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From Cue to Recall

The Temporal Dynamics of Long-Term Memory Retrieval

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Abstract

A fundamental function of long-term memory is the ability to retrieve a specific memory when encountering a retrieval cue. The purpose of this dissertation was to further our understanding of such cued recall by investigating the temporal dynamics from the presentation of the retrieval cue until the target memory is recalled. Retrieval cues are often related with several memories. When such a retrieval cue is presented, the associated memories will compete for retrieval and this retrieval competition needs to be handled in order to retrieve the sought after target memory. Study 1 and Study 2 investigated the temporal dynamics of such *competitive semantic* cued recall. Interestingly, previous research has shown that the ability to retrieve the currently relevant target memory comes with a cost, namely retrieval-induced forgetting of the competing memories. These studies also investigated the role of competitor activation and target retrieval in this forgetting phenomenon. Study 1 investigated the electrophysiological correlates of reactivation of competing currently irrelevant memories and the role of such competitor activation in retrieval-induced forgetting. Competitor activation was related to an FN400 event-related potential (ERP) effect and this effect predicted increased levels of retrieval-induced forgetting, indicating that this forgetting effect is dependent on competitor activation. Study 2 examined processes involved in target retrieval in a similar competitive semantic cued recall task. The main finding in this study was that attempts to retrieve the target memory were related to a late posterior negativity ERP effect. Another important finding was that behavioural and ERP measures of target retrieval were unrelated to retrieval-induced forgetting. Retrieval cues can sometimes elicit involuntary retrieval of unwanted memories. Such memory intrusions are a core symptom of post-traumatic stress disorder. Study 3 investigated the temporal dynamics of such memory intrusions. One of the key findings was that memory intrusions were related to a negative slow wave ERP effect possibly reflecting the activation of the intruding memory in working memory. Taken together the findings in the dissertation indicate that cued recall involves several cognitive processes ranging from early automatic memory reactivation to conscious processes such as working memory activation and recollection. The findings have implications for cognitive theories of memory and have relevance for several clinical conditions including depression and post-traumatic stress disorder.

Key words Cued recall, long-term memory, ERP, retrieval-induced forgetting, Think/No-Think, memory intrusions

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Abstract

A fundamental function of long-term memory is the ability to retrieve a specific memory when encountering a retrieval cue. The purpose of this dissertation was to further our understanding of such cued recall by investigating the temporal dynamics from the presentation of the retrieval cue until the target memory is recalled. Retrieval cues are often related with several memories. When such a retrieval cue is presented, the associated memories will compete for retrieval and this retrieval competition needs to be handled in order to retrieve the sought after target memory. Study 1 and Study 2 investigated the temporal dynamics of such *competitive semantic* cued recall. Interestingly, previous research has shown that the ability to retrieve the currently relevant target memory comes with a cost, namely retrieval-induced forgetting of the competing memories. These studies also investigated the role of competitor activation and target retrieval in this forgetting phenomenon.

Study 1 investigated the electrophysiological correlates of reactivation of competing currently irrelevant memories and the role of such competitor activation in retrieval-induced forgetting. Competitor activation was related to an FN400 event-related potential (ERP) effect and this effect predicted increased levels of retrieval-induced forgetting, indicating that this forgetting effect is dependent on competitor activation.

Study 2 examined processes involved in target retrieval in a similar competitive semantic cued recall task. The main finding in this study was that attempts to retrieve the target memory were related to a late posterior negativity ERP effect. Another important finding was that behavioural and ERP measures of target retrieval were unrelated to retrieval-induced forgetting.

Retrieval cues can sometimes elicit involuntary retrieval of unwanted memories. Such memory intrusions are a core symptom of post-traumatic stress disorder. Study 3 investigated the temporal dynamics of such memory intrusions. One of the key findings was that memory intrusions were related to a negative slow wave ERP effect possibly reflecting the activation of the intruding memory in working memory.

Taken together the findings in the dissertation indicate that cued recall involves several cognitive processes ranging from early automatic memory reactivation to conscious processes such as working memory activation and recollection. The findings have implications for cognitive theories of memory and have relevance for several clinical conditions including depression and post-traumatic stress disorder.

Populärvetenskaplig sammanfattning på svenska

Från ledtråd till framplockning: temporal dynamik vid framplockning från långtidsminnet

En av de mest fundamentala funktionerna för vårt långtidsminne är funktionen att kunna plocka fram ett specifikt minne när vi stöter på en ledtråd som är relaterad till detta minne. Ett vardagsexempel på sådan ledtrådsstödd långtidsminnesframplockning är om en vän frågar dig hur långt ett maraton är (en ledtråd som sökningen i långtidsminnet kan baseras på) och du lyckas plocka fram att ett maraton är 42195 meter långt. Syftet med den här avhandlingen var att undersöka den temporala dynamiken vid ledtrådstödd framplockning ur långtidsminnet, från presentationen av ledtråden till dess att minnet är framplockat. Eftersom deltagarna i studierna inte är medvetna om alla processer som är involverade vid minnesframplockning, så är det nödvändigt att mäta deras hjärnaktivitet för att kunna undersöka tidsförloppet vid minnesframplockning. I samtliga studier i den här avhandlingen mättes deltagarnas hjärnaktivitet med en metod som kallas för elektroencefalografi som något förenklat innebär att hjärnaktivitet mäts med hjälp av elektroder som appliceras på deltagarnas skalp/hårbotten. När denna metod mäter hjärnaktivitet tidslåst till en viss händelse kallas den för händelserelaterade potentialer som förkortas som ERP på engelska.

Ledtrådar är ofta relaterade med flera ledtrådar. Om någon till exempel frågar dig om vad du fick i julklapp av din mamma förra julen kan minnen av vad du fick i julklappar av andra släktingar samma år samt minnen av vad du fick i julklapp av din mamma tidigare år aktiveras. Dessa minnen tävlar då om framplockning och för att kunna plocka fram att du fick strumpor i julklapp av din mamma den här julen behöver du kunna hantera tävlan från andra irrelevanta minnen. Tidigare forskning har visat att framplockning av det eftersökta minnet (strumporna) kommer med en kostnad, nämligen glömska av de tävlande minnena. Detta fenomen kallas för framplockningsinducerad glömska.

Den första studien i den här avhandlingen studerade aktivering av tävlande minnen vid ledtrådsstödd minnesframplockning och vilken roll aktivering av tävlande minnen spelar i framplockningsinducerad glömska. Huvudfyndet i den studien var att en

ERP-effekt som kallas för FN400 var relaterad till aktivering av tävlande minnen. Denna ERP-effekt var även relaterad till senare glömska av de dessa minnen. Ju större FN400-effekt desto fler tävlande minnen glömde deltagarna. Detta resultat tyder på att aktivering av tävlande minnen är en förutsättning för framplockningsrelaterad glömska och är förenligt med den så kallade inhibitionsteorin av framplockningsinducerad glömska. Enligt denna teori rekryteras kognitiva kontrollmekanismer för att dämpa tillgängligheten till tävlande minnen för att på så sätt underlätta framplockning efter det relevanta minnet. Denna inhibition/dämpning leder till minskad tillgänglighet för de tävlande minnena, vilket i sin tur resulterar i att vi tillfälligt har svårt att plocka fram dessa minnen.

I Studie2 undersöktes istället processer relaterade till försök att plocka fram det relevanta eftersökta minnet. Målet med den här studien var att separera processer relaterade till framplockningsförsök och processer relaterade till framgångsrik framplockning av det eftersökta minnet. ERP resultaten visade att en sen negativering över posteriora elektroder (en så kallad LPN-effekt) var relaterad till misslyckade framplockningsförsök. I Studie 1 och 2 fick deltagarna en ledtråd som bestod av en kategori och en ordstam (till exempel Frukt – Ki___) och uppgiften gick ut på att plocka fram ett ord ur det semantiska långtidsminnet som passade in på ledtråden (Kiwi). LPN-effekten är sannolikt relaterad till generering av ord som passar in på ledtråden och/eller till att övervaka framplockningen och testa om framplockade ord passar in på ledtråden. Framgångsrik framplockning av det eftersökta minnet (Kiwi) var istället relaterad till en anterior positivering. Ett viktigt fynd i den här studien var att varken beteendemått eller ERP-mått på framplockning av det eftersökta minnet var relaterat till framplockningsinducerad glömska av tävlande minnen. Detta fynd tyder på att denna glömskeeffekt är oberoende av framplockning av det eftersökta minnet och är förenligt med inhibitionsteorin.

I den tredje och sista studien i avhandlingen undersöktes den temporala dynamiken vid ofrivillig minnesframplockning. Motiveringen till att göra denna studie var att ofrivillig minnesframplockning är vanligt i flera kliniska tillstånd som till exempel depression och post-traumatiskt stressyndrom. I denna studie fick deltagarna först memorera orelaterade ordpar (dinosaurie - stol). Sedan visades det vänstra ordet i grön eller röd färg. Om ordet visades i grönt skulle deltagarna tänka på det ord som de hade lärt sig att associera med det presenterade ordet. Om ordet visades i rött skulle deltagarna däremot försöka att inte tänka på ordet som de lärt sig att associera med det presenterade ordet. Efter varje uppgift fick deltagarna skatta i vilken utsträckning de hade tänkt på det associerade ordet i föregående uppgift. Vi använde dessa skattningar för att dela in ERP-datan från den röda uppgiften i lyckade försök att undvika att tänka på ordet och ofrivillig framplockning av ordet som de skulle undvika att tänka på. Ett av huvudfynden i den här studien var att ofrivillig framplockning var relaterat till en negativ ERP-effekt som var utsträckt i tiden. Denna effekt är sannolikt relaterad till aktivering av minnet som plockats fram ofrivilligt i arbetsminnet.

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Sammantaget belyser avhandlingen den temporala dynamiken från presentation av ledtråd till minnesframplockning. Resultaten tyder på att flera kognitiva processer är involverade i ledtrådsstödd framplockning ur långtidsminnet. Tidigt i tidsförloppet fann vi ERP effekter som är relaterade till riktning av visuell uppmärksamhet till ledtråden. Dessa processer följdes av automatisk aktivering av associerade minnen som i sin tur följdes av medvetna kontrollerade processer som arbetsminnesaktivering och framplockning av information från instuderingstillfället. Resultaten har relevans för kognitiva teorier om långtidsminnesframplockning och har relevans för kliniska tillstånd som till exempel post-traumatiskt stress syndrom.

List of Papers

I. Hellerstedt, R., & Johansson, M. (2014). Electrophysiological correlates of competitor activation predict retrieval-induced forgetting. *Cerebral Cortex, 24*(6), 1619-1629. doi: 10.1093/cercor/bht019

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II. Hellerstedt, R., & Johansson, M. (submitted). Competitive semantic memory retrieval: temporal dynamics revealed by event-related potentials.

III. Hellerstedt, R., Johansson M., & Anderson, M.C. (submitted). Tracking the intrusion of unwanted memories into awareness with event-related potentials.

Abbreviations

EEG	Electroencephalography
ERP	Event related potential
fMRI	Functional magnetic resonance imaging
FN400	Frontal negativity onsetting 400 milliseconds post stimulus onset
LPN	Late posterior negativity
LPP	Late parietal positivity
MS	Milliseconds
MVPA	Multivariate pattern analysis
N2	Event related potential component (the second negative peak)
NSW	Negative slow wave
P3	Event related potential component (the third positive peak)
PET	Positron emission tomography
PSW	Positive slow wave
PTSD	Post-traumatic stress disorder

Introduction

Long-term memory enables us to encode, store, and retrieve information over time (Tulving, 2000). It is fundamental for human cognition and a prerequisite for learning. Long-term memory also defines who we are. Without access to the experiences that we have encoded cumulatively during our lives we would not be the same persons as we are today. Furthermore, long-term memory enables us to understand our immediate surrounding in the present and makes it possible to predict the future. In this way, long-term memory guides our behaviour. Long-term memory is so fundamental to our everyday life functioning that we take it for granted and often do not even notice it. The most common situation when we notice our long-term memory is ironically when we fail to retrieve something. We have all experienced how frustrating it can be to know that we know something and still be unable to retrieve it. In order to explain why long-term memory retrieval sometimes fails it is necessary to investigate the neurocognitive processes that underlie this phenomenon.

The purpose of this dissertation was to further our knowledge of the temporal dynamics of long-term memory retrieval. More specifically, the purpose was to investigate the time course of a particular kind of long-term memory retrieval called cued recall. Cued recall refers to retrieval of a specific memory trace that is associated with a given cue. The cue can either be external and perceived perceptually or internally generated. An example of cued recall in everyday life is if someone asks you about the name of the jazz piano player that is famous for his Köln concert and you correctly recall that his name is Keith Jarrett.

A challenge that researchers interested in cognitive processes face is that being able to perform a certain cognitive behaviour like long-term memory retrieval is not the same thing as being able to tell *how* to perform this behaviour. When examining the neurocognitive processes involved in cued recall it is consequently not possible to simply ask the participants about *what* neurocognitive processes they utilize to perform the long-term retrieval or *when* they recruit these processes. Instead it is necessary to measure the participants' brain activity to investigate this question. In order to examine the *temporal dynamics* of cued recall it is necessary to employ a method with a high temporal resolution. The method that was used in this dissertation, electroencephalography, can measure brain activity with a time resolution of down to one millisecond (ms) and is hence a well suited method for this research question.

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There are several different kinds of memories that are stored in separate memory systems (Squire, 1992). This dissertation focused on declarative memories, i.e. memories that we can verbalize and that we have conscious access to. Declarative memory can be divided into episodic and semantic memories (Tulving, 1972). Episodic memories are memories for life events and are tied to a specific time and place (e.g. the memory of presenting a poster at a conference on a memory conference in Dubrovnik in 2012). Semantic memories are memories that are not bound to a specific time or place, like for example facts and vocabulary. Study 1 and 2 investigated semantic cued recall. This kind of retrieval is important for everyday life functioning, but the temporal dynamics of it has only been studied in a few studies (e.g. Cansino, Ruiz, & López-Alonso, 1999; Rass, Landau, Curran, & Leynes, 2010). Study 3 investigated the temporal dynamics of intrusion of unwanted memories into awareness.

Each of the three studies of this dissertation aimed to examine an aspect of the temporal dynamics of cued recall that had not been studied before. The aim of Study 1 was to investigate competitor reactivation during retrieval competition. Study 2, aimed at isolating processes related to retrieval attempts and retrieval success during semantic cued recall. Finally, Study 3 aimed to elucidate the time course of involuntary memory retrieval. The motivation for examining the temporal dynamics of involuntary retrieval in this study was predominantly that such memory intrusions is a core symptom in post-traumatic stress disorder (PTSD; American Psychiatric Association, 2013) and common in several clinical conditions (e.g. Reynolds & Brewin, 1999).

A secondary purpose of this dissertation was to investigate one of the most long-standing questions in memory research, namely the question of why we forget. More specifically we aimed to investigate why retrieval can cause forgetting of related memories, a phenomenon referred to as retrieval-induced forgetting (M. C. Anderson, Bjork, & Bjork, 1994). Study 1 investigated the role of activation of competing memories in this phenomenon. This line of research was continued in Study 2, where we examined the relation between target retrieval and retrieval-induced forgetting. Previous studies have suggested that we can suppress memories that we do not want to think of (M. C. Anderson & Green, 2001; M. C. Anderson et al., 2004). Study 3, investigated the functional significance of memory intrusions in such suppression-induced forgetting (M. C. Anderson & Hanslmayr, 2014). These two forgetting phenomena will be described in more detail in chapter 2.

