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Retrieval Inhibition in Autobiographical Memory

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Introduction

Autobiographical memory (AM) retrieval is a complex process that involves the processing of episodic, semantic, and emotional information with strong personal relevance (Conway & Williams, 2008). It can be either a voluntary process, like in constructive memory search (Schacter & Addis, 2007), or an involuntary process, like in the case of memory intrusions of emotionally unpleasant or traumatic events (Berntsen, 1998). Voluntary retrieval of AMs is effortful and slow, i.e., it takes time to consciously retrieve a specific AM. In contrast, involuntary retrieval is fast and spontaneous, i.e., an AM intrudes without any conscious or deliberate attempt to retrieve it.

Voluntary retrieval of an AM requires constructive memory search (Cabeza & St Jacques, 2007; Schacter & Addis, 2007). For example, try to remember the last time you went to the movies. Unless this was very recently, you will actuate a protracted, time-consuming memory search to retrieve the appropriate information. You may more or less voluntarily search for the memory within an associative network of complex AM information, including episodic, semantic, and emotional representations. Doing so, retrieval success will depend strongly on the search path or retrieval route that, voluntarily or involuntarily, is selected (see Mace, chapter 3, this volume). In the first step, episodic retrieval cues (e.g., you remember a specific movie you went to with your friend Julia), semantic cues (e.g., you think of people munching popcorn), or emotional cues (e.g., you bring to mind that movies

always make you cry) may be generated. Then, on the basis of the generated cues, a targeting search path will be constructed to recall the relevant information.

During such memory search, cueing most likely elicits not only relevant information, i.e., information pointing to the target memory, but elicits also irrelevant information that points to nontarget memories. Retrieval of a specific AM thus may fail because irrelevant information is sampled instead of relevant ones. Crucially, to overcome interference of irrelevant information and prevent spurious recall, inhibitory processes may operate to reduce the accessibility of irrelevant information and enhance that of the relevant one (for reviews, see Anderson, 2003; Bäuml, 2008; Bjork, 1989). To date, the idea that inhibition is involved in AM retrieval lacks basic research. The investigation of AM retrieval with experimental paradigms in which the action of inhibitory processes has been suggested, therefore, is eligible. Such research is raring to go (Barnier et al., 2007; Barnier, Hung, & Conway, 2004; Joslyn & Oakes, 2005; Wessel & Hauer, 2006).

While AM search often happens voluntarily, recall of past events may also happen involuntarily. This is particularly the case for emotional events that are recalled more vividly, with greater contextual detail, and with greater recollective experience than emotionally neutral memories (Buchanan, 2007). These recall characteristics may be desirable for pleasant AMs, they are less desirable, however, for involuntary retrieval of unpleasant memories. Traumatized and depressed people often suffer from involuntary retrieval of distressing memories they are unable to forget (see Williams & Moulds, chapter 15, this volume). These “flashback” memories can lead to strong memory disturbances in traumatized individuals with posttraumatic stress disorder (PTSD), characterized by intrusions of highly emotional memory fragments and the inability to voluntarily recall other important aspects of the trauma, often at the same time.

Intrusions and amnesia may be related in PTSD, because unwanted traumatic “flashbacks” may interfere with and thus impair deliberate recall of other aspects of the trauma. In addition to processes like interference and blocking, ineffective retrieval inhibition of highly emotional aspects of the traumatic event may play a role in trauma-related memory disturbances as well. The idea that inefficient cognitive control is involved in PTSD is an interesting proposal for clinical psychology (see Verwoerd & Wessel, chapter 14, this volume). Therefore, the investigation of memory disorders in PTSD with experimental paradigms in which inhibitory processes are likely to play a crucial role is eligible. Recently, first steps were taken to investigate the role of retrieval inhibition in PTSD (for a review, see Geraerts & McNally, 2008).

The chapter begins with an introduction of commonly used experimental paradigms in research on retrieval inhibition in episodic memory. Basic behavioral findings and the role of emotion in these paradigms will be reviewed. After summarizing recent physiological findings in the study of retrieval inhibition, neural substrates of AM retrieval will be addressed. Comparing the results from the two lines of studies, we will conclude that inhibitory processes may play a crucial role in AM construction and the suppression of unpleasant or traumatic AMs. Inhibitory control in AM retrieval thus may be an important piece of the puzzle towards an understanding of how we recall the past.

Experimental Paradigms for the Study of Inhibitory Processes

In the following, we summarize findings from three experimental paradigms in which the action of inhibitory processes has repeatedly been suggested: retrieval-induced forgetting, directed forgetting, and think/no-think impairment. Whereas retrieval-induced forgetting reflects unintentional forgetting, directed forgetting and think/no-think impairment reflect intentional forms of forgetting. In retrieval-induced forgetting, the selective retrieval of previously encoded information has been shown to impair later recall of related material without an explicit intention to forget (Anderson, Bjork, & Bjork, 1994). In directed forgetting and think/no-think impairment, it has been found that the explicit instruction to forget or to stop thinking of previously encoded information can lead to intentional forgetting of target material (Anderson & Green, 2001; Geiselman, Bjork, & Fishman, 1983). In all these cases, the action of retrieval inhibition, involuntarily or voluntarily, has been suggested to serve the goal-directed use of human memory.

Retrieval-induced forgetting

Involuntary retrieval inhibition has been examined in the retrieval-practice paradigm (Anderson, Bjork, & Bjork, 1994). In this paradigm, effects of selective retrieval of a subset of previously studied items on later memory performance for the retrieved and nonretrieved items are examined. When using verbal material, participants often study categorized item lists (e.g., FRUIT-*apple*, FRUIT-*banana*, DRINK-*soda*) and then repeatedly practice half of the items from half of the categories using a word-stem completion task (e.g., FRUIT-*ap*_____). Following this retrieval-practice phase and a subsequent distractor task, participants' recall performance is tested on a final memory test. The typical finding on this test is that recall of practiced

items (*apple*) is enhanced and recall of unpracticed items from practiced categories (*banana*) is impaired, relative to control items from unpracticed categories. The impairment in recall of the unpracticed material is referred to as retrieval-induced forgetting (RIF).

