dependent criterion shifts have been shown in studies investigating the list-strength effect. Hirshman (1995) found that, after studying lists with higher mean strength, the subjects' criterion was stricter than following lower strength lists (but see Stretch & Wixted, 1998, for inconsistent findings). In a similar vein, subjects might have lowered their criterion in the selective retrieval, because the mean item strength was lower in the selective retrieval than in the reexposure condition. While a more liberal criterion led to higher false alarm rates than in the reexposure condition, it did not result in a higher hit rate, because the unpracticed items in the selective retrieval condition are assumed to be weakened by inhibition as compared to the reexposure condition.

The finding of a forgetting effect in the selective retrieval condition suggests that the absolute strength of unpracticed items in the selective retrieval condition was affected by inhibition. In the reexposure condition, no forgetting was found, indicating that the unpracticed items' memory strength was not affected in this condition. However, an influence of relative competition on recognition tests cannot be entirely excluded. For example, the presentation of the probe-item during the recognition test could activate related items. This would lead to a search set with more than one item and competition among these items for being sampled. In Experiment 3, this alternative interpretation could be declined because of the results from the reexposure condition. If the forgetting effect in the selective retrieval condition was due to the activation of strong, practiced items during recognition of the unpracticed items, forgetting should also have emerged in the reexposure condition, which was not the case.

Conclusion

The results from Experiment 3 strongly support an inhibitory account of retrieval-induced forgetting. Absolute memory strength of unpracticed items, as measured by a recognition test, was reduced by selectively retrieving, but not by restudying a subset of previously encoded items. Thereby, the results from Experiment 3 support the view that retrieval-induced forgetting is a retrieval-specific effect that can hardly be explained by strength-dependent competition.

Experiment 4

Bäuml et al. (2005) investigated the dynamics of recall within the retrieval-practice paradigm using recall latencies. In their experiment, the authors tested whether retrieval-induced forgetting was due to (i) the suppression of an item's memory representation (following the inhibitory account, see Anderson, 2003), to (ii) an unbinding of the item from the cue (as suggested by e.g., Geiselman, Bjork, & Fishman, 1983), or to (iii) the slowing of the processing of previously interfering items (an approach derived from the negative priming literature; e.g., Tipper & Cranston, 1985). Bäuml et al. (2005) constructed the item material such that each item type (practiced, unpracticed, controls) was tested with a different subcategory cue. This way, the search set during recall was delimited to one item type, which created a pure-list situation with (assumed) equal item strengths within each list.

With this particular experimental setting, each of the above described three accounts of retrieval-induced forgetting predicted different mean latencies: (i) equal mean latencies for unpracticed items and control items, because suppression of the memory representations would neither affect sampling rate nor search set size; (ii) faster mean latencies for unpracticed than control items, because unbinding would reduce the search set size; and (iii) slower mean latencies for unpracticed than control items, because of the slowing in processing. As there was no difference between unpracticed and control items, the results indicated that retrieval-induced forgetting did not affect the size of the search set (as predicted by the unbinding account) and did not affect the sampling rate (as predicted by the retrieval-slowing account). Thus, the findings by Bäuml et al. (2005) support an inhibitory account of retrieval-induced forgetting, and are well in line with the view that effects of inhibition become manifest at the recovery and not the sampling stage of the final recall (e.g., Healey et al., 2010; Hicks & Starns, 2004; Spitzer & Bäuml, 2007; Veling & van Knippenberg, 2004).

Concluding that the effects of inhibition cannot be observed at the sampling stage of recall might be premature, however, due to some methodological limitations of previous studies. Bäuml et al. (2005) employed a pure-strength paradigm in their study, limiting each search set to items with equal item strength. In a mixed-list paradigm, items with different strengths are part of one search set, which changes the predictions based on the relative-strength rule during the sampling stage of recall. As studies on the list-strength effect have shown (e.g., Malmberg & Shiffrin, 2005; Ratcliff et al., 1990; Tulving & Hastie, 1972; Wixted et al., 1997), recall performance for strong items from a mixed-strength list (i.e., with strong and weak items together in one list) is higher than for equally strong items from a pure-strength list (i.e., with only strong items on a list). According to relative strength models, list strength affects the sampling stage of recall. The relative strength of strong items from a mixed-strength list is higher, because some of their competitors are weak, whereas strong items from pure-strength lists have exclusively strong competitors. This difference should result in shorter mean latencies for strong items from mixed-strength lists than strong items from pure-strength lists.

Wixted et al. (1997) evaluated these predictions by manipulating item strength and comparing response latencies across pure-strength and mixed-strength lists. Item strength was varied by repeatedly presenting all items of a list (pure-strength) or only a subset of these items (mixed-strength). They showed that across pure-strength lists, response latencies did not vary with item strengths in these lists. In the mixed-strength lists, response latencies were smaller for strong than for weak items. Moreover, mean latencies of strong items from mixed-lists were smaller than latencies of equally strong items from pure-strength lists. The opposite was true for weak items. Thus, response latencies varied corresponding to the predictions of the relative strength model for mixed-strength and pure-strength lists.

Applied to the retrieval-practice paradigm, this approach offers a possibility to proof a central assumption of the inhibitory account of retrieval-induced forgetting: Inhibition weakens an item's memory representation. If true, this should be observable in the recall latencies, but only in a mixed-strength paradigm. In the classical retrieval-practice paradigm, one would assume that after the study phase, all of the items have the same strength. In a selective retrieval condition, the strength of a subset of these items is increased by repeatedly retrieving them during retrieval practice. Additionally, unpracticed items are weakened by inhibition. Thus, the selective retrieval condition produces a mixed-strength list. In the control condition without a practice phase, the items' strengths remain untouched (a pure-strength list). At the final recall test, the search sets are limited by the category cue. Consequently, the relative strength rule would predict smaller mean latencies for practiced (strong) items than control items, because strong items have a sampling advantage over unpracticed (weak) items. The unpracticed items should show greater mean latencies than control items, because of the disadvantage in competition they have compared to strong items within the search set.

However, this would not indicate the additional weakening by inhibition, but only their sampling disadvantage compared to the strong items (i.e., blocking). Thus, another condition is required, which offers a mixed-strength list situation without additional weakening of the unpracticed items by inhibition. Because of the retrieval-specificity of retrieval-induced forgetting, restudying a subset of items will not trigger inhibition (Bäuml & Aslan, 2004). However, such a reexposure condition will still create a similar mixed-strength situation as a retrieval-practice condition, because a subset of items is strengthened by reexposure. These strong items will have a sampling advantage over items that had not been reexposed. Because reexposure will not additionally weaken the unpracticed items (as no inhibition is involved), it represents a good baseline for the selective retrieval condition.

Table 5 gives a numerical example of the sampling situation in a free recall test, based on the assumptions of the relative strength rule. A category in the control condition corresponds to a pure-strength list; a category in the selective retrieval and the reexposure condition corresponds to a mixed-strength list. After study, all of the items have the strength 1. In the selective retrieval and the reexposure condition, practiced items are strengthened (to strength 2). Because unpracticed items interfere during selective retrieval, inhibition reduces their strength (to strength 0.5). Unpracticed items in the reexposure condition are not weakened, because no inhibition is involved (and therefore remain at strength 1).

Strengths in the control condition remain unchanged at the study level (strength 1). The recall latencies are calculated according to the relative strength rule [$s_k / \sum s_i$].