This introduction concludes with a description of the dissertation's outline. Research is often a cumulative process and this dissertation is no exception. The next chapter will set the stage by introducing the memory theories that the dissertation is based on. The following chapter introduces theories of forgetting. Forgetting measures were used to control that the tasks were competitive (Study1 and 2) and that the participants attempted to avoid retrieval (Study 3). The third chapter introduces the event related potential technique that was used in all three studies in the dissertation.

This chapter also contains a selective review of previous research on the temporal dynamics of memory retrieval using the event-related potential method. The fourth chapter describes the aims, the methods and the main finding in each of the three studies that were included in the dissertation. In the fifth and final chapter, I discuss and integrate the main findings from the three studies and suggest directions for future research.

1. Theories of Memory

Introduction

Before considering the temporal dynamics of long-term memory retrieval I am providing a brief introduction to relevant memory theories that this dissertation is based on. The purpose of this chapter is to position the dissertation within a theoretical framework and to define key concepts. This chapter will primarily focus on theories of long-term memory. I will however begin the chapter with a short introduction to theories of short-term memory and working memory, since these memory systems interact with long-term memory systems during retrieval. More specifically, the retrieval cue needs to be maintained in short-term/working memory while the participant search after the sought after memory representation in long-term memory. In addition, at the time of retrieval the long-term memory representation is activated in short-term/working memory as long as it is kept in awareness (Atkinson & Shiffrin, 1968; Baddeley, 2003; Cowan, 1999). Finally, when a memory representation has been retrieved from long-term memory it needs to be compared with the retrieval cue in working memory in order to decide whether the correct memory representation was retrieved or not.

Short-Term Memory and Working Memory

The temporal duration of storage is one way to classify memory systems. By employing this logic, memory has been divided into short-term and long-term memory systems. Short-term memory refers to storage over a few seconds whereas long-term memory refers to retention over longer time periods (Tulving, 2000). Apart from the difference in retention time, which is evident in the names of these two memory systems, they also differ in storage capacity. While short-term memory capacity is limited to a few items, the capacity of long-term memory is considered to be virtually unlimited. Short-term memory and working memory are two different concepts that refer to storage over short time periods. There are two main differences between these two concepts. The first difference is that short-term memory is considered to be a passive storage system whereas working memory not only stores information, but also manipulates this information if necessary (Baddeley & Hitch,

1974). One example of such manipulation is mental arithmetic. In order to subtract one digit from another it is necessary to maintain the digits in working memory while retrieving the rules of subtraction from long-term memory and performing the calculation. All these processes are dependent on working memory. Another difference is that short-term memory is considered to be a unitary system (Atkinson & Shiffrin, 1968) whereas working memory consists of several subsystems (e.g. Baddeley, 2003). One of the most influential models of working memory, consists of separate stores for verbal and spatial information as well as an episodic buffer for currently activated representations in long-term memory and a central executive system that executes manipulation of the information stored in the other systems (Baddeley, 2003). The model of working memory that is used the most in this dissertation is Cowan's embedded-processes model (Cowan, 1999). According to this model, working memory consists of three embedded processes: a long-term store, a short-term store and the focus of attention. The long-term store refers to all memory representations that are stored in long-term memory. A minority of these memory representations are currently activated in the short-term store. Importantly, this activation is not sufficient for a memory representation to enter awareness. In order for a memory representation to enter awareness the central executive must direct attention towards the activated memory representation, so that it becomes the focus of attention. The focus of attention process in Cowan's model consequently refers to the sub proportion of the activated memories in the short-term store that currently are in awareness. This model is especially relevant for Study 3 that investigated the intrusion of unwanted memories into awareness during involuntary long-term memory retrieval.

Long-Term Memory Systems

Memory researchers have tried to describe the organization of long-term memory by either dividing it into systems or into processes. System theories have divided memory into distinct systems based on the content of the stored information, levels of awareness and their neural basis. Process theories have instead divided memory into distinct processes based on the cognitive operations that are performed in a certain task. These two perspectives complement each other and both contribute to this dissertation's theoretical foundation.

One prominent system theory of long-term memory divides long-term memory into explicit and implicit memory (Schacter, 1987). Explicit memory denotes conscious retrieval of stored memory representations, whereas implicit memory refers to improved performance in a task (e.g. a word fragment completion task) due to prior perceptual experiences (e.g. exposure to words that complete the word fragments) in the absence of conscious recollection of stored memories.

An influential taxonomy of long-term memory was proposed by Squire and colleagues (Cohen & Squire, 1980; Squire, 1992). They categorized long-term memory into declarative and non-declarative memory. In principle, this distinction maps quite well onto Schacter's explicit/implicit distinction (Schacter, 1987). Declarative memory refers to memories that we can verbalize and that can be accessed via conscious retrieval. Memory of specific episodes from our lives (e.g. a concert that we went to last weekend) and specific facts (e.g. that Rome is the capital of Italy) are examples of declarative memories. This is undoubtedly what most people refer to when they use the word memory. Non-declarative memory on the other hand denotes various kinds of learning that are more difficult to verbalize and based on perceptual and motoric rather than cognitive processes that we do not have conscious access to. Habits, procedural skills, perceptual learning and reflexes are examples of such non-declarative memories. Research on patients with amnesia has provided support for the distinction between declarative and non-declarative memory systems, by showing that they can be dissociated. That is, injury to a specific brain region can lead to impairment in one of these systems while leaving the other system intact. The typical finding is that damage to the medial temporal lobes impairs declarative memory, but not non-declarative memory (Squire, 1992).

Tulving has further divided declarative memory into episodic and semantic memory (Tulving, 1972). Semantic memory refers to knowledge about the world. Examples of semantic memories are facts and vocabulary. Semantic memories are not associated with a specific life experience at a particular time and place. On the contrary, episodic memory refers to memories of personal experiences that are related with a specific time and place. Episodic retrieval allows us to mentally travel back in time to the encoding episode and re-experience it. Episodic memory is not only considered to be crucial for mental time travel back to the encoding episode, but also for imagining the future (Schacter, Addis, & Buckner, 2007; Tulving, 2002). The idea is that we use our previous experiences when we imagine possible future events. The association between episodic memory and future thinking has received support from neuropsychological studies showing that patients with damage to the medial temporal lobes both are impaired at recalling events from the past and in imagining the future (e.g. Tulving, 1985b). Moreover, neuroimaging studies has suggested that overlapping neural networks are involved in these two tasks (Schacter et al., 2007). In order to be able to retrieve information from episodic memory, Tulving proposed that it is necessary to enter a specific cognitive set, in which cues primarily are processed as probes of episodic memory. This cognitive set is referred to as retrieval mode (Tulving, 1985a). According to Tulving, episodic memory is a recently evolved memory system which is uniquely human and stems from semantic memory (Tulving, 2002). The idea that the ability to remember specific events and to plan for the future is unique for human has been questioned by recent research. It has for example been shown that scrub-jay birds can retrieve detailed information about where and when they caught a specific kind of food (Clayton, Bussey, & Dickinson,

2003). In addition, evidence have been provided that the scrub-jay birds can adjust their anticipated hunting behaviour based on this information, indicating that they can plan for the future (Clayton et al., 2003). Another example of future thinking in a non-human species comes from observational studies of captivated chimpanzees, reporting that these animals can plan attacks on future zoo visitors by collecting stones before the visitors arrive at the zoo (Osvath, 2009; Osvath & Karvonen, 2012). There is still an on-going debate regarding the uniqueness of human episodic memory and the comparison between species is complicated by the fact that other species have different language systems, since declarative memory is considered to be dependent upon language.

In summary, multiple distinctions have been suggested throughout the history of memory research to describe the organization of long-term memory. The present dissertation focused on declarative long-term memory. More specifically, Study 1 and Study 2 investigated semantic long-term memory retrieval whereas episodic long-term memory retrieval was investigated in Study 3.

Long-Term Memory Processes

Instead of organizing long-term memory into separate systems that stores different kinds of content, process theories divide long-term memory into several cognitive processes that are used to accomplish various memory tasks (e.g. Roediger, 1990). According to these theories, tasks that involve the same processes will recruit the same brain areas whereas tasks that are associated with different processes will recruit separate brain regions. Neuropsychological and neuroimaging data indicating that specific brain regions are engaged to perform a particular task (e.g. memory retrieval) independent of the content of the information that is involved in the process (e.g. auditory vs visual stimuli) have been interpreted as evidence for memory being divided into separate memory processes rather than into distinct memory systems. Tulving has defined the concept memory as the ability to encode, store and retrieve information over time (Tulving, 2000). These three processing stages are described below. Since retrieval is central for this dissertation, this process will be described in more detail.

Encoding

Encoding refers to acquiring new information and integrating this information in long-term memory. Early theories like the modal model theorized that the likelihood of encoding a stimulus into long-term memory was dependent on the time spent actively maintaining this item in short-term memory (Atkinson & Shiffrin, 1968). According to this model, information is acquired through our sensory organs, stored in perceptual short-term stores and then transferred to short-term memory. If the information is not actively rehearsed in short-term memory it will quickly be replaced by other information and lost. In order to remain in short-term memory and to be transferred into long-term memory the information needs to be rehearsed actively. The more the item is rehearsed, the more likely it is to be encoded into long-term memory. This model was later challenged by studies showing that other factors than time spent on rehearsal predicted successful long-term memory encoding (Craik & Lockhart, 1972; Craik & Tulving, 1985). In these studies encoding success was related to the level of processing during encoding attempts. More specifically, deep compared to shallow encoding was associated with higher performance in an ensuing memory test. It was for example shown that deep semantic processing of words (judging if a word was semantically congruent with the rest of the sentence) led to higher memory performance on a subsequent memory test compared with shallow perceptual encoding tasks (judging if a word was written in lower or upper case letters). This led to the development of the levels of processing framework that holds that different cognitive processes like attention and semantic memory interacts during encoding and that successful encoding is dependent on the depth of processing.

Memories are not stored in a single brain structure, but rather distributed in brain regions that are involved in processing of different perceptual aspects of the stimulus or event (e.g. Eichenbaum, Yonelinas, & Ranganath, 2007). Brain regions devoted to processing of information from a specific sensory modality (e.g. the occipital cortex for visual stimuli) initially process the incoming stimuli and projects them to multimodal association areas in the cortex. A ventral processing stream codes for what the stimulus is and is often referred to as the *what stream*. Another more dorsal processing stream codes for information about where, in space, the stimulus has been encountered and this stream is consequently referred to as the *where stream*. Given that the brain areas that code for declarative memories are distributed throughout the cerebral cortex, it can appear paradoxical that injuries to a single brain area, the medial temporal lobe, is related to an inability to encode new declarative memories (Scoville & Milner, 1957). The reason for this is that both the where and the what processing streams projects to the medial temporal lobe (Eichenbaum et al., 2007; Preston & Eichenbaum, 2013; Ranganath, 2010). More specifically, the *what stream* projects to the perirhinal cortex and the lateral enthorinal area, whereas the *where stream* projects to the parahippocampal cortex and the medial enthorinal area. The two processing streams then project to the hippocampus where they converge. As a

consequence of this anatomical organization, the hippocampus has been theorized to be involved in binding item information from the *what stream* with context information from the *where stream*. According to the hippocampal index theory, the hippocampus stores an index that describes the pattern of cortical activation during encoding (Teyler & DiScenna, 1986; Teyler & Rudy, 2007). When a retrieval cue that is related to the encoded memory is presented later, there will be a partial reinstatement of the cortical activity pattern that was present during encoding. Information regarding this partial reinstatement reaches the hippocampus via the *what* and the *where* processing streams. If the cue is efficient enough to trigger the hippocampal index, the hippocampus will send feedback to the cerebral cortex that causes pattern completion, that is a reinstatement of the activation pattern that was present during encoding (e.g. Yassa & Stark, 2011). When pattern completion occurs, we re-experience the encoding episode via memory retrieval. The opposite of pattern completion is pattern separation, the separation of similar cortical activation patterns into distinct orthogonal memory representations (Yassa & Stark, 2011). The formation of new episodic memories is dependent on this process. Without pattern separation encoding of new information would be impossible without overwriting similar old memories. Two sub regions in the hippocampus; the dentate gyrus and the CA3 subfield have been shown to be involved in this important mnemonic process.

In addition to the anatomical position of the hippocampus, there are also neurons within the hippocampus that seem to be well suited for coding of episodic memories. Rodent studies have shown that there are, so called *place cells*, in the hippocampus that code for spatial position, (O'Keefe & Dostrovsky, 1971), and other neurons that code for time, referred to as *time cells* (Eichenbaum, 2013; 2014). Time and place is fundamental parts of episodic memory, so these cells may contribute to the formation of the hippocampal indexes and the ability to remember memories in a temporal order.

Although associative memory generally is considered to be dependent on the hippocampus, a growing body of evidence suggests that a unitization encoding strategy can make associative memory dependent on the perirhinal cortex (Haskins, Yonelinas, Quamme, & Ranganath, 2008). Unitization refers to the process of combining two memory representations into a single memory representation (Graf & Schacter, 1989; Mayes, Montaldi, & Migo, 2007; Murray, 2013). Two words (e.g. police and car) can for example be encoded as a single compound word (police-car). Neuropsychological studies has shown that patients with hippocampal lesions can recognize associated word pairs if and only if these word pairs have been unitized during encoding (Quamme, Yonelinas, & Norman, 2007). Associative encoding was used in all three studies in this dissertation and given that the tasks were relatively difficult, the participants may have adopted a unitization strategy to facilitate encoding. This is especially likely in Study 3, since multiple encoding opportunities were given for each word pair in this study.

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Consolidation/Storage

Consolidation denotes the stabilisation of memory representations after acquisition (Dudai, 2004). It has been known since the beginning of the 20th century that memories are vulnerable after acquisition and that they may be forgotten if similar interfering information is presented within a few minutes after encoding (Müller & Pilzecker, 1900). Periods of sleep after encoding has been associated with increased memory performance in an ensuing test compared with periods of wakefulness of equal length (for review see Diekelmann & Born, 2010). More specifically, a sleep stage referred to as slow-wave sleep, has recently been suggested to be involved in integrating new information with pre-existing memories and is theorized to be important for memory consolidation (Diekelmann & Born, 2010).

As described above the brain regions that code for different perceptual aspects of an experience are active simultaneously during encoding. On the cell level, the neurons in these regions fire in synchrony, leading to strengthening of the synapses between the neurons that fire together through long-term potentiation. Over time, this strengthening leads to a consolidated, more stable memory trace. The role of the hippocampus in consolidation is currently under debate (Frankland & Bontempi, 2005). According to system consolidation models, the hippocampus is involved in the encoding of a memory trace. The memory trace does however grow independent of the hippocampus when strong associations have been formed between the regions of the cerebral cortex that codes for the memory trace, via consolidation processes (Squire & Alvarez, 1995). This theory is based on the neuropsychological finding that patients with medial temporal lobe lesions still can retrieve remote autobiographic memories with great detail, indicating that retrieval of these memories are independent of the medial temporal lobe (Bayley, Hopkins, & Squire, 2003). The system consolidation theory holds that semantic memories are decontextualized episodic memories that have been independent of a specific time and place via consolidation mechanisms.