RIF has been observed in free and cued recall tests (e.g., Anderson, Bjork, & Bjork, 1994; Macrae & MacLeod, 1999), in item and category recognition tests (e.g., Hicks & Starns, 2004; Spitzer & Bäuml, 2007, 2009), and in implicit memory tests, like lexical-decision tasks and other conceptual implicit memory tests (e.g., Perfect, Moulin, Conway, & Perry, 2004; Veling & van Knippenberg, 2004). In addition, RIF has been found in so-called independent-probe tests in which retrieval cues are used at test that had not been presented in any previous phase of the experiment (e.g., Anderson & Spellman, 1995; Aslan, Bäuml, & Pastötter, 2007). RIF is not restricted to verbal material and has been observed with various stimuli and experimental settings, including visuospatial material (Ciranni & Shimamura, 1999), eyewitness event memory (Saunders & MacLeod, 2002), foreign language acquisition (Levy, McVeigh, Marful, & Anderson, 2007), and AM retrieval (Barnier, Hung, & Conway, 2004; Wessel & Hauer, 2006).

RIF is not restricted to episodic memories but affects semantic memories as well. Bäuml (2002) provided evidence that RIF may be the result of semantic generation. After the study of a list of category exemplars, participants generated new, previously not presented exemplars of the studied categories. On the final memory test, such semantic generation caused episodic forgetting of the originally studied items. Johnson and Anderson (2004) then extended the finding by showing that selective retrieval can induce semantic forgetting. After generating exemplars of a category, participants' ability to recall a semantically related item on a free-association test was impaired. This suggests that not only episodic memories, but also semantic memories, can be subject to RIF.

RIF is a retrieval-specific effect (Anderson, Bjork, & Bjork, 2000; Bäuml, 2002; Ciranni & Shimamura, 1999). Only retrieval (FRUIT-*ap*____), but not relearning (FRUIT-*apple*), of a subset of previously studied items can induce forgetting of the not-reprocessed material. The idea is that during attempts to selectively retrieve target information, the representation of related unpracticed information is involuntarily inhibited to reduce interference, impairing memory performance of the unpracticed items on the final test (Anderson, 2003). Instead of deactivating any particular retrieval route between the interfering items and their cue(s), involuntary retrieval inhibition is suggested to affect the representation of the unpracticed item itself (Anderson & Spellman, 1995; Spitzer & Bäuml, 2007), causing a recovery problem for the inhibited item (Bäuml, Zellner, & Vilimek, 2005). Following Tulving and Pearlstone's (1966) terminology, RIF thus may be regarded as a form of item unavailability rather than item inaccessibility (Bäuml, 2007, 2008).

Directed forgetting

Voluntary retrieval inhibition has been examined in the directed forgetting (DF) paradigm in which participants are cued to intentionally forget previously studied material. Two methods have been used in the literature to induce directed forgetting: the list method (Bjork, LaBerge, & LeGrand, 1968) and the item method (Muther, 1965).

In list-method directed forgetting (LM-DF), participants study two lists of items and, after study of List 1, are cued to either forget or continue remembering this list before studying List 2. On a later memory test, forget-cued participants typically show impaired recall of List-1 items and improved recall of List-2 items, compared to remember-cued participants; the two effects are referred to as List-1 forgetting and List-2 enhancement. In item-method directed forgetting (IM-DF), participants study a single list of items and the presentation of each single item is followed closely by a cue to either remember or forget the item. On a later memory test, in which participants are asked to recall all of the previously presented items, to-be-remembered items are typically better memorized than the to-be-forgotten items.

Whereas IM-DF is present in recall tests, recognition tests, and even implicit memory tests, LM-DF is present in recall tests only and is absent in recognition and implicit memory tests (e.g., Basden & Basden, 1996; Basden, Basden, & Gargano, 1993; Davis & Okada, 1971; MacLeod, 1989, 1999). DF effects are present irrespective of output order of to-be-remembered and to-be-forgotten information (e.g., Geiselman, Bjork, & Fishman, 1983; Zellner & Bäuml, 2006), indicating that the forgetting does not reflect effects of blocking or output interference at test (see Bäuml, 2008). DF is also a fairly general phenomenon and has been observed with verbal (e.g., Geiselman et al., 1983; MacLeod, 1999), visual (e.g., Basden & Basden, 1996), and autobiographical material (e.g., Barnier et al., 2007; Joslyn & Oakes, 2005). Crucially, DF is not the result of demand characteristics, because it was found to be still present if money was offered to participants as reward for each recalled to-be-forgotten item (MacLeod, 1999).

With respect to theoretical explanations of DF, it has repeatedly been suggested that retrieval inhibition offers the best account of LM-DF, but that a selective rehearsal account provides the best explanation of IM-DF (Basden, Basden, & Gargano, 1993; Bjork, 1989). In LM-DF, the proposal is that, by inhibiting List-1 items, the forget cue deactivates retrieval routes to List-1 items, thus making them less accessible on a subsequent recall test. Being less accessible, List-1 items are also less likely to interfere with List-2 items, which simultaneously improves access to List-2 items (e.g., Geiselman et al., 1983; for a noninhibitory account, see Sahakyan & Kelley, 2002, or Sheard &

MacLeod, 2005). The loss of accessibility via retrieval inhibition seems to affect the whole List 1 rather than single items (Kimball & Bjork, 2002). Accordingly, when participants alternately learn items intentionally and incidentally and are instructed to forget the intentionally learned items, incidentally learned List-1 items are just as well forgotten as the intentionally learned items (Geiselman et al., 1983). Following Tulving and Pearlstone's (1966) terminology, LM-DF thus seems to be due to a loss of accessibility via retrieval routes to List 1 rather than a reduction in items' availability (Bäuml, 2008).