Table 5. Hypothetical item strengths and corresponding response latencies in mixed-strength lists created by selective retrieval (SR) and reexposure (RE) practice and in a pure strength list (C =control condition without practice between study and test).

Type of list		Item Strengths						Mean Strength		Mean latencies	
		Practiced (P+)			Unpracticed (P-)			P+	P-	P+	P-
		s1	s2	s3	s4	s5	s6	s	s	τ	τ
Mixed	SR	2	2	2	0.5	0.5	0.5	2	0.5	3.75	15
	RE	2	2	2	1	1	1	2	1	4.5	12
Pure	C	1	1	1	1	1	1	1		6	

Based on these assumptions, two effects should be observable by measuring recall latencies during free recall: (i) faster latencies for practiced than control items and slower latencies for unpracticed than control items in the selective retrieval and the reexposure condition, reflecting biased competition due to the strengthening of a subset of items in a category, which occurs in both the selective retrieval and the re-exposure condition; and (ii) slower latencies for unpracticed and faster latencies for practiced items in the selective retrieval than in the reexposure condition, reflecting the additional weakening of a subset of items, that is, the lowering of their relative strength, due to inhibition.

Methods

Subjects

36 students at the University of Regensburg (19-31 years old, 31 women, five men) participated in the experiment. All subjects had German as their native language, and received course credit or 5 € for participation.

Materials

Stimuli were 108 German nouns from 18 semantic categories, drawn from several published norms (Mannhaupt, 1983; Scheithe & Bäuml, 1995). Each category consisted of six items (mean rank = 9.5, *SD* = 2.6) with unique word-stems with respect to their category. Each category was divided into two sets consisting of three "to-be-practiced items" (practiced in the intermediate phase of the reexposure and the selective retrieval condition), and three "unpracticed items".

Design

An outline of the experimental design can be seen in Figure 20. The experiment consisted of three blocks (within-subjects design), each of which comprised a study phase, an intermediate phase, and a test phase. Blocks differed in the list that was provided and the type of CONDITITON (selective retrieval, reexposure, control) conducted during the intermediate phase: In the selective retrieval condition, category labels and word stems of one set of three to-be-practiced items (SPORT - Hoc___) per category were presented. Subjects were instructed to retrieve the corresponding items. In the reexposure condition, category labels of one set of three intact to-be-practiced items (SPORT - Hockey) per category were presented; subjects were instructed to restudy the items to enhance their performance on the recall test (e.g., Bäuml & Aslan, 2004). Both practice procedures were repeated once in the intermediate phase (1st and 2nd Cycle).

The practice procedure created two types of items in the selective retrieval condition, practiced items (SRp) and unpracticed items (SRu). In the same manner, in the reexposure condition, practiced items (REp) can be distinguished from unpracticed items (REu). In the control condition, no practice of studied items took place, and subjects performed a distracter task instead. Thus, in the control condition, only one item type was created (CON). The detrimental effect (forgetting) was defined as the difference between unpracticed items in either the selective retrieval or the reexposure condition and control items. The beneficial (enhancement) was defined as the difference between practiced items from either the selective retrieval or the reexposure condition and control items. The assignment of list to condition and of item set to item type (practiced vs. unpracticed) was counterbalanced across subjects; the order of blocks was randomized.

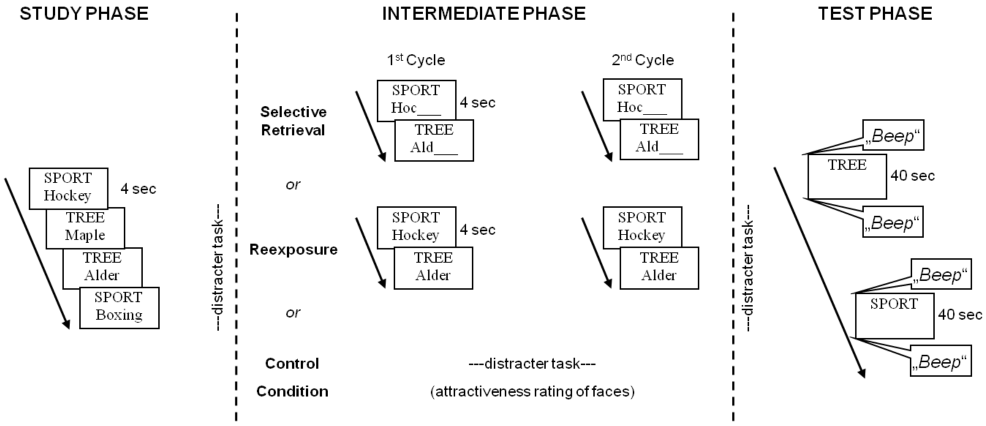

Figure 20. The experimental procedure as employed in the present study. The experiment consisted of three blocks, each block comprising a study phase, an intermediate phase, and a test phase. In the study phase of each block, items were studied together with their category cue. In the test phase of each block, all of the studied items were tested using a category cued free recall test. Start and end of the recall was signaled by a tone. The intermediate phase varied with condition: in the selective retrieval condition, a subset of the previously studied items was retrieved on two consecutive cycles; in the reexposure condition, the same subset of items was restudied on two consecutive cycles; in the control condition, no practice took place and subjects conducted a distracter task instead.

Procedure

Experiment 4 comprised a study phase, an intermediate phase and a test phase. As the study and the intermediate phase were identical to those conducted in Experiment 3, details can be found on page 82.

Test Phase

After the intermediate phase, a category-cued recall test was conducted. Subjects were instructed to recall as many studied items as possible belonging to the specified category. Order of categories in the test phase was randomized. As a memory cue, the category name was presented on the computer screen with a simultaneously presented tone. The tone was the starting signal for subject's recall and marked the beginning of the recall epoch on the audio-recording system. The category name was presented for 40 sec and ended by another tone that signaled the end of the recall epoch. Subjects' answers were recorded by a computer program in a pulse code modulation-waveform format with a sampling rate of 44 kHz and a 16-bit resolution. Latencies were assessed by means of the computer program Cool Edit 2000 (Version 4.1, Syntrillium Software Corporation, Pheonix, Arizona). The voice onset of each recalled item was located manually in the spectogram. Only correct answers were included in the latency analysis. Mean recall frequency and mean latencies were used as dependent variables.

Measure of Latency

The recall epoch was divided into 40 bins of 1 sec length. The time elapsed since the beginning of the recall period was measured for each of the five item types (SRp, SRu, REp, REu, CON), and correct answers were assigned to the respective bin. The observed latency distributions were fitted by an ex-Gaussian distribution (see Appendix), using a maximum likelihood estimation procedure. The ex-Gaussian distribution is a convolution of a normal (Gaussian) and an exponential distribution. This convolution is used to describe a serial, independent two-stage process of memory retrieval, including (i) initiating memory search and establishing a memory set, and (ii) the ongoing search for target items. The

Gaussian stage has mean μ and standard deviation σ, the exponential stage has mean τ and standard deviation τ. τ represents the mean latency of the items. Asymptotic standard errors (ASEs) for each parameter were obtained from the Hessian matrix of second partial derivatives. Using these standard errors, paired t-tests were conducted comparing τ values between conditions (degrees of freedom: summed degrees of freedom for each parameter estimate).