An alternative theory, the multiple trace theory, argues that episodic memories always are dependent on the medial temporal lobe (Nadel & Hardt, 2011). Based on neuropsychological data suggesting that patients with medial temporal lobe lesions can encode new semantic memories (Bayley & Squire, 2002; C. Stark, Stark, & Gordon, 2005), the multiple trace theory argue that semantic memory is not dependent upon the medial temporal lobe (Nadel & Hardt, 2011). While system consolidation theory views consolidation as a process that starts and ends once, multiple trace theory considers it to be a continuous process that is restarted when a memory trace is retrieved. Consistent with multiple trace theory, episodic memory traces has been demonstrated to enter a fragile state comparable to the initial encoding state when they are retrieved (Sara, 2000). The restart of the consolidation after retrieval is referred to as reconsolidation. Studies of reconsolidation of episodic memories in humans have shown that memory traces are fragile and prone to

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alterations in content during reconsolidation (Forcato, Rodríguez, Pedreira, & Maldonado, 2010). This line of evidence suggests that it may be possible to reduce the negative affective component of unwanted memories during reconsolidation in psychotherapy. In addition to reducing the negative affective component, recent work suggests that disruption of reconsolidation after memory reactivation can reduce the intrusiveness of experimentally induced traumatic memories (James et al., 2015).

A new theory of consolidation was recently developed that integrates elements of system consolidation theory and multiple trace theory. This theory is referred to as competitive trace theory (Yassa & Reagh, 2013). Somewhat simplified, this theory claims that features are added and subtracted from a memory trace each time it is reinstated via pattern completion (performed by the hippocampus). When a retrieval cue is presented only parts of the cortical activity that the cue elicits will be overlapping with the cortical pattern associated with the original encoding experience. According to the competitive trace theory, the role of the hippocampus is to bind together the traces that are activated every time a memory is reactivated and to store the pattern in a new hippocampal index. Besides binding together the features that are overlapping between the initial encoding and the reactivation, the hippocampus also decontextualize non-overlapping features between encoding and reactivation. Over multiple reactivations a strong association is formed between the features that have been shared at each encoding and the co-reactivation of these features is no longer dependent on the hippocampus. Other features that are unique for each reactivation are weakened and ultimately lost, making the memory decontextualized. An advantage of the competitive trace theory is that it can account for how a memory can be altered during reactivations. This theory holds that a memory trace is reconsolidated each time it is reactivated and that alterations of a memory can survive if the altered features are reactivated together with the original memory trace multiple times. This theory also accounts for how features of a memory trace can be lost over time, namely if these features are not reactivated during later subsequent reactivations.

Retrieval

Tulving has defined retrieval as the act of recovering previously encoded information from long-term memory (Tulving, 1999). Retrieval is a cue-dependent process. The likelihood of retrieval success is dependent on the specificity of the provided cue. In *free recall* tasks the cue usually points towards an encoding context and the task is to retrieve the memory representations that were presented in this context. The external cue is not specific enough to reactivate all the memories from the encoding context, so the participant will need to generate more specific cues in order to successfully retrieve all memories from the encoding context. In *cued recall*, a specific cue is given that is related to a particular memory from the encoding context, making the task easier than *free recall*. In *cued recall* there is a partial reactivation of the cortical regions that coded for the memory during encoding. Recognition memory refers to situations

where all the information that was presented during encoding is represented as a copy cue, giving rise to a complete reinstatement and a high likelihood of successful retrieval.

An important principle of memory retrieval is that the probability of retrieval success is dependent on the degree of overlap between the encoding situation and the retrieval situation (Tulving & Thomson, 1973). This phenomenon is often referred to as the encoding specificity. One of the most famous demonstrations of this phenomenon was made by Godden and Baddeley who showed that change compared with no change, in physical context between encoding and test leads to reduced memory performance (Godden & Baddeley, 1975). A similar principle is that overlap in cognitive processing during encoding and test is related to retrieval success, a principle that is referred to as transfer appropriate processing (Morris, Bransford, & Franks, 1977). In other words, overlap in tasks between the encoding and test situation is related to higher performance relative to change in task between encoding and test.

Recent studies have suggested that we automatically segment the stream of perceptions that we continuously experience into events (Kurby & Zacks, 2008; Radvansky & Zacks, 2010). Event segmentation is closely related to pattern separation. When internally generated or externally presented cues cause a sufficiently large change in cortical activation patterns, the hippocampus will pattern separate and store distinct hippocampal indexes for the two activation patterns. In this way, we will remember these two experiences as separate events. Research on event segmentation has showed that retrieval is more likely to be successful if encoding and retrieval occurs within the same event in comparison to if there is an event boundary between encoding and retrieval. It has for example been shown that walking through doorways, an action that leads to event segmentation, can lead to reduced access to memories encoded in the room that was left (Radvansky, Tamplin, & Krawietz, 2010). This effect holds even if the participant re-enters the room where the memory was encoded, indicating that this phenomenon is separate from the encoding specificity phenomenon.

Intention

The importance of involuntary memory retrieval has been realised since Ebbinghaus pioneering work, in which he divided explicit memory into voluntary and involuntary explicit memory (Ebbinghaus, 1885/1964). Involuntary retrieval denotes spontaneous, non-deliberate retrieval of memories, in the absence of an active retrieval attempt (Berntsen, 1996). The spontaneous nature of involuntary retrieval makes it more difficult to study this process in comparison to voluntary retrieval and it has consequently not been studied to the same extent. Outside the laboratory, involuntary retrieval has been reported to be as frequent as voluntary retrieval when it comes to retrieval of autobiographical memories (Rubin & Berntsen, 2009). Similarly to voluntarily retrieved memories, involuntarily retrieved memories also tend to be recent, novel and emotional, suggesting that memories that have been retrieved involuntarily are relevant to the present and guides our behaviour in the same way that voluntarily retrieved memories do (Berntsen, 2010). When memories are unwanted, we are likely to actively attempt to suppress retrieval of these memories when encountering a cue that reminds us of this memory. In Study 3, we investigated the temporal dynamics of memory intrusions in relation to failed suppression attempts. The reason why this study focused on memory intrusions was that such involuntary retrieval of unwanted memories is a core symptom of PTSD (American Psychiatric Association, 2013) and is present in several clinical disorders including depression (Reynolds & Brewin, 1999) and social phobia (Hackmann, Clark, & McManus, 2000). Previous functional magnetic imaging (fMRI) studies of unintentional retrieval has revealed that the dorsolateral prefrontal cortex is activated to a greater extent during voluntary compared with involuntary retrieval, indicating that this region is involved in cognitive control processes that are absent in involuntary retrieval (Hall et al., 2014; Kompus, Eichele, Hugdahl, & Nyberg, 2011).

Recognition

I focus on cued recall in this dissertation, so recognition memory will only be mentioned briefly. As described above, recognition memory refers to situations when a copy cue is presented and we are able to decide that we have encountered this cue on a previous occasion. One large on-going debate is whether recognition memory depends on a single process or two processes (Wixted, 2007). Single process models views recognition as a threshold function. According to these models, recognition is based on memory strength. Encoding leads to an increase in memory strength and stimuli that have been encountered in the encoding phase of a recognition experiment are consequently more likely to be recognized compared with extra study items, since their memory strength is more likely to exceed the threshold. Dual process models of recognition memory distinguish between recognition based on recollection of details from the encoding episode, referred to as recollection, and recognition based on the feeling of familiarity (Jacoby, 1991; Mandler, 1980). The familiarity and recollection

concepts are most easily explained with a practical example. Envision yourself going for a run in a park. After a couple of kilometres you suddenly see a person that you recognize feeding mallards next to a pond. Your recognition decision is based on familiarity if you recognize this person without being able to recall whom it is or where you have met her. The recognition decision is instead based on recollection if you can remember that the person is your new dentist that you met at the dentist clinic two months ago.

Episodic Cued Recall

The cortical regions that code for perceptual experiences during encoding are reactivated during episodic memory retrieval (Danker & Anderson, 2010; J. D. Johnson & Rugg, 2007; Khader, Burke, Bien, Ranganath, & Rösler, 2005a). According to the hippocampal index theory, the pattern of cortical activation is stored in an index in the hippocampus (Alvarez & Squire, 1994; Norman & O'Reilly, 2003; Teyler & DiScenna, 1986; Teyler & Rudy, 2007). When a retrieval cue is presented, there will be a partial reinstatement of the cortical pattern of activations that was present during encoding. If the pattern generated by the cue is similar enough to the pattern that has been stored in the hippocampal index, neurons in the hippocampus will complete the pattern of cortical activity that was present during encoding, leading to the experience of episodic memory retrieval (Yassa & Stark, 2011). This theory has received support from neuroimaging studies. Consistent with the hippocampal index theory, the hippocampus have been shown to be activated both during encoding and during retrieval (e.g. Nyberg, Mclntosh, Houle, Nilsson, & Tulving, 1996). Moreover, cortical regions involved in processing of a certain sensory modality (e.g. vision) have been shown to be reactivated during retrieval of information that was encoded in this modality (e.g. Nyberg, Habib, & McIntosh, 2000). Similarly, encoding retrieval overlap in cortical activation patterns have been demonstrated for stimulus categories that are known to be processed by distinct regions in the cerebral cortex (Danker & Anderson, 2010; J. D. Johnson & Rugg, 2007; Khader et al., 2005a). Recent advancements in fMRI methods has made it possible to track the reactivation of cortical patterns associated with a single stimulus during retrieval by comparing cortical activation patterns between study and recall (Ritchey, Wing, LaBar, & Cabeza, 2013; Wimber, Alink, Charest, Kriegeskorte, & Anderson, 2015; Wing, Ritchey, & Cabeza, 2014). These studies provide strong evidence for cortical reinstatement during episodic memory retrieval.

Besides the cortical regions that are related to reinstatement of perceptual processing of a specific stimulus or event during retrieval, other cortical regions are more generally involved in episodic cued recall. The parietal cortex has for example repeatedly been reported to be activated during episodic memory retrieval and has been suggested to be involved in directing attention to internal memory representations during retrieval search or alternatively in maintaining the retrieved memory representation in working memory (Cabeza, Ciaramelli, Olson, &

Moscovitch, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). The attention to memory model holds that ventral regions in the parietal cortex is related to directing attention towards external perceptual representations, whereas dorsal regions in the parietal cortex are related to attending to internal long-term memory representations (Cabeza et al., 2008).

Another region that repeatedly has been related to episodic memory retrieval is the prefrontal cortex (Buckner & Wheeler, 2001; Habib, Nyberg, & Tulving, 2003; Wagner et al., 1998). Retrieval of verbal material is associated with increased activity in the left prefrontal cortex, whereas retrieval of non-verbal visual memories is related to right prefrontal activity (Wagner et al., 1998). The anterior left ventral prefrontal cortex has been linked to cue specification during episodic retrieval (Dobbins, Foley, Schacter, & Wagner, 2002). Cue specification denotes active generation of cues, based on semantic associations that aid memory retrieval. If you find out that you mistakenly have left your computer at home when you arrive at work, you may for example aid retrieval of the episodic memory of where you put it this morning by retrieving semantic memories of where you usually store your computer. Retrieval monitoring, i.e. evaluation of whether retrieved information match the retrieval cue is also dependent on the left prefrontal cortex but on other subregions, namely the posterior dorsolateral and the frontopolar left prefrontal cortex (Dobbins et al., 2002). The semantic cued recall tasks in Study 1 and Study 2 of this dissertation involved continuous retrieval monitoring when the participants compared retrieved semantic memories with the retrieval cues. Of further relevance for these two studies, the prefrontal cortex has also been suggested to be recruited during competitive retrieval tasks. More specifically, the anterior cingulate cortex, a medial anterior structure, has been related to detection of retrieval-competition and the lateral prefrontal cortex has been related to inhibition of competing memory traces (Kuhl, Dudukovic, Kahn, & Wagner, 2007; Wimber et al., 2015; Wimber, Rutschmann, Greenlee, & Bäuml, 2009). Finally, activity in the right dorsolateral prefrontal cortex has been related to retrieval suppression of unwanted memories (M. C. Anderson et al., 2004; Benoit & Anderson, 2012; Benoit, Hulbert, Huddleston, & Anderson, 2014; Depue, Curran, & Banich, 2007). This finding is of relevance for Study 3, where the participants attempted to avoid memory intrusions by suppressing retrieval.

Semantic Cued Recall

Different aspects of semantic memory, like colour, shape, vocabulary, action related information and so on, are distributed in the cerebral cortex. These features have been theorized to be bound together by a semantic hub in the temporal pole (Patterson, Nestor, & Rogers, 2007). Consistent with this theory, neuropsychological studies have shown that lesions in the temporal pole, in patient groups (e.g. semantic dementia) have been related to decreased performance in several semantic memory tasks.

Semantic memory retrieval have been related to activity in the left inferior prefrontal cortex (Badre & Wagner, 2007; Snyder, Feigenson, & Thompson-Schill, 2007; Thompson-Schill, 2003). More specifically, the anterior part of this brain region has been related to controlled search in semantic memory whereas the mid and posterior inferior frontal region has been associated with selection between retrieved competing alternatives.

Interactions Between Episodic and Semantic Long-Term Memory systems

The episodic and the semantic long-term memory systems often interact during retrieval. Semantic information can for example be retrieved to aid episodic retrieval via cue specification (Dobbins et al., 2002). Similarly, retrieval of an episodic memory of a conversation with a friend can facilitate semantic retrieval of a fact that was discussed during that conversation. It is conceivable to consider retrieval competition to be dependent on interactions between these two memory systems as well. The likelihood of reactivation of a particular competing memory trace upon cue presentation should both be dependent on whether this memory trace recently has been associated with the cue in an episodic event and on the general semantic association strength between the retrieval cue and the memory trace. The interaction between episodic and semantic causes of memory reactivation was utilized in Study 1 to study differential levels of retrieval competition. First, we presented competitors both in the high- and the low-competition conditions to increase the likelihood that they were reactivated and competed for retrieval in the subsequent semantic cued recall task. Second, our manipulation of retrieval competition levels was based on the fact that memories with a strong compared with weak semantic association strength with the cue were more likely to be reactivated and compete for retrieval. Another example of interactions between episodic and semantic long-term memory is that pre-existing semantic knowledge or expertise is important for pattern separation. Experts within a given domain will be able to distinguish between two similar but different experiences that novices consider being similar and this will affect later memory for this experience.

2. Theories of Forgetting

Introduction

Besides investigating the temporal dynamics of cued recall, a secondary purpose of the dissertation project was to investigate mechanisms underlying forgetting. In this chapter I will describe the two forgetting effects that were examined in this dissertation (i.e. retrieval-induced forgetting and suppression-induced forgetting) and provide a theoretical framework of forgetting.