In IM-DF, the dominant theoretical view is the selective rehearsal account, according to which participants fail to adequately encode to-be-forgotten items because they terminate rehearsal in response to the forget cue. As a consequence, these items receive less rehearsal than to-be-remembered items, which can account for the observed IM-DF effects in both recall and recognition tests (e.g., Basden, Basden, & Gargano, 1993; MacLeod, 1999). The selective rehearsal account arose from behavioral research. Recent physiological examinations of IM-DF, however, suggest that inhibitory processes may contribute to the forgetting as well (e.g., Wylie, Foxe, & Taylor, 2008).

There is strong evidence from both behavioral and physiological studies that IM-DF is due to differences in processing at the time the cue to remember or forget is presented. In contrast, in LM-DF, the presence of a forget instruction has been shown to be not sufficient to produce List-1 forgetting, but is effective only if there is additional List-2 encoding (Pastötter & Bäuml, 2007). The crucial role of postcue encoding has also been shown when dividing participants' attention during List-2 encoding by means of a secondary task which reduces List-1 forgetting (Conway, Harries, Noyes, Racsmany, & Frankish, 2000), and when increasing the amount of List-2 encoding which increases List-1 forgetting (Pastötter & Bäuml, in press). In line with a recent physiological finding (Bäuml, Hanslmayr, Pastötter, & Klimesch, 2008), LM-DF thus is suggested to be initiated during postcue encoding.

Think/no-think impairment

A third form of intentional forgetting is think/no-think (TNT) impairment (Anderson & Green, 2001). The TNT paradigm is a memory adaptation of the go/no-go task, which is typically used to study control of prepotent motor responses. Initially, participants study several cue-target pairs (e.g., coffee-table) and are trained to answer with the appropriate target upon presentation of its cue. After training, participants engage in a TNT task in which they are instructed to either repeatedly retrieve (think) or actively suppress retrieval (no-think) of a target at its cue presentation. On a cued-recall test on the targets, memory performance is typically enhanced for the think items

and impaired for the no-think items, relative to baseline items that are neither remembered nor suppressed during the TNT phase.

TNT impairment was found both when the original cue (e.g., Anderson & Green, 2001; Depue, Banich, & Curran, 2006) and when semantically related independent probes were provided in explicit memory tests (e.g., Anderson & Green, 2001; Anderson et al., 2004). However, no studies have yet been reported examining TNT impairment in recognition or implicit memory tests, at least when comparing performance of target items to an appropriate baseline condition (see Marx, Marshall, & Castro, 2008, for speeded recognition data without baseline reference). Importantly, TNT impairment has also been found when money was offered to participants as reward for each recalled no-think item (Anderson & Green, 2001). Thus, TNT impairment should not be the result of demand characteristics.

Anderson and Green (2001) argued that TNT impairment is caused by active retrieval suppression of no-think items (for a noninhibitory account, see Bulevich, Roediger, Balota, & Butler, 2006, or Hertel & Calcaterra, 2005). According to the inhibitory account, during no-think trials, the memory representation of the targets is reduced so that later accessibility of the targets is lowered regardless of which cue is provided and which retrieval route is used. According to this view, no-think trials affect the items' later availability; the impairment, therefore, should be observable across a wide range of memory tests, including recall tests, recognition tests, independent-probe tests, and even implicit memory tests. Currently, the evidence for TNT impairment is restricted to cued recall and independent-probe tests, awaiting further tests of the inhibition proposal using recognition and implicit memory tests.

In the TNT paradigm, retrieval suppression is suggested to build up slowly and, therefore, repeated TNT trials are necessary to effectively suppress retrieval of no-think targets (Depue, Curran, & Banich, 2007). Indeed, most TNT studies suggest that the forgetting in this paradigm typically arises only if the number of TNT trials is fairly high (>10 trials) and does not arise if the number of such trials is relatively low (<5 trials; Depue et al., 2006).

Emotion and Retrieval Inhibition

Prior research has shown that emotion guides human judgment and cognitive processing (for a review, see Clore & Huntsinger, 2007). In particular, emotion can affect the retrieval of AMs (for a review, see Buchanan, 2007). This influence is exerted at either a state-specific level, i.e., retrieval of emotionally neutral events in a specific affective state, or an item-specific level, i.e., retrieval of a specific emotional event in a neutral state. Thus, with respect to the role of emotion in retrieval inhibition, two related but separate

questions arise. The first question is whether the affective state experienced during retrieval inhibition modulates the forgetting. The second question is whether the forgetting differs for emotional and nonemotional contents.

Affective state

In RIF, the first question has recently been addressed by Bäuml and Kuhbandner (2007). They examined how affective states experienced during retrieval modulate RIF by inducing positive, negative, and neutral moods immediately before the retrieval-practice phase. Their results showed that repeated retrieval did not cause forgetting of nonretrieved items when participants were in negative moods, whereas when subjects were in positive or neutral moods, reliable RIF was found. The absence of RIF in negative moods is consistent with the view that negative moods induce predominantly item-specific processing, i.e., processing of items by their features and distinctive qualities (e.g., Clore & Huntsinger, 2007). Because item-specific processing reduces interference from related information, retrieval inhibition should be reduced and RIF be eliminated, which is exactly what the data showed.

