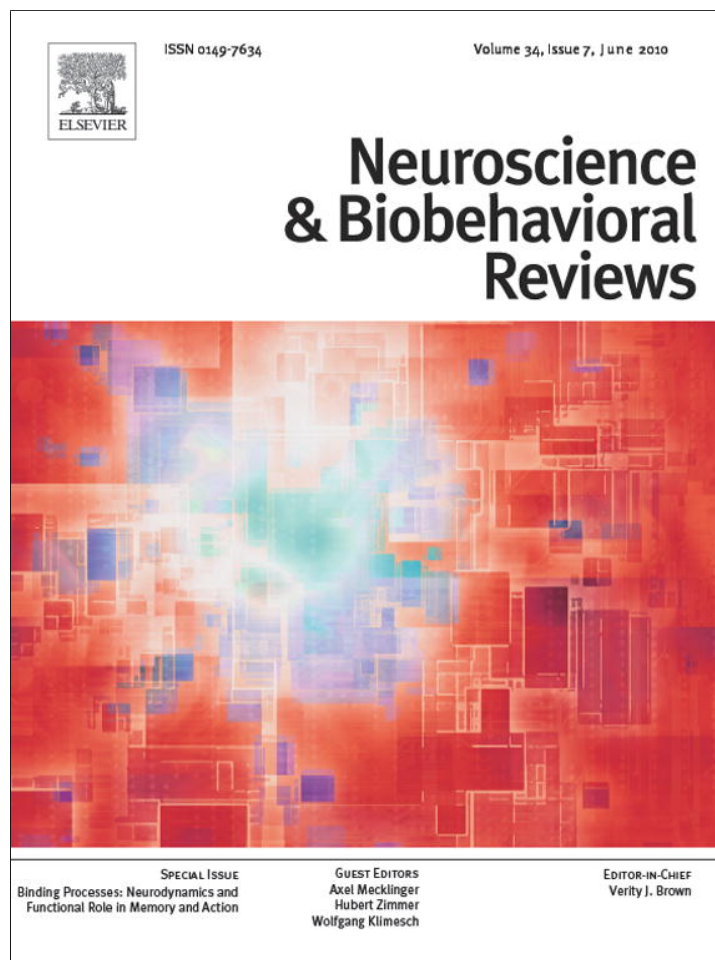


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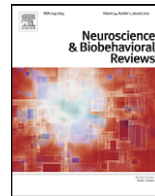
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Review

The control of long-term memory: Brain systems and cognitive processes

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ABSTRACT

This paper provides a selective review of controlled memory retrieval, i.e., processes, that operate on long-term stored information in the service of current goals and task demands. Binding mechanisms that combine fragments of long-term stored information in response to a retrieval cue, are central for the understanding of the interaction between a retrieval cue and memory-stored information. The paper summarizes empirical evidence showing that ERP slow waves are highly sensitive to the initiation and maintenance of retrieval orientations. It is argued that similar mechanisms of controlled memory retrieval operate in the service of successful remembering and the suppression of unwanted memories (forgetting). The mechanisms can be grouped into two classes: those that enhance retrieval cue processing (cue bias) and those that directly act on memory representations and modulate their accessibility (target bias). From a neuroanatomical point of view, the former class of processes reflects selection mechanisms for internal actions that rely on the integrity of the prefrontal cortex (PFC), whereas the second class of processes can be identified with selective attention mechanisms for which the posterior parietal cortex (PPC) plays an important role.

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The ability to remember past experiences is an essential part of our self. But our memory system can do much more than simply recognize that a particular event was encountered previously. From a memory psychology point of view, remembering is thought to involve the interaction between a retrieval cue and an internal representation which in turn leads to the reconstruction of parts or the whole episode. A retrieval cue can either be provided by the environment or be self-generated, as in situations in which an actual retrieval cue does not reactivate a memory representation and further internal representations have to be generated to guide memory research and the retrieval of context appropriate memories. Binding mechanisms, the mechanisms by which fragments of long-term stored information are bound together in response to a

retrieval cue, are central for the understanding of the cue–memory interaction (see Zimmer et al., 2006 for an overview). Binding mechanisms are not only relevant in binding together incidental and disparate features that comprise the memory for an event during learning (Knowlton and Eldridge, 2006). They are also relevant at retrieval, when the event is re-experienced and has to be brought in line with retrieval goals and intentions. Here, binding mechanism may link task-relevant information in long-term memory, i.e., item and context features that comprise an event, and bind it with top-down goal-relevant signals. The ensemble of processes that guide the interaction between retrieval cues and internal representations in the service of task-appropriate behavior is referred to as controlled memory retrieval.

In 1983, Tulving introduced the concept of “mental time travel” to refer to our ability to relive experiences, to remember past experiences, and to flexibly search memory for behaviorally relevant information by the internal generation of retrieval cues.

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According to this view, episodic memory not only allows to recollect the personal past, it also entails the capacity to focus attention on our own subjective experiences (i.e., auto-noetic awareness). The primary task of our memory system is to guide the interaction between retrieval cues and memory representations by binding together item presentations and their associated contextual features. This, in turn, allows the individual to infer the context in which an item was initially encountered. According to [Tulving \(1983\)](#), a prerequisite of successful episodic retrieval is that an individual is in a so-called retrieval mode, a cognitive state that ensures that an external or internal event is treated as a retrieval cue. Hence, retrieval mode is also a prerequisite for auto-noetic awareness (see also [Wheeler et al., 1997](#)).

Following Tulving's seminal work, a lot of neuroscientific research has focused on the prefrontal cortex as the critical brain system for the supervision of episodic retrieval and auto-noetic awareness. In recent years, however, stimulated in part by new brain imaging techniques and sophisticated data analyses methodologies, new theoretical developments arose in this area. These models not only suggest a more detailed functional taxonomy of retrieval processes, they also challenge the view of the PFC being the sole brain system relevant for controlled memory retrieval.

The present article will focus on event-related potential (ERP) indices of controlled memory retrieval, in particular ERP slow waves. Event-related slow waves appear as a negative or positive deflection in the averaged ERP with a minimum duration of about 400 ms and a maximum duration of several seconds. Even though a coherent account on the generating cellular mechanisms of positive and negative slow wave activity is still lacking, there is increasing evidence that they arise from the enhanced and long-lasting firing of neo-cortical pyramidal cells adjacent to the scalp electrode sites at which they are recorded ([Rockstroh et al., 1982](#); [Birbaumer et al., 1990](#)). Volume conduction models also suggest that remote cortical and subcortical structures play a negligible role in the generation of ERP slow waves ([Nunez, 1990](#)). Thus, even though ERP slow waves do not allow to unequivocally localize the generating structures, qualitative differences in the scalp topography of slow wave activity in two experimental conditions can be interpreted as evidence that the two conditions engage functionally distinct cognitive operations. By this ERP slow waves are a valuable tool to inform and to constrain cognitive models of controlled memory retrieval (for a further discussion of neural dissociations see [Henson, 2006](#); [Simons, 2009](#)).