Defining Forgetting

Tulving defined forgetting as the inability to recall something now that could be recalled on an earlier occasion (Tulving, 1974). A topic that has been debated within memory research is whether forgotten memories are completely erased (referred to as catastrophic forgetting) or if they can be retrieved if a more specific cue is provided. In the memory literature a distinction is made between availability and accessibility. Memory traces can be available in memory, but inaccessible at a given occurrence due to the absence of an efficient retrieval cue. In support of this idea there are evidence that previously forgotten memories can be retrieved if a more diagnostic cue is provided (Tulving & Pearlstone, 1966). Tulving & Pearlstone (1966) has for example demonstrated that that participants were able to recall words from a word list that they has failed to retrieve in a free recall task if they were given cues that were related to specific words in the word list (cued recall). This line of evidence suggests that forgetting can be caused by retrieval failure rather than total erasure. It is however not possible to scientifically test the catastrophic forgetting theory. This theory is hence not very useful from a scientific point of view, although it can be of relevance for philosophical discussions about forgetting. In the research studies in this dissertation, forgetting was defined as the inability to retrieve the cued memory within the provided response time window. Importantly, we do not claim that the forgotten memories could not have been retrieved with more specific retrieval cues or that the memory traces have been erased. Instead we do claim that the memory trace's **accessibility** has been reduced to the extent that it was not recallable within the given time window with the provided cue.

A Brief Overview of Forgetting Theories

Decay Theory

In his seminal paper, Ebbinghaus (1885/1964) showed that memory performance decreased as a function of time. This line of evidence gave rise to the decay theory of forgetting which postulates that all memory traces decay over time and will be lost if they are not recalled repeatedly.

Interference Theory

In the empirical work that gave rise to the idea of consolidation, Müller and Pilzecker (1900) found that memories are vulnerable to interference from similar information that is presented shortly after encoding. Based on this pioneering work, McGeogh criticized decay theory and argued that forgetting was caused by retrieval failure due to interference from information encountered during the retention interval (the time between encoding and test) rather than time itself (McGeoch, 1932). His argumentation was also based on studies showing that memory performance was reduced if the participants were awake compared with if they were asleep during the retention interval even when the time between encoding and test was equal in both conditions. McGeogh argued that the forgetting in the awake-condition was caused by interference from experiences during the retention interval. Interference theory distinguishes between two types of interference: proactive and retroactive interference. Proactive interference refers to negative consequences of learning information *prior* to acquiring the target information, whereas retroactive refers to negative effects of learning new information *after* the encoding of the target information.

Another complementary distinction has been suggested between input and output interference (Tulving & Arbuckle, 1963). Input interference refers to the empirical finding that the more information that needs to be encoded the less probable recall is for a particular item. The probability that a word will be remembered is for example greater if this word is included in a wordlist of ten compared with a list of 40 words. Input interference is closely related to another concept, namely cue overload (O. C. Watkins & Watkins, 1975). Cue overload refers to the finding that retrieval success declines as a function of the number of items that are related to the same cue. Retrieval of the target (e.g. Apple) is for example more likely to be successful if the retrieval cue (e.g. Green) has been related to one additional item (e.g. Grass) in contrast to if it has been associated with several other items (e.g. Grass, Leaf, Cucumber). Turning to output interference, this concept denotes the empirical phenomenon that the probability of retrieval success is dependent on output order (Tulving & Arbuckle, 1963). In other words, a specific target item is more likely to

be remembered if the participant attempts to retrieve it first compared to if other items are retrieved before the target. The probability of retrieval success declines as a function of output position.

Inhibition Theory

Inhibition theory is based on interference theory and shares the core assumption that retrieval competition occurs when multiple memory traces are associated with the same cue. The difference between the two theories is that inhibition theory assumes that control mechanisms are recruited to resolve retrieval competition and enable retrieval of the target memory trace (M. C. Anderson, 2003; M. C. Anderson et al., 1994; M. C. Anderson & Spellman, 1995; B. J. Levy & Anderson, 2002). The concept of inhibition has traditionally been used to refer to a general decrease in memory performance independent of the reason for the decrease. In contrast, the inhibition theory uses the concept to specifically refer to a cognitive control mechanism that is recruited actively to reduce the accessibility of the competing memory traces. An important tenet in this theory is that inhibition operates directly on the competing memory traces rather than on the association between these traces and the retrieval cue. Support for the inhibition theory has primarily been provided in studies using the directed forgetting, the retrieval-practice, and the Think/No-Think paradigms (M. C. Anderson, 2003; M. C. Anderson & Hanslmayr, 2014; M. C. Anderson & Huddleston, 2012). The inhibition theory is of particular relevance for this dissertation, since Study 1 tested the competition dependence assumption of this theory, Study 2 tested the strength independence assumption of this study and Study 3 tested the idea that inhibition can be recruited intentionally to suppress retrieval.

Retrieval-Induced Forgetting

Introduction

An enormous amount of information is stored into our long-term memory every day of our lives. In order to function in everyday life we need to be able to selectively retrieve a specific memory among all the stored memories in long-term memory. This problem is similar to the problem a librarian encounters when she/he wants to find a particular book in a huge library. As described in the interference section above, selective memory retrieval is more difficult when the available memory cue not only is related to the target memory, but also to competing irrelevant memories. Retrieval-induced forgetting refers to the phenomenon that such competitive selective memory retrieval causes forgetting of the competing memories (M. C. Anderson, 2003; M. C.

Anderson et al., 1994; Murayama, Miyatsu, Buchli, & Storm, 2014; Storm & Levy, 2012). Competitive selective retrieval situations are common in everyday life. For example, when I leave my office at the department of psychology after a workday, I need to recall where I parked my bike on that particular day in the face of memories of where I parked it other days. Retrieval-induced forgetting has been suggested to be adaptive, since the forgetting of no longer relevant information (e.g. where I parked my bike last week) may facilitate the retrieval of information that is relevant in the present (where I parked my bike today;M. C. Anderson, 2003). For the same reason, forgetting due to event segmentation (e.g. when walking through a doorway) has been theorized to be adaptive because it facilitates retrieval of information that is relevant for the present context (the room that we enter; e.g. Radvansky, Tamplin, & Krawietz, 2010). The mechanisms underlying retrieval-induced forgetting were investigated in Study 1 and Study2 in this dissertation.

The Retrieval-Practice Paradigm

Retrieval-induced forgetting can be studied in the laboratory with the retrieval-practice paradigm (M. C. Anderson et al., 1994). This paradigm consists of an encoding phase, a retrieval practice phase and a test phase. The participants study category-exemplar-word pairs (Fruit - Mango, Fruit - Apple, Bird - Robin, Bird - Eagle) in the encoding phase. In the subsequent retrieval-practice phase, the participants engage in retrieval practice of half of the exemplars from half of the categories (Bird - R___?). All category-exemplar word pairs are tested in the final test phase (Fruit - M___?, Fruit - A___?, Bird - R___?, Bird - E___?). Retrieval-induced forgetting denotes the typical finding that retrieval practice leads to impaired memory performance for non-practiced exemplars (Eagle) from practiced categories (Bird) compared with non-practiced exemplars from non-practiced categories (Mango, Apple). A modified semantic version of the retrieval-practice paradigm was used in Study 1 and Study 2 in this thesis. Instead of practicing studied exemplars as in the standard episodic version, the participants retrieved extra study items from semantic long-term memory in these studies. This semantic cued recall task has previously been shown to cause retrieval-induced forgetting of related memories (Bäuml, 2002).

Theoretical Accounts of Retrieval-Induced Forgetting

The Associative Blocking Account

The associative blocking account is based on interference theory (Raaijmakers & Jakab, 2013). According to this account, successful retrieval-practice leads to an increase in associative strength between the practiced exemplar (e.g. Robin) and the category cue (Bird). When the category cue later is presented in the final test, the practiced exemplars are assumed to be reactivated and block retrieval of the non-practiced exemplars from the practiced categories (e.g. Eagle), due to their relatively stronger associative strength with the category cue (Bird).

The strength of the associative blocking account is that it is the most parsimonious theory of retrieval-induced forgetting. Its' main weakness is that the factor causing retrieval-induced forgetting according to this account, the strengthening of the cue-target association when retrieval practice is successful, has been shown to be unrelated to this forgetting phenomenon. If retrieval-induced forgetting is caused by strengthening of the association between practiced items (e.g. Robin) and the category cue (Bird), then there should be a positive relationship between retrieval success and retrieval-induced forgetting (i.e. the more retrieval success, the more retrieval-induced forgetting of non-practiced items from the same category). In conflict with predictions from the associative blocking account, a meta-study including 52 studies recently showed that there was no relationship between target retrieval success when restricting the analysis to studies that had controlled for output interference (Murayama et al., 2014). Furthermore, retrieval-induced forgetting has been shown in experiments when target retrieval success was impossible (Storm & Nestojko, 2010; Storm, Bjork, Bjork, & Nestojko, 2006). In these studies, Storm and colleagues provided the participants with retrieval practice cues consisting of a category from the study phase plus a word stem that did not match any exemplar in the category, making cue completion impossible. Equal levels of retrieval-induced forgetting have been reported in this impossible retrieval practice task as in the standard version. We examined the role of target retrieval in retrieval-induced forgetting further with behavioural and electrophysiological methods in Study 2.

Another empirical finding that is inconsistent with the associative blocking account is that retrieval-induced forgetting has been shown to be cue-independent. The term cue-independency refers to the finding that retrieval-induced forgetting is present even when the category cue used in the encoding and retrieval-practice phase is not presented in the final memory test (M. C. Anderson, 2003; Storm & Levy, 2012). Retrieval-induced forgetting has for example been seen in recognition paradigms where the category cue is not presented at all (Gómez-Ariza, Lechuga, Pelegrina, & Bajo, 2005; HicksStarns, 2004; Spitzer & Bäuml, 2007; Veling & van Knippenberg, 2004) and in studies in which the cue has been exchanged between retrieval-practice and the final test (e.g. encoding phase: Vegetable – Tomato, retrieval-practice phase: Vegetable – T___?, test phase: *Red* – T___? Tomato!; M. C. Anderson & Bell, 2001;

M. C. Anderson & Spellman, 1995; M. C. Anderson, Green, & McCulloch, 2000). The reason why it is difficult to reconcile these results with the associative blocking account is that this theory claims that it is the presentation of the category cue in the test phase that causes blocking of non-practiced items associated with the same category. If the category cue is not presented in the final test then there should be no blocking and no retrieval-induced forgetting of non-practiced items from practiced categories. Proponents of the associative blocking account have argued that the tests of cue-independency may not be truly cue independent, because the participants may have retrieved the studied category cue (e.g. Vegetable) covertly to facilitate retrieval of the exemplar (Tomato; Camp, Pecher, Schmidt, & Zeelenberg, 2009). Covert retrieval of the category cue could potentially facilitate retrieval in effortful cued recall tasks like the cue exchange paradigm and it should also be noted that several studies have failed to replicate retrieval-induced forgetting with this paradigm (Camp, Pecher, & Schmidt, 2007; Perfect, Moulin, Conway, & Perry, 2002). It is however more difficult to explain retrieval-induced forgetting in tasks that are not facilitated by retrieval of the category cue, like recognition tasks (Gómez-Ariza et al., 2005; HicksStarns, 2004; Spitzer & Bäuml, 2007; Veling & van Knippenberg, 2004) and the lexical decision task (Veling & van Knippenberg, 2004) with the associative blocking account. It is unlikely that the participants' judgement of whether the presented stimulus is a word or not in the lexical decision task, or the decision of whether it has been presented in the encoding phase or not in recognition tests would benefit from covert retrieval of the category cue. The covert cueing hypothesis thus seems to be an unlikely explanation of these findings.

The Context Account

Another account of retrieval-induced forgetting was recently developed by Jonker and colleagues (Jonker, Seli, & MacLeod, 2013; 2015). This theory claims that the retrieval-induced forgetting phenomenon can be explained by similarities between the retrieval-practice and the test phase. According to this theory, the presentation of the category cue (Bird) will reactivate the retrieval-practice context for practiced categories (for the Bird category, but not for the non-practiced Fruit category in my example). The reactivation of the retrieval practice context leads to increased accessibility to the practiced items (Robin) and reduces the likelihood of retrieving non-practiced items from practiced categories (Eagle). The context account claims that the practiced categories reactivate the retrieval practice context for two reasons. The first is temporal proximity; the retrieval-practice context is more recent than the encoding context. The second reason is task similarity, the test context is more similar to the retrieval-practice context compared with the encoding context, since both the test and the retrieval-practice phase involves retrieval.

Retrieval success in the retrieval-practice phase is not necessary for retrieval-induced forgetting according to the context account, so this theory is consistent with some findings in the literature (e.g. retrieval success independence) that the associative

blocking account is inconsistent with. However, similarly to the associative blocking account, this theory predicts that retrieval-induced forgetting is dependent on the presentation of the category cue in the test phase, because it is the category cue that is supposed to reactivate different contexts for practiced and non-practiced category cues and it is this difference in context reactivation that is theorized to cause the retrieval-induced forgetting phenomenon. The finding of retrieval-induced forgetting in recognition tests and other cue independent tests is thus inconsistent with the context account.

The Inhibitory-Control Account

The most prominent account of retrieval-induced forgetting is the inhibitory-control account. This account is based on the inhibition theory of forgetting described above. The basic idea is that the presentation of the category cue in the retrieval-practice phase (Bird - Robin) leads to retrieval competition (re-activation of Eagle) and that inhibitory control mechanisms are recruited to resolve this interference by lowering the accessibility of the competing memory representations (M. C. Anderson, 2003; M. C. Anderson et al., 1994). This reduction in accessibility leads to reduced memory performance in the final cued recall test for inhibited exemplars.

Inhibitory control is theorised to operate directly on the competing memory representations (e.g. Eagle) rather than on the association between the category cue and the competing representations (Bird - Eagle), so consistent with existing data this theory predicts that retrieval-induced forgetting should be observed even when the category cue is not presented in the test phase. This account is consequently the only account that is consistent with this finding.

There are also other properties of retrieval-induced forgetting that are consistent with the inhibitory-control account, but inconsistent with the other two accounts. One such example is competition dependence. This property is of extra relevance for this dissertation since it was tested in Study 1. According to the inhibitory-control account, cognitive control is recruited to solve retrieval competition. If there is no retrieval competition, there is no need for competition and there should be no retrieval-induced forgetting. For the same reason, items that are strongly associated with the category cue (Fruit - Apple) should be more likely to be reactivated during retrieval-practice and hence be more likely to be inhibited and forgotten compared with items that are weakly associated with the cue (Fruit - Litchi). Several studies have provided evidence for the competition dependence of retrieval-induced forgetting (M. C. Anderson et al., 2000; Bauml & Samenieh, 2010; Bäuml, 1998; Hanslmayr, Staudigl, Aslan, & Bäuml, 2010; B. J. Levy, McVeigh, Marful, & Anderson, 2007; Storm, Bjork, & Bjork, 2007). Other studies have however failed to demonstrate the competition dependency of retrieval-induced forgetting (Jakab & Raaijmakers, 2009; Jonker & MacLeod, 2012; Raaijmakers & Jakab, 2012). As noted by Levy and Storm (2012) most of these studies have failed to control for output interference in the final test, so the retrieval-induced forgetting effects in the low-competition conditions

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could potentially be due to output interference in these studies, obscuring a difference between high- and low-competition conditions in retrieval-induced forgetting. Jonker and colleagues (2012) did however control for output interference, so all failures to replicate the competition dependence of retrieval-induced forgetting can not be accounted for with this explanation. Another explanation for the diversity in findings could be that competition levels have been manipulated in various ways and some of these manipulations may not lead to increased competition. For example, Jakab and Raaijmakers manipulated item strength by presenting some items more times than others and by manipulating the presentation order of the items in the encoding phase. Although these manipulations unarguably lead to increased item strength they may not lead to increased competition, because competition is dependent on the association strength between retrieval cue and the item rather than the strength of the item itself. Future studies on the competition dependency of retrieval-induced forgetting would benefit from distinguishing between association and item strength. In summary, there is an ongoing debate regarding whether the competition dependence property of retrieval-induced forgetting is valid and given that this is a central tenet of the inhibitory-control account, it is surprising that relatively few studies have investigated this assumption. This was the reason why we tested this assumption in Study 1.