Analysis of Output Interference

In the selective retrieval and the reexposure condition, mean output positions during free recall were analyzed for unpracticed and practiced items, respectively. The output index was computed as a difference score for each subject and each condition. The mean output position of unpracticed items was subtracted from the mean output position of the practiced items. Thus, positive values reflect early output of practiced items, negative values reflect early output of unpracticed items.

Results

Recall Totals

During the retrieval-practice phase, 88.3 % (*SE* = 1.4 %) of the items were correctly recalled, confirming that retrieval of practiced items was successful. In the test phase, an average of 86.9 % (*SE* = 1.3 %) of the SRp items and 54.5 % (*SE* = 2.8 %) of the SRu items were remembered. Recall rates were 86.4 % (*SE* = 2.0 %) for the REp items and 56.5 % (*SE* = 2.9 %) for the REu items. In the control condition, subjects remembered 62.1 % (*SE* = 2.2 %) items on average (see Fig. 21).

In both the selective retrieval and the reexposure condition, subjects remembered reliably more practiced items than items in the control condition [$t_{35} > 11$, $p < .001$, for both paired comparisons]. Significant forgetting (unpracticed items vs. control items) was found in the selective retrieval condition [$t_{35} = 3.7$, $p <$

.001] and in the reexposure condition [t_{35} = 2.2, $p < .05$]. Recall rates of unpracticed items did not differ between the selective retrieval and the reexposure condition [t_{35} = .7, $p > .47$].

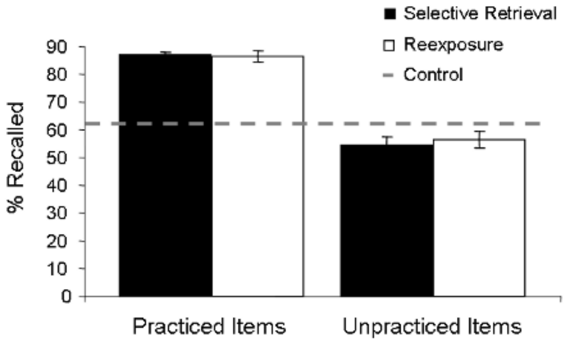

Figure 21. Recall totals. Forgetting, as indicated by the difference in recall rates between unpracticed and control items (dashed line), is depicted on the right (error bars indicate S.E.). In both the selective retrieval and the reexposure condition, fewer items were recalled than in the control condition. On the left, enhancement, as indicated by the difference in recall rates between practiced items and control items, is depicted. In both the selective retrieval and reexposure condition, more items were recalled than in the control condition (dashed line).

Recall Latencies

Response latencies were grouped into 1 sec bins and plotted as a function of time (Figure 22). Each data point, representing one bin, contains the absolute frequency of items recalled. The best fitting ex-Gaussian distribution for each item type is also depicted in Figure 22. A summary of the parameter estimates, found by the maximum likelihood estimation, is given in Table 6.

Table 6. Ex-Gaussian Fits of Latency Distributions.

	Initial stage		Mean latency	Goodness-of-Fit			
	μ (ASE)	σ (ASE)	τ (ASE)	N	χ^2	df	p
SRp	1.55 (.06)	0.26 (.31)	3.65 (.16)	563	34.43	11	<.001
SRu	1.78 (.17)	0.43 (.21)	6.06 (.37)	353	40.49	16	<.001
REp	1.56 (.07)	0.27 (.30)	3.90 (.18)	560	25.72	12	<.05
REu	1.62 (.15)	0.30 (.36)	5.99 (.34	366	40.63	16	<.001
CON	1.56 (.06)	0.25 (.27)	4.68 (.17)	805	99.35	16	<.0001

Gaussian Stage

In the selective retrieval condition, μ was 1.55 sec (*ASE* = .06) for the practiced items, and 1.78 sec (*ASE* = .17) for the unpracticed items. In the reexposure condition, μ was 1.56 sec (*ASE* = .07) for the practiced items and 1.62 sec (*ASE* = .15) for the unpracticed items. For items in the control condition, μ was 1.56 sec (*ASE* = .06). Paired comparisons showed that μ did not differ significantly across conditions and item types ($p > .2$, for all tests).

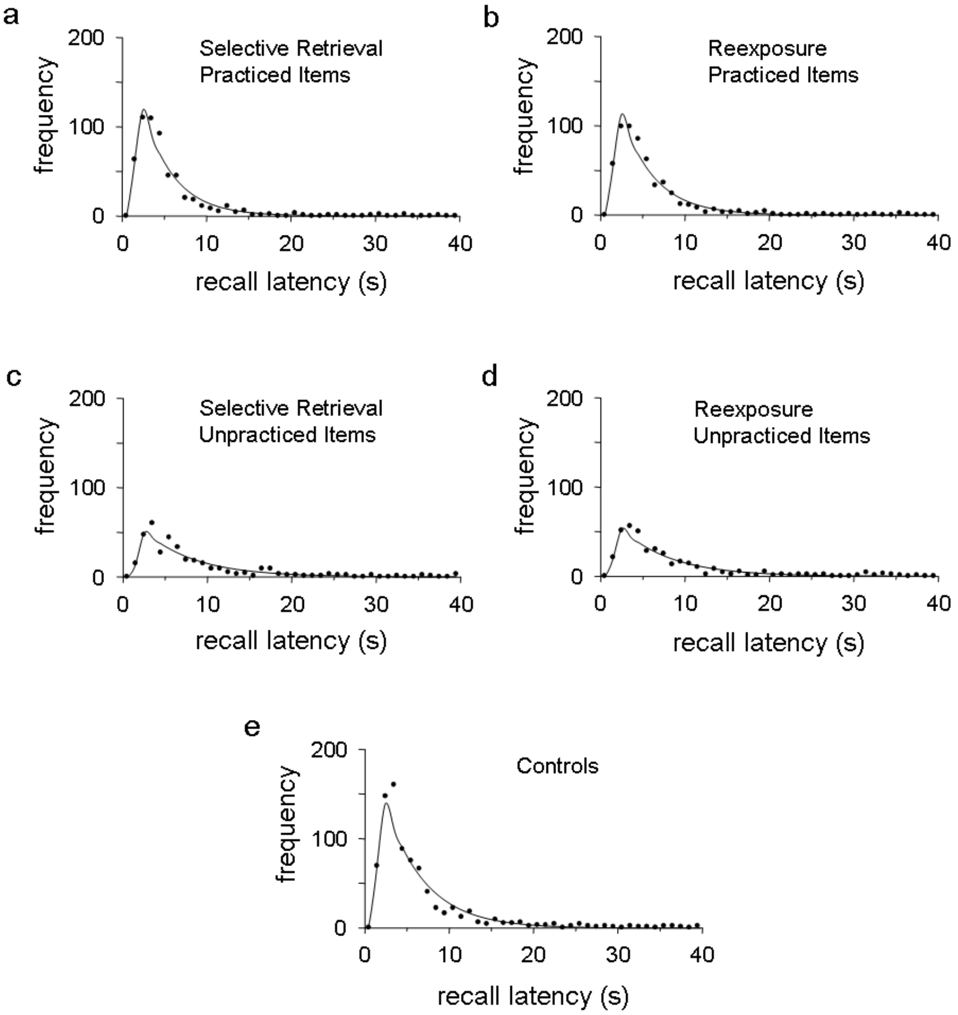

Figure 22. Recall latencies. Latency distributions (absolute frequency recalled for every 1-sec bin) for the practiced items from (a) the selective retrieval and (b) the reexposure condition; for unpracticed items from (c) the selective retrieval and (d) the reexposure condition; and (e) for control items from the control condition. The solid lines depict the best fitting ex-Gaussian functions (see Appendix for equation). Table 6 shows the parameter estimates.

Exponential Stage

In the selective retrieval condition, mean response latency (τ) was 3.65 sec (*ASE* = .16) for practiced items (SRp) and 6.06 sec (*ASE* = .37) for unpracticed items (SRu). In the reexposure condition, τ was 3.90 sec (*ASE* = .18) for practiced items

(REp) and 5.99 sec (*ASE* = .34) for unpracticed items (REu). For control items (CON), a τ of 4.68 sec (*ASE* = .17) was computed. Paired comparisons showed that the difference between SRp and CON items was significant [$t_{74} = 4.41$, $p < .0001$], as well as the difference between REp and CON [$t_{74} = 3.15$, $p < .005$]. Mean latencies of SRu and CON items differed significantly [$t_{74} = 3.39$, $p < .005$], as well as mean latencies of REu and CON items [$t_{74} = 3.45$, $p < .001$]. Neither the difference between SRp and REp [$t_{74} = 1.04$, $p = .30$], nor the difference between SRu and REu [$t_{74} < 1$] were significant.

Output Interference

The mean output index was .72 (*SE* = .12) in the selective retrieval condition, and .35 (*SE* = .11) in the reexposure condition. The difference between the conditions was significant [$t_{35} = 2.29$, $p < .05$], implicating earlier mean output of practiced items in the selective retrieval than in the reexposure condition.

To further investigate the relationship between forgetting and output position, the subject sample was split into a high and a low forgetting group, for the selective retrieval and the reexposure condition, respectively, and compared their output index. The output index did not differ significantly between high and low forgetters, neither in the reexposure [$t_{34} = 1.65$, $p = .108$] nor in the selective retrieval condition. [$t_{34} < 1$].

Discussion

The present experiment investigated the impact of inhibition on previously interfering items during free recall. The effects of selective retrieval and reexposure were compared, assuming that the former, but not the latter induces inhibition of interfering items that leads to retrieval-induced forgetting on a later recall test (Bäuml & Aslan, 2004). Concerning recall totals, in the selective retrieval and the reexposure condition, significant forgetting of the unpracticed items was found. The forgetting effect did not differ between the conditions.

The difference between the conditions that would have been expected on the basis of an inhibitory account of retrieval-induced forgetting was probably superimposed by an effect of test type. In category cued or free recall, strengthened items are typically recalled first. The early retrieval of these items leads to inhibition of the not strengthened items during the test, a finding referred to as output interference (see Anderson, 2003). Because reexposure and selective retrieval both strengthened a subset of items, the unpracticed items in both conditions were subject to output interference. Compared to items from a control condition without strengthening of a subset of items, unpracticed items from the reexposure and the selective retrieval condition were exposed to more output interference during category cued recall than control items. Thus, less unpracticed items from the reexposure than the control condition were recalled due to output interference, mimicking a retrieval-induced forgetting effect without inhibition during the retrieval-practice phase. As the output interference analysis showed, practiced items were recalled before unpracticed items in the reexposure and the selective retrieval condition. However, the difference in output position between practiced and unpracticed items was bigger in the selective retrieval condition than in the reexposure condition, indicating that unpracticed items in selective retrieval were subject to relatively more output interference than in the reexposure condition.

Recall Latencies

Recall latencies were recorded during free recall and used to estimate the parameters of an ex-Gaussian distribution. This distribution has been shown to adequately describe the temporal dynamics of free recall (Rohrer & Wixted, 1994; Wixted & Rohrer, 1993; Wixted et al., 1997). Two critical parameters are estimated from the recall latencies: The first parameter characterizes the initial Gaussian stage of the ex-Gaussian distribution. It is interpreted as the initiation and delimitation of a search set by a retrieval cue. The second parameter defines the exponential stage of the ex-Gaussian distribution (mean latency). It describes the sampling process itself, and has been shown to be inversely related to the relative strength of the items (see Wixted et al., 1997).

Concerning the initial stage, the estimated parameters did not differ across conditions, suggesting that the experimental manipulation did not affect the initiation of the retrieval process. Mean latencies, defining the exponential stage of the ex-Gaussian, differed across conditions. Practiced items in the selective retrieval and the reexposure condition were recalled faster than control items. The opposite was true for weak items. This finding of a positive list-strength effect replicates previous work on that topic. Wixted et al. (1997) strengthened items by repeatedly presenting them to the subjects and found a positive list-strength effect on recall latencies. These former and the present results converge on the view that the relative strength of an item is crucial to its recall position in a free or category cued recall test.

Inhibition and Recall Latencies

It was hypothesized that the impact of inhibition on the relative strength of interfering items can be captured by comparing mean latencies of unpracticed items from a selective retrieval and a reexposure condition. Mean latencies of unpracticed items were expected to be larger in the selective retrieval than in the reexposure condition. Additional to the sampling disadvantage that is due to the mixed-strength situation, inhibition suppresses the unpracticed items' memory representations in the selective retrieval but not in the reexposure condition. Finding a deficit in the sampling of unpracticed items that is due to inhibition would strongly support the inhibitory account of retrieval induced forgetting, in particular the view that inhibition weakens an item's memory representation.

However, the results did not confirm this hypothesis. Mean recall latencies for unpracticed items did not differ across conditions, leading to the conclusion that inhibition does not affect the sampling stage of recall. This view is in line with previous work on recall latencies and retrieval-induced forgetting. Bäuml et al. (2005) found no effect on recall latencies in free recall and suggested that the locus of inhibition is the recovery stage of recall. In a similar vein, Verde (2009) argued that strength dependent competition and inhibition both contribute to forgetting, with the former being located at the sampling stage and the latter being located at the recovery stage of recall.

Alternatively, an effect of inhibition on recall latencies might have been present but overshadowed by other factors in Experiment 4. For example, differential strengthening of to-be-practiced items in the selective retrieval and the reexposure condition could have superimposed an effect of inhibition on recall latencies. If reexposure strengthened the practiced items more than selective retrieval, practiced items would be recalled faster in the reexposure than in the selective retrieval condition. Consequently, unpracticed items would suffer from more output interference in the reexposure than in the selective retrieval condition. This relative slowing of the recall of unpracticed items in the reexposure condition would then mimic the slowing of the recall in the selective retrieval condition, even if only the latter one is caused by inhibition. The results from the output interference analysis do not support this view. The difference in output positions between practiced and unpracticed items was bigger in the selective retrieval than the reexposure condition.

Another possible explanation for the null effect of inhibition on recall latencies can be derived from the differentiation of contextual and item-specific features of studied items, inspired by temporal context models (e.g., Howard & Kahana, 2002; Malmberg & Shiffrin, 2005; Mensink & Raaijmakers, 1988). Whereas item-specific features can be described as all the features that are intrinsic to an item, like its semantic meaning, contextual features are commonly related to temporal, spatial, or emotional states associated with the item at encoding (see Murnane, Phelps, & Malmberg, 1999). Depending on the retrieval situation, item-specific or context features can both be decisive for successful recall. According to relative strength models like SAM, free recall tests rely strongly on the activation of contextual features of studied items. The list strength effect in free recall is assumed to emerge due to a contextually cued retrieval (Shiffrin, Ratcliff, & Clark, 1990).