In LM-DF, Bäuml and Kuhbandner (2009) examined how affective states modulate intentional forgetting. On the basis of the finding that the mechanism(s) underlying LM-DF operate(s) during List-2 encoding (Bäuml, Hanslmayr, Pastötter, & Klimesch, 2008; Pastötter & Bäuml, 2007, in press), positive, negative, and neutral moods were induced immediately before List-2 encoding. The forget instruction caused List-1 forgetting when participants were in neutral or negative moods, but did not cause forgetting when participants were in positive moods. The absence of List-1 forgetting in positive moods is consistent with the view that positive moods induce spreading activation processes (e.g., Clore & Huntsinger, 2007), which may lead to reactivation of List-1 items during List-2 encoding and thus may eliminate the LM-DF effect.

No studies have yet been reported examining the role of mood in IM-DF and TNT impairment.

Emotional content

The question whether inhibitory forgetting differs for emotional and nonemotional contents has been addressed in RIF studies (e.g., Barnier, Hung, & Conway, 2004; Kuhbandner, Bäuml, & Stiedl, 2009), LM-DF studies (e.g., Barnier et al., 2007; Wessel & Merckelbach, 2006), and IM-DF studies (e.g., Korfine & Hooley, 2000; McNally, Metzger, Lasko, Clancy, & Pitman, 1998). All of these studies suggest that the forgetting is present and comparable in amount for positive, negative, and nonemotional contents. These findings arose for both simple word lists and AMs.

In contrast, in the TNT paradigm, Depue, Banich, & Curran (2006) showed that item material with negative content produces stronger TNT impairment than nonemotional material. This finding is consistent with the view that emotional material is more accessible than nonemotional material (Hamann, 2001) and thus more susceptible to mechanisms of voluntary retrieval suppression. No item material with positive content was included in this study. Marx, Marshall, & Castro (2008) compared the effects of positive and negative content as well as the effect of high and low arousal in TNT impairment. TNT effects were strongest for highly arousing positive material and lowly arousing negative material. These results partly deviate from the results of Depue et al. (2006), possibly because Marx et al. compared recall of no-think items directly with recall of think items, rather than with baseline items. Still, the findings suggest that retrieval of emotional information can be more easily suppressed than retrieval of nonemotional information.

Neural Substrates of Retrieval Inhibition

Physiological studies in the domain of cognitive control have shown that two prefrontal cortex (PFC) regions play a fundamental role in guiding behavior when interference occurs. Whereas the anterior cingulate cortex (ACC) is suggested to detect interference between competing responses (Botvinick, Cohen, & Carter, 2004), the right lateral prefrontal cortex (LPFC) is meant to resolve interference by inhibiting irrelevant responses (Aron, Robbins, & Poldrack, 2004). Thus, interference detection in the ACC is thought to implement cognitive control mechanisms exerted by lateral PFC. Recent physiological research in memory retrieval has in fact implicated PFC regions in the suppression of irrelevant information to guide access to relevant memories. These and related findings are reviewed next.

Retrieval-induced forgetting

Prior behavioral work suggests that RIF affects the availability of the non-practiced information via involuntary retrieval inhibition (Anderson, 2003; Bäuml, 2008). The findings of recent physiological studies examining the neural correlates of RIF during the retrieval-practice phase (Johansson, Aslan, Bäuml, Gäbel, & Mecklinger, 2007; Kuhl, Dudukovic, Kahn, & Wagner, 2007; Wimber, Rutschmann, Greenlee, & Bäuml, 2009) and the final testing phase (Spitzer, Hanslmayr, Opitz, Mecklinger, & Bäuml, 2009; Wimber, Bäuml, Bergström, Markopoulos, Heinze, & Richardson-Klavehn, 2008) support this inhibitory account of the forgetting.

Because RIF is a recall-specific effect (e.g., Ciranni & Shimamura, 1999), the neural correlates of RIF can be examined by comparing the (inhibitory)

retrieval-practice condition with a (noninhibitory) relearning condition, thus isolating the putative inhibitory component. Johansson, Aslan, Bäuml, Gäbel, and Mecklinger (2007) used this rationale and analyzed event-related brain potential (ERP) components in an electroencephalogram (EEG) study. The authors found an early onset and sustained increase in prefrontal ERP positivity during retrieval practice compared to relearning. Because prefrontal positivity was predictive of RIF, the activity was suggested to reflect the differential involvement of involuntary retrieval inhibition in retrieval as compared to relearning.

Wimber, Rutschmann, Greenlee, and Bäuml (2009) used functional magnetic resonance imaging (fMRI) to investigate the neural processes underlying RIF. Following the same rationale as Johansson, Aslan, Bäuml, Gäbel, and Mecklinger (2007), brain activity between a retrieval-practice and a relearning condition was compared. Selective retrieval was associated with increased brain activity in the hippocampus, the posterior temporal and parietal association cortices, and the dorsolateral prefrontal cortex (DLPFC). Again, the prefrontal brain activity was predictive of later RIF, albeit negative in direction. The authors suggested that the negativity of the correlation may be due to the multiplicity of retrieval-practice trials. According to this view, successful retrieval inhibition on early practice trials may reduce the need for inhibitory control on subsequent practice trials and thus exhibit an overall decrease of inhibition-related activation over the whole retrieval-practice phase.

Kuhl, Dudukovic, Kahn, and Wagner (2007) directly compared brain activity between a first and a third retrieval practice trial to test for decreases in inhibitory control demands. Consistent with the Wimber, Rutschmann, Greenlee, and Bäuml (2009) interpretation, they found that repeated retrieval was accompanied by reduced brain activity in the ACC and the right lateral PFC. Prefrontal brain activity was predictive of later RIF which increased with reduced prefrontal activation across repeated retrieval attempts. Thus, RIF seems to be mediated by activations in anterior cingulate and lateral prefrontal activity, indicating interference and inhibition.

Recent studies also examined the neural substrates of RIF on the final memory test when the impairment should be observed. An fMRI study by Wimber et al. (2008) showed that RIF is reflected by an increase in left prefrontal brain activity. More precisely, RIF was specifically related to activation in the left anterior ventrolateral prefrontal cortex (VLPFC; but see Kuhl, Kahn, Dudukovic, & Wagner, 2008), a brain region that has been suggested to subserve selective retrieval of weakened memory representations stored in temporal regions (Badre & Wagner, 2007). Consistently, Wimber et al. (2008) observed a functional coupling of left anterior VLPFC with the posterior lateral temporal cortex. The finding that RIF is modulated by activity in these brain regions supports the view that RIF reflects retrieval inhibition directly affecting the memory representation of unpracticed items.

Spitzer, Hanslmayr, Opitz, Mecklinger, and Bäuml (2009) examined the effects of prior retrieval practice on evoked ERPs and oscillatory power measures during a final recognition test. Whereas ERPs are phase-locked to stimulus onset, oscillatory power measures pick up dynamic changes of brain activity nonphase-locked to stimulus onset. Spitzer et al. found that RIF was characterized by reduced amplitudes of the P2 ERP component at frontal electrode sites, reduced theta power (4 to 7 Hz) at distributed sites, and reduced gamma power (60 to 85 Hz) at occipital sites. Because theta power has been suggested to reflect – among other things – items' memory strength and occipital gamma power the activation of sensory memory networks, these results suggest that RIF leads to a deactivation of items' memory representations and a weakening of the material's sensory representation.

In sum, during retrieval practice, selective retrieval of the relevant information is facilitated by inhibiting the interfering irrelevant information as revealed by modulations of brain activations in the ACC, right lateral PFC, and the hippocampus. On the final test, RIF then is related to activation of the left VLPFC functionally coupled with temporal cortex activation, suggesting that involuntary retrieval inhibition directly affects unpracticed items' representations. The latter conclusion is further supported by results from EEG studies.

Directed forgetting

While LM-DF has been studied extensively in behavioral research (Bäuml, 2008; MacLeod, 1998), little effort has yet been made to understand the underlying physiological mechanisms. To date, the only physiological study relating LM-DF to brain activity was conducted by Bäuml, Hanslmayr, Pastötter, and Klimesch (2008), who measured participants' electrophysiological activity and investigated the effects of the forget cue on brain oscillations.

On the basis of the behavioral finding that List-2 encoding is a necessary precondition for LM-DF (Pastötter & Bäuml, 2007, *in press*), Bäuml, Hanslmayr, Pastötter, and Klimesch (2008) recorded EEGs during study of List-2 items, analyzing oscillatory brain activities. They found two effects of the forget cue in the alpha frequency range (11–13 Hz): a reduction of alpha phase coupling between electrode sites, which was related to List-1 forgetting, and an increase of alpha power, which was related to List-2 enhancement. Because phase coupling between electrode sites is regarded as a measure of the synchrony between distant neural assemblies (e.g., Lachaux, Rodriguez, Martinerie, & Varela, 1999) and coherent firing between distant neuronal populations has been regarded as a mechanism subserving binding processes (e.g., Miltner, Braun, Arnold, Witte, & Taub, 1999), the decrease in alpha phase coupling could reflect the unbinding of List-1 items and the

deactivation of the retrieval routes to List-1 items. Because results from recent studies suggest that alpha oscillations serve as an active inhibitory filter for the brain (e.g., Klimesch, Sauseng, & Hanslmayr, 2007), the finding of the effect in the alpha frequency range supports the view that DF is mediated by inhibition.

It has recently been argued that LM-DF might be noninhibitory and be caused by an internal context change (Sahakyan & Kelley, 2002). The context-change account of LM-DF claims that the forget cue induces a change in participants' internal context, which should impair List-1 recall due to a mismatch between encoding and retrieval context. Examining oscillatory brain activity in the context-change paradigm, however, it was recently found that oscillatory activities in the context-change paradigm differ largely from those in LM-DF (Pastötter, Bäuml, & Hanslmayr, 2008), thus indicating that the LM-DF effects do not reflect the result of an internal context change.

In IM-DF, the original view has been a strengthening view according to which to-be-forgotten and to-be-remembered items differ in the degree to which they are rehearsed and strengthened during encoding (MacLeod, 1998). However, recent imaging and electrophysiological studies which examined brain activity during encoding (Paz-Caballero, Menor, & Jiménez, 2004; Wylie, Foxe, & Taylor, 2008) and retrieval (Nowicka, Jednoróg, Wypych, & Marchewka, 2009) suggest that inhibitory processes may also contribute to IM-DF.

At the encoding stage, Paz-Caballero, Menor, and Jiménez (2004) examined ERPs at the time of cuing participants to either remember or forget words on a trial-by-trial basis. They found enhanced early prefrontal positivity but decreased late parietal positivity in response to the forget cue (for the latter finding, see also Paller, 1990). The prefrontal effect of cuing was related to subsequent forgetting of items in a recognition task. Due to the frontal location of the effect, the early positivity was suggested to reflect some form of voluntary encoding suppression of to-be-forgotten items. Similar in procedure, Wylie, Foxe, and Taylor (2008) examined brain activity associated with IM-DF in an fMRI study. They found a network of brain regions more activated when participants received a forget instruction compared to when they received a remember instruction. In this network, the right VLPFC was most active for to-be-forgotten items that were not recognized on the subsequent recognition task, indicating that this brain region is specific to successful intentional forgetting of items.

At the retrieval stage, Nowicka, Jednoróg, Wypych, and Marchewka (2009) investigated changes in electrophysiological brain activity. Analyzing ERPs during recognition of previously learned to-be-remembered and to-be-forgotten items, they found a typical left parietal old/new effect for to-be-remembered items reflected by enhanced positivity for correctly recognized old items compared to new items (Rugg & Curran, 2007). The old/new effect

was absent for to-be-forgotten items that were recognized despite the prior forget instruction (see also Ullsperger, Mecklinger, & Müller, 2000). More important, missed to-be-forgotten items yielded a left parietal ERP component that was more negative-going compared to correctly rejected new items and was suggested to reflect effective retrieval inhibition of to-be-forgotten information.

Together, recent physiological findings suggest that both LM-DF and IM-DF may be mediated by inhibitory processes, preventing the to-be-forgotten items from being remembered. In LM-DF, the forgetting has been found to be related to a reduction in alpha phase coupling which was interpreted as evidence for inhibition of retrieval routes to to-be-forgotten information. In IM-DF, cueing to forget an item is accompanied by an increase in right prefrontal brain activity, which may reflect active suppression of items' further processing. During retrieval, the availability of the to-be-forgotten information then is reduced and retrieval is inhibited as reflected by reduced parietal brain activation.

Think/no-think impairment

Behavioral research on TNT impairment has shown that the instruction to avoid recollection of target material can impair its subsequent memory performance. This detrimental effect has been suggested to arise from voluntary retrieval suppression (Anderson & Green, 2001). Two recent fMRI studies and an ERP study examining brain activity in the TNT phase underpin the role of inhibitory processes in TNT impairment (Anderson et al., 2004; Depue, Curran, & Banich, 2007; Hanslmayr, Leipold, Pastötter, & Bäuml, 2009).

Anderson et al. (2004) contrasted brain activity between think and no-think trials. They found that various prefrontal regions, including the ACC and bilateral DLPFC and VLPFC, were more activated in suppressing retrieval in no-think trials than in achieving memory retrieval in think trials. At the same time, hippocampal and left parietal activations were reduced in no-think trials compared to think trials. Both prefrontal cortical and hippocampal activations predicted the magnitude of subsequent forgetting. These findings suggest that voluntary retrieval suppression is an active process that recruits prefrontal brain regions to avoid conscious recollection elicited in the hippocampus.

Depue, Curran, and Banich (2007) used unpleasant stimuli that have been shown to have a larger impact on TNT impairment than nonemotional stimuli (Depue, Banich, & Curran, 2006). Using a baseline reference, they related brain activity with either the think or no-think condition. Whereas right DLPFC and VLPFC showed an increase in activity during no-think trials, activity in the hippocampus and the amygdala was decreased in the

no-think condition (and increased in the think condition) compared to the baseline reference. Crucially, prefrontal and hippocampal activity were found to predict TNT impairment.

Hanslmayr, Leipold, Pastötter, and Bäuml (2009) compared ERP waveforms between the first and the second half of no-think trials and identified a decrease in positivity over right frontal and left parietal electrode sites predicting later TNT impairment. In particular, to investigate anticipatory effects of TNT impairment, Hanslmayr et al. presented the TNT instruction prior to the memory cue allowing participants to prepare for memory suppression. Interestingly, a decrease in positivity was already found at TNT instruction before presentation of the memory cue and this anticipatory ERP effect predicted both the later memory cue ERP effect and TNT impairment. Therefore, the anticipatory effect was suggested to reflect top-down control preparing for retrieval suppression.

Together, neuroimaging in the TNT phase suggests that the volition to avoid conscious recollection of both emotional and nonemotional information recruits prefrontal brain regions which are known to impose cognitive control by inhibitory mechanisms. Retrieval suppression of the no-think information is mediated by right prefrontal regions, down-regulating the activity in the hippocampus and the amygdala. ERP investigation suggests that items' memory representations can be affected via anticipatory retrieval suppression to keep unwanted memories from entering consciousness.

Neural Substrates of AM Retrieval

AM retrieval has been related to processing in a distributed neural network, including the PFC, the medial temporal lobe, and posterior regions (for a review, see Maguire, 2001, or Svoboda, McKinnon, & Levine, 2006). Because AMs usually are recalled with a sense of reliving and emotional intensity, brain regions involved in sensory and emotional processing are typically related to AM retrieval as well (Cabeza & St Jacques, 2007). In this section, we address physiological findings in AM construction and the retrieval of unpleasant AMs. Thereafter, we will discuss the possible role of retrieval inhibition in constructive AM search and the suppression of unpleasant AMs.

AM construction

AM retrieval is a constructive process (Schacter & Addis, 2007), in which relevant information is widely distributed across the brain and has to be bound together to form a coherent memory. Two consecutive processes of AM retrieval may be distinguished. Initially, a search process is activated to

access a specific memory. Then, after recovery of the memory, an elaboration process is activated to maintain and elaborate the selected information. The access process includes attempts to reactivate relevant information as well as emotional processing and top-down control that guides the search. The elaboration process involves vivid imagery as well as controlled attentional and working memory operations to keep the selected information in mind for elaboration.

Brain regions that are mostly involved in constructing AMs are the hippocampus, the amygdala, the ACC, and both right and medial PFC regions (Daselaar et al., 2008). Hippocampal activity is suggested to be strongly modulated by prefrontal activations, which are assumed to guide conscious recollection of information mainly represented in posterior regions by top-down control on the hippocampal binding process (Hassabis & Maguire, 2007; Schacter, Addis, & Buckner, 2007). In PFC, different sub-regions implement different functions in cognitive control. The proposal is that the ACC detects interference (Botvinick, Cohen, & Carter, 2004) and integrates emotional processing (Burianova & Grady, 2007), the right LPFC exerts inhibitory control (Aron, Robbins, & Poldrack, 2004), and the medial PFC contributes to self-referential processing (Gusnard, 2005). With respect to emotional intensity of AMs, Greenberg et al. (2005) found a high correlation of amygdala and right VLPFC activity, suggesting a strong interaction between emotional processing and AM construction.