Consistent with the inhibitory-control account, retrieval-induced forgetting has been shown to be absent in several clinical conditions that are associated with deficits in inhibitory control including attention deficit hyperactivity disorder (Storm & White, 2010), depression (Groome & Sterkaj, 2010), schizophrenia (Soriano, Jiménez, Román, & Bajo, 2010), obsessive compulsive disorder (Demeter, Keresztes, Harsányi, Csigó, & Racsmány, 2014) and PTSD (Amir, Badour, & Freese, 2009). Furthermore, in line with the inhibitory-control account, retrieval-induced forgetting has been related to motor inhibition (Schilling, Storm, & Anderson, 2014) and is absent when executive control is taxed by a secondary task during retrieval practice (Ortega, Gómez-Ariza, Román, & Bajo, 2011; Román, Soriano, Gómez-Ariza, & Bajo, 2009). Further support for the role of inhibitory control in retrieval-induced forgetting comes from neuroimaging studies demonstrating that increased activity in the lateral prefrontal cortex, a region that is associated with cognitive control, during retrieval-practice is related to subsequent retrieval-induced forgetting of competing memories (Kuhl et al., 2007; Wimber et al., 2009; 2015; 2008; 2011). These results are consistent with predictions from the inhibitory-control account and are difficult to reconcile with the two non-inhibitory theories.

Suppression-induced forgetting

Introduction

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Some life events are so painful that we would rather forget them. There is a long-standing controversy in psychology of whether it is possible to actively suppress these unwanted memories or not. Recent research suggests that repeated attempts to suppress retrieval in a cued recall task can lead to subsequent forgetting of the probed associate, indicating that active suppression of unwanted memories is possible (M. C. Anderson et al., 2004; M. C. Anderson & Green, 2001; M. C. Anderson & Huddleston, 2012). This finding is referred to as suppression-induced forgetting (M. C. Anderson & Hanslmayr, 2014). Retrieval suppression is however not always successful. In empirical studies, the participants typically only manage to forget 8% of the items and it may be even more difficult to suppress memories in everyday life, given that the retrieval cues are likely to be multimodal and more effective in triggering the unwanted memory than in the laboratory setting. In Study 3 we investigated the temporal dynamics of involuntary memory retrieval, when the active attempt to suppress retrieval fails and the unwanted memory intrudes into awareness. Furthermore, we studied the relationship between memory intrusions and ensuing suppression-induced forgetting, since previous research has suggested that the ability to reduce the frequency of memory intrusions over retrieval suppression attempts predicts suppression-induced forgetting (B. J. Levy & Anderson, 2012).

The Think/No-Think Paradigm

The idea that it might be possible to stop retrieval was inspired by research on motor stopping, the ability to voluntarily stop the execution of a movement. In motor stopping research there is a classic paradigm called the go/no-go task. In this paradigm, the participants are instructed to press a button every time stimulus A (e.g. a green fixation cross) is presented and to avoid pressing the same button when stimulus B (e.g. a red fixation cross) is presented (e.g. Criaud & Boulinguez, 2013). Inspired by this task, the Think/No-Think paradigm was developed to investigate if it is possible to stop retrieval in the same way that it is possible to stop a motor response. The Think/No-Think paradigm consists of three phases, a learning phase, a Think/No-Think phase and a test phase (M. C. Anderson & Green, 2001).

The learning phase is usually divided into three stages. In the first stage, word pairs are presented (e.g. Pen – Dinosaur, Chair – Book) and the task is to form an association between the words in each pair. This presentation stage is followed by a test-feedback cycle stage where the subjects are given the left hand words (referred to as stimulus words, e.g. Pen) and are instructed to retrieve the right hand word (the response word, e.g. Dinosaur). In the end of each trial, the participants are given the correct response word as feedback. The participants perform this test-feedback stage until they reach a learning criterion that varies between studies, but usually is set to approximately 50 to 75 % of the word pairs. In the final stage of the learning phase the participants perform one additional test without feedback. Only correctly remembered word pairs in this test are included in the data analysis, based on

Tulving's definition of forgetting stating that previous retrievability is a prerequisite of later forgetting (Tulving, 1974).

The learning phase is followed by a Think/No-Think task. In this task the stimulus words (e.g. Pen) are presented in green or red type font. When a stimulus word is presented in green (Think condition), the participants are instructed to think of the response word that previously was associated with this word (Dinosaur). When a stimulus word is shown in red (e.g. chair) they are instead instructed to prevent the overlearned response word (Book) from intruding into awareness. The participants are instructed to push the response word out of awareness if they experience an intrusion.

The Think/No-Think phase is followed by a surprise cued recall test of all words from the encoding phase, including baseline word pairs that were not included in the Think/No-Think phase of the experiment. The classic finding is that performance is reduced for No-Think items compared with baseline items, indicating that retrieval suppression attempts can cause forgetting of the suppressed memory trace (M. C. Anderson et al., 2004; M. C. Anderson & Green, 2001; M. C. Anderson & Huddleston, 2012). However, it should be noted that this Suppression-induced forgetting effect has not always been replicated (Bergström, Velmans, de Fockert, & Richardson-Klavehn, 2007; Bulevich, Roediger, Balota, & Butler, 2006; Hertel & Calcaterra, 2005; Mecklinger, Parra, & Waldhauser, 2009). Anderson and Huddlestone (2012) performed a meta-analysis of 32 published studies to test whether the effect is robust when combining the published data and found a significant Suppression-induced forgetting effect both in same-cue and independent-cue tests.

Theoretical Accounts of Suppression-Induced Forgetting

Associative Blocking Account

Similarly to retrieval-induced forgetting, there is an on-going debate regarding if the Suppression-induced forgetting effect is caused by inhibition (M. C. Anderson & Green, 2001) or by interference (e.g. Tomlinson, Huber, Rieth, & Davelaar, 2009). According to the associative blocking account, the participants generate distractive thoughts during No-Think trials. An association is formed between these distractive thoughts and the stimulus word. It is standard to repeat the No-Think task eight to 16 times in the Think/No-Think paradigm and the associative blocking account theorizes that the stimulus word becomes more strongly associated with the distractive thoughts than with the response word due to this repetition. When the stimulus word is presented in the final cued recall test, the distractive thought will consequently block retrieval of the response word in the No-Think condition. Studies have been conducted to compare associative blocking and inhibition within the same experiment (Benoit & Anderson, 2012; Bergström, de Fockert, & Richardson-

Klavehn, 2009). In these experiments, the subjects were instructed to think of a different word in the associative blocking condition, whereas they were instructed to accomplish the task without generating distracting thoughts in the direct suppression condition. Both studies employed a between-subjects design, meaning that one group received associative blocking instructions and the other group received direct suppression instructions. Although both associative blocking and direct suppression instructions led to a Suppression-induced forgetting effect, electrophysiological and fMRI data indicated that distinct brain regions were associated with the two different instructions, suggesting that separate neural mechanisms caused the forgetting in the two conditions. Consistent with the inhibitory-control account, increased brain activity in the right dorsolateral prefrontal cortex, a region associated with cognitive control, was only predictive of subsequent forgetting in the direct suppression instruction group (Benoit & Anderson, 2012). Moreover, as predicted by the inhibitory-control account, decreased activity in the hippocampus, presumably indicating suppressed retrieval, was only observed in the direct suppression instruction group.

Inhibitory-control account

The inhibitory-control account theorizes that executive control is recruited during No-Think trials to stop retrieval and reduce the accessibility of the response word. In line with predictions from this theory, the suppression-induced forgetting effect correlates with performance in the stop-signal task (the better the performance in the stop signal task the larger the suppression-induced forgetting effect); a motor inhibition task (Depue, Burgess, Willcutt, Ruzic, & Banich, 2010b). Moreover, both tasks were related to increased activity in the right dorsolateral prefrontal cortex indicating that the neural mechanisms recruited to perform these two tasks may be related. Similarly, the N2 event-related potential component that is elicited both in the stop-signal task and in the Think/No-Think task has been shown to be correlated with each other, further suggesting that overlapping neurocognitive mechanisms are involved in these two tasks (Mecklinger et al., 2009). The evidence for the relation between the N2 component and suppression-induced forgetting are described in more detail in chapter 3.

In line with the inhibitory control interpretation, the No-Think task has been shown to be related to increased activity in the dorsolateral prefrontal cortex and reduced activity in the hippocampus in several studies (M. C. Anderson et al., 2004; Benoit et al., 2014; Depue et al., 2007; Benoit:2012dc B. J. Levy & Anderson, 2012). A problem in these studies is however that they have lacked a perceptual non-retrieval baseline condition and instead compared two active tasks with each other. It is therefore impossible to separate the contributions of retrieval (Think condition) from the contributions of retrieval suppression (No-Think condition) in these contrasts, meaning that the described reduction in hippocampal activity in the No-Think task instead could be related to increased activity in the hippocampi during memory

retrieval in the think task. In Study 3, we included a perceptual non-retrieval baseline, with an aim to overcome this problem. The hippocampal effect has however been shown to correlate with subsequent forgetting of No-Think items (e.g. M. C. Anderson et al., 2004), suggesting that it reflects a reduction in hippocampal activity in the No-Think condition, in line with predictions from the inhibitory-control account. Support for the inhibitory-control account is also provided by studies showing that the Suppression-induced forgetting effect is absent in clinical groups that are theorized to have inhibitory control deficits like attention deficit hyperactivity disorder (Depue et al., 2010a), PTSD (Catarino, Küpper, Werner-Seidler, Dalgleish, & Anderson, 2015) and depression (Hertel & Gerstle, 2003; Hertel & Mahan, 2008; Joormann, Hertel, Brozovich, & Gotlib, 2005; Joormann, Hertel, LeMoult, & Gotlib, 2009).

3. Event-Related Potentials

Introduction

To be able to retrieve information from long-term memory is not equal to knowing how to do it. It is hence not sufficient to use introspection methods when studying memory retrieval. To gain insights into the cognitive processes that are involved in retrieval and when they are recruited it is necessary to measure the underlying brain activity. The event-related potential (ERP) technique was used to measure brain activity in all studies included in this thesis. The main reason for using this method is that it has a high temporal resolution, making it well suited for examining the time course of cognitive processes. Another advantage of this method compared with hemodynamic methods like fMRI and positron emission tomography (PET) is that it measures brain activity directly instead of indirectly via blood flow. Given that the ERP method was used in all studies in this dissertation, an introduction to this method is provided below.

Electroencephalogram and Event-Related Potentials

Brain activity gives rise to small voltage fluctuations that can be measured by placing electrodes on the scalp. This measure is called electroencephalography (EEG). The EEG signal stems from summated post-synaptic potentials from ten thousands to millions of neurons in the cerebral cortex that are active simultaneously. Event-related potentials are voltage fluctuations that are time-locked to specific sensory-, cognitive- or motor processes. These are small (on the level of microvolts) and hidden within the EEG signal. Since the rest of the EEG is not time locked to a specific event, it is possible to detect the ERPs within the EEG by time locking to the onset of a stimulus and by averaging over multiple trials of the same task (e.g. retrieval from long-term memory). In this way, the noise in the EEG-signal is reduced and the embedded ERP waveform is detectable. The ERP waveform is characterised by several positive and negative peaks that have been related to various sensory, cognitive and motor processes. These peaks are referred to as ERP components. The mapping of the peaks to these processes is based on the polarity, the latency, the spatial distribution over the scalp and the relation to behavioural measures (e.g. response accuracy or response

time). The processes that are studied in memory research and other fields within cognitive neuroscience are often more prolonged in time and involve multiple ERP components. These processes are described in ERP effects. The term ERP effect refers to a difference in ERP amplitude between two conditions in a specified time window. An important principle in ERP methods and other methods for measuring brain activity is that the cognitive process of interest needs to be contrasted with a baseline condition. In Study 1 and Study 2 successful retrieval trials were for example compared to unsuccessful retrieval trials to investigate the ERP correlates of retrieval success. The reason why it is necessary to include a control condition is that the ERP waveforms contain a lot of brain activity that is unrelated to the cognitive process of interest (e.g. early sensory processes related to viewing a word on a screen). In order to isolate the brain activity related to the cognitive process of investigation (e.g. retrieval success) it is necessary to compare this condition (e.g. successful retrieval trials) with a control condition (e.g. unsuccessful retrieval trials) that only differs from the experimental condition in the cognitive process that we want to investigate. In this way it is possible to isolate the parts of the ERP waveform that are related to the cognitive process of interest.

ERP Correlates of Long-Term Memory Processes

ERPs have been used to study the temporal dynamics of both encoding and retrieval (e.g. Friedman & Johnson, 2000). For the present purposes this overview will focus on ERP correlates of memory processes related to long-term memory retrieval.

Recognition Memory

The majority of the studies of the temporal dynamics of long-term memory retrieval have investigated recognition memory. These studies have provided support for and contributed to the development of dual processes models of recognition memory (Mecklinger, 2000; Rugg & Curran, 2007; Yonelinas, 2002). The most common comparison in ERP studies of recognition memory is between correctly recognized old items and correctly rejected new items. Differences in ERP amplitude between these item classes are referred to as old/new effects. In general, old items (i.e. hits) are related to more positive going ERPs in comparison to correctly rejected items (i.e. correct rejections). There is no such old/new effect when contrasting old items mistakenly judged as new (i.e. misses) and new items incorrectly judged as old (i.e. false alarms). This pattern of results suggests that the old/new effect reflects retrieval rather than an obligatory signature of stimulus repetition. It should however be noted that studies of false recognition have shown that false recognition of lures can give rise

to similar old/new effects for falsely recognized lures (e.g. Curran, Schacter, Johnson, & Spinks, 2001).

Two old/new ERP effects with distinct latency and spatial distribution have been suggested to reflect familiarity and recollection respectively. An early anterior positive going deflection for old item ERPs 300-500 ms after the presentation of the stimulus has been related to familiarity (Mecklinger, 1998; 2000; Rugg & Curran, 2007; Smith, 1993). This effect is referred to as the FN400 effect. The FN400 has also been associated with enhanced access to semantic information due to repetition, referred to as conceptual priming (Paller, Voss, & Boehm, 2007; Voss & Federmeier, 2011; Voss & Paller, 2010) and there is currently an ongoing debate regarding if the FN400 reflects familiarity or conceptual priming (Lucas, Voss, & Paller, 2010; Paller, Lucas, & Voss, 2012; Rosburg, Mecklinger, & Frings, 2011; Stenberg, Hellman, Johansson, & Rosén, 2009; Stenberg, Johansson, & Hellman, 2010).