If this differentiation of an item's features held true, the null effect found in the present experiment could be explained by assuming that inhibition suppresses the unpracticed items item-specific features, but not the contextual features. Such a view is in line with a pattern-suppression account of retrieval-induced forgetting (Anderson & Spellman, 1995), according to which overlapping, common features of targets and competitor items do not get suppressed. Given that target and competitor items share contextual features to a large extent, the contextual features of the competitor item would be insusceptible to inhibition during retrieval-practice. However, future research needs to be done to clarify this issue on the basis of experimental evidence.

Conclusion

In Experiment 4, the effects of inhibition on the relative strength of interfering items were investigated by analyzing recall latencies during free recall. Although theoretically expected, recall latencies for unpracticed items in the selective retrieval and the reexposure condition did not differ. Thus, the hypothesis that inhibition affects the sampling stage of recall could not be confirmed. Together with the results from Experiment 3 and from previous work (Bäuml et al., 2005), the present results converge on the view that retrieval-induced forgetting is an effect of inhibition reducing the absolute strength rather than the relative strength of interfering items.

Part IV

General Discussion

Selectively retrieving past memories is a highly dynamic process. Cognitive models assume that competing memories are activated by a common cue, such that interference arises and triggers inhibition, which in turn suppresses the initially activated, interfering memories (Anderson & Spellman, 1995). The present thesis made an effort to embrace this dynamic behavior on a methodological and theoretical level. A two-step strategy was pursued to unravel the dynamics of selective memory retrieval. First, the inhibitory mechanism was explored at the time at which it is assumed to operate, that is, during the practice phase of the retrieval-practice paradigm. Brain oscillations were analyzed in order to disentangle the neural functioning of inhibition. Second, the effects of inhibition on the absolute and relative strength of interfering items were investigated. Absolute item strength was tested by employing a recognition test procedure in the retrieval-practice paradigm. Measuring response latencies during free recall gave insight into the impact of inhibition on the sampling of interfering items, which depends on their relative strength.

Brain Oscillations Mediating Inhibition as it Operates

Theta Oscillations and Inhibition

In two Experiments, EEG data was analyzed during selective retrieval from memory. In both experiments, retrieval-induced forgetting was found, suggesting that neural signatures of an inhibitory mechanism suppressing interfering items during retrieval could theoretically be captured. Experiment 1 investigated the oscillatory correlates of inhibition during retrieval from episodic memory. The retrieval-practice paradigm was modified in order to isolate the engagement of an inhibitory mechanism. More specifically, repeated cycles of selective retrieval (see Kuhl et al., 2007, for a similar procedure) and repeated cycles of reexposure were conducted, such that, in line with the focus of the present thesis on retrieval dynamics, oscillatory activity could be compared across cycles. During the first cycle of selective retrieval practice, a high level of interference is thought to trigger the engagement of an inhibitory mechanism that resolves this competition. Consequently, during the second cycle of retrieval practice, less inhibition should be needed, because competition should have been resolved (at least partly) already during the first cycle. Experiment 1 showed that theta oscillations specifically mirrored this hypothesized pattern of the dynamics of inhibition. A reduction in theta amplitude was found across retrieval cycles. No such reduction was found when comparing consecutive cycles of reexposure. The reduction in theta amplitude across cycles of retrieval predicted later retrieval-induced forgetting. No such correlation was found in any other frequency band. This unique feature supports the conclusion that theta oscillatory activity reflects the dynamics of inhibition in episodic memory retrieval.

Experiment 2 was the first study to investigate the neural correlates of inhibition during retrieval from semantic memory. The procedure of the study was paralleled to that from Experiment 1, with the difference that the episodic encoding phase of the retrieval-practice paradigm was removed (see Johnson & Anderson, 2004, for a similar procedure), such that subjects had to generate items from semantic memory rather than retrieve them from episodic memory. Following the reasoning of Experiment 1, oscillatory activity was compared across repeated cycles of semantic retrieval-practice, assuming that semantically related memories initially interfere during retrieval and are inhibited, such that less and less inhibition is needed across cycles of semantic retrieval-practice. However, theta amplitude was not reduced across cycles in Experiment 2, but even showed the opposite trend.

The absence of the hypothesized effect in the theta band in Experiment 2 could be due to the fact that the forgetting effect in the Experiment 2 was rather small. Possibly, retrieval from semantic memory elicited only low levels of interference among category member, triggering low levels of inhibition throughout the repeated cycles of semantic retrieval. Thus, one could argue that the need for inhibitory control differed only marginally across cycles, and that this difference was too small to be captured by theta oscillations in the EEG. Therefore, the finding that theta oscillations reflect the dynamics of inhibition during selective retrieval from episodic memory (Experiment 1) cannot be extended to retrieval from semantic memory. Thus, the generalizability of an oscillatory correlate of inhibition across memory systems remains an open question to future research.

A recent study also investigated oscillatory correlates of inhibition in the retrieval-practice paradigm (Hanslmayr et al., 2010). The results from Experiment 1 are in line with the findings by Hanslmayr et al. (2010) in showing that theta oscillations reflect inhibitory processes during selective memory retrieval. In contrast to Hanslmayr et al. (2010), the present study controlled for effects of repetition priming. Because no difference in theta amplitude was found across repeated cycles of reexposure, the effect found across retrieval cycles cannot be attributed to repetition priming. Moreover, comparing oscillations across repeated cycles of selective retrieval allowed for disentangling the engagement of inhibition from its effects, a problem that was central to the brain-behavior correlation found by Hanslmayr et al. (2010). On the basis of the results of Experiment 1, the negative relationship between theta oscillations and retrieval-induced forgetting found by Hanslmayr et al. (2010) can be interpreted as reflecting the effects of inhibition.

A factor that might potentially limit the comparability between Experiment 1 and the study by Hanslmayr et al. (2010) is the difference in data analyzes. Hanslmayr et al. (2010) found evoked theta oscillations to be predictive of individual differences in retrieval-induced forgetting. In contrast to induced oscillatory activity, evoked oscillations are phase-locked to the stimulus onset. The present experiment did not distinguish between evoked and induced oscillatory activity. Thus, it remains subject to future research whether the phase-timing of theta oscillations plays a crucial role in inhibition during selective memory retrieval.

The view that theta oscillations index inhibition during selective retrieval from episodic memory is in line with previous fMRI findings. In their study, Kuhl et al. (2007) interpreted the reduction in BOLD signal in prefrontal areas across repeated cycles of selective retrieval as reflecting a decreased need of inhibitory control. Localizing the sources of the theta effect in Experiment 1 offered the possibility to relate brain oscillatory analyses closer to those previous fMRI findings. Indeed, the difference in theta amplitude was localized in the ACC, the brain region that showed BOLD signal changes predictive of later retrieval-induced forgetting in previous fMRI studies (Kuhl et al., 2007; Wimber et al., 2009).

Theta Oscillations and Interference

Previous EEG studies established a link between cognitive interference and theta oscillations. For instance, in classic interference paradigms (e.g., Stroop task, Flanker task), prefrontal theta oscillations varied with interference level (Cavanagh, Cohen, & Allen, 2009; Hanslmayr et al., 2008). These and other studies indicated that mid-frontal theta oscillatory activity is generated in the ACC (Gevins et al., 1997; Hanslmayr et al., 2008), complementing imaging studies pointing to the ACC as the neural source for interference detection (Botvinick, Braver, Barch, Carter, & Cohen, 2001). In the memory domain, a relation between theta amplitude and the size of the to-be-retained memory set was found in working memory tasks (Jensen & Tesche, 2002; Mecklinger, Kramer, & Strayer, 1992). Concerning episodic memory, Khader and Rösler (2010) showed that midline frontal theta is related to the level of interference during retrieval from episodic memory. Varying the amount of interference via the number of members that belonged to a particular category (the so called fan - effect), theta power increased with increasing fan size. Thus, there is converging evidence that theta oscillations can reflect the presence of interference during episodic memory retrieval.

The effects found in the theta band in Experiment 1 could thus also be interpreted as reflecting the level of interference that is present during retrieval. In the selective retrieval condition, a high initial level of interference is assumed, which should (at least partly) be resolved by inhibition during the first retrieval cycle, resulting in a lower level of interference during the second cycle. In the reexposure condition, the level of interference should not differ between repeated cycles, as no interference is assumed to arise initially (e.g., Anderson, 2003; Bäuml et al., 2010). Oscillations in the theta frequency band show exactly this pattern.

Selective retrieval induced a higher level of theta activity compared to the reexposure condition in the first cycle, along with a decrease in theta amplitude from the first to the second cycle in the selective retrieval condition that was not found in the reexposure condition.

Localizing the present theta effect to the ACC may suggest that theta activity reflects interference resolution by inhibition in the present experimental task (e.g., Posner, Petersen, Fox, & Raichle, 1988). Alternatively, however, ACC activity may mediate interference detection, but not its resolution (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Botvinick, et al., 2001), suggesting that ACC activity only monitors the amount of interference present during retrieval, but does not reflect the direct engagement of inhibition as a control mechanism for interference resolution. Recent imaging work supports the latter view, showing that both ACC (interference detection) and lateral prefrontal areas (inhibition) are involved in retrieval-induced forgetting (Kuhl et al., 2007; Wimber et al., 2009). If so, the present theta effect is likely to reflect *the effects* of inhibition rather the inhibitory mechanism itself.

As described earlier, the finding of no retrieval-induced forgetting on the final recall test is typically attributed to a deficit in inhibitory function (e.g., Anderson, 2003). However, if theta oscillations indeed reflect the level of interference, the results of Experiment 1 suggest an alternative explanation. Whereas high forgetters showed high theta amplitudes during the first retrieval cycle, low forgetters showed a low level of theta activity which did not change from the first to the second retrieval cycle. Intriguingly, theta activation in the low forgetters generally mimicked the pattern found in the reexposure condition, during which no interference is assumed to arise. Thus, the low forgetters in the present study seem to show a deficit in interference detection rather than a deficit in inhibitory function. The finding mirrors results from an fMRI study by Kuhl et al. (2007). In this study, high forgetters showed large initial activation of the ACC, which was reduced on a subsequent retrieval cycle, whereas low forgetters' level of ACC activation was low and remained unchanged during both early and late cycles of retrieval.

Alpha Oscillations and Semantic Memory Processes

In Experiment 1 and Experiment 2, similar effects in the alpha band were found. Across cycles of retrieval, alpha desynchronization was decreased. Previous studies related oscillatory activity in the alpha band to semantic memory processes (see Klimesch et al., 2010, for a review). Both of the present experiments involved semantic processing. In Experiment 1, semantically categorized word material was encoded. During selective retrieval, activation of the cue (the item's category and its word stem) triggered the activation of semantic associations in long-term memory. In Experiment 2, the activation of semantic memory was more direct, because subjects had to generate items that were not encoded before. Thus, both experiments involved spreading activation in the semantic memory system, but to a different extent. The reduction of alpha desynchronization across cycles may reflect the decrease in the engagement of semantic memory processes across cycles. As discussed before, with an increasing number of cycles, episodic memory processes become dominant, rendering the activation of semantic networks more and more unnecessary.

Related to this notion, Klimesch (1996) has proposed a role for alpha oscillations in delimiting the search set during retrieval from long-term memory via mediating thalamico-cortical projections. One major source of alpha oscillations is the thalamico-cortical circuitry. Evidence from vision research suggests that the thalamus acts as the crucial gateway between sensory input and higher cortical areas (e.g., Lopes da Silva, van Lierop, Schrijer, & Leeuwen, 1973; Lörincz, Kékesi, Juhász, Crunelli, & Hughes, 2009). Considering the numerous connections between the hippocampal region and the thalamus (see Aggleton et al., 2010, for a review), the thalamus could also gate the flow of information during memory search. Alpha oscillations, theoretically originating from the thalamus, could mediate the delimitation of a search set. The decrease in desynchronization across cycles would then reflect the down-sizing of the search set due to successful retrieval attempts, as explained below.

Tendentiously, the present results support this assumption. In Experiment 2, a large search set (all of the possible category exemplars) within the semantic memory network had to be activated to successfully generate an item, reflected by large and widespread alpha desynchronization over multiple electrode sites. As episodic memory processes become dominant across cycles of Experiment 2, such large-scale activation is rendered unnecessary. Therefore, the decrease in alpha desynchronization across cycles of retrieval from semantic memory could well reflect the narrowing of the search set within semantic memory. Compared to the situation in the first cycle of semantic generation (Experiment 2), the memory cue that was provided in Experiment 1 was more specific, because it targeted only the previously encoded items as possible candidates. Consequently, the search set was smaller in Experiment 1, which might have caused the alpha deactivation to not be as dominant and widespread as in Experiment 2. However, as long as there is no direct experimental evidence for an involvement of thalamico-cortical alpha oscillations in memory search, this interpretation of the effect found in the alpha band remains speculative.

Inhibitory Effects on Absolute vs. Relative Item Strength

Inhibition and Absolute Strength

The second part of the work was dedicated to the question of how retrieval inhibition affects the absolute and the relative strength of interfering items. Experiment 3 investigated the absolute strength of an item in a recognition test procedure. In line with previous work (Gómez-Ariza et al., 2005, Hicks & Starns, 2004, Spitzer & Bäuml, 2007, Verde, 2004), retrieval induced forgetting was found in the recognition test, suggesting that the absolute strength of previously interfering, unpracticed items was reduced by inhibition. Extending previous work, Experiment 3 showed that the reexposure did not reduce the absolute strength of unpracticed items in a recognition test. This result speaks against an explanation of the forgetting effect by strength dependent competition (Verde, 2009).

Experiment 4 investigated the effect of inhibition on the relative strength of an item by analyzing response latencies during free recall. No difference between mean latencies of unpracticed items from the reexposure condition and unpracticed items from the selective retrieval condition emerged. The results of Experiment 3 and 4 converge on the view that retrieval-induced forgetting is driven by a reduction in the absolute strength of interfering items, rather than the relative strength.

Previous studies reasoned that that inhibition is located at the recovery stage of recall (Bäuml et al., 2005; Verde, 2009). The present results are in line with this view. Two-stage models of recall assume a sampling and a recovery stage to be contributing to the retrieval of an item. Whereas the relative strength of an item (its strength in relation to all of the items in a search set) defines the probability of that item for being sampled at the sampling stage, the absolute strength (irrespective of other items) is decisive for exceeding the recovery threshold (e.g., Raaijmakers & Shiffrin, 1981; Rohrer, 1996). In Experiment 3, a recognition test was used for assessing the absolute strength of previously interfering items. Because recognition tests provide the item itself as a retrieval cue, the search set should be limited to one item (the probe). If so, the influence of the strength of other, competing items on the recognition performance is minimized (if not zero). Although two-stage models of recall describe conceptually different recall situations, the results from the recognition tests support the view that inhibitory processes are located at the recovery stage of recall.

Inhibition and Relative Strength

The null effect found in Experiment 4 gives reason to inspect the theoretical assumptions of the inhibitory account of retrieval-induced forgetting more thoroughly. In particular, the question of how exactly inhibition suppresses an item needs further discussion. Inhibition theory claims that the representation of an interfering item is suppressed by inhibition (Anderson & Spellman, 1995). Such weakening of an item was expected to be captured by recall latencies in Experiment 4, because recall latencies are assumed to reflect an item's relative strength in a search set (see Wixted et al., 1997). The relative strength of an item is simply a function of its own strength in relation the sum of strengths of all other items in a search set. Thus, a decrease in an item's strength due to inhibition implies a decreased relative strength of that item. This decreased strength should lead to an increase in mean latency for those items. However, Experiment 4 showed no such effect on inhibited items' mean latencies.

As one possible explanation, an effect of inhibition on the relative strength may not be detectable by response latencies, because inhibition affects different features than those responsible for the sampling process. Such an interpretation can be derived from temporal context models (e.g., Mensink & Raaijmakers, 1988; Howard & Kahana, 2002) that differentiate between context features and item-specific features. On the basis of these models, a possible explanation for the null effect in Experiment 4 is that inhibition weakens the item-specific features only, but sampling relies on the relative strength of the context features. However, direct evidence for a differential effect of inhibition on contextual and item-specific features is lacking.

Theoretically, one can think of other parameters that account for the null effect of inhibition on the sampling stage of recall. For example, the relative strength rule might only model the strengths of the associations between items and the cue. In this case, if inhibition directly reduces the strength of an item representation, no effect of retrieval practice on the sampling of unpracticed items would be found. However, a previous study showed that the association between cue and item was not affected by inhibition (Bäuml et al., 2005). Therefore, future research needs to thoroughly investigate the relationship between inhibition and competition among items, as described by relative strength models. In this process, the question of how exactly inhibition resolves interference should play a prominent role to clarify the theoretical concepts of inhibition and interference and their interrelationship.

Theoretical Implications

The behavioral results of Experiment 1 and 3 support the retrieval-specificity of retrieval-induced forgetting, a central assumption of the inhibitory account (Anderson, 2003). Replicating prior behavioral work (Anderson et al., 2000; Bäuml & Aslan, 2004; Ciranni & Shimamura, 1999), Experiment 1 showed that selective retrieval, but not reexposure, of a subset of studied items leads to retrieval-induced forgetting of related, unpracticed items during cued recall. Extending previous work, Experiment 3 showed that such a retrieval-specific effect could also be found in a recognition test.

The results of Experiment 3 also indicated that inhibition affects the absolute strength of interfering items. Together with the results from Experiment 4, they suggest that retrieval inhibition can be found in tests relying on absolute rather than relative item strength. In terms of a two-stage model of recall (e.g., Raaijmakers & Shiffrin, 1981; Rohrer, 1996) the results imply that inhibition affects the recovery stage of recall.

The results from the oscillatory analysis of Experiment 1 also yield theoretical implications in favor of an inhibitory account of retrieval-induced forgetting. The finding that the reduction in theta amplitude was selectively related to the forgetting and not the enhancement effect is well in line with the assumption that an inhibitory mechanism causes the impairment (but not the enhancement), and undermines a blocking account of retrieval-induced forgetting (see Jakab & Raaijmakers, 2009). According to non-inhibitory accounts, forgetting is a by-product of the strengthening of to-be-practiced items during retrieval practice. Thus, forgetting and enhancement are necessarily interlinked, an assumption that was not confirmed in the Experiment 1. Neither were enhancement and forgetting correlated, nor was the oscillatory correlate predictive of both effects.

The brain-behavior relationship found in Experiment 1 gives rise to intriguing theoretical implications. It was found that the larger the decrease in theta from the first to second cycle was, the more items were forgotten on the final memory test. Confirming this relationship, the subject sample was split on the basis of the behavioral data into high forgetters and low forgetters. High forgetters showed high theta amplitudes in the first cycle, which were then reduced in the second cycle. By contrast, low forgetters showed low amplitudes already in the first cycle, and these amplitudes remained unchanged in the second cycle. Depending on the functional interpretation of theta oscillations - inhibition or interference - different implications arise. If theta oscillatory activity reflects inhibitory processes, the present brain-behavior relationship supports the standard view that the failure to find retrieval-induced forgetting is due to a deficit in inhibitory functioning. If theta oscillations index interference, the present results implicate that the low-forgetters did not experience interference during the first cycles of selective retrieval. As a consequence, no inhibition was triggered, and no items were inhibited. If the latter interpretation holds true, the failure to find retrieval-induced forgetting is due to a failure to detect interference, rather than a deficit in inhibition.

This view would shed new light on neuropsychological findings and results from developmental studies. The failure to find retrieval-induced forgetting in ADHD patients or Schizophrenics (Soriano et al., 2009; Storm & White, 2010), as well as healthy kindergarteners (Aslan & Bäuml, 2010) might be due to inefficient detection of interference and not an inhibitory deficit. However, these groups of subjects are known to have a general deficit in inhibitory functioning (see Bjorklund & Harnishfeger, 1990; Schachar et al., 2007, Weisbrod et al., 2000). Therefore, the question of whether the failure of finding retrieval induced forgetting is due to a deficit in inhibitory functioning or a deficit in interference detection remains subject to future research.

As outlined in the introductory section, inhibition is assumed to be an executive control process (see, Anderson, 2003, for a review). According to this view, prefrontal cortex mediates the inhibitory top-down control of interfering information. The results from Experiment 1 support this notion in showing that theta oscillations over frontal electrode sites predicting retrieval-induced forgetting were localized to the ACC. In line with this view, several previous studies showed that neural activity in the prefrontal cortex is crucially involved in mediating retrieval-induced forgetting (Johansson et al., 2007; Kuhl et al., 2007; Wimber et al., 2009).

Based on the assumption that a central executive control process mediates memory inhibition, one may assume that the top-down control of interfering information generalizes across different memory systems. However, the present findings do not support such a view. The oscillatory correlate of inhibition in episodic memory (Experiment 1) was not found if contents from semantic memory had to be selectively retrieved. Because the null effect in Experiment 2 has to be considered with caution (the difference in inhibitory engagement across cycles of semantic retrieval-practice might have been too small to be captured by theta oscillations), a careful reevaluation of the oscillatory correlates of inhibition in semantic memory seems appropriate to decide whether an oscillatory correlate inhibition generalizes across different memory systems.

Conclusions

The present work provided insights into the functioning and the effects of inhibition during selective memory retrieval from two perspectives. In two electrophysiological experiments, the oscillatory correlates of inhibition were investigated at the time at which it is assumed to operate. Theta oscillations indexed inhibition during selective retrieval from episodic memory, alpha and beta oscillations reflected the engagement of semantic memory processes across repeated cycles of selective retrieval. However, inhibition during retrieval from semantic memory was not indexed by theta oscillations. Thus, an oscillatory correlate of inhibition generalizing across memory systems was not found. In the second part, the effects of inhibition on the absolute and relative strength of interfering items were investigated. Employing a recognition test procedure, retrieval-specific impairment of the absolute strength of previous competitors was found, a finding replicating and extending previous work. No effect of inhibition on the relative strength of interfering items was found during free recall, as measured by recall latencies. The results of both experiments converge on the view that retrieval-induced forgetting is mainly driven by a reduction in absolute competitor strength, rather than by a reduction of the relative strength during the sampling stage of recall. Together, the results elucidate the nature of inhibitory mechanisms during retrieval from long-term memory, revealing the neural dynamics of inhibition during selective retrieval, and, how inhibition affects the representation of interfering memory information.

Future Challenges

Disentangling Interference and Inhibition

A major issue in the present thesis was to unravel the concepts of interference and inhibition. In Experiment 1, the theta effect followed the theoretically predicted dynamics of inhibition as well as the dynamics of interference, and could thus not be interpreted unambiguously. Disentangling the concepts of interference and inhibition is difficult, because the catenation of both concepts is part of the inhibitory framework which states that interference triggers the inhibitory mechanism (see Anderson, 2003). Future studies will have to seek for a way to separate interference from inhibition. An approach to solve this issue could be to temporally separate interference from inhibition, for example, by activating relevant and irrelevant items via the presentation of a cue before the assignment of a target item within the search set. Like this, inhibition is triggered at the point in time the selective retrieval process is initiated and, thus, after interference arises.

Another approach could be to manipulate the functioning of the inhibitory process itself. Román et al. (2009) showed that an additional task during the practice phase of the retrieval practice paradigm disrupts retrieval-induced forgetting. Thus, overloading executive control resources could be a way to specifically impair inhibitory functioning. Like this, selective correlates of interference and inhibition could be investigated. However, finding a manipulation that selectively impairs inhibition and not interference is a challenging task.

Inhibition and Contextual vs. Item-Specific Features

The finding of a null effect of inhibition in mean latencies in Experiment 3 is challenging with regard to the inhibitory framework, which claims that the representation of an interfering item is suppressed by inhibition (Anderson & Spellman, 1995). This weakened representation of suppressed items was expected to affect recall latencies. Thus, in the light of the present null effect found in

Experiment 3, there is need to clarify exactly which features of an item are impaired by inhibition. An approach to solving this issue could be made by assuming that an item consists of contextual and item-specific features, as stated in the One-Shot Hypothesis of context storage (Malmberg & Shiffrin, 2005). Based on temporal context models (e.g., Mensink & Raaijmakers, 1988; Howard & Kahana, 2002), the authors suggest that the two types of features can be selectively strengthened. Whereas the strength of item features increases with study time, the strength of context features does not. Malmberg and Shiffrin (2005) account for this dissociation by stating that context features are established early during encoding, and, after the context feature is stored, attention is drawn to the item-specific features. Thus, an extended presentation of an item (termed "massed presentation") will strengthen its item-specific features, but not its contextual features. Contrarily, if items are repeatedly presented in a list (termed "spaced presentation"), the context is also encoded and strengthened each time.

Malmberg and Shiffrin (2005) claim that, in free recall, the sampling probability of an item is a function of the overlap between the cue and an item's contextual features. The more overlap, the more likely the item will be sampled. In a list-strength paradigm, this assumption can be examined by comparing the impact of massed and spaced repetition within mixed-strength lists. According to the One-Shot Hypothesis, spaced presentation creates stronger contextual features, creating a tendency for these items to be sampled before weak items (list-strength-effect). Massed presentation, on the other hand, does not produce a difference in the strength of contextual features between strong and weak items. Therefore, no list-strength effect is expected on free recall. In a series of experiments, Malmberg and Shiffrin (2005) found that the predictions of the One-Shot Hypothesis held true for recall totals. Only spaced presentation produced a reliable list-strength effect. Massed presentation did enhance recall performance of strong items, but did not impair weak items.

In a first step, a future study could validate the predictions of the One-Shot Hypothesis by investigating recall latencies in a list-strength experiment varying the type of item presentation (massed vs. spaced). The second step would be to incorporate the massed and spaced procedure in the retrieval-practice paradigm.

Measuring recall latencies in such an experimental setting can shed light on the question whether inhibition selectively impairs item-specific and not contextual features of interfering information.

Alpha Oscillations and Memory Search

As described earlier, the thesis comprises two major parts that differed methodologically as well as on the theoretical level. Experiment 1 and 2 investigated the oscillatory correlates of inhibition "as it operates" during the retrieval-practice phase. The behavioral Experiments 3 and 4 explored the effects of inhibition on the sampling and recovery stage of a later recall period. At fist glance, both parts seem hard to merge into a common experimental setting. However, the finding that alpha desynchronization is related to the retrieval from semantic memory, and the fact that recall latencies offer a possibility to estimate the size of a subject's memory search set offers an intriguing possibility to combine both parts.

The key assumption in this context would be a role for alpha oscillations in delimiting the search set during retrieval from long-term memory, as proposed by Klimesch (1996). This assumption could be tested in a latency experiment that collects EEG data during free recall, while manipulating the search set size, for example, via the length of the presented list at study. If alpha oscillations delimit the search set during retrieval, they should vary with the manipulated list length and predict the estimated parameter for search set size. Furthermore, advanced localizing methods could be used to explore the sources of the alpha oscillatory activity. Previous research found that one major source of alpha oscillations is the thalamico-cortical circuitry (e.g., Lopes da Silva et al., 1973; Lörincz et al., 2009). With such an experiment, evidence for the importance of thalamico-cortical networks in memory search, that is, in delimiting a search set, could improve the understanding of the functioning of human memory on a theoretical and neural level.

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Appendix

Ex-Gaussian distribution:

$$f\left(x\right)=\left(\frac{e^{\frac{\mu}{\tau}-\frac{x}{\tau}+\frac{\sigma^2}{2\tau^2}}}{\tau\sqrt{2\pi}}\right)\int_{-\infty}^{\left(\frac{x}{\sigma}-\frac{\mu}{\sigma}-\frac{\sigma}{\tau}\right)} e^{-\frac{y^2}{2}}dy$$

The ex-Gaussian distribution is a convolution of a normal distribution and an exponential distribution. Applied to response latencies in free recall, the Gaussian stage describes the initial pause that is frequently encountered before the first item is retrieved. The Gaussian stage is characterized by its mean μ and its standard deviation σ. The exponential stage describes the ongoing memory search and is defined by its mean τ. These parameter estimates are unbiased when the best fitting function is found by maximum likelihood estimation, and this technique produced the estimates given in Table 6.

A derivation of the ex-Gaussian distribution is given in Rohrer and Wixted (1994). Previous studies demonstrated that the ex-Gaussian precisely describes recall distributions (Rohrer & Wixted, 1994; Wixted & Rohrer, 1993; Wixted et al., 1997).