In this selective review I will first discuss relevant contemporary models in the area of controlled memory retrieval. I will focus on two memory-relevant cognitive states, i.e., retrieval mode and retrieval orientation, the situations in which they are adapted, and their neural correlates as revealed by event-related potential (ERP) measures. The review will first concentrate on retrieval processing initiated by a retrieval cue (retrieval attempts) and then discuss preparatory (pre-retrieval) processes that are engaged prior to retrieval and influence the way a retrieval cue is processed. Next, the functional role of retrieval processing will be discussed. A special focus will be on the commonalities and differences of control mechanisms in the service of successful remembering and suppression of unwanted memories (i.e., forgetting). The final section will discuss the role of three brain systems, the PFC, the medial temporal lobes (MTL), and the posterior parietal cortex (PPC) in mediating controlled memory retrieval.

1. Retrieval attempts

In their seminal 2000 paper, [Rugg and Wilding \(2000\)](#) proposed a fourfold classification of the subprocesses recruited by controlled memory retrieval: retrieval mode, orientation, effort, and success.

Following [Tulving \(1983\)](#) model, *retrieval mode* is assumed to constitute a tonically maintained state, entry to which allows to treat a stimulus as an episodic retrieval cue. From this it follows that any neural correlates of retrieval mode should be tonically present for the duration of an episodic retrieval task and should be observable in response to an episodic task cue. [Düzel et al. \(1999\)](#) were among the first to show that the right PFC is critically involved in the maintenance of retrieval modes. [Düzel et al. \(1999\)](#) recorded ERP slow wave activity elicited by task cues that either indicated an upcoming episodic (recognition memory) task or a semantic classification task. During the episodic task, there was a pronounced positive going slow wave (relative to the semantic task) over right fronto-polar recording sites. Together with a corresponding PET activation pattern in the right anterior PFC, the authors took these results to suggest that the right PFC is critically engaged in the initiation and tonic maintenance of an episodic retrieval mode.

In the following several studies addressed the issue whether a retrieval mode is constant across different episodic memory tasks or whether different forms of processing are applied to an episodic retrieval cue depending on the to-be-retrieved materials.

The general logic behind investigations of retrieval orientations is to compare neural activity elicited by identical retrieval cues and to vary the kind of information to be retrieved. In order to separate the ERP correlates of retrieval attempts from other forms of retrieval processing (i.e., retrieval success), ERPs to new items are contrasted according to retrieval task. Since new items have not been studied in the experimental context, any ERP differences between them can be considered as correlates of retrieval attempts.

An illustrative example is a study by [Dzulkifli and Wilding \(2005\)](#). In the study phase participants performed one of two encoding tasks on visually presented words. They either had to think of a concrete use for the object denoted by the word (function task) or to indicate how difficult it is to draw the object (drawing task). This was followed by two retrieval phases in which words from both encoding task were presented together with new (unstudied) words. Participants responded "old" to targets from one target destination and "new" to non-targets and unstudied items. Target destination was varied across the two retrieval phases. [Dzulkifli and Wilding \(2005\)](#) found pronounced slow wave differences in the ERPs to new items at frontal and central recording sites, which took the form of more positive going slow waves in the function task. Importantly, task performance (% correct responses to new items) did not vary across tasks. By this, differences in task difficulty cannot account for the ERP differences evoked by the new items. Thus, the ERP difference is a consequence of attempting to retrieve the function or drawing encoding task and presumably reflects processes that optimize the interaction between the retrieval cue and the memory trace. The selective processing of a retrieval cue has been labeled cue bias by [Anderson and Bjork \(1994\)](#). Cue bias refers to an ensemble of processes that constrain, specify or maintain the internal representation of the retrieval cue in pursuit of successful memory retrieval. In case of the aforementioned study it ensures that remembering of only one of the two study tasks is optimized.

Differential ERP patterns to items with no study history contrasted according to retrieval task were also reported in other studies. [Herron and Rugg \(2003\)](#) examined memory for previously studied words or pictures using words as retrieval cues. In separate test blocks, old responses were required for test items corresponding to either study words or study pictures and new responses were required for items from the other study category and completely new items. ERPs to new words were more negative going in the picture than in the word condition. However, in contrast to the aforementioned study by [Dzulkifli and Wilding](#)

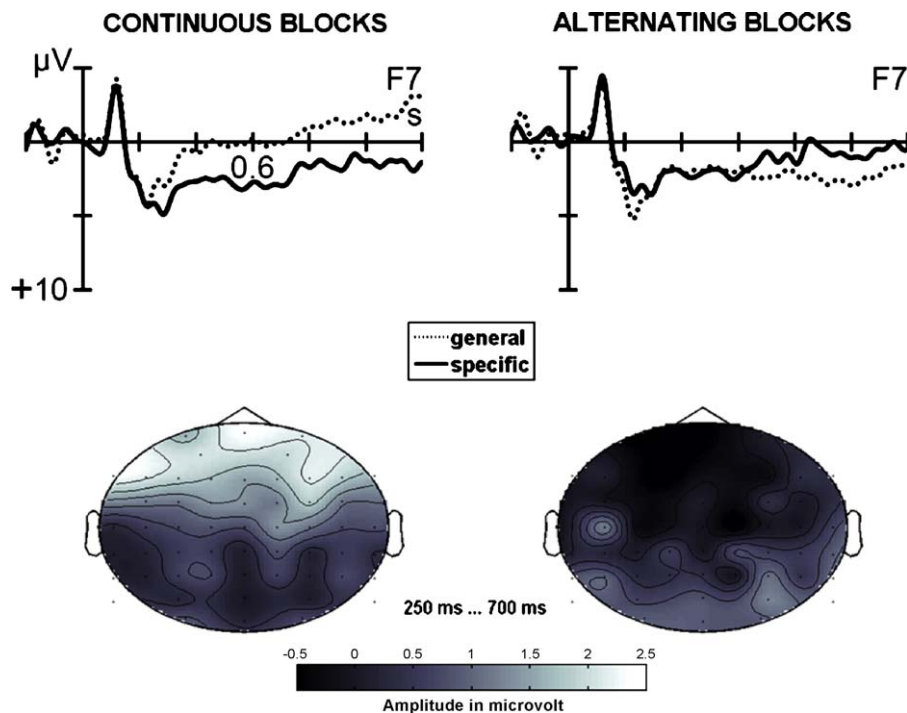


Fig. 1. (Top) ERPs elicited by correct rejections of new words in continuous (left) and alternating (right) task blocks in the general and specific task at the left frontal electrode site F7. (Bottom) Topographical maps for ERP difference waves (specific minus general) within continuous (left) and alternating (right) test blocks for a time interval from 250 to 700 ms after stimulus onset.

these effects were restricted to a smaller time window (300–900 ms) and topographically more wide-spread.

Though the Herron and Rugg (2003) findings suggest that physically identical retrieval cues can elicit differential ERP activity as a function of retrieval task, they do not allow to decide whether these retrieval orientation effects are indeed related to the sought-after information (i.e., pictures or words). In fact, as the manipulation of study material (pictures and words) and similarity between study materials and test cues (words) was confounded in the latter study, the effects could simply reflect the degree of similarity between the study and test items. To overcome this shortcoming, Hornberger et al. (2004) conducted a study in which study materials were auditory words and pictures and test items were visually presented words. Replicating the Herron and Rugg (2003) findings, ERPs to unstudied test words were more negative going when pictures were the sought-after materials. This suggests that the ERP retrieval orientation effects do not depend on cue–target similarity and are also obtained under conditions of constant cue–target similarity.