Recollection has instead been associated with a positive going modulation for hits compared with correct rejections 400-800 ms post stimulus presentation (Mecklinger, 2000; Paller & Kutas, 1992; Rugg & Curran, 2007; Wilding & Rugg, 1996; Wilding, Doyle, & Rugg, 1995). This old/new effect is typically maximal over left parietal electrode sites. Although the late posterior positivity (LPP) have been demonstrated to co-vary with the amount of source information that is retrieved in recognition tasks (Wilding, 2000; Wilding et al., 1995; Wilding & Rugg, 1996), recent research suggests that participants can reject studied, nontarget items correctly in memory exclusion tasks without generating an LPP (Elward, Evans, & Wilding, 2013; Herron & Rugg, 2003a; Herron & Wilding, 2005; Rosburg, Johansson, & Mecklinger, 2013). An interpretation of these findings is that the participants employ a strategy where they reject non-target items based on that they do not elicit source retrieval as efficiently as target items. Recognition of two associated items has traditionally been associated with an LPP effect, suggesting that this kind of recognition is based on recollection (e.g. Donaldson & Rugg, 1998). However, recent research suggests that the associative recognition is reflected in an FN400 if the two items are unitized into a single memory representation during encoding, indicating that familiarity is involved in associative recognition of unitized items (Bader, Mecklinger, Hoppstädter, & Meyer, 2010; Diana, Van den Boom, Yonelinas, & Ranganath, 2011; Jäger, Mecklinger, & Kipp, 2006; Rhodes & Donaldson, 2007; Tibon, Gronau, Scheuplein, Mecklinger, & Levy, 2014; Wiegand, Bader, & Mecklinger, 2010). Retrieval of source information has often been related to a late posterior negativity ERP effect (Johansson & Mecklinger, 2003). This effect has been suggested to reflect action monitoring in tasks with high levels of response conflict and retrieval of attribute conjunctions that are associated with the recognized item.

A third right frontal old/new effect has been reported in studies that require the participants to retrieve episodic information about the recognized items (e.g. Senkfor & Van Petten, 1998; Trott, Friedman, Ritter, Fabiani, & Snodgrass, 1999; Wilding & Rugg, 1996). This effect starts approximately 600 ms after stimulus presentation

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and lasts until the end of the recording epoch. The effect has been suggested to reflect post retrieval evaluation processes (Friedman & Johnson, 2000; Mecklinger, 2000).

Cued Recall

ERP studies of cued recall have mainly focused on episodic cued recall. Inspired by the old/new logic in recognition memory research, these studies have predominantly compared retrieval of previously encountered stimuli (old, episodic cued recall) with generation of new items that have not been presented previously in the experiment (new, semantic cued recall). Word stems completed with previously encoded words have for example been contrasted to word stems completed with words that has not been presented earlier in the experiment (e.g. Allan & Rugg, 1997; 1998; Allan, Doyle, & Rugg, 1996; R. Johnson, Kreiter, Zhu, & Russo, 1998). The typical finding in these studies is that episodic compared with semantic cued recall is associated with an anterior positive slow wave (PSW; e.g. Allan et al., 1996; Allan & Rugg, 1997; 1998; Allan, Robb, & Rugg, 2000; Allan, Wolf, Rosenthal, & Rugg, 2001; Angel, Fay, Bouazzaoui, & Isingrini, 2010a; Osorio, Ballesteros, Fay, & Pouthas, 2009). The PSW has been reported to be greater in amplitude for explicit compared with implicit recall/priming in a similar episodic word-stem completion task (Badgaiyan & Posner, 1997). In this study, the participants were exposed to a list of words before engaging in a word fragment completion task. In the implicit recall/priming condition, the participants were instructed to complete the word stems with the first word that came to mind. In the explicit condition, the participants were instead instructed that some of the word stems could be completed with words from the list and that they should try to complete the word-stems with words from the list when this was possible.

Inspired by the recognition memory ERP literature, other researchers have divided the episodic cued recall PSW into an anterior and posterior effect using the same word-stem completion paradigm (Angel, Fay, Bouazzaoui, & Isingrini, 2010a; Angel, Fay, Bouazzaoui, Baudouin, & Isingrini, 2010b; Angel, Fay, Bouazzaoui, Granjon, & Isingrini, 2009; Fay, Isingrini, Ragot, & Pouthas, 2005). These researchers have suggested that the anterior PSW may reflect a similar neurocognitive process as the anterior old/new effect (the FN400) and that the posterior old/new effect may be associated with recollection processes. These two PSW effects have been used to investigate effects of aging on episodic cued recall. Only the posterior PSW has for example been shown to be affected in older adults with high executive ability, whereas both the anterior and the posterior PSW has been reduced in older adults with low-executive ability (Angel, Fay, Bouazzaoui, & Isingrini, 2010a). This finding is in line with the recollection interpretation of the posterior PSW, since behavioural studies have previously indicated that recollection is more impaired than familiarity in older adults (Yonelinas, 2002). A problem with the distinction between anterior and posterior PSW effects is that the two proposed effects overlap in time and have the

same polarity (Angel, Fay, Bouazzaoui, & Isingrini, 2010a; Angel, Fay, Bouazzaoui, Baudouin, & Isingrini, 2010b; Fay et al., 2005), making it difficult to motivate why they should be treated as two separate effects rather than a single effect. This is the reason why the positive going cued recall effect has been interpreted as a single PSW effect with an anterior maximum in most studies.

Studies investigating suppression of episodic cued recall, using the Think/No-Think paradigm, have related retrieval ERPs (the Think condition) to a positive going modulation over left parietal electrode sites compared with suppressed retrieval (the No-Think condition; Bergström et al., 2007; 2009; Bergström & de Fockert, 2009; Chen et al., 2012; Depue et al., 2013; Hanslmayr, Leipold, Pastötter, & Bäuml, 2009; Mecklinger et al., 2009; Waldhauser, Lindgren, & Johansson, 2012b). This effect has been interpreted to reflect recollection in the Think condition and suppressed recollection in the No-Think condition. This effect is usually referred to as a late posterior positivity (LPP) effect rather than a posterior PSW effect. A similar posterior PSW/LPP effect has been reported for incidental cued recall (Kompus et al., 2011). In this experiment, the participants encoded colour photographs that were paired with natural sounds. In the subsequent incidental retrieval task, the participants were presented to words and the task was to categorize these words based on concreteness. Half of the words corresponded to a photograph or a sound from the encoding phase and the participants were instructed to indicate if they incidentally/unintentionally retrieved the photograph or the sound while working with the categorization task. Taken together, the data from this incidental retrieval study and the Think/No-Think paradigm suggest that the LPP/posterior PSW is independent of retrieval intention, but can be avoided voluntarily via cognitive control.

Interestingly, semantic cued recall has also been related to a PSW ERP effect when comparing successful and unsuccessful cued recall in a word fragment completion task (Rass et al., 2010) and in the scrabble task (Cansino et al., 1999). Although successful semantic cued recall is associated with a reduced PSW in comparison to episodic cued recall, semantic retrieval success is hence also associated with a PSW. This pattern of results suggests that the cognitive process that the PSW reflects is present in both episodic and semantic retrieval. Future studies should directly compare the topographical distribution of the semantic and the episodic cued recall PSW effect to investigate if they have separate or common underlying neural sources.

Working Memory Maintenance

The participants needed to maintain the retrieved memory representations in working memory before responding in all three studies in this dissertation. The reason for this was that both oral (Study 1 and 2) and manual (Study 3) responses elicit muscle artefacts in the EEG recording that makes it more difficult to detect evoked responses

related to memory retrieval. To avoid artefacts in the recording epoch, the participants consequently waited until a response cue appeared on the screen, indicating that the recording epoch was over, before delivering their response.

Working memory maintenance of information is reflected in a negative slow wave ERP effect (NSW; for reviews see (Drew, McCollough, & Vogel, 2006; Ruchkin, Grafman, Cameron, & Berndt, 2003). The topography of the NSW is distinct for different sensory modalities. Auditory working memory maintenance has e.g. been associated with an anterior NSW (e.g. Guimond et al., 2011; Lefebvre et al., 2013) whereas maintenance of visual stimuli have been related to a posterior NSW (e.g. Lefebvre et al., 2013; Pun, Emrich, Wilson, Stergiopoulos, & Ferber, 2012). Within the visual domain separate topographies have been demonstrated for the NSW corresponding to maintenance of spatial, verbal and color information (Rösler, Heil, & Hennighausen, 1995). Of relevance for the studies in this dissertation, maintenance of verbal material has been reflected in a left anterior NSW in both the visual and the auditory domain (Ruchkin et al., 2003). The NSW has not only been reported in working memory studies, but also in long-term memory experiments where a retrieved memory representation needs to be held in working memory until the response is given (Khader, Heil, & Rösler, 2005b; Rösler et al., 1995). This NSW effect has been shown to be greater in amplitude when many in contrast to few items needs to be held in working memory (Khader et al., 2005a; 2007; Rösler et al., 1995). Similarly, an anterior NSW has been related to the buildup of retrieval competition when different memories that are associated with the same retrieval cue are retrieved on consecutive trials (Kizilirmak, Rösler, & Khader, 2014; Kizilirmak, Rösler, & Khader, 2012). The NSW is typically significant during the whole time period that the participants are required to maintain information in long-term memory meaning that it usually is significant until the end of the recording epoch in ERP experiments (e.g. Kizilirmak et al., 2012). In fact, it has been shown to be significant up to seven seconds after stimulus presentation in studies using long recording epochs (e.g. Rösler et al., 1995).

Cognitive Control of Long-Term Memory Retrieval

All studies in this dissertation involved cognitive control of memory retrieval (for a review of ERP correlates of cognitive control of memory retrieval see Mecklinger, 2010). In Study 1 and 2 the participants needed to handle retrieval competition from previously encoded irrelevant memories and in Study 3 the subjects tried to suppress retrieval of unwanted memories.

The Role of the N2 Effect in Retrieval Suppression
The N2 effect has been predictive of suppression-induced forgetting in three Think/No-Think studies and has been suggested to reflect inhibition of the unwanted

memory (Bergström et al., 2009; Mecklinger et al., 2009; Waldhauser et al., 2012b). Although the interpretation of the N2 effect as an ERP marker of inhibition is widely accepted (for reviews see M. C. Anderson & Hanslmayr, 2014; Mecklinger, 2010), the results in studies trying to relate this component with suppression-induced forgetting have been mixed. Given that this effect has relevance both for Study 2, where we observed an N2-like effect, and for Study 3 where we used the paradigm where this effect has been observed, I will provide a brief review of the support for the inhibition interpretation of this effect. Mecklinger and colleagues (2009) were the first to report a relationship between the N2 and suppression-induced forgetting. The inhibition interpretation of the N2 effect was based on two findings in this study. First, when comparing ERPs from subsequently remembered items and subsequently forgotten items in the No-Think condition in the Think/No-Think task (this analysis is referred to as subsequent memory analysis), they observed significantly greater N2 amplitude for subsequently forgotten compared with remembered items. Second, N2 amplitude in the Think/No-Think task correlated positively with N2 amplitude in a motor-inhibition task. This is compelling given that the motor N2 is thought to reflect motor inhibition. However, even though the described findings suggest a relationship between the N2 and inhibition there is one reason for being careful in making this interpretation, namely that there was no reliable suppression-induced forgetting effect in the final test in this study. Bergström and colleagues (2009b) replicated relationship between the N2 effect and suppression-induced forgetting in a subsequent memory analysis. However, although there was a suppression-induced forgetting effect in this study, there was no correlation between N2 amplitude and forgetting. Instead, a reduction in the component that precedes the N2, i.e. the P2 component, predicted suppression-induced forgetting. Finally, Waldhauser et al. (2012) also replicated the association between the N2 and forgetting in a subsequent memory analysis. In this study there was a similar relationship between the next negative component, the N3, and forgetting in the subsequent memory analysis. Suppression-induced forgetting occurred in that study, but consistent with previous studies there was no correlation between forgetting and the N2, although there was a correlation between response time in the final test and the N2 (greater N2 amplitude predicted slower response times). Taken together three out of the six published Think/No-Think ERP studies have observed a relationship between the N2 and forgetting in a subsequent memory analysis. No study has however observed a significant correlation between N2 amplitude and suppression-induced forgetting. The pattern of results becomes even more difficult to interpret given that two additional effects, the P2 and the N3 also has been suggested to reflect inhibition. Importantly, I am not arguing that the N2 does not reflect inhibition. The argument being made here is rather that the results are mixed and that more research is needed before any conclusions can be drawn.

The Positive Slow Wave and the Late Posterior Negativity

Cognitive control during competitive memory retrieval has previously been related to an anterior PSW onsetting approximately 200 ms after stimulus presentation (Johansson, Aslan, Bäuml, Gäbel, & Mecklinger, 2007). Another ERP effect that repeatedly has been related to difficult retrieval situations, with a high risk of errors, is the late posterior negativity (LPN; for review see Johansson & Mecklinger, 2003). This effect has been suggested to reflect error detection or error monitoring during memory retrieval. The LPN has for example correlated negatively with false alarm rates in false recognition studies, indicating that participants with a large LPN were less prone to mistakenly rate a new item as old in a recognition test (Nessler, Mecklinger, & Penney, 2001). The LPN effect has also been related to selection among multiple memory representations that has been retrieved from long-term memory (Kizilirmak et al., 2012).

4. Research Studies

The main aim of this dissertation was to investigate the temporal dynamics of long-term memory retrieval. More specifically, we aimed at investigating the time course of the following three cognitive processes: retrieval competition, search processes during competitive semantic retrieval attempts, and involuntary retrieval.

Study 1

The purpose of this study was two-fold: to test the inhibitory-control account of retrieval-induced forgetting and to investigate the ERP correlates of competitor reactivation during competitive long-term memory retrieval. A fundamental tenet of the inhibitory-control account is the competition-dependence assumption. According to this assumption, competition is recruited to suppress competing memories during selective memory retrieval. Only competing memories should hence be inhibited and suffer from retrieval-induced forgetting. Previous behavioural studies testing the competition-dependence of retrieval-induced forgetting have provided mixed results. Some results have suggested that the assumption is valid (M. C. Anderson et al., 2000; Bäuml, 1998; Bäuml & Samenieh, 2011; Hanslmayr et al., 2010; B. J. Levy et al., 2007; Storm et al., 2007), whereas other studies have reported conflicting findings (Jakab & Raaijmakers, 2009; Jonker & MacLeod, 2012; Raaijmakers & Jakab, 2012).

A limitation of behavioural methods is that they can not investigate reactivation of competitors at the time when it occurs. Instead they measure the consequences of retrieval competition in a later memory test. Recording of ERPs during competitive retrieval enabled us to investigate reactivation of competing memories directly at the time when this is hypothesized to occur. A challenge for studies investigating the neural mechanisms underlying retrieval competition is an overlap in time of competitor reactivation and retrieval of the target. It is hence difficult to isolate the neural activity related to competitor reactivation from the neural activity related to target retrieval. Previous studies have used a spatial approach to disentangle these two processes (Jost et al., 2012; Kuhl, Rissman, Chun, & Wagner, 2011; Waldhauser, Johansson, & Hanslmayr, 2012a). We used a complementary temporal approach in this study. Memory was probed by the sequential presentation of two cues: one category cue to reactivate recently encoded competitors followed by a target-specific

word-stem cue. The purpose was to separate competitor reactivation from target retrieval in time and to utilize the high temporal resolution of ERPs to isolate the neural correlates of competitor reactivation and target retrieval. If the competitor dependence assumption is valid, the ERP correlates of competitor reactivation should be related to retrieval-induced forgetting. Competition levels were manipulated by varying the pre-experimental associative strength between the competitors and the category cue. In the high competition condition, the competitors had a strong association with the category cue (e.g. Fruit - Apple), while the targets had a weak category-exemplar associative strength (e.g. Fruit - Litchi), to maximize the level of competition. The opposite pattern (weak associative strength for competitors and strong association strength for targets) was used in the low-competition condition to minimize the level of competition.

The experiment consisted of three phases: encoding, competitive retrieval, and test. In the encoding phase, the participants studied category-exemplar word pairs (Fruit - Apple). In the ensuing retrieval-practice phase, the participants generated items from half of the categories from the high- and the low-competition conditions respectively. The remaining categories served as behavioural baseline conditions. In the competitive retrieval phase the task was to retrieve an item from semantic long-term memory that completed a category-plus-word-stem cue (e.g. Fruit – Ma___?). Importantly, the categories had already been presented in the encoding phase, but none of the studied exemplars matched the word-stem cue. The category-cue and the word-stem cue were presented separately, and the idea was that the category-cue (Fruit) should reactivate the recently encoded competitors (e.g. Apple), whereas target retrieval should not be possible before the target specific word-stem cue (Ma___?) was presented. In the final test phase, a category-plus-initial-letter cued recall test (Fruit – A___?) was given for all the studied category exemplars.

Three predictions were postulated based on the competition dependence assumption of the inhibitory-control account. First, competitors with strong associative strength in the high-competition condition should be reactivated and inhibited to greater extent during competitive retrieval and would hence be more prone to retrieval-induced forgetting compared to competitors in the low-competition condition. Second, a competition level sensitive ERP modulation was expected in the category cue time window, reflecting competitor reactivation. Third, this ERP effect should be related to retrieval-induced forgetting, indicating that retrieval-induced forgetting was dependent on competitor-reactivation.

All three predictions were confirmed by the results. First, the retrieval-induced forgetting effect was larger in the high- than the low-competition condition. Second, there was a competition sensitive ERP modulation in the category cue time window, in the form of a reduction in the FN400 effect. This ERP effect started approximately 300 ms and lasted until 900 ms after the presentation of the category cue. Third, this effect interacted with forgetting in the category cue time window. That is, the FN400 effect was greater for participants that showed higher levels of retrieval-induced

forgetting. As expected, target retrieval was instead related to a widespread PSW effect in the word-stem cue time window. The temporal separation of competitor reactivation and target retrieval was hence successful. In summary, the results provide strong support for the competition dependence of retrieval-induced forgetting and suggest that a reduction in the FN400 ERP effect can be used as a neural marker of competitor reactivation during semantic cued recall.

Study 2

While we focused on the role of competitor activation in retrieval-induced forgetting in Study 1, we investigated the role of target retrieval in Study 2. We had two aims: a) to test if retrieval-induced forgetting is independent of the strengthening between the target and the retrieval cue, as proposed by the inhibitory-control account, and b) to further our understanding of temporal dynamics of competitive semantic cued recall by isolating ERP correlates of retrieval attempt and retrieval success.

The reason for investigating the role of target retrieval in retrieval-induced forgetting was that the associative blocking account and the inhibitory-control account have opposite predictions regarding the relationship between target retrieval and retrieval-induced forgetting. The associative blocking account holds that strengthening of the association between the retrieval cue and the target memory via target retrieval is the mechanism underlying retrieval-induced forgetting, so according to this theory there should be a positive relationship between target retrieval and forgetting (i.e. the more target retrieval, the more retrieval-induced forgetting of competing memories). On the contrary, the inhibitory-control account proposes that inhibition is independent of target retrieval success and consequently predicts that there should be no relationship between target retrieval and retrieval-induced forgetting.

A similar semantic cued recall paradigm was used as in Study 1. Participants studied category-exemplar word pairs (e.g. Fruit – Apple, Occupation – Teacher) before engaging in a semantic competitive retrieval task. Similarly to Study 1, a category cue (Fruit) and a word stem cue (Ma___?) were presented sequentially and the participants were instructed to retrieve an exemplar from semantic long-term memory that matched the category-plus-word-stem cue (Mango!). The category cues had been presented in preceding encoding phase, but none of the studied exemplars completed the word-stem cue, making the task a competitive semantic cued-recall task.

To test the strength independence assumption and to enable investigation of the processes involved in retrieval attempts, we added a non-retrieval *presentation baseline condition* to the experimental design. In this condition, an intact category-exemplar word pair was presented on the screen and the task was to covertly read this word and to say it aloud when a question mark appeared on the screen in the end of the trial.

With an aim to isolate brain activity related to search processes in semantic long-term memory, i.e. retrieval attempt from retrieval success, we included an *impossible retrieval condition*. In this condition a word stem that did not match any exemplar in the previously presented category was given, making the semantic retrieval task impossible and consequently extended in duration. This impossible retrieval condition also served a second purpose, namely to test if unsuccessful retrieval attempts can induce retrieval-induced forgetting, as suggested by two prior studies (Storm et al., 2006; Storm & Nestojko, 2010). To summarize, there were three conditions in this experiment: a possible retrieval condition, an impossible retrieval condition, and a presentation baseline condition.

As in Study 1, the participants' memory for all studied exemplars was tested in the final cued recall test. We tested the role of target retrieval in retrieval forgetting in two ways using behavioural measures: a) we investigated if impossible retrieval induced retrieval-induced forgetting compared with the presentation baseline condition, and b) we examined if there was a correlation between retrieval success in the possible retrieval condition and retrieval-induced forgetting of related items in the same condition in the final recall test. The associative blocking account holds that retrieval-induced forgetting is dependent on strengthening between the target and the retrieval cue. When retrieval is unsuccessful there should be no strengthening between the cue and the target and hence no blocking, so this theory predicts that the impossible retrieval condition will not induce retrieval-induced forgetting. The associative blocking account also predicts that there should be a positive correlation between target retrieval in the competitive semantic retrieval task and retrieval-induced forgetting of related memories in the final test (the more successful retrievals, the more retrieval-induced forgetting). The inhibitory-control account instead predicts that RIF is independent of target retrieval (i.e. strength independent). Inhibition should be recruited even when retrieval is unsuccessful, so the impossible retrieval condition is also predicted to cause retrieval-induced forgetting according to this theory. In addition, the inhibitory control account predicts that there should be no relationship between target retrieval success and retrieval-induced forgetting.

All the behavioural results suggested that retrieval-induced forgetting is independent of target retrieval and are consistent with the inhibitory-control account. We observed retrieval-induced forgetting in the impossible retrieval condition compared with the presentation baseline condition in the final test. Moreover, there was no correlation between target retrieval in the competitive semantic retrieval task and retrieval-induced forgetting in the final test.

Besides these behavioural tests, we also tested the relationship between target retrieval in the competitive semantic retrieval task and ensuing retrieval-induced forgetting in the final test with electrophysiological methods. The ERP-method makes it possible to measure the mechanisms underlying retrieval-induced forgetting when they occur in the competitive semantic retrieval phase rather than indirectly by measuring reduced performance in the ensuing memory test, as is done with behavioural

methods. The logic of the ERP analysis was the following: retrieval attempt related processes should be evident in contrasts between the impossible retrieval condition and the perceptual baseline condition whereas retrieval success related processes should be apparent in comparisons between successful and unsuccessful retrieval trials within the possible retrieval condition.

Retrieval attempts were expected to be reflected in an LPN given that this ERP component have been related to search processes in competitive and difficult retrieval situations like the one in the present experiment (Johansson & Mecklinger, 2003; Kizilirmak et al., 2012). Retrieval success was instead predicted to be reflected in a PSW effect, since this effect has previously been related to retrieval success in semantic cued recall tasks (e.g. Cansino et al., 1999; Hellerstedt & Johansson, 2014; Rass et al., 2010).

We observed that retrieval attempts were related to three ERP effects: a P3-like effect, an anterior negative peak and an LPN. The P3-like effect started approximately 300 ms after the presentation of the word-stem cue compared with the baseline condition and was maximal over posterior electrode sites. The P3 effect has been related to allocation of cognitive resources in previous studies and may indicate allocation of cognitive resources to the relatively more difficult retrieval tasks (Polich, 2007). This P3 effect was followed by a negative peak that was maximal over anterior regions. This negative peak has a similar topography as the N2 effect that has been associated with inhibition in Think/No-Think studies (Bergström et al., 2009; Mecklinger et al., 2009; Waldhauser et al., 2012b). As anticipated, retrieval attempts were also associated with an LPN. This LPN may reflect retrieval-monitoring during sustained, iterative retrieval search, retrieval of conjunction attributes during generation of candidates to complete the word-stem cue or selection among retrieved semantic long-term memory representations (Johansson & Mecklinger, 2003; Kizilirmak et al., 2012). Unexpectedly, none of the retrieval attempt effects correlated with retrieval-induced forgetting as predicted by the inhibitory-control account. Although this finding is inconsistent with the inhibitory-control account, which suggest that retrieval attempts are sufficient for inducing retrieval induced forgetting, it should be noted that the comparison between failed retrieval trials (impossible retrieval condition and retrieval failures in the possible retrieval condition) is likely to involve multiple cognitive processes besides inhibition (e.g. retrieval monitoring as discussed above), so the ERP analysis could be considered to be a less direct test of the inhibitory-control account compared with the associative blocking account.

As predicted, retrieval success was reflected in a widespread PSW effect with an anterior maximum onset approximately 400 ms after the presentation of the word stem and lasting until the end of the recording epoch. Inconsistent with the associative blocking account, this ERP index of retrieval success did not correlate with ensuing retrieval-induced forgetting.

In summary, the results in this study suggest that retrieval-induced forgetting is independent of target retrieval. The results are difficult to reconcile with the associative blocking account and supports the inhibitory-control account (except the absence of a relationship between ERP processes related to retrieval attempts and retrieval-induced forgetting). Above and beyond the contribution to the retrieval-induced forgetting literature, the present results elucidate the temporal dynamics of competitive semantic retrieval by isolating ERP correlates of retrieval attempts from retrieval success. The present study was the first to observe an LPN in a semantic retrieval task. Both the LPN and the PSW has traditionally been reported in studies of episodic cued recall, so the results suggest these ERP effects reflect processes that are general for declarative long-term memory retrieval.

Study 3

The aim of Paper 3 was to investigate the temporal dynamics of memory intrusions. Recent work has advanced the understanding of the neurocognitive mechanisms underlying suppression of memory retrieval; however, no study has to the best of our knowledge examined the temporal dynamics of memory intrusions. We used a modified version of the Think/No-Think paradigm that included phenomenological ratings of whether the participants experienced memory intrusions on a trial-by-trial basis (cf Benoit et al., 2014; B. J. Levy & Anderson, 2012).

The experiment consisted of a learning phase, a Think/No-Think phase, and a test phase. The participants were trained on unrelated word pairs (e.g. chair - book) until they could recall 73.3% of the response words (right hand word) when given the stimulus word (the left hand word) as a cue. This learning phase also contained single words (e.g. fire -). In the subsequent Think/No-Think phase, the stimulus words were shown in green or red type font colour in the centre of the screen. The participants were instructed to actively retrieve the response word when a stimulus word was presented in green (Think condition), whereas they were instructed to prevent the response word from entering awareness if the stimulus word was shown in red (No-Think condition). If the participants failed to prevent the response word from entering awareness during No-Think trials they were instructed to purge the intruding response word out of awareness and keep it out of awareness until the end of the trial. The single words were presented in yellow font colour and the participants were instructed to read the yellow words and keep them in awareness until the end of the trial. This condition was used as a perceptual baseline condition in the ERP analysis. After each trial, the participants rated the extent to which they thought of the response word in the foregoing trial. This phenomenological measure was used to divide trials in the No-Think condition into memory intrusions and avoided retrievals. The Think/No-Think phase was followed by a surprise cued recall

test. In this test, memory was tested for all the word pairs from the encoding phase including a behavioural baseline condition that was excluded from the Think/No-Think phase.

The ERP analysis was based on four planned comparisons. First, we compared the voluntary retrieval condition with the perceptual baseline condition to investigate the ERP correlates of voluntary retrieval. Second, we contrasted ERPs elicited by memory intrusions in the No-Think condition with ERPs elicited by the perceptual baseline to reveal the ERP correlates of memory intrusions. Third, we compared memory intrusions with voluntary retrievals to investigate differences between these two kinds of retrieval. Finally, we contrasted memory intrusion trials with avoided retrieval within the No-Think condition to examine how the awareness of a memory intrusion affected the ERP effects.

Given that the temporal dynamics of memory intrusions have not been studied before, we considered the most parsimonious prediction to be that memory intrusions should be reflected in the same ERP effects as observed for voluntary retrieval. We expected voluntary retrieval to be reflected in the following three ERP effects: first, the presentation of the stimulus word was expected to lead to an automatic activation of the lexical representations of the response word, as indicated by a FN400 effect, similarly to how this effect reflects reactivation of paired competitors in Study 1. Second, based on previous studies, voluntary retrieval was expected to be associated with an LPP effect, indicating recollection (Bergström et al., 2007; 2009; Bergström & de Fockert, 2009; Chen et al., 2012; Depue et al., 2013; Hanslmayr et al., 2009; Mecklinger et al., 2009; Waldhauser et al., 2012b). Finally, we anticipated that voluntary retrieval would be reflected in an NSW effect late in the trial when the retrieved response word was maintained in working memory.

I will first describe the behavioural results before discussing the ERP results. Overall, the behavioural results replicated the findings from previous Think/No-Think studies. Repeated suppression attempts lead to suppression-induced forgetting for No-Think items compared with behavioural baseline items. Replicating previous studies that have collected reports of memory intrusions, we observed a reduction in intrusion frequency between the first and the second half of the Think/No-Think phase and the reduction in intrusions over repetitions predicted suppression-induced forgetting. More specifically, a steeper reduction in memory intrusions over repetitions were related to increased levels of suppression induced forgetting.

As expected, we observed an FN400 effect for both voluntary retrieval and memory intrusions, presumably reflecting the reactivation of a conceptual or lexical representation of the response word. Interestingly, the memory intrusion FN400 predicted enhanced levels of suppression-induced forgetting. In other words, the greater the FN400 effect the more forgetting of No-Think items in the final test. There was no difference in FN400 amplitude between memory intrusions compared

with avoided retrieval, indicating that additional processes were needed in order for the response word to intrude into awareness.

We expected both voluntary retrieval and memory intrusions to be related to an NSW effect, indicating the activation of the response word in working memory. Consistent with predictions, we observed an NSW effect in both conditions approximately 550 ms into the recording epoch. These findings suggest that this ERP effect may index the entrance of the response word in working memory and that it may be a useful indirect measure of the entrance of the response word in awareness. This interpretation predicts four key findings. First, the NSW effect should be greater for memory intrusion trials compared with avoided retrieval trials. Second, the duration of the NSW effect should be shorter for memory intrusions compared with voluntary retrieval, since the participants were instructed to purge the response word out of awareness when they noticed an intrusion in the No-Think condition. Third, if the NSW reflects the activation of the response word in working memory it should mirror the reduction in the frequency of intrusions across blocks of the Think/No-Think task observed in the phenomenological reports of memory intrusions and hence be smaller in the second compared to first half of the Think/No-Think phase. Finally, working memory maintenance is traditionally related with enhanced likelihood of transfer to long-term memory, so if the NSW reflects working memory activation it should predict remembering in the ensuing test. Strikingly, all four predictions were confirmed, suggesting that the NSW may be used to index the activation of the unwanted response word in working memory.

The NSW was more anterior for voluntary retrieval compared with memory intrusions. This finding is in line with previous fMRI studies reporting that intentional retrieval is related to increased activity in dorsolateral prefrontal cortex compared with incidental retrieval (Hall et al., 2014; Kompus et al., 2011). The central topography of the memory intrusion NSW also opens up for a complementary interpretation. The topography of the intrusion NSW effect is similar to the error-related negativity, so it may partly reflect error-detection when the participants noticed that the response word had intruded into awareness even though the task was to avoid retrieval. Importantly, the working memory and the error-detection interpretations are complementary rather than exclusive, since both processes are likely to be involved in memory intrusions.

We expected both voluntary retrieval and memory intrusions to be related to an LPP effect, reflecting recollection (Paller & Kutas, 1992; Smith, 1993; Wilding & Rugg, 1996). There was a significant LPP effect at electrode P7 in the 900-1300 ms time window for voluntary retrieval compared with the perceptual baseline. Replicating previous studies, we observed a reduction in the LPP for avoided retrieval compared with voluntary retrieval (Bergström et al., 2007; 2009; Bergström & de Fockert, 2009; Chen et al., 2012; Depue et al., 2013; Hanslmayr et al., 2009; Mecklinger et al., 2009; Waldhauser et al., 2012b). This reduction in the LPP has previously been interpreted as avoidance of recollection (Bergström et al., 2007). Surprisingly,

however, there was no LPP effect for memory intrusions. There was actually even a reduction in the LPP for memory intrusions compared with the perceptual baseline. This finding suggests that recollection as reflected in the LPP can be avoided, when it does not contribute to the task at hand, as has previously been suggested in the strategic retrieval literature (e.g. Herron & Rugg, 2003b). Moreover, the finding that the NSW was present for intrusions while the LPP was not suggest that the absence of an LPP can not be used as a conclusive marker that the unwanted memory did not enter awareness.

In summary, replicating Study 1, we observed that the FN400 was a) related to reactivation of an associated memory and b) predictive of ensuing forgetting, indicating that this effect reflects memory interference that signals the need for cognitive control. The results also suggest that the NSW may index the activation of the unwanted memory in working memory. Finally, the finding that voluntary retrievals but not memory intrusions was reflected in an LPP indicate that these two kinds of retrieval are qualitatively different. Consistent with the strategic retrieval literature, this finding also suggests that recollection, as indicated by the LPP, only is recruited when it contributes to the task.

5. General Discussion

Integrating the Principle Findings

What did we learn from this dissertation that was unknown at the outset? While previous ERP research mainly has focused on retrieval success, this dissertation project elucidates the processes operating between the presentation of the retrieval-cue and the retrieval of the target memory. Taken together the three studies suggest that cued recall involves a cascade of processes. In this section I will integrate the main findings from the three studies and describe what we have learned about the journey from the presentation of the retrieval cue until the target memory is recalled.

Processes Generally Involved in Declarative Memory Retrieval

The earliest effects that we observed are likely to reflect allocation of visual attention to retrieval cues that are associated with more difficult tasks. Posterior P3-like effects were enhanced for cues related to the most demanding tasks in both Study 2 and Study 3. One interpretation of these effects is that the participants prepare themselves for a difficult task by updating working memory to allocate attentional resources to this task.

These perceptual effects were followed by the reactivation of associated memories, as indicated by the FN400 effect. The finding that reactivation of memories associated with the retrieval cue is reflected in the FN400 is one of the main findings in this dissertation. This link between the FN400 and reactivation was first observed in Study 1 where it was associated with reactivation of competing memory representations and then replicated in Study 3 where it reflected reactivation of an overlearned pre-experimentally unrelated stimulus (the response words). The FN400 has previously been related with processing of the *retrieval cue* in recognition tasks and has been suggested to reflect familiarity or conceptual priming. The novel finding in this dissertation is that the FN400 can reflect reactivation of *an associated memory* rather than processing of the *retrieval cue* in cued recall tasks. Importantly, it is possible that the FN400 effect reflects different processes in recognition and cued recall, so the interpretation of the FN400 in the present study should be viewed as an interpretation of the FN400 in cued recall tasks. Further research is needed to investigate if this functional role of the FN400 also is valid in recognition tasks. Our

interpretation that the FN400 reflects reactivation of associates in cued recall was supported by the observed relation between the FN400 and forgetting of the reactivated memory in a subsequent memory test (the greater the FN400 effect, the more forgetting in the ensuing test) in both Study 1 and Study 3. There was no such link between the FN400 and forgetting when the reactivated memory was the sought-after target memory in the Think condition in Study 3. This pattern of results suggests that the FN400 effect signals the need for cognitive control if the reactivated memory is in conflict with the task at hand. Another aspect of the functional significance of the FN400 that was discovered in this dissertation project was that the participants were unaware of the reactivation (according to the phenomenological reports of memory intrusions in Study 3) and that the participants were unable to avoid this reactivation via cognitive control (in the No-Think task in Study 3). These two findings indicate that the FN400 reflects an automatic process. In summary, we extend previous research by showing that the FN400 ERP effect is involved in cued recall and reflects automatic reactivation of associated memories.

Processes Specifically Involved in Semantic Cued Recall

The processes occurring after the reactivation of memories associated with the retrieval cue was separate for semantic (Study 1 and Study 2) and episodic (Study 3) cued recall. I will start with describing the semantic cued recall.

The FN400 was followed by an LPN in semantic cued recall (Study 1 and Study 2). This finding extends previous studies on *episodic* memory retrieval by showing that the processes that the LPN reflects also are involved in *semantic* memory retrieval. This effect was observed during failed retrieval attempts and is likely to reflect processes involved in controlled search in semantic long-term memory. The exact process that the LPN reflects in semantic long-term memory search is difficult to disentangle in the present studies. The task in Study 1 and 2 involves construction of possible candidates that potentially complete the cue, continuous retrieval monitoring when comparing generated candidates with the retrieval cue, and selection among generated memory representations. All these processes have been suggested to be related to the LPN effect (Johansson & Mecklinger, 2003; Kizilirmak et al., 2012). Interestingly, the LPN was attenuated when retrieval was successful. This result is consistent with the interpretation that the LPN was involved in search processes that were discontinued when retrieval was successful and is in line with all three interpretations.

Retrieval success has not been studied to the same extent in *semantic* as in *episodic* cued recall. The results of Study 1 and Study 2 suggest that retrieval success is related to widespread PSW effects onsetting approximately 400 ms after the presentation of the word stem cue and lasting until the end of the recording epoch. The findings are similar to the results in the episodic cued recall literature and suggest that overlapping

processes are involved in successful target retrieval in semantic and episodic word-stem-cued-recall tasks.

Processes Specifically Involved in Voluntary Episodic Cued Recall and in Memory Intrusions

For episodic cued recall (Study 3), working memory activation as indexed by an NSW effect followed the early, automatic memory reactivation. We extend prior work showing that the NSW reflects working memory activation following long-term memory retrieval (for reviews see Drew et al., 2006; Ruchkin et al., 2003), by demonstrating that the NSW is sensitive to the intrusion of unwanted memories into awareness, possibly reflecting the temporary maintenance of the intruding memory representation in working memory.

The working memory activation was followed by recollection as indicated by an LPP effect. Importantly, while this effect was observed for voluntary retrieval it was absent for memory intrusions. This finding suggests that the LPP reflects processes that can be avoided via cognitive control or alternatively non-mandatory processes that only are recruited when recollection contributes to the task at hand. In contrast to prior suggestions, our results indicate that a reduction in the LPP can not conclusively be used as a marker of retrieval, since memories could intrude into working memory in the absence of an LPP.

Implications for Theories of Retrieval-Induced Forgetting

Besides elucidating the temporal dynamics of cued recall, the present dissertation also investigated the role of competitor activation (Study 1) and target retrieval (Study 2) in retrieval-induced forgetting. Both the behavioural and the ERP results demonstrate that retrieval-induced forgetting is dependent on competitor activation and independent of target retrieval. These findings are consistent with the inhibitory-control account and difficult to reconcile the associative blocking account.

Limitations

A limitation of Study 1 was that the associative strength between the exemplar and the target was manipulated for competitors and targets simultaneously. A complete balance of the design would make the experiment too lengthy to be able to complete within one recording session and would require a larger stimulus material. Given that it was only possible to include two conditions we selected the two conditions that we expected to be related to the highest and lowest levels of interference, thus

maximizing the interference manipulation. Competitors with strong associative strength were expected to cause more competition if the target had a weak associative strength and this pattern was hence selected for the high-competition condition. Applying a similar logic, competitors with weak associative strength were expected to cause less competition for strongly compared with weakly associated targets and this pattern of associative strength was hence chosen for the low-competition condition. A consequence of manipulating the associative strength simultaneously is that it is not possible to conclusively disentangle the effect of competitor-cue associative strength from the effect of target-cue associative strength on retrieval-induced forgetting. In other words, the increased retrieval-induced forgetting effect in the high-competition condition could be due to the weak associative strength between the target and the cue rather than increased retrieval competition due to strong competitor-cue associative strength. We find it unlikely that the increment in retrieval-induced forgetting was related to the target given that the only ERP effect that correlated with forgetting was predictive of forgetting in the category cue time window before the target was specified by the word stem cue. Another consequence of the manipulation of target-cue associative strength was that performance was higher in the competitive retrieval task in the low-competition condition where the targets were strongly associated with the category cue. An alternative interpretation of the reduction in the FN400 effect could hence be that it reflects retrieval effort in the more difficult high-competition condition because of the weaker target-cue association strength. We find this unlikely for two reasons. First, the FN400 effect was significant prior to the specification of the target and should hence be independent of target-cue association strength. Second, when collapsing the two levels of competition conditions and comparing successful and unsuccessful retrieval trials there was no difference between conditions in the FN400 time window suggesting that this effect was unrelated to target retrieval success.

To ensure that we had enough involuntary retrieval trials to enable ERP analysis of involuntary retrieval in Study 3, the participants were trained until they could recall 73.3% of the stimuli. While this did indeed render sufficient amounts of involuntary retrieval trials to investigate the process that we were most interested in, a side effect of the high performance was that we did not have enough unsuccessful voluntary retrieval trials to be able to divide the voluntary retrieval condition into successful and unsuccessful trials in this study. It was consequently not possible to test if the effects that we interpreted as recollection and maintenance of retrieved memory representations in working memory were related to retrieval success as they should be if our interpretations are valid.

Directions for Future Research

Research has a tendency to stimulate new questions rather than conclusively answering old questions. I conclude with suggestions for future studies based on the research questions that this dissertation project has given rise to.

What Kind of Representations Does the FN400 Reflect Reactivation of?

We observed that the FN400 is sensitive to reactivation both in episodic and semantic cued recall. A question for future research is to investigate if the FN400 only is sensitive to reactivation of verbal representations or if it also is observed for other kinds of representations like pictorial or auditory representations. Even within the verbal domain it remains to be investigated whether the FN400 reflects reactivation of conceptual or lexical representations.

The Functional Role of the LPN in Semantic Cued Recall

Another question for future research is to examine the functional significance of the LPN in Semantic Cued Recall. The LPN in Study 2 could be associated with retrieval of attribute conjunctions during construction of candidates for completing the word stem, error detection after retrieval of memories that are incompatible with the cue, or both these processes. An important difference between these two interpretations of the LPN effect is that the retrieval of attribute conjunctions interpretation predicts that the LPN should *precede* semantic retrieval independently of whether the retrieved item was correct or not, whereas the error detection interpretation predicts that the LPN should only be present *after* retrieval of exemplars that did not match the cue. It may be possible to disentangle these two interpretations of the LPN during retrieval attempts by letting the participants press a button every time they retrieve an exemplar from long-term memory. If the LPN effect reflects retrieval of attribute conjunctions, it should be present in the time window between the presentation of the word-stem cue and the button press indicating retrieval (in a stimulus locked ERP analysis), whereas it should be apparent after the button press (in a response locked ERP analysis) if it reflects conflict detection.

Neural Indices of Memory Intrusions

Using the ERP method in Study 3, it was impossible to disentangle involuntary retrieval from error detection. The NSW effect could thus reflect both these processes. New analysis tools for examining overlap in brain activity patterns between encoding and retrieval have recently been developed. These methods are based on the

idea that the neural networks in the cerebral cortex that are activated while perceiving a stimulus during encoding will be reactivated during retrieval. Although such multivariate pattern analysis (MVPA) methods primarily have been used with fMRI, pattern reactivation during retrieval has recently also been demonstrated with methods with higher temporal resolution like EEG. By analysing EEG data with MVPA it may be possible to separate memory intrusions from error detection. The logic of this analysis being that there should be an overlap in activation patterns between encoding and memory intrusions whereas there should be no such overlap between encoding and error-detection.

Study 3 of this dissertation is a first step towards identifying neural indices of memory intrusions. Such neural indices of memory intrusions could potentially be used to study effects of clinical interventions aimed at reducing intrusion frequency in patient groups that suffer from memory intrusions of traumatic memories. Before considering using the NSW as an index of memory intrusions in clinical populations, however, it is necessary to investigate if the relationship between memory intrusions and the NSW effect generalizes to everyday experiences and emotional memories.

Another important question for future research is to investigate whether reductions in intrusion frequency and suppression-induced forgetting is related to reductions in emotional response to the retrieval cue. In other words, is retrieval suppression of the verbalized representation accompanied by a similar absence of or reduction in emotional response to the retrieval cue? This kind of studies is important for investigating if methods for reducing memory intrusion frequency like retrieval-suppression, associative blocking and taxing visual working memory during reconsolidation also lead to reduced emotional responses in clinical groups.

Concluding Remarks

Although long-term memory retrieval often is described as a single process, the present dissertation project illustrates that it consists of several processes ranging from perception and attention processes to automatic memory reactivation via activation in working memory to voluntarily recruited processes like recollection. Even though some of the observed ERP effects have been described earlier in the recognition literature the results also indicate that cued recall may involve processes that are not involved in recognition. Automatic reactivation of associates and working memory activation are two examples of processes that we have demonstrated in cued recall that are unlikely to be recruited in a standard recognition memory task. These findings suggest that research on memory retrieval will need to utilize a diversity of tests of memory in the future to be able to generalize findings to real life situations.

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