Daselaar et al. (2008) examined brain activity during AM access and elaboration using fMRI. Participants were asked to provide a memory of a specific past event in response to a generic cue word. Imaging showed that the initial accessing of AMs engaged the hippocampus, the retrosplenial cortex, right and medial PFC regions, and the ACC. In contrast, subsequent elaboration recruited the visual cortex, the precuneus, and left PFC regions. Daselaar et al. also examined emotion- and reliving-modulated brain activity. For this purpose, participants rated the emotional intensity an AM actually induced and how much they felt they were reliving the initial event again. Emotion-modulated activation was observed in the amygdala and the frontopolar cortex. Reliving-modulated activation was observed in the visual cortex, right inferior PFC, and the anterior and posterior cingulates. Interestingly, whereas emotion-related areas were selectively activated during initial memory search, reliving-related areas were selectively activated during AM elaboration.

During AM retrieval, autobiographical information dynamically interacts with episodic and semantic information within a network of long-term memory representations (Conway & Pleydell-Pearce, 2000; Conway & Williams, 2008). The question of how AM retrieval overlaps with episodic and semantic memory retrieval has recently been addressed by Burianova and Grady (2007), examining brain activations that are common or unique to

autobiographical, episodic, and semantic memory search. Despite some differences in activated brain regions among the three memory types, their results provide evidence for a common temporo-frontal retrieval network involving left and right VLPFC as well as the hippocampus – brain regions that have also been associated to involuntary and voluntary retrieval inhibition. Accordingly, Burianova and Grady (2007) suggested that AM retrieval engages inhibitory processes that may be similar to episodic and semantic memory retrieval.

Together, physiological findings suggest that AM construction is related to a distributed neural network including frontal and medial temporal regions. In part, prefrontal brain activations may reflect inhibitory processes in the service of successful AM construction. At the end of the chapter, we will discuss the possible role of retrieval inhibition in AM retrieval. Before doing so, we address the neural substrates of emotional AMs, with the focus on unpleasant events.

Retrieval of unpleasant AMs

The retrieval of emotional AMs recruits the same regions that are involved in the retrieval of nonemotional AMs, along with a set of additional regions typically associated with emotional processing, including the amygdala and medial PFC. Within this network of brain regions, the retrieval of emotional AMs seems to be primarily related to interactions between the hippocampus, the amygdala, and the PFC. Thereby, whereas the medial PFC is more involved in the retrieval of pleasant AMs, findings from both neuropsychology and neuroimaging suggest that the amygdala is involved mainly in the retrieval of unpleasant AMs (for a review, see Buchanan, 2007).

Neuropsychological research has shown that patients with amygdala damage show impaired retrieval of unpleasant emotional events (Buchanan, Tranel, & Adolphs, 2005, 2006). Buchanan et al. (2005) showed that patients with MTL damage limited to the hippocampus retrieved emotional AMs similar to healthy participants, in terms of both the number and affective quality of these AMs. In contrast, patients with damage to both the amygdala and the hippocampus retrieved fewer unpleasant AMs and rated their unpleasant memories as less intense, significant, and vivid compared to other participants. Buchanan et al. (2006) also examined whether right and left amygdala play a different role in the retrieval of emotional AMs, in patients with either left or right MTL damage. Results showed that patients with right-sided damage, but not with left-sided damage, retrieved less unpleasant AMs and rated them as less intense compared to healthy participants. Together with the Buchanan et al. (2005) study, these results suggest that the right amygdala – and its connection to PFC – may be a necessary component of the neural circuitry required for retrieval of unpleasant, highly intense AMs.

Neuroimaging studies also related the retrieval of emotional AMs to activation in the amygdala (for a review, see Cabeza & St Jacques, 2007). For instance, Daselaar et al. (2008) contrasted emotion- and reliving-modulated activation during AM retrieval and demonstrated that the first was greatest in the amygdala and anterior PFC, whereas the second was greatest in the visual cortex. Also in line with neuropsychological results is the finding that pleasant AM retrieval seems to activate the medial PFC, whereas unpleasant AMs seem to activate the right MTL (Markowitsch, Vandekerckhove, Lanfermann, & Russ, 2003). Emotional AMs have also been found to be related to greater activity in the hippocampus (Addis, Moscovitch, Crawley, & McAndrews, 2004) and bilateral amygdala-hippocampal interactions (Greenberg et al., 2005). Together, imaging findings suggest that the amygdala has a functional role in remembering unpleasant AMs.

Consistent with these findings, physiological research in the study of trauma and PTSD suggests that the three major brain regions involved in trauma-related memory disturbances are the amygdala, the medial prefrontal cortex, and the hippocampus (for a review, see Shin, Rauch, & Pitman, 2006). There is evidence that, whereas the amygdala is highly responsive to trauma-related memories, activation in the medial PFC, including the ACC and medial frontal gyrus, is largely decreased in PTSD. This pattern of amygdala hyperactivation and PFC deactivation may be associated to typical memory disturbances in PTSD with intrusions of highly emotional memories and the inability to recall other aspects of the trauma, possibly because of ineffective retrieval inhibition of involuntary memory intrusions.

Together, physiological findings suggest that the retrieval of unpleasant AMs is strongly related to activity in the amygdala and the PFC. Prefrontal brain activations thus may represent in part inhibitory processes, reflecting retrieval inhibition of unpleasant and traumatic AMs.

Future Lines of Research

We suggest that AM retrieval is regulated by inhibitory control. More precisely, inhibitory processes may affect irrelevant AMs to facilitate retrieval of relevant AMs. In this sense, retrieval inhibition would be an adaptive mechanism in AM retrieval to access relevant AM information within almost infinite possible ramifications of episodic, semantic, and emotional cues associated to various information along the search path. Retrieval of unpleasant AMs or traumatic events may also depend on inhibitory processes. Indeed, there is evidence from research in episodic memory that unpleasant material can be unintentionally and intentionally forgotten. The crucial question is whether this finding generalizes to unpleasant and trauma-related AMs.

To examine the role of retrieval inhibition in AM retrieval, two lines of research should be taken in future research. First, in behavioral experiments, inhibitory paradigms should be used to examine whether effects of emotional and neutral material found with simple item lists can be extended to AMs. This line of research is raring to go in healthy populations (Barnier, Hung, & Conway, 2004; Barnier et al., 2007; Joslyn & Oakes, 2005; Wessel & Hauer, 2006) as well as clinical populations (McNally, Clancy, Barrett, & Parker, 2004; McNally, Clancy, & Schacter, 2001; McNally, Metzger, Lasko, Clancy, & Pitman, 1998; McNally, Ristuccia, & Perlman, 2005). Second, in physiological experiments, inhibitory paradigms should be used to examine unintentional and intentional forgetting of emotional and neutral AMs instead of simple item material. No studies have yet been published addressing this second issue.

Regarding the first line of research and behavioral work in healthy populations, in RIF, Barnier, Hung, and Conway (2004) let participants generate specific emotional or nonemotional AMs in response to negative, positive, and neutral cue words. As in the standard RIF procedure, each cue word was associated to a number of other memories. After retrieval practice on some AMs, participants tried to recall all of their originally generated memories on a final recall test. A standard RIF effect was found for previously generated emotional and nonemotional AMs. Recently, Wessel and Hauer (2006) replicated the Barnier et al. (2004) finding for negative material, but did not observe RIF for positive material. In LM-DF, Barnier et al. (2007) adapted the standard LM-DF procedure to directed forgetting of unpleasant, pleasant, and emotionally neutral AMs. Participants generated a specific AM in response to a list of generic cues. After presentation of this list, they were instructed to either forget or continue remembering AMs associated to cues of this list. Next, a second list of cues was presented and again an AM had to be generated in response to each generic cue. Across various experiments, Barnier et al. found a standard directed forgetting effect for precue generated unpleasant, pleasant, and neutral AMs. Also in LM-DF, but within a diary paradigm outside the laboratory, Joslyn and Oakes (2005) investigated intentional forgetting of AMs. Participants were asked to keep a diary for two weeks. After the first week, they were instructed either to forget or continue remembering the first week's events. After a second week of keeping the diary, all participants returned to the laboratory and were asked to recall events of both weeks. Consistent to the controlled LM-DF experiment in the laboratory (Barnier et al., 2007), significant directed forgetting for AMs from the first week was found. Together, these findings provide first evidence that inhibitory processes may play a crucial role in AM retrieval.

In clinical populations, the ability to forget trauma-related and neutral words has been examined in LM-DF and IM-DF (McNally, Metzger, Lasko, Clancy, & Pitman, 1998; McNally, Clancy, & Schacter, 2001; McNally,

Clancy, Barrett, & Parker, 2004; McNally, Ristuccia, & Perlman, 2005). Irrespective of method, clinical populations showed the same reliable forgetting of words as healthy controls, regardless of valence and relatedness of material to trauma. Thus, it seems that traumatized people do not differ in encoding or retrieval of trauma-related words. However, using simple words as substitutes for real AMs may underestimate the role of inhibitory processes in forgetting autobiographical trauma memories. Thus, further behavioral and physiological research in PTSD is needed to investigate inhibitory forgetting of unpleasant and traumatic AMs. In doing so, the TNT paradigm may be particularly promising. In contrast to other inhibitory paradigms, the forgetting in TNT has been found to be larger for unpleasant items compared to emotionally neutral material (Depue, Banich, & Curran, 2006). This finding suggests that retrieval of unpleasant information can be more easily suppressed than nonemotional information. Whether this effect holds for trauma-related material has still to be shown.

Conclusions

Inhibitory paradigms can be used to explore certain forms of unintentional and intentional forgetting in the laboratory. Doing so, evidence has arisen that inhibitory processes mediate the modulation in accessibility of irrelevant or to-be-forgotten information. Thereby, different inhibitory mechanisms have been suggested to reduce the accessibility of memory representations. The mechanisms differ in whether they affect the representation of irrelevant information itself or affect its retrieval routes, and whether they are initiated involuntarily or voluntarily.

Both unintentional and intentional forgetting, as examined in RIF, DF, or TNT impairment, are meant to arise from active inhibitory processes triggered by prefrontal brain regions. In particular, the ACC and the right LPFC are suggested to regulate brain activity in the service of selective retrieval and forgetting of irrelevant information. The ACC is meant to signal the need for inhibitory control, which is then exerted by the right LPFC. Thus, inhibitory processes down regulate memory-related activity in the hippocampus, the amygdala, and posterior regions. In addition, they may reduce the synchronicity of brain activity between relevant brain regions.

A review of physiological findings revealed a remarkable overlap of brain regions involved in AM retrieval with brain regions related to retrieval inhibition. Indeed, during AM search, mostly involved brain regions are the hippocampus, the amygdala, the ACC, the right LPFC, and medial PFC regions. Hippocampal and amygdala activity is suggested to be modulated by prefrontal activations which more or less guide memory search. Within this temporo-frontal network of AM retrieval, the amygdala becomes involved in

the retrieval of unpleasant or traumatic AMs. With its strong interconnections to the hippocampus and PFC, it then plays a crucial role in voluntary and involuntary retrieval of emotional AMs.

We think that future examination of inhibitory forgetting of AMs will be promising with both behavioral and physiological experiments. Based on first evidence that both neutral and emotional AMs can be unintentionally and intentionally forgotten, future behavioral work should further specify the possible role of retrieval inhibition in AM retrieval, in both healthy and clinical populations. Future imaging studies will help to discover exactly what processes mediate selective remembering and intentional forgetting of autobiographical events, and to what extent these processes are functionally and neurally equivalent to inhibitory brain processes, as they are involved in selective retrieval and intentional forgetting of simple item lists.

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