An important issue concerns the initiation of retrieval orientations in situations with inconsistent retrieval demands. Do retrieval orientations require consistent retrieval goals for a series of trials and, in turn, can only be adapted and maintained when retrieval goals are constant throughout a series of trials? Alternatively, retrieval orientations could reflect item-specific processing in the sense that they can be adjusted in response to a single retrieval cue. In the latter case, they should also be observable in situations with inconsistent retrieval demands, as for example when frequent switches between different retrieval tasks are required.

A few ERP studies explicitly addressed this issue (Johnson and Rugg, 2006; Werkle-Bergner et al., 2005; Wilding and Nobre, 2001). In the Werkle-Bergner et al. (2005) study we compared task performance and ERP indices of retrieval orientations in two task situations. In a continuous task situation, retrieval requirements were held constant within each test block, whereas in the

alternating task situation the retrieval requirements changed on a trial-by-trial basis. In one retrieval task, the participants made old/new judgments for previously studied words (general task). The other retrieval task required the additional retrieval of a word's character style (specific task). The difference between the two retrieval situations is that the latter requires more extended retrieval cue processing in order to make study information (i.e., character style) available. The ERPs to new words in both retrieval tasks in the continuous and alternating task situation are illustrated in Fig. 1.

In the continuous task situation, the ERPs show remarkable task-related differences. When perceptual details of the studied words were the sought-after materials, the ERPs were more positive going at bilateral frontal recording sites. This effect started at around 250 ms and extended for several hundred milliseconds. Notably, this effect of retrieval orientation was virtually absent in the alternating situation, suggesting that the requirement to frequently switch between different retrieval demands may have hindered the participants from entering task-specific retrieval orientations. In other words, adapting a task-specific retrieval orientation requires the completion of several successive retrieval attempts. The same conclusions were drawn by Wilding and Nobre (2001), manipulating continuous and alternating processing requirements across experiments, and by Johnson and Rugg (2006), using words as test items and pictures or words as target materials.

Werkle-Bergner et al. (2005) further explored the specific processing requirements in the alternating task situation. This condition demanded the alternation between two retrieval tasks (T1 and T2) in a fixed and predictable order (i.e., T1–T1–T2–T2–T1–T1–T2–T2). The kind of retrieval task was indicated by an instructional cue that preceded the test item by 300 ms. On a behavioral level, the processing costs in the alternating condition are evident by so-called general switch costs (Rogers and Monsell, 1995), i.e., subjects made more errors and had longer response times for recognition memory judgments in the alternating than in

the continuous task situation. These behavioral effects are paralleled by pronounced differences in the ERPs to new items in both task situations. These effects were most pronounced at frontal and anterior–frontal recordings and took the form of more positive going slow wave activity in the alternating than in the continuous task situation. Prior to discussing the functional role of these effects, it is important to recapitulate that two sorts of trials were included in the ERPs to new items in the alternating task situation. Switch trials, in which the retrieval task has changed relative to the preceding trial, and stay trials, in which the retrieval task was the same as in the preceding trials. The additional processing costs for switch trials on the behavioral level (specific switch cost) take the form of longer reaction times and more errors for switch trials as compared to stay trials. We examined the extent to which both trial types contribute to the anterior–frontal positive slow wave pattern in the alternating task situation. The positive slow wave pattern was highly similar for both trial types between 500 and 750 ms, whereas the ERPs were even more positive going for switch than stay trials at right frontal recordings in a late, post-response period (see [Werkle-Bergner et al., 2005](#), for details).

These results suggest that, in addition to the initiation of task-specific retrieval orientations, another form of control processes is initiated by the requirement to flexibly change between different retrieval demands. The ERP correlate of these control processes is an anterior–frontal positive slow wave. As this effect is not modulated by the actual task requirements, (i.e., to switch to another retrieval task) it is reasonable to assume that it does not reflect task-specific retrieval processing but rather more general control requirements brought up by the dual task situation of holding two retrieval sets active simultaneously, controlling competing memory traces and alternating between two sets of target materials. Interestingly, a similar anterior–frontal positive slow wave was reported by [Johnson and Rugg \(2006\)](#) in an alternating task situation using an unpredictable task sequence and different retrieval tasks.

While the aforementioned task- and block-related ERP effects were present at around the same time as the putative ERP correlates of retrieval success (i.e., the parietal old/new effect), a third aspect of controlled memory retrieval was only manifest in a post-response period. Consistent with studies that have identified similar late positive slow wave activity over right frontal recording sites with post-retrieval monitoring ([Mecklinger, 1998](#); [Wilding and Rugg, 1996](#)), the late positivity to switch as compared to stay trials could reflect increased post-decisional monitoring and evaluation demands for low confidence recognition memory decisions. The long response times and enhanced error rates that were obtained for recognition memory judgments in switch trials are consistent with this view.

2. Preparatory processes

Another important issue is whether task-specific retrieval processing can be adapted in a preparatory way even before a retrieval cue is presented and information can be recovered from memory. How do these preparatory processes influence retrieval processing initiated by the retrieval cue? [Herron and Wilding \(2004\)](#) directly explored these issues. In their study, participants were cued on a trial-by-trial basis to perform a semantic retrieval task or one of two episodic retrieval tasks (memory for spatial location and encoding task). ERPs were recorded time-locked to the task cues, that preceded the retrieval cues for which memory judgments had to be given by 2 s. While accuracy did not differ between switch and stay trials, response times were longer for switch trials.

Interestingly, the authors found different ERP slow wave patterns to the two preparatory cues in the episodic tasks:

preparing the retrieval of the spatial locations was associated with pronounced left fronto-central positive slow wave activity as compared to preparing to retrieve an encoding operation. This data supports the view that task-specific retrieval processing can be adapted upstream, i.e., even before a retrieval cue, that allows the recovery of information from episodic memory is presented. They also show that preparation to retrieve varies according to the kind of episodic information to be retrieved.

The preparatory effects by [Herron and Wilding \(2004\)](#) were obtained for stay trials only, even though memory performance was not better in stay than in switch trials. This suggests that preparing for retrieval does not necessarily enhance the likelihood that information is recovered upon presentation of a retrieval cue. Notably, as the authors did not find preparatory effects for switch trials, they were not able to determine whether preparatory retrieval processing can occur after only one trial with a particular retrieval demand.

We approached this issue in a further study with unpredictable retrieval demands ([Benoit et al., 2009](#)). At issue was, whether task-specific retrieval processing can be adjusted in one single switch trial in response to a preparatory task cue that signals the upcoming retrieval task. We assumed that even though retrieval orientations cannot be adjusted in response to a single retrieval cue (as suggested by the aforementioned studies), this does not preclude the possibility that some form of task-specific retrieval processing can be initiated by preparatory cues even before information is recovered from episodic memory.

In this study ([Benoit et al., 2009](#)) we used a modified version of the task switching paradigm employed in the [Werkle-Bergner et al.](#) study. We extended the interval between the preparatory cue and the retrieval cue to 1000 ms. In addition, there was a second alternating task situation with an unpredictable task sequence. In finding reliable general and specific switch costs, the behavioral results of the [Werkle-Bergner et al.](#) study were replicated. Importantly, the specific switch costs (i.e., the higher processing costs for switch than stay trials) were modulated by the task factor: response times were longer when switching to the easier-to-perform general task. This asymmetrical pattern of switch costs suggests that retrieval preparation is more demanding in the case of the easier-to-perform task.

Replicating the [Werkle-Bergner et al. \(2005\)](#) findings, attempts to retrieve the words' character style in the specific task were associated with bilateral frontal slow wave activity in the continuous task situation but not in the two alternating situations. This confirms the view, that retrieval orientations cannot be adjusted in response to a single retrieval cue, presumably due to the fact that enhanced processing requirement in the alternating situations hinders task-specific retrieval cue processing. Interestingly, task-specific effects in the alternating situation, though absent in response to the retrieval cue, were obtained in the cue-elicited ERPs. As illustrated in [Fig. 2](#), these task-specific preparatory effects were present at posterior recordings sites for switch trials only.

They were characterized by a greater positivity to the cue indicating the general task. These task effects were prominent in the 400 ms preceding the retrieval cue and were obtained in both alternating conditions. These cue-elicited task effects are somehow similar to the findings of [Johnson and Rugg \(2006\)](#), who also found more positive going cue-elicited ERPs at parietal sites in switch trials than in stay trials. In the blocks with unpredictable task sequences, this positive slow wave to switch trials was preceded by a larger P300, signaling the updating of working memory contents by the unpredictable task cue ([Donchin and Coles, 1988](#)). It is conceivable that these task-specific effects elicited by the cue reflect processes that support a task set reconfiguration, i.e., attempts to activate the appropriate retrieval orientation even

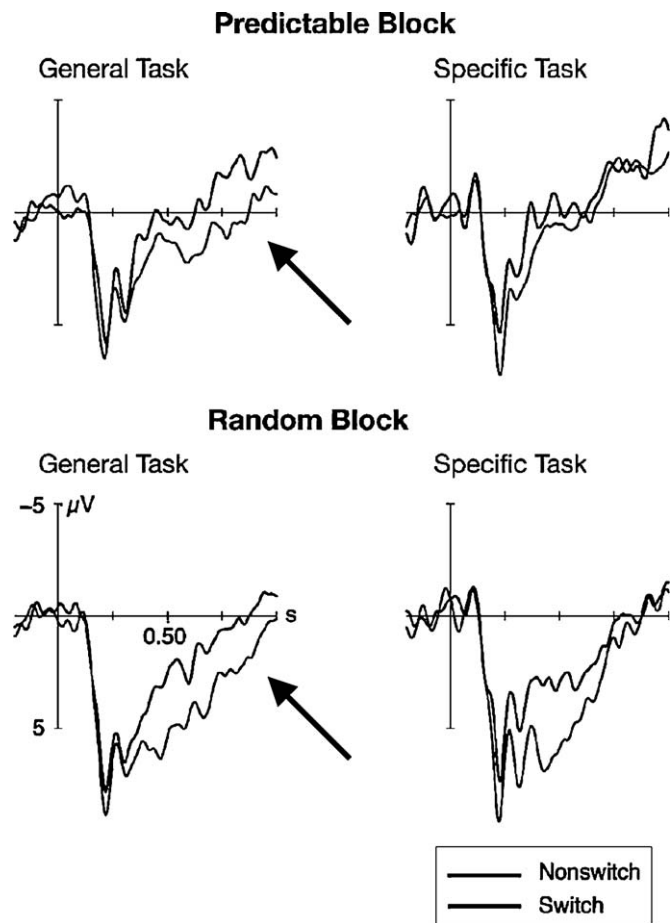


Fig. 2. ERPs elicited by the preparation cues at parieto-occipital recording site POz in the general and specific task in the study by Mecklinger et al. (2005) signaling that the retrieval demands will change (switch trials) or will remain unchanged (stay trials).

prior to the presentation of the retrieval cue. Interestingly, these processes were not sufficient to evoke task-specific processing of the retrieval cues, as no ERP correlates of differential retrieval orientations were obtained upon presentation of the retrieval cues in the alternating conditions. The differential cue-elicited slow wave pattern is paralleled by the asymmetrical switch costs on the behavioral level, i.e., the slow wave was most pronounced when the cue indicated that the task set of the general task (for which switch costs were larger) has to be activated. Consistent with the “task-set-inertia” hypothesis (see Allport et al., 1994), that proposes that asymmetrical switch costs reflect the additional processing demands required to overcome the interference from a strongly imposed task, the positivity preceding the retrieval cue in the general task may reflect the greater attentional selection demands to overcome interference from the strongly imposed task set of the specific tasks. An alternative interpretation is that the cue effects reflect enhanced attentional focusing on the targeted class of memory representations that occurs prior to the presentation of the task cue. This analogy between selective attention and memory retrieval in interpreting the task cue effects is also supported by neuroanatomical considerations. The task cue effects were selectively observed over posterior (parietal) recording sites that overlie posterior parietal brain regions that – in brain imaging studies – have been identified with top-down attention processing in memory (Cabeza et al., 2008; Wagner et al., 2005) and non-memory tasks (Corbetta and Shulman, 2002). Even though the neural generators of scalp recorded ERP data cannot unequivocally be determined it is conceivable that the preparatory ERP effects

observed in the Benoit et al. study are due to activity in regions identified with top-down attentional processing in brain imaging studies. Attentional focusing on the targeted memory representations is a retrieval strategy which has been labeled “target bias” by Anderson and Bjork (1994). Target bias refers to a set of processes set in train in response to a task cue that directly operate on memory (target) representations and in turn increase their accessibility. This strategy may be highly efficient in alternating task situations with unpredictable retrieval demands which due to the high processing demands prevent the initiation of a task-specific retrieval orientation upon presentation of the test items (see Johnson and Rugg, 2006, for similar arguments).

3. The mechanism supporting selective retrieval processing

An important issue concerns the nature of selective processing of retrieval cues, as reflected in the ERPs elicited by new items. One possibility is that the processes indexed by the differential ERP effects to retrieval cues reflect operations that maximize the overlap between processes engaged at encoding and retrieval (Rugg et al., 2002). This view is closely related to the transfer-appropriate processing account (Craik and Lockhart, 1972), according to which memory performance is a function of the degree to which cognitive processes at encoding are re-activated during retrieval. A variety of recent brain imaging studies provided direct support for this account by showing that successful memory retrieval is associated with the reactivation of neural activity from the prior study phase (see Polyn and Kahana, 2008, for a review). In an illustrative study, Polyn et al. (2005) used a pattern classification algorithm to identify neural activation patterns in the fMRI signal that are associated with three different classes of study materials. Applying these material-specific classifiers to the fMRI signals in a subsequent recall phase, they found that the material-specific activation pattern from the study phase was reinstated before the recall of the items (see also Sederberg et al., 2007) for similar results obtained with high frequency EEG oscillations). Evidence for the reinstatement of encoding related processes during episodic retrieval was also provided in a recent fMRI study by Johnson and Rugg (2007). However, in contrast to the Polyn et al. (2005) study, only a small number of brain regions, including three posterior regions and the medial frontal cortex, showed overlap between the study and test phases, as predicted by the transfer-appropriate processing principle. The majority of regions activated at retrieval were activated by both retrieval tasks with no overlap with task-specific encoding activity. A logical limitation of the latter studies is that it cannot be unambiguously decided, whether successful remembering is the effect or the cause of a reactivated brain activation pattern.

As the aforementioned ERP studies did not analyse similarities between ERPs elicited in the study and test phases (but see Khader et al., 2005 for a different approach), inferences on the reinstatement of study information and how this may be reflected in the test phase ERPs can only be indirect. For example, some of the data reviewed so far have been accounted for by differential conceptual-semantic processing demands in the test phases (Hornberger et al., 2004). To illustrate this view, in the studies by Herron and Rugg (2003) and Hornberger et al. (2004) the ERP correlates of retrieval orientation were characterized by more negative going ERPs (resembling the N400 component) to sought-after materials which are dissimilar to the retrieval cue. It was proposed that in cases of low cue–target overlap, it is efficient to constrain cue processing to those features of the retrieval cues that are selectively shared by the sought-after memory representation. In the aforementioned studies, in which words were used as cues and pictures as target materials, the only shared attributes would be on the conceptual-semantic level. The enhanced N400-like

negativity to the cues would in turn reflect the enhanced conceptual-semantic processing demands in case of low cue–target similarity (Hornberger et al., 2004).

This latter account, however, is limited to situations in which study items and retrieval cues are very dissimilar and concordance can only be established on the conceptual level. It cannot explain ERP effects of retrieval cue processing in situations in which constraining cue processing to the conceptual-semantic level is not beneficial for memory retrieval. For example in the Werkle-Bergner et al. (2005) study, in which words were used as test cues and the target material was either the word itself or the word matching in character type, conceptual features of the target are not at all diagnostic. The same holds for two other ERP studies on retrieval orientation: Ranganath and Paller (1999) used pictures as retrieval cues and the target information either entailed perceptually detailed information or not. In the Dzulkipli and Wilding (2005) study, the sought-after information was the task performed at study. In these situations, other mechanisms that support the selective processing of retrieval cues in order to maximize cue–target overlap must be initiated. One possible mechanism could be the maintenance of the cue features in working memory. This in turn would make these features available for the search for matching memory representations. Three of the aforementioned studies (Werkle-Bergner et al., 2005; Benoit et al., 2009; Ranganath and Paller, 1999) found extended positive slow wave activity over frontal recording sites when the task requires the retrieval of perceptually detailed information. It is possible that these ERP effects reflect working memory processes set in train for the maintenance and specification of the features of the test cue (see Ranganath and Paller, 1999, for similar arguments).

The different instances of selective retrieval processing are illustrated in Fig. 3. An ensemble of processes are initiated before and after the presentation of a retrieval cue in pursuit of successful remembering. They can broadly be divided into two classes, cue bias and target bias. As outlined above, according to Anderson and Bjork (1994) cue bias refers to an ensemble of processes which are applied to the internal representations of the retrieval cue in order to optimize the cue–memory trace interaction. In more detail, they

increase the cue–target overlap by constraining, specifying, or maintaining task dependent cue representations.

While cue-bias strategies, presuppose the consecutive execution of several retrieval attempts, another form of selective retrieval processing, i.e., target bias in the Anderson and Bjork (1994) terminology can be initiated even by one single trial. It is anticipatory in nature, i.e., it can be established upstream to the recovery of information from memory on the basis of a preparatory cue alone. In the task cue interval, target bias is associated with positive ERP slow waves at posterior recording sites. This ERP effect is most pronounced under inconsistent retrieval demands and covaries with the processing costs that arise from switching from one retrieval task to the other.

From a functional point of view this form of retrieval processing operates directly on memory (target) representation and serves to increase the accessibility of these representations even before a retrieval cue is presented. This target-bias mechanisms, by analogy, is similar to selective attention. As in selective attention situations for external events, it allows to shift attention to internal mnemonic representations (Anderson and Bjork, 1994; see also Cabeza et al., 2008, for similar arguments). By this, they assist in memory retrieval by enhancing the activation and accessibility of some parts of memory and by decreasing the activation of memory competitors.

4. The other side of the coin: the control of unwanted memories

Besides the recovery of previous memories, another important aspect of controlled memory retrieval concerns the control of unwanted and task-inappropriate memory. The main function of controlled memory retrieval, the guidance of the interaction between a retrieval cue and memory representations in pursuit of task-appropriate remembering implies that these processes should also be initiated in the service of suppressing irrelevant memories.

A paradigmatic case of suppressing task-inappropriate memories is retrieval-induced forgetting. It describes the interesting phenomenon, that practicing the retrieval of one part of learned materials impairs the memory for unpracticed materials, relative to a control condition for which no retrieval practice occurs. An illustrative example is a task in which participants learn lists of category–exemplar pairs (fruit–orange, drink–scotch, fruit–banana). Then they practice the retrieval of half of the exemplars in a cued stem recall test (fruit–or_____). In a final cued recall test they are encouraged to recall all exemplars upon presentation of the category names as cues. Recall of unpracticed materials from a practiced category (banana) is impaired relative to unpracticed baseline items (scotch). Retrieval-induced forgetting has been attributed to (inhibitory) control mechanisms which are initiated in situations in which a retrieval cue (fruit) is associated with several target memories (orange, banana, apple, etc.) (Anderson, 2005; Bäuml et al., 2005). Thus, successful retrieval practice entails strengthening the cue–target association for the practiced materials and also (as revealed by the below-baseline performance of unpracticed materials) inhibiting the association between the cue and unpracticed materials. This constitutes a typical target-bias situation as the decreased activation of non-practiced exemplars arises from an activity reducing control mechanism that operates directly on memory representations.

The control mechanisms mediating retrieval-induced forgetting to a large extent have been indirectly inferred from behavioral data, i.e., memory performance following retrieval practice phases. To directly examine the putative control mechanisms while they operate, we set out to examine ERP correlates of retrieval processing in the retrieval practice phase

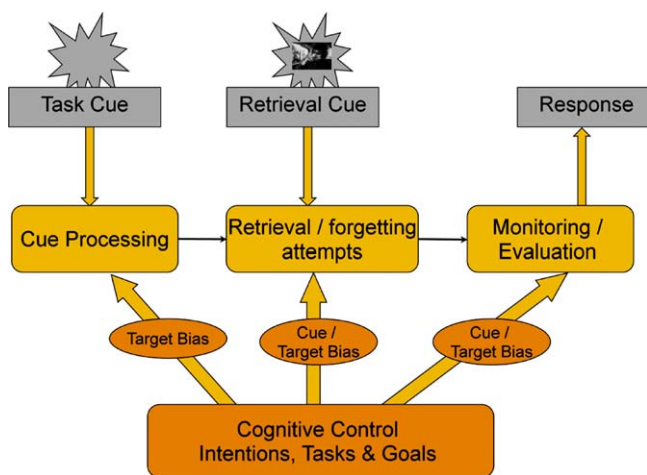


Fig. 3. Diagram illustrating the different instances of selective retrieval processing. Processes initiated by a task cue are preparatory in nature and modulate the accessibility of a memory trace before information is recovered from memory. The processes initiated by the retrieval cue are applied to the internal representation of the retrieval cue and serve to optimize the cue–memory trace interaction or take the form of monitoring and evaluating the outcome of the retrieval process. While cue-bias strategies are characteristic for retrieval cue processing, target-bias strategies that modulate the accessibility of memory traces can be employed prior to retrieval cue presentation or, thereafter, i.e., in the service of enhancing relevant or suppressing irrelevant memories or monitoring the output of retrieval (for further details see text).

(Johansson et al., 2007). We assumed that any ERP effect of retrieval-induced forgetting should be set in train by the practice cues in the retrieval practice phase and should be systematically related to the amount of forgetting of non-practiced materials. A standard retrieval-induced forgetting paradigm was used, and ERPs were recorded in an intermediate phase in-between the study and final recall phase. In this phase, participants performed two different tasks. They either practiced the retrieval of the category exemplars of a prior learning phase, or, in a second (baseline) condition, the category exemplars were represented for relearning. As expected, memory performance for non-practiced materials was lower following retrieval practice as compared to the relearning condition. Conversely, for practiced materials no influence of the kind of reprocessing in the intermediate phase (relearning vs. retrieval practice) was obtained. The ERPs elicited by cues in the relearning and retrieval practice condition are illustrated in Fig. 4.

Pronounced differences emerged at frontal and anterior-frontal recordings which took the form of more pronounced positive slow wave activity in the retrieval practice than in the relearning condition. To examine whether this slow wave activity to practiced materials is related to the subsequent forgetting of non-practiced materials, we calculated a forgetting index (relearning minus retrieval for non-practiced materials). Next, the frontal and anterior-frontal slow wave activity in the relearning and retrieval condition were subjected to a stepwise regression analysis with the forgetting index as dependent variable. Notably, the frontal slow wave in the retrieval condition accounted for 33% of the variance in later forgetting. This result suggests that the processes reflected in the anterior slow wave to practiced materials directly operate on the memory representations of non-practiced material which, in turn, show higher forgetting than in the control condition. These processes subserve the control of competing memory traces and – as revealed by the aforementioned regression analysis – decrease the accessibility of the non-practiced materials in pursuit of successful retrieval of the practiced items.

The anterior-frontal slow wave, obtained in the Johansson et al. (2007) study, is somewhat reminiscent of the slow waves reported by Werkle-Bergner et al. (2005) and Johnson and Rugg (2006) in situations of alternating retrieval demands. In fact, in all three studies, slow wave activity is largest at anterior-frontal recordings, starts between 200 and 400 ms after stimulus onset, and lasts for several 100 ms. On the basis of these commonalities, it is tempting to speculate that this anterior-frontal slow wave pattern in all three studies reflects common mechanisms of control that are set

in train to flexibly regulate the accessibility of competing memory traces in the service of successful memory performance.

An objection against the equation of controlled memory retrieval in explicit memory tasks and in retrieval-induced forgetting could be that in the former case there is the explicit goal to remember. Conversely, retrieval-induced forgetting is a by-product of retrieving other materials and by this non-intentional. By this view, retrieval-induced forgetting, due to its unintentional character, would not require cognitive control (see Anderson, 2005, for a discussion of the goal vs. control issue). From this, it follows that retrieval-induced forgetting and controlled memory retrieval should not have mechanisms in common and any ERP correlates of retrieval practice in the retrieval-induced forgetting paradigm cannot reflect functionally similar control mechanisms as those observed in explicit memory tasks. A way to solve this issue is to examine ERP correlates of forgetting in situations in which the putative control process is initiated by a “forget” instruction itself, rather than by the successful retrieval of other materials.

An experimental paradigm in which forgetting constitutes the explicit goal of the individual is directed forgetting. In this paradigm, participants are given instructions to forget learned items either on the item level or on the list level (Golding and MacLeod, 1998). Recall deficits for items that were associated with a forget instruction are thought to reflect selective rehearsal of the to-be-studied words (Anderson, 2005; Ullsperger et al., 2000). The results of directed forgetting studies, however, are sometimes difficult to interpret, as multiple causes, such as retroactive interference or shallow encoding for recall deficits for forget-items, exist. Another way to probe intentional forgetting of unwanted memories is the think/no-think paradigm (Anderson and Green, 2001). In a typical task, subjects study weakly related word pairs and are then trained to retrieve the second word upon presentation of the first word as cue. Next, they enter the think/no-think condition, which requires them to exert control over memory retrieval. In think trials, they are presented with the first word and are required to recall and say aloud the second words, as before. In no-think trials, however, they are instructed to neither recall the word nor to think about this word. By this, they have to stop not only the vocal response but also the act of retrieval. The think/no-think instruction is repeated for several times. The critical test for intentional forgetting is a subsequent cued recall test in which subjects are given cue words and are asked to give the correct response to each. The main finding of Anderson and Green (2001) was that memory declined for no-think words below the level of words that were not represented at all in the think/no-think phase.

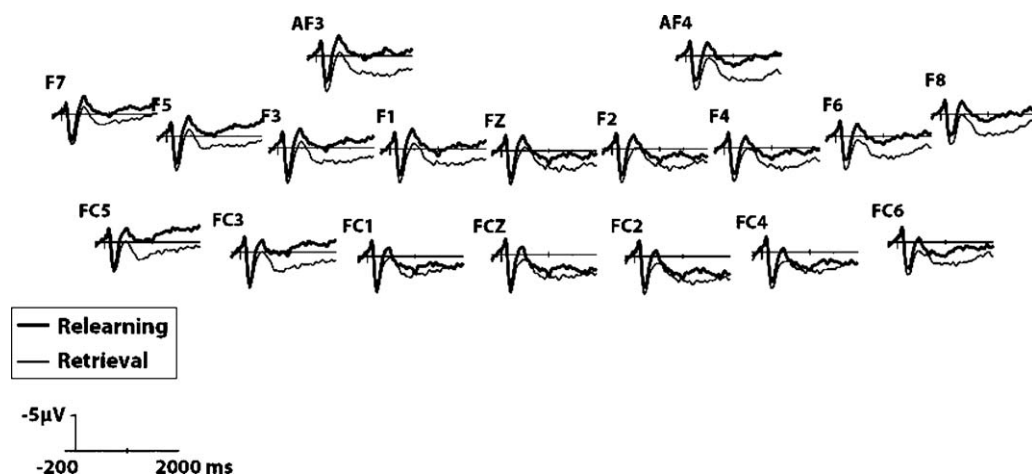


Fig. 4. ERPs at anterior frontal, frontal and fronto-central recording sites elicited by the cues in the retrieval practice and the relearning phase in the study by Johansson et al. (2007).

This finding suggests that control mechanisms are voluntarily recruited to prevent unwanted memories to come to mind. We were interested in whether intentional forgetting, as operationalized in the think/no-think paradigm, has mechanisms in common with other situations requiring cognitive control of memory retrieval. This would be another instance of a target-bias strategy as intentional forgetting should result from an activity reducing control mechanism that directly operates on non-relevant memory representations.

In this study, the think/no-think paradigm was adapted to the needs of an ERP study. (Mecklinger et al., 2009) Participants learned word pairs up to a criterion of 66% correct recall of the second word. Then they entered the think/no-think condition, in which each word was repeated 16 times with either a think or a no-think instruction, as indicated by color cues. ERPs were recorded in this phase of the experiment. Memory performance in the final cued recall test, in which the first words of the study pairs were used as retrieval cues, was above 90%. While recall was better for words from the think phase than from the baseline condition, no behavioral effects of forgetting were obtained, i.e., recall of words from the prior no-think phase did not fall below the baseline condition. Notably, several studies failed to find below-baseline performance for no-think items, even when exactly the same experimental procedures as in the Anderson and Green (2001) study were applied. This suggests that forgetting effects are not a robust phenomenon but are prone to processing strategies and also modulated by individual differences (see Bulevich et al., 2006, for a discussion).

The ERPs recorded in the think/no-think phase (collapsed across all 16 repetitions of each trial type) are illustrated in Fig. 5.

The ERP waveforms in both conditions start to differ at around 150 ms after onset of the retrieval cue. These effects were characterized by an enhanced P2 to think trials, presumably reflecting enhanced attentional processing elicited by the color cue in the think condition (see also Bergström et al., 2007). This effect was followed by a prominent negativity (N2) to no-think trials that peaked around 400 ms. Notably, negativities of similar kinds are usually found in motor stopping tasks where they have been identified with the ability to stop prepotent motor responses (Kok et al., 2004). This implies that similar mechanisms are involved in stopping memory retrieval and motor stopping (see Mecklinger et al., 2009 for a more extended discussion). At parietal recording sites, the N2 was followed by a pronounced positivity, which was larger for think than for no-think trials. Former studies have identified parietal positivities with similar temporal characteristics with recollection-based remembering (i.e., the parietal old/new effect, see Friedman and Johnson, 2000, for a review). Our findings thus suggest that the parietal positivity is not only sensitive to retrieval success but also modulated by mere attempts to avoid memory retrieval (as operationalized by the no-think condition). A final ERP correlate of differential cue processing was obtained at frontal and anterior frontal recording sites. It was characterized by larger positive slow wave activity in the no-think condition. Notably, even though the latter effect was present for about 300 ms and by this phasic in nature, it is somehow similar to the anterior-frontal positive slow wave elicited by retrieval of practiced materials in the Johansson et al. (2007) study. By this, it is tempting to speculate that both ERP effects reflect common mechanisms in the service of intentional forgetting (no-think trials) and in the service of retrieving materials in light of memory competitors (retrieval practice). It is conceivable that these mechanisms are directly involved in the regulation of competing memory traces, i.e., reducing the accessibility of task-inappropriate memory representations in no-think trials and for non-practiced materials in the retrieval practice phase.

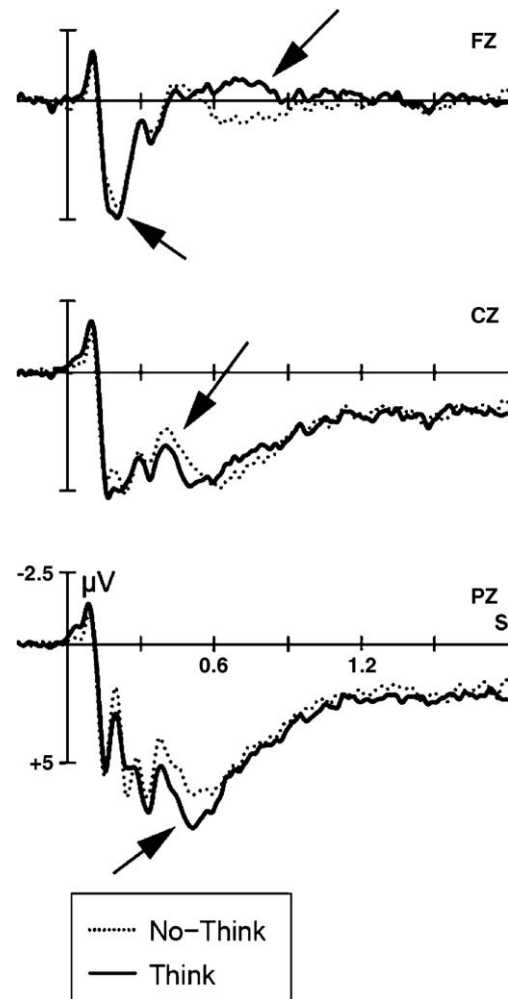


Fig. 5. ERPs elicited by think and no-think trials in the think/no-think phase at three midline recording sites in the intentional forgetting study reported by Mecklinger et al. (2009).

Taken together, the aforementioned results support two main conclusions: first, common mechanisms of selective retrieval processing are initiated in the service of successful remembering and the suppression of unwanted memories. Second, controlled memory retrieval is initiated in response to retrieval cues, irrespective of whether the suppression of unwanted memories is the intentional goal or is rather a by-product of the intention to retrieve other materials. Even though, the retrieval-induced forgetting paradigm does not entail the explicit goal to forget, increasing the accessibility of practiced materials seems to require the control of competing materials. The aforementioned studies suggest that retrieval-induced forgetting and intentional forgetting share similar control mechanisms and anterior frontal slow wave correlates.

5. Functional neuroanatomy of controlled memory retrieval

This review so far has discussed controlled memory retrieval, i.e., processes initiated either before or after the presentation of a retrieval cue, that optimize the internal representation of the cue or directly operate on memory representation and, in turn, modulate their accessibility in the service of current goals and task demands. This selective retrieval processing entails on the neural level the binding and unbinding of fragments of long-term stored information. Examples are the binding of items and their contextual features in a prior study episode, the separation

between features bound to an episode and features that constitute an entry in semantic memory or the binding of features from a study and a test phase in order to optimize the reinstatement of study phase information. These aspects of selective retrieval processing can reliably be monitored by ERPs to items with no study history in the test phase of recognition memory tasks. From a functional point of view, it has been proposed that these ERP effects reflect operations that maximize the overlap between processes engaged at encoding and retrieval (Rugg et al., 2002). The ensemble of mechanisms that support controlled memory retrieval can be subdivided in two classes, according to a taxonomy proposed by Anderson and Bjork (1994). Cue-bias strategies, i.e., processes that maximize the cue–target overlap by constraining, specifying, or maintaining task depended cue representations, and target-bias strategies, processes that directly act on memory representations and influence their accessibility. Target-bias strategies are suitable not only for increasing the accessibility of relevant memory representations, they also play a crucial role in reducing the activity of non-relevant memory representations in the service of intentional forgetting.

A final issue concerns the brain systems that mediate controlled memory retrieval. A large body of literature suggests that controlled memory retrieval is realized by interactions between the MTL memory system and the PFC (see Simons and Spiers, 2003, for a review). According to this view, the PFC continuously monitors memory-related activity in the MTL. It houses an ensemble of control mechanisms that allow the specification and maintenance of retrieval cues, the search through memory, and the seeking of concordance between the cue and memory representations. This PFC–MTL interaction, in turn, modifies memory-related MTL activity and modulates its accessibility in future situations. In this framework, a division of labor in the PFC has been proposed, with ventro-lateral PFC regions being critical for cue specification and the maintenance of cue and target information, and the dorso-lateral PFC being involved in comparing cue and target information and in elaborating and monitoring the outcome of this comparison. Additionally, it has been suggested that anterior PFC regions are recruited by complex retrieval situations, e.g., operations that act on internally generated information, while medial or orbital PFC regions are engaged by the retrieval of reward-related or autobiographical memories (Simons, 2009). The PFC–MTL interaction view of controlled memory retrieval is substantiated not only by a large body of neuropsychological and brain imaging studies. It also receives support by neuroanatomical considerations. There are, for example, strong reciprocal connections between both brain regions some of which passing through the unicate fascicle, a small fiber bundle connecting ventral PFC and anterior MTL regions, lesion to which selectively impair recollection and autobiographical memories (Levine et al., 1998).

The PFC–MTL interaction view has recently been challenged by brain imaging studies showing consistent memory-related activation in the posterior parietal cortex (PPC). A review of the large literature on memory and the PPC is beyond the scope of this article (for reviews see Wagner et al., 2005; Cabeza et al., 2008). However, two illustrative studies showed that the lateral PPC (left inferior parietal cortex) is sensitive to “perceived oldness”, i.e., it shows stronger activation for items classified as “old” irrespective of memory status (hits and false alarms) than for items classified as new (correct rejections and misses) (Kahn et al., 2004; Wheeler and Buckner, 2003). Conversely, medial PPC regions (the precuneus extending into retrosplenial cortex) were shown to be sensitive to retrieval success, i.e., they showed larger activation for hits than for correct rejections (see Wagner et al., 2005, for an overview; Von Zerssen et al., 2001). Interestingly, lateral PPC regions seem to be sensitive to a special form of selective retrieval processing. They showed greater activation when a retrieval

orientation for the recollection of contextual information from a study episode was initiated and maintained (Dobbins et al., 2002). These recollective-orienting effects generalize to different forms of contextual (perceptual vs. conceptual) episodic details (Dobbins and Wagner, 2005) and were present irrespective of whether the source decisions were correct or incorrect.

These findings suggest that the PPC, similar to the PFC, is critically involved in differential retrieval processing. Consistent with the important role of the PPC for externally and internally driven attention (Corbetta and Shulman, 2002), it has been proposed that the PPC is associated with the shifting of attention to mnemonic representations (Cabeza et al., 2008) and/or the maintenance of attention on bound item–context representations (Johansson and Mecklinger, 2003). The allocation of attention to memory representations directly enhances their accessibility and is of high relevance when memory decisions are difficult (as for example the recovery of episode details) or when a target memory is not directly elicited by a retrieval cue. By this, the attention to internal representations view bears similarities with target-bias strategy as proposed by Anderson and Bjork (1994).

The attention to internal representations account for the PPC also receives some indirect support by recent ERP recognition memory studies. There is converging evidence from an increasing number of ERP studies that negative slow wave activity over posterior brain regions, observable at around the time memory decisions are given (i.e., the Late Posterior Negativity, LPN), reflects the binding of study items with their contextual attributes and the allocation of attention to task-relevant memory representations (see Johansson and Mecklinger, 2003, for a recent review; Friedman et al., 2005). According to this view the LPN reflects (attentional) mechanisms that allow to recover item–context associations when such information is not readily available and, in turn, the accessibility of stored information has to be enhanced. Consistent with this account, the LPN has been found to be more pronounced in associative memory task than in item memory tasks, is elicited by successful and unsuccessful source retrieval, and is also sensitive to the amount of source-specifying attributes that can be recovered to guide memory decisions (Mecklinger et al., 2007). Though scalp recorded ERP components do not allow strong inferences on their underlying neural generators, on the basis of the functional resemblance of the LPN and the aforementioned PPC effects in brain imaging data, it is tempting to speculate that the LPN reflects mnemonic functions of the PPC.

Taken together, there is increasing evidence that the PPC in close collaboration with the PFC and the MTL, contributes in important ways to controlled memory retrieval. While the MTL is critically involved in the generation of memories guided by external and internal cues, the PFC provides top-down control by continuously modifying and elaborating MTL activations. The main role of the PPC seems to be the orientation and shifting of attention towards mnemonic information in situations in which target memories are not automatically elicited by a retrieval cue. The high relevance of the dorsal PPC for attention to memory has also been accentuated in a recent model of Cabeza et al. (2008). Consistent with the present model, they assume that the dorsal PPC in episodic retrieval plays a similar role as in top-down attention, namely the allocation of attentional resources according to goals and task demands. Corbetta and Shulman (2002). In addition they propose that the ventral PPC is critical for stimulus driven (bottom up) attention to internal information (as for example in involuntary remembering in response to an appropriate cue), even though the Cabeza et al. (2008) model can account for a large number of neuropsychological and neuroimaging findings, including the different contribution of dorsal and ventral PPC regions to memory retrieval, differential retrieval processing

for familiarity and recollection, mnemonic consequences of PFC lesions, its major limitation is that it contains only vague assumptions on the division of labor between PFC and PPC during controlled memory retrieval.

What might be the functional relation between the PFC and PPC in controlled memory retrieval? Both regions are highly interconnected and by this, may be commonly involved in setting up and maintaining retrieval goals. Their interaction is highly relevant for binding together those parts of long-term memory that comprise an event and the current situational context by which retrieval goals are set. Specifying the neural binding mechanism underlying selective retrieval processing in detail is beyond the scope of this review. However, it has been proposed that interactive binding mechanisms are of high relevance when top-down, goal-relevant signals have to be bound with bottom up memory signals (see Murre et al., 2006 for a comprehensive of neural binding mechanism).

Most brain imaging studies found coactivations of lateral PFC and PPC regions in situations that require selective retrieval processing, though most studies solely focus on PFC activation. The PFC might be more involved in action-related control mechanisms, like updating retrieval goals, cue specification, and action selection among competing alternatives. In light of the important role of the PFC in managing overt behavior (Miller and Cohen, 2001), memory retrieval can be considered as an internal action that requires similar control mechanisms as external actions. An illustrative example for the functional similarities between the control of action and the control of memory is given by a situation in which a retrieval cue activates several memories and we can selectively recollect the event we are seeking despite competing memories. This is functionally equivalent to a situation in which the features of an external event (e.g., a color word written in a non-matching ink color as in Stroop tasks) activate several motor responses and only the task-appropriate one is selected. In this framework it is possible, that the ERP slow wave activity over frontal brain regions elicited by unstudied items in a variety of memory tasks, that has been identified with cue specification and maintenance of cue features, reflects mechanisms in pursuit of the action selection requirements of the PFC.

Conversely, the PPC might be critically involved in directly modulating the accessibility of memory representations by focusing attention on task-relevant information and making this information more salient for action selection mechanisms housed by the PFC. These attentional mechanisms bear similarities to those operating on external events and are recruited when memory retrieval and decisions are effortful and target memories cannot directly be retrieved. Notably, these attention selection mechanisms can be anticipatory in nature, i.e., they can be initiated even without overt response selection requirements. This view is tentatively supported by the above reviewed ERP findings (Johnson and Rugg, 2006; Mecklinger et al., 2005), showing enhanced slow wave activity over posterior recording sites prior to the presentation of a retrieval cue.

In sum, this selective review summarized empirical evidence showing that ERP slow waves are highly sensitive to the initiation and maintenance of retrieval orientations. It illustrates that these mechanisms can be grouped into two classes; those that enhance retrieval cue processing and those that directly act on memory representations and modulate their accessibility. From a brain systems point of view, the former class of processes reflects selection mechanisms for internal actions and rely on the integrity of the PFC, whereas the second class of processes can be identified with selective attention mechanisms for which the PPC plays an important role. Not much is known so far on the nature of the interactions between the PFC, the PPC, and the MTL, by which long-term stored item and context features are

bound together and made available for current task demands. The view that the PFC mediates the selection of internal (memory) actions whereas the PPC is more engaged in preparing and allocating attention to mnemonic representations as outlined in the present paper may act as a working model and will await further empirical validation. In any case, understanding how exactly attention mechanisms in the PPC change representations in MTL memory systems and how, in turn, this MTL-PPC interplay is modulated by goal oriented activity in the PFC remains an important endeavor for future neurocognitive memory research.

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