Sleep-associated and circadian effects on future-directed memory

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Dipl. Psych. Christine Barner
aus Kirchheim / Teck

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2. Berichterstatter: PD. Dr. Susanne Diekelmann

“It’s a poor sort of memory that only works backwards” the Queen remarked.

“What sort of things do YOU remember best?” Alice ventured to ask.

“Oh, things that happened the week after next,” the Queen replied in a careless tone"

Lewis Carroll 1871
Through the Looking Glass, Chapter 5

To Runa

SUMMARY

Memories reflect past experiences, yet their function is to bear appropriate behavior in the present and adapt it to future situations. The memory for intentions and plans explicitly relates to future behavior and can be counted among ‘future-directed memory’. Circadian (lat. *circa*, ‘approximately’ and *diem*, ‘day’) rhythms keep time for many bodily functions, of which the sleep-wake cycle is probably the most obvious. Cognitive functions of different domains among others memory functions likewise underlie circadian variations. The aim of this thesis is to shed light on the role of sleep and time of day in future-directed memories. Sleep has been shown to benefit the consolidation, i.e. the stabilization and reorganization of new memories. Only recently has sleep been proven effective in consolidating intentions. Study 1 of this thesis uncovers conditions for a beneficial sleep effect on intentions and study 2 addresses the question of whether the memory for plans is also consolidated during sleep. Cognitive functions - for example memory and attention - fluctuate throughout the course of a day, in parallel with arousal levels of the endogenous circadian system. Better performance during the day is succeeded by a decline towards the night, which is called the time-of-day effect. For some cognitive domains, performance is higher at preferred times of the day and worse at non-preferred times of the day; this is known as the synchrony effect. Study 3 of this thesis addresses whether intentions underlie a time-of-day effect or a synchrony effect and whether attention modulates these potential effects. Results show that intentions benefit from sleep as long as they are still pending and only if they are instructed in temporal proximity to the initial learning session. These findings highlight the importance of the time after encoding as a sensitive period, in which experiences determine whether memories undergo consolidation during subsequent sleep. Furthermore, the present work delivers tentative evidence that the memory for plans is consolidated during sleep. This result should be interpreted with caution because the beneficial effect of sleep is not present in all measures and because the experiment lacks a circadian control. Thirdly, intentions underlie a time-of-day effect. Independent of circadian preference and the level of available attention, intentions are realized more successfully during evening hours compared to morning hours. This has been shown in 3 out of 4 measures. Together, these results show that future-directed memories are consolidated during sleep only under certain conditions and that they underlie an attention-independent time-of-day effect in the absence of a synchrony effect.

ZUSAMMENFASSUNG

Erinnerungen spiegeln vergangene Erfahrungen wieder. Ihre Funktion liegt darin, angemessenes Verhalten in der Gegenwart hervorzubringen und es an zukünftige Situationen anzupassen. Das Gedächtnis für Absichten und Pläne bezieht sich ausdrücklich auf zukünftiges Verhalten und kann demnach zum „auf die Zukunft gerichteten Gedächtnis“ gezählt werden. Zirkadiane (lat. *circa*, “ungefähr” und *diem*, “Tag”) Rhythmen geben den Takt für viele Körperfunktionen vor, wovon der Schlaf-Wach-Zyklus wahrscheinlich der offensichtlichste ist. Kognitive Funktionen unterschiedlicher Domänen, darunter die Gedächtnisfunktionen, unterliegen ebenfalls zirkadianen Schwankungen. Ziel dieser Arbeit ist es, die Rolle des Schlafes und der Tageszeit für auf die Zukunft gerichtetes Gedächtnis zu beleuchten. Schlaf wirkt sich förderlich auf die Konsolidierung, das heißt, die Stabilisierung und Reorganisation, von neuen Gedächtnisinhalten, aus. Kürzlich wurde gezeigt, dass Schlaf auch die Konsolidierung von Absichten fördert. Studie 1 dieser Arbeit deckt Voraussetzungen für einen förderlichen Schlafeffekt auf Absichten auf und Studie 2 befasst sich mit der Frage, ob das Gedächtnis für Pläne ebenfalls im Schlaf konsolidiert wird. Kognitive Funktionen wie Gedächtnis und Aufmerksamkeit schwanken im Tagesverlauf parallel zum Niveau der physiologischen Erregung des endogenen zirkadianen Systems. Auf höhere Leistungen am Tag folgt eine Verschlechterung zur Nacht hin, was als Tageszeiteffekt bezeichnet wird. In manchen kognitiven Domänen sind die Leistungen zur bevorzugten Tageszeit besser und zur nicht-bevorzugten Zeit schlechter, was unter dem Synchronie-Effekt bekannt ist. Studie 3 dieser Arbeit befasst sich mit der Frage, ob Absichten einem Tageszeit- oder Synchronie-Effekt unterliegen und ob diese potentiellen Effekte durch Aufmerksamkeit moduliert werden. Die Ergebnisse zeigen, dass Intentionen vom Schlaf profitieren, wenn sie über die Schlafperiode hinweg aktiv sind und wenn sie in zeitlicher Nähe zur anfänglichen Lernsituation instruiert werden. Diese Befunde heben die Zeit nach der Enkodierung als eine kritische Phase hervor, in welcher die dort gemachten Erfahrungen bestimmen, ob Inhalte im nachfolgenden Schlaf konsolidiert werden. Zweitens liefert die vorliegende Arbeit erste Belege, dass das Gedächtnis für Pläne im Schlaf konsolidiert wird. Dieses Ergebnis sollte mit Vorsicht interpretiert werden, da der förderliche Effekt von Schlaf nicht in allen Maßen zu finden ist und keine zirkadiane Kontrolle vorhanden ist. Drittens unterliegen Intentionen einem Tageszeiteffekt. Unabhängig von der zirkadianen Präferenz und dem zur Verfügung stehenden Aufmerksamkeitsniveau

werden Intentionen am Abend erfolgreicher ausgeführt als am Morgen. Dies wurde in 3 von 4 Maßen gezeigt. Zusammengenommen konnte ich in diesen Arbeiten zeigen, dass auf die Zukunft gerichtetes Gedächtnis im Schlaf nur unter bestimmten Bedingungen konsolidiert wird und dass dieses Gedächtnis einem aufmerksamkeitsunabhängigen Tageszeiteffekt unterliegt, ohne dass die präferierte Tageszeit eine Rolle spielt.

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ABBREVIATIONS

ANOVA	analysis of variance
ANCOVA	analysis of covariance
EEG	electroencephalography
EMG	electromyography
EOG	electrooculography
LC	locus coeruleus
LTD	long-term depression
LTP	long-term potentiation
MCTQ	Munich ChronoType Questionnaire
MEQ	Morningness-Eveningness Questionnaire
MSFsc	midpoint of sleep on work-free days corrected by the sleep dept participants build up during working days compared to work-free days
NREM	non-rapid-eye movement
PM	Prospective Memory
PSQI	Pittsburgh Sleep Quality Index
PVT	Psychomotor Vigilance Task
REM	rapid-eye-movement
SCN	suprachiasmatic nucleus
SD	standard deviation
SEM	standard error of the mean
SSS	Stanford Sleepiness Scale
SWS	slow wave sleep
S1	sleep stagee 1
S2	sleep stage 2
TMR	targeted memory reactivation
W	wake

LIST OF RELEVANT PUBLICATIONS

This thesis is based on the following publications and manuscripts:

Barner, C., Seibold, M., Born, J., & Diekelmann, S. (2017). Consolidation of prospective memory: Effects of sleep on completed and reinstated intentions. Frontiers in Psychology, 7(2025). http://doi.org/10.3389/FPSYG.2016.02025

Barner, C., Altgassen, M., Born, J., & Diekelmann, S. (2018). Effects of sleep on the realization of complex plans. *Journal of Sleep Research*, 2*8*(1). http://doi.org/10.1111/jsr.12655

Barner, C., Schmid, S. R., & Diekelmann, S. (2019). Time-of-day effects on prospective memory. *Behavioral Brain Research, 376*.

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STATEMENT OF CONTRIBUTION

I hereby declare that I wrote this thesis by myself with no further support or aid from other sources or persons than stated below.

Study 1: Consolidation of prospective memory: Effects of completed and reinstated intentions.

Experiment 1 was designed and planned by S. Diekelmann and J. Born. Data collection was realized by K. Kanje, under the supervision of S. Diekelmann and was analyzed, interpreted and visualized by S. Diekelmann. The respective part of the manuscript was written by S. Diekelmann. I planned experiment 2 together with S. Diekelmann and J. Born, collected data, analyzed it including sleep scoring, interpreted the results together with S. Diekelmann, created the figures and wrote the first draft of the manuscript. I designed experiment 3 together with S. Diekelmann and J. Born. Data collection was realized by M. Seibold under my supervision. I analyzed data except for sleep scoring, which was done by M. Seibold, interpreted the results together with S. Diekelmann, created the figures and wrote the first draft. All authors edited the manuscript for study 1.

Study 2: Consolidation of complex plans.

I designed the study together with S. Diekelmann and J. Born. M.-J. Kater collected data under my supervision. I performed the analysis, including sleep scoring, and created the figures. M. Altgassen supported application and analysis of the Dresden Breakfast Task. I interpreted the results and wrote the first draft of the manuscript. S. Diekelmann contributed to the interpretation of the results and edited the draft together with M. Altgassen and J. Born.

Study 3: Time-of-day effects on prospective memory.

I designed the study together with S. Diekelmann. Data collection was realized by S. R. Schmid under my supervision. I analyzed the data, created the figures, interpreted the results and wrote the first draft of the manuscript. S. Diekelmann contributed to the interpretation of the results and edited the draft together with S. R. Schmid.

INTRODUCTION

Memories enable us to remember experiences in the past, to act in an appropriate way in the present and to adapt behavior to future situations (Schacter, Addis, & Buckner, 2007). While research on memory of the past has a long-standing tradition of more than 100 years, future-directed memories have only recently risen on the academic horizon, although they were already mentioned in the 1980ies (Ingvar, 1985; Schacter et al., 2007). The capability of mentally travelling back in time and travelling forth into the future seems to have provided a selective survival advantage (Klein, Robertson, & Delton, 2011) and is an essential prerequisite for creative thinking. Constructing possible scenarios enabled gifted human beings to produce masterpieces in many artistic domains, for example in literature (e.g. Hemmingway´s 'The old man and the sea'), and enable us to think ahead. The construction of possible future scenarios in everyday life - like planning breakfast preparation or intending to realize a task like brewing the tea as soon as the water has boiled - is an essential prerequisite for successful goal-directed behavior. The memory for such plans and intentions can be termed 'future-directed memory'.

Human beings not only swing back and forth in their minds between the future and the past (Schacter et al., 2007, 2012), but also oscillate between two poles of consciousness: wakefulness and sleep (Schmidt, Collette, Cajochen, & Peigneux, 2007). Alertness increases while shifting from the extreme pole of deep sleep to the other pole of being wide awake. With each gradual step towards more alertness, cognitive functions, including memory functions vary. Sleep is required in order to reliably distinguish whether mental representations derive from truly experienced episodes in the past, from representations of the present perceptions, from representations of future or possible events. A lack of sleep can lead to erroneous memories (Diekelmann, Landolt, Lahl, Born, & Wagner, 2008), has been associated with hallucinations (Babkoff, Sing, Thorne, Genser, & Hegge, 1989; Meyhöfer, Kumari, Hill, Petrovsky, & Ettinger, 2017) and has been associated with the collapse in many cognitive performance measures - like vigilance and memory functions (Schmidt et al., 2007).

One important function of sleep, which has been investigated intensively in the last decades, is the role of sleep in the consolidation of memory. While being ’off-line’, the brain is highly active in order to re-process newly encoded information and to stabilize this information for long-term storage and successful retrieval. This has been shown for many memory domains directed to the past, and recently also turned to the field of future-directed memory. For instance, information which is relevant in the future seems to be specifically prone to consolidation, which is in line with the active system consolidation hypothesis, which states that memories are consolidated selectively and in an active process (Rasch & Born, 2013). The first part of this thesis aims at elucidating the role of sleep in the consolidation of future-directed memory of different types and by addressing conditions for successful consolidation.

During sleep, alertness is at its nadir and cognitive functions undergo ‘off-line’ processes like consolidation. During the course of a normal day, alertness swings from lower to higher levels and back. In synchrony with alertness, fluctuations have been shown for physiological parameters of the circadian system like body temperature, cortisol and melatonin (Bailey & Heitkemper, 2001; Benloucif et al., 2005), as well as for cognitive performance parameters like vigilance, working memory and executive functions (Schmidt et al., 2007). Diurnal fluctuations in future-directed memory have been studied sparsely, despite their relevance during the course of a day. At many workplaces, plans and intentions have to be carried out throughout the course of a day. Stable performance levels are inevitable, for example in the medical sector. Dentists should remember their intention to fit a crown before permanent fixation, both in the morning and in the evening after a long working day. Failures in the realization of plans and intentions at specific times of the day have contributed to accidents and industrial incidents in the past. The second part of this thesis aims at enlightening the role of diurnal fluctuations in future-directed memory by investigating a series of different tasks at two times of a normal day.

Memory systems and processes of memory formation

Memory is conceptualized as a multifaceted system. Different structures and networks in the brain cooperate dynamically in order to enable individuals to retain information throughout a large time scale, from seconds to years. Classical psychological theories distinguish a temporary storage from a long-term storage. A temporary storage can retain (and in some models manipulate) information in the time range of milliseconds to seconds (Aben, Stapert, & Blokland, 2012; Atkinson & Shiffrin, 1966; Baddeley, 2000). Long-term memory retains memories from seconds to years (Squire, 2004; Squire & Zola, 1996). Short-term memories and long-term memories directed to the past code for representations of past events and facts. Conversely, memory of the future (future-directed memory) codes for hypothetical events or facts occurring in the future.

Memory systems

In this section the focus will be long-term memory, since it is the kind of memory which benefits from consolidation over longer periods, including sleep. Long-term memory is divided into two major systems: declarative and non-declarative memory (Squire & Zola, 1996) (Figure 1). Declarative memory is the storage for semantic and episodic information (Tulving, 1985). Semantic memory, the memory for facts and general knowledge of the world, retains information independent of the scenery in which it has been learned (for example, that Paris is the capital of France). Episodic memory, in contrast, is the memory for events in the past, which can be memorized vividly, including information about the spatiotemporal context of the event (like a visit to a museum). Both, semantic and episodic memory can be explicitly and consciously retrieved and verbally expressed by a person. Declarative memory is classically associated with intact functioning of the medial temporal lobe, including hippocampal and parahippocampal regions and neocortical association areas (Eichenbaum, 2000). In order to construct a mental image of possible future events or facts, i.e. future-directed cognition, the declarative memory system contributes knowledge of past events and facts (Szpunar, Spreng, & Schacter, 2014). In contrast to declarative memory, non-declarative memory is an implicit system, comprising several heterogeneous subsystems, including: striatum, neocortex, amygdala and cerebellum (Squire, Knowlton, & Musen, 1993; Squire & Zola, 1996). Non-declarative memories cannot be verbally expressed or explicitly retrieved, but are rather recalled through actions or by reactions to stimuli. Non-declarative memory comprises procedural learning of skills or habits, like riding a bicycle. It further comprises priming, which refers to the facilitated reaction to a perceptual stimulus due to prior exposure to the same stimulus; and simple classical conditioning, which depicts a cue-action association based on repeated co-occurrence of a previously neutral cue to an already existing response to a stimulus. Brain areas involved in non-declarative systems might also be involved in future-oriented memories, specifically future-oriented actions like realizing plans in the future (Szpunar et al., 2014) (see section ‘future-directed memory’).

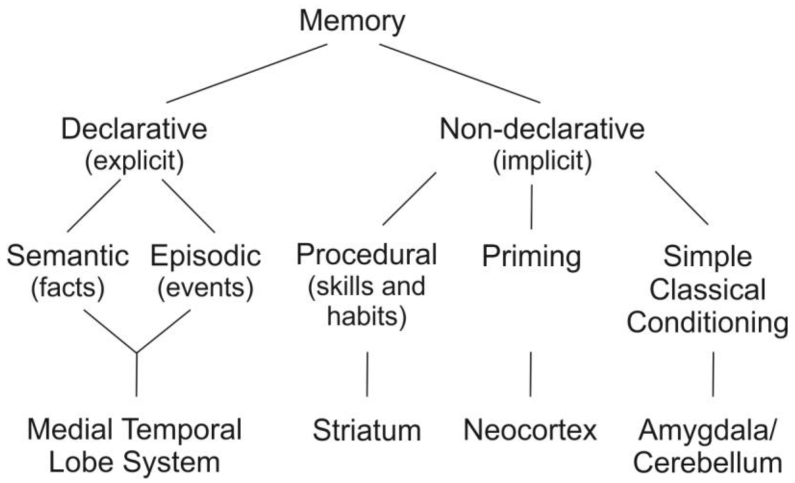

Figure 1 Taxonomy of long-term memory systems including underlying brain structures. Adapted from Squire & Zola (1996).

Stages of memory formation

Memories emerge in a multi-stage process including: encoding, consolidation, retrieval and reconsolidation. After initial information uptake (encoding), memory traces are usually in a label state. For new memories to move from label state to being integrated into existing knowledge and to be functionally useful, post-encoding stabilization and reorganization is needed (Dudai, Karni, & Born, 2015). This post-encoding process is called consolidation (Müller & Pliezecker, 1900). After both successful encoding and consolidation, memories can be retrieved. Whenever memories are actively retrieved or cued, they can become labile again. In this state, they are prone to transformations and depend on reconsolidation to persist (Nader & Einarsson, 2010; Nader & Hardt, 2009).

Consolidation has been investigated at two different levels, a synaptic level and a system level. At the level of synaptic consolidation, plastic experience-dependent changes at local synapses and cells represent newly encoded information in neuronal circuits and thereby constitute the basis of memory storage in the brain (Takeuchi, Duszkiewicz, & Morris, 2014). On a molecular basis, long-term potentiation (LTP), facilitates the excitability of posts-synaptic neurons by repeated co-activation of pre- and postsynaptic neurons (Bliss & Lømo, 1973) and long-term depression (LTD) attenuates synaptic excitability (Murakoshi & Yasuda, 2012; Zhou, Homma, & Poo, 2004).

The framework of the ‘revised synaptic tagging and capture hypothesis’ (Redondo & Morris, 2011) elaborates, that for permanent memory storage, four steps are required. Firstly, in the early phase of long-term potentiation, synapses that experienced potentiation during memory encoding, receive a tag which holds the potential for longer-lasting synaptic changes. Secondly, during late-long-term potentiation, new, plasticity-related proteins are synthesized and distributed. Thirdly, the tagged synapses capture these proteins under certain conditions, and fourthly allow the stabilization of synaptic strength. A core aspect of this hypothesis is that plasticity-related proteins cannot only be synthesized at the synapse which was involved during learning, but also by other synapses before or after learning. Thus, on a behavioral level, not only the learning input but also other experiences shortly before and after might modulate further consolidation of new information (Ballarini, Moncada, Martinez, Alen, & Viola, 2009; Dunsmoor, Murty, Davachi, & Phelps, 2015); this is known as *behavioral tagging* (Moncada, Ballarini, & Viola, 2015). For instance, if the presentation of pictures of animals and tools is followed by the presentation of other pictures of these categories but only one category is paired with electrical shocks (e.g. pictures of animals only), the originally seen pictures of this category (e.g. animals) are recognized better than the original pictures of the other category (Dunsmoor et al., 2015).

Apart from memory consolidation on a synaptic level, consolidation entails longer-lasting processes on the level of whole brain areas, occurring in the time-frame of up to years after encoding. Memories are re-shaped and re-organized over different brain regions, a process termed systems consolidation. According to the standard model of consolidation (Frankland & Bontempi, 2005) (Figure 2), two learning systems absorb newly encoded information in parallel.

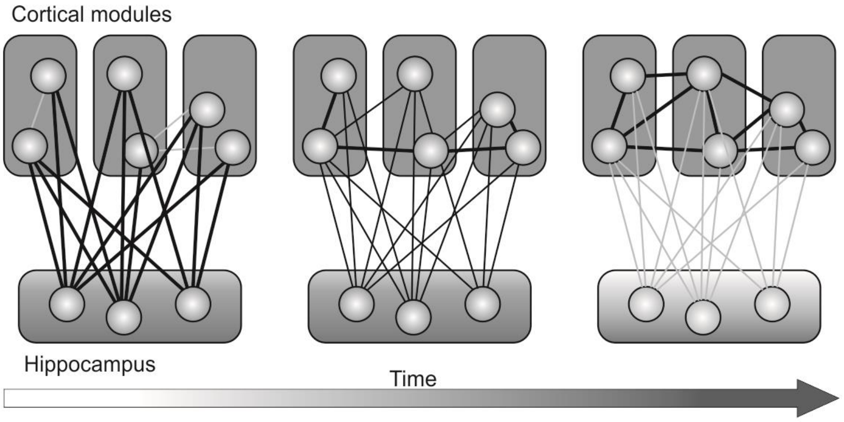

Figure 2 Standard model of systems consolidation. New information is encoded in primary and associative cortical areas and hippocampal areas in parallel. The fast-learning hippocampus acts as a temporary storage retaining a high density of information for gradually training cortical slow-learning areas in storing information for the long-term. Over time, cortical representations become independent from hippocampus. Adapted from Frankland & Bontempi, 2005.

A fast learning system enables highly plastic short-term encoding, with fast decaying traces for flexible reactions to the environment. For declarative memory, this fast-learning system is located in the medial temporal lobe, mainly in the hippocampus, which receives afferent signals from cortical association areas for spatial and temporal integration of multimodal information (Eichenbaum, 2004). A second learning system is able to retain information on the long-term, but encodes this information much more slowly. For declarative memory, this function relies on primary cortical areas and cortical association areas. The hippocampus functions like a buffer, retaining information and gradually training cortical areas for long-term storage. This training consists of repeated activation of hippocampal memory traces, which often occurs in absence of any conscious engagement in retrieval (Carr, Jadhav, & Frank, 2011), e.g. during sleep (Wilson & McNaughton, 1994), leading to gradually strengthening of the memory traces and their integration into existing cortical networks. Due to this hippocampal-neocortical dialogue, cortical traces become gradually more independent of hippocampal functioning (Haist, Bowden Gore, & Mao, 2001), storing memories of the past for later retrieval.

Future-directed memory

Retaining memories for later realization is an essential human skill, even for something as mundane as preparing breakfast. The memory for future-directed cognition, like the memory for simulations, predictions, intentions and plans (Szpunar et al., 2014) can be called ‘future-directed memory’ (Figure 3). While psychological concepts and neuroscientific approaches on memory of the past have been developed for many years, future-directed memory has only recently attained attention. The ability to ‘think about the future’, as Suddendorf, Bulley, & Miloyan (2018) define, is the capability of prospection, which is now being addressed more systematically. Szpunar, Spreng, & Schacter (2014) distinguish four modes of prospection (Figure 3): *simulation*, defined as the process of building a mental representation of the future; *prediction,* defined as the prospective evaluation of the probability of a future outcome or one´s reaction to a predicted outcome; *intention,* which refers to the process of setting a goal and is often operationalized in the concept of prospective memory - the memory for intentions to be carried out at an appropriate time in the future; and *planning,* the act of stepwise defining and organizing the achievement of a desired aim. According to Szpunar et al. (2014), these modes are hierarchically structured procedures, with the lower level processes (like *simulation)* being necessary for the successful realization of higher order processes (like prospective memory) (Terrett et al., 2015). In order to create a *plan* of how to prepare breakfast, one has to *simulate* the final table layout, *predict* the consequences of setting the alarm for cooking the eggs and build the *intention* to switch off the egg boiler when the eggs are ready.

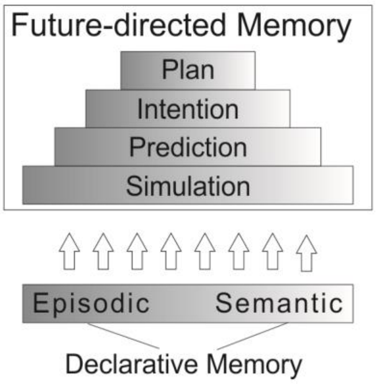

Figure 3 Future-directed memory for plans, intentions, predictions and simulations are structured hierarchically with lower components as necessary features of higher components, e.g. predicting consequences of a future event involves the simulation of this event. Future-directed memories rely on classical long-term memory systems of the past. Episodic and semantic contribution can vary according to the content of the memory. Figure adapted from (Szpunar et al., 2014).

The future-related modes of cognition are conceptualized as to rely on the classical memory systems described above (Szpunar et al., 2014). In fact, similar brain structures are involved when memory is directed to future scenarios compared to past representations (Schacter et al., 2012). To further expand upon breakfast preparation, in order to make breakfast (planning mode), general knowledge about breakfast preparation should be retrieved from the declarative semantic memory system, for example that each person receives a plate. The formation of future-directed memory including its consolidation might underlie the same or at least similar (sleep-related and time of day-related) processes as the formation of classical memories.

Apart from the contribution of memory functions, the successful realization of plans and intentions depends on several other factors like. Factors like motivation (including anticipated cognitive and affective evaluation of an action and perceived self-efficacy) and self-regulation (including self-monitoring, awareness of standards and effort) contribute in getting goal realization started, keeping goal realization going or finalizing an action (Rhodes & de Bruijn, 2013; Sheeran & Webb, 2016; Sniehotta, Scholz, & Schwarzer, 2005). According to the action control framework of Rhodes and de Bruijn´s (2013) these factors are essential for closing the often observed gap between an intention/plan and its realization. The motivation for an action can be influenced for example by the evaluation of the anticipated outcome of this action (Keer, Conner, Van den Putte, & Neijens, 2014). This anticipation is part of the *prediction* mode of cognition (Szpunar et al., 2014). Due to the hierarchic structure of future-directed memories, planning and prospective memory entail the hierarchically lower *prediction* mode. Predicted evaluations can occurs on the cognitive level, e.g. by the anticipation of positive consequences like the usefulness of an action**,** and can occur on the affective level, e.g. by the anticipation of negative feelings of regret (Keer et al., 2014). For instance, individuals basing their intentions more on affective evaluation, i.e. on the anticipated feelings succeeding an action, compared to cognitive evaluation, realize their intentions and plans more efficiently (Keer et al., 2014). Furthermore, strategies of self-regulation influence the success of intention/plan realization. Coping planning, for example, is a strategy for keeping goal realization going, by defining behavior to deviate obstacles, i.e. 'I intend to do behavior A when I encounter obstacle B' (Rhodes & de Bruijn, 2013; Sniehotta, 2009). Likewise, using a diary for self-monitoring one´s progress, is another self-regulation strategy which is effective in supporting intention/plan realization (Harkin et al., 2016; Sheeran & Webb, 2016). Although these influencing factors on intention/plan realization were kept constant in the present studies, it cannot be excluded that they excerpt effects on future-directed memory in the present studies.

Prospective memory

The concept of prospective memory is taken as the first example of future-directed memories. Prospective memory is referred to as the ability to retain intentions and realize them at a specific time in the future. Within Szpunar´s et al. (2014) framework of future-oriented cognition, it is included in the mode of *intention*, which covers different types of intentions including for example goal intentions ('I intend to reach goal X'), behavioral intentions ('I intend to do behavior Y in order to achieve goal X'), implementation intentions ('If situation Z is encountered, then I will initiate goal-directed behavior Y!) (Gollwitzer, 1999; Gollwitzer & Sheeran, 2006; Sheeran & Webb, 2016) and self- and other generated intentions (Armitage, 2009). Prospective memory is the memory for a specific intended behavior bound to the memory for the respective context in which this behavior should be carried out. For example, the memory that 'as soon as the water boils' (reflecting the context), 'I will pour the water in the tea cup' (reflecting the intended behavior)'. Prospective memory is influenced by different factors. For example, a recent meta-analysis shows it benefits from explicit implementation intentions (Chen et al., 2015). Likewise, it has been shown that it is influenced by the affective state, i.e. if individuals find themselves in sad mood (induced by a video clip) while realizing prospective memory, they perform better than in happy mood (Rummel, Hepp, Klein, & Silberleitner, 2012), but habitual negative mood related to depression or anxiety seems to alter prospective memory unfavorably in most occasions (Kliegel & Jäger, 2006).

Prospective memory in the present studies is instructed as behavioral intention including an implementation intention. Furthermore, prospective memory is primarily generated by the experimenter, but in some of the tasks, a delay between instruction and realization requires participants to keep the instruction in memory and remember it at a previously defined occasion.

Prospective memory, in contrast to retrospective memories, is retrieved without any explicit instruction at the correct time. Thus, the realization of prospective memory requires the self-initiated retrieval of an action (Einstein & McDaniel, 2005). If a cue in the environment indicates the appropriate time, this is termed event-based prospective memory, like pouring the water into the tea cup as soon as it has boiled (Altgassen, Koban, & Kliegel, 2012) or pressing a specific button as soon as a certain cue word appears on the screen during a lexical decision task (deciding whether words on the screen are real words or non-existing words) (Scullin & McDaniel, 2010). For time-based prospective memory, the appropriate time for realizing an intention is a specific time in the future, e.g. remembering to remove the teabag after 3 minutes (Altgassen et al., 2012), or pressing a button 20 minutes after the beginning of another task (Esposito, Occhionero, & Cicogna, 2015). Thus, prospective memory realization is often measured by whether specific actions are realized at the right time (e.g. pouring water into the cup or removing a teabag).

Prospective memory usually entails a prospective component, the memory for the fact *that* something has to be done (e.g. remembering that something has to be done as soon as the water has boiled), and a retrospective component, the memory for *what* has to be done (e.g. remembering that the water has to be poured into the cup) (Einstein & McDaniel, 1990). The retrospective component is thus closely linked to the classic retrospective memory systems with episodic and semantic contribution (Figure 3). Another feature of prospective memory is the focality of a prospective memory cue. Focal cues can be recognized by activating the same processes that are required for the ongoing task (e.g. detecting a cue word in an ongoing lexical decision task which also requires word processing), while non-focal cues require different processes than the ongoing task (e.g. detecting a cue syllable embedded in an ongoing lexical decision task) for successful recognition (McDaniel & Einstein, 2000). According to the multiprocess framework, prospective memory can be retrieved either spontaneously, because a cue within the ongoing task activates an intention, or it can be retrieved through the application of attention–based monitoring strategies (Einstein et al., 2005; McDaniel & Einstein, 2000; Scullin, McDaniel, & Shelton, 2013). Monitoring for prospective cues induces 'costs', termed the 'task interference effect', which results in slower reactions to the ongoing task items (Einstein et al., 2005; Hicks, Marsh, & Cook, 2005). Whether one or the other retrieval strategy dominates, depends on factors like the focality of the cue (Cona, Bisiacchi, Sartori, & Scarpazza, 2016; Einstein & McDaniel, 2005; McDaniel & Einstein, 2000) or if the occurrence of a cue is expected or not (Scullin et al., 2013).

Successful prospective memory requires multiple phases, including the formation/encoding, the retention, the initiation and the execution of an intention (Kliegel, Martin, McDaniel, & Einstein, 2002; Kliegel, McDaniel, & Einstein, 2008). The retention phase can be regarded as an analogous phase to the stage of consolidation for memories of the past. During the retention phase, intentions are discussed to be held in a status of heightened activation compared to other information (the 'intention superiority effect'; Goschke & Kuhl, 1993; Marsh, Hicks, & Bink, 1998). Another possibility is that the intended action is stored in memory together with the cue, which announces the realization, thereby forming a cue-action association (McDaniel, Quynn, Einstein, & Breneiser, 2004). Classical executive functions like planning, problems solving, cognitive flexibility and non-verbal fluency contribute to successful prospective memory. During the phase of intention formation, the executive function of planning is required. The phase of intention initiation is marginally associated with the executive function of problem solving. The phase of intention execution is related to cognitive flexibility, planning (marginally) and non-verbal fluency. Yet, during the phase of retention, executive functions seem to play a minor role (Kliegel et al., 2002). Phase-specific neuronal underpinnings of prospective memory can be distinguished. The retrieval of an intention has been shown to activate a ventral fronto-parietal network, the retention of an intention has been shown to activate a dorsal fronto-parietal network (Cona, Scarpazza, Sartori, Moscovitch, & Bisiacchi, 2015; McDaniel, LaMontagne, Beck, Scullin, & Braver, 2013). According to a recent meta-analysis (Cona et al., 2016), another modulator for brain activation is the focality of prospective memory cues. Non-focal prospective memory incorporates more brain regions involved in top-down, attention-based processes, and focal prospective memory activates more regions involved in automatic, bottom-up processes.

Although the different phases in prospective memory have been considered more and more in recent years, the phase of retention has not been investigated thoroughly. The time window for the retention phase has usually been operationalized relatively short in the time range from seconds to minutes, in which a designated ongoing activity is realized (e.g. Altgassen et al., 2012; Esposito et al., 2015; Landsiedel & Gilbert, 2015). Less research has been devoted to longer retention intervals (e.g. Diekelmann, Wilhelm, Wagner, & Born, 2013b; Leong, Koh, Chee, & Lo, 2019; Leong, Koh, Tandi, Chee, & Lo, 2018; Scullin & McDaniel, 2010) and the specific effect of sleep on retention has been addressed in very few studies (Diekelmann, Wilhelm, Wagner, & Born, 2013a; Diekelmann et al., 2013b; Leong, Koh, et al., 2019; Scullin & McDaniel, 2010). This thesis has realized longer retention intervals including other activities than a designated ongoing task for testing the role of sleep in the consolidation of prospective memory and the conditions under which sleep-dependent consolidation occurs (study 1). Shorter retention intervals have been realized for addressing time-of-day effects on prospective memory (study 3).

Planning

Planning is the second concept serving as an example for testing the role of sleep-dependent consolidation on future-directed memories. Within Szpunar´s et al. (2014) framework of future-oriented cognition, it is included via the mode of *planning.* Planning is referred to as ‘the predetermination of a course of action aimed at achieving some goal’ (Hayes-Roth & Hayes-Roth, 1979). Planning can be described as a two-fold function consisting of the act of defining steps that are expected to solve a problem and to carry out these steps (Grafman, 1989; Sorel & Pennequin, 2008). Planning tasks in the laboratory and even more outside the laboratory often incorporate several complex intentions with different overlapping sub-intentions and sometimes one intention being nested in the realization of another. Thus, planning concepts exceed the if-then structure of implementation intentions, yet implementation intentions can be part of a plan, reflecting the hierarchical structure of future-directed cognition (Szpunar et al., 2014).

A typical task assessing planning capabilities is the ‘Tower of Hanoi’, which requires participants to move a pyramid of discs from the first of three pegs to the last peg, following certain rules like for example that just one disk can be moved at a time. Classical planning tasks are often realized immediately after instruction and have been examined in several studies, for example in the elderly (Balachandar, Tripathi, Bharath, & Kumar, 2015; Sorel & Pennequin, 2008) or in patient groups like schizophrenia (Holt, Wolf, Funke, Weisbrod, & Kaiser, 2013; Knapp, Viechtbauer, Leonhart, Nitschke, & Kaller, 2017) or Parkinson’s Disease and in participants with sub-clinical signs of dementia (Köstering, McKinlay, Stahl, & Kaller, 2012). During the immediate realization of a classical planning task, a defined behavior is carried out while the next step is simultaneously being defined. Thus, defining steps and carrying them out is closely interlinked.

In order to realize mental plans after a certain delay successfully, the plans require being encoded, retained in memory and retrieved from memory at a later time for realization. The intermediate stage between encoding and retrieval of information has been conceptualized as ‘consolidation’ for declarative memory and as ‘retention’ for prospective memory. However, to the knowledge of the author of this thesis, an equivalent stage for the retention of plans has not been conceptualized explicitly. The realization of plans and intentions not always occurs immediately. Longer retention intervals inherently include night intervals, such that plans and intentions remain uncompleted throughout sleep episodes. This thesis aims at separating mental planning (i.e. encoding of a plan) from the realization phase (i.e. retrieval stage) and introduces a retention interval of ~12 hours in study 2 after explicit mental planning, in order to address the role of sleep in the consolidation of planned behavior.

Sleep and memory

Sleep is an evolutionary, highly preserved state among the animal kingdom (Siegel, 2008; Vorster & Born, 2015). It is a behavior characterized by reduced reactivity to external stimuli, a typical body posture and by homeostatic regulation (Miyazaki, Liu, & Hayashi, 2017; Tobler, 1995). Its function is still a matter of debate, although a huge variety of candidate theories exist. Among others, sleep saves energy consumption, clears waste products off the brain and serves immunological and cognitive functions (Krueger, Frank, Wisor, & Roy, 2016; Siegel, 2005). Among the cognitive functions, long-term memory formation seems to be specifically dependent on sleep, which has been demonstrated in the last century (Rasch & Born, 2013).

Aserinsky & Kleitman (1953) initialized the revelation of the today known sleep stages with the discovery of rapid-eye movement (REM) sleep: a state distinguished by prompt eye-movements, low muscle tone and wake-like patterns in the electroencephalogram (EEG). In humans, REM sleep can be distinguished from the stages of non-rapid-eye movement (NREM) sleep. Sleep depth increases from NREM sleep stage 1 to sleep stage 4 according to Rechtschaffen & Kales (1986) and from stage 1 to stage 3 according to more recent classification criteria (Iber, Ancoli-Israel, & Quan, 2007). Rechtschaffen & Kales´ (1986) criteria are applied in this work, if not indicated otherwise. In order to better classify sleep, sleep stages are assigned to 30s epochs of recordings in the EEG, electrooculography (EOG) and electromyography (EMG) recordings. Stage 1 describes a transitional state from wake to sleep and from one to another sleep stage. It is characterized by less than 50% of alpha activity (8-13 Hz) (Berry, 2012) and occasionally includes slowly rolling eye movements. Sleep stage 2 is the lightest of the stable NREM sleep stages, with the typical hallmarks of ‘sleep spindles’ (discrete waxing and waning events in the range of 12-14 Hz, < 0.5s) and ‘K-Complexes’ (lower-frequency, high amplitude biphasic deflections, > 0.5s). With increasing sleep depth in sleep stage 3 and 4, lower frequencies in the delta band (< 2 Hz), including the slow oscillations (>1 Hz) (Acherman & Borbély, 1997), become more and more prominent. They comprise between 20% and 50% of an epoch in S3 and more than 50% in S4. These deeper sleep stages, 3 and 4, are termed slow wave sleep (SWS). SWS and REM sleep alternate throughout one night in cycles of approximately 90 minutes with higher portions of SWS during the first half of the night and higher portions of REM sleep during the second half of the night.

Sleep is crucial for effective cognitive functioning, including memory functioning. Acute sleep deprivation impairs the stages of encoding and retrieval of declarative memories (Cousins, Sasmita, & Chee, 2018; Drummond et al., 2000; Yoo, Hu, Gujar, Jolesz, & Walker, 2007) and non-declarative memories (Smith, 1995). Likewise, sleep loss impairs memories directed to the future, like for example prospective memory (Esposito et al., 2015; Fabbri, Tonetti, Martoni, & Natale, 2014; Grundgeiger, Bayen, & Horn, 2013) and planning (Blatter, Opwis, Münch, Wirz-Justice, & Cajochen, 2005; Horne, 1988; Smith, 1995). A study assessing prospective memory in good and in bad sleepers (Fabbri et al., 2014) asked participants to press a button when they went to bed and when they got up. Good sleepers pressed the button more often after waking up than bad sleepers. Two possible explanations could account for this result: Good sleep facilitates reprocessing of the encoded information and thus facilitates the stage of consolidation; or good sleep restores cognitive capacities and thus facilitates the stage of retrieval.

Sleep and memory consolidation

That sleep promotes the stage of memory consolidation, is widely accepted (Diekelmann & Born, 2010; Rasch & Born, 2013). Many studies support the dual-process hypothesis that declarative, hippocampal tasks (e.g. word pair learning) profit more from SWS, while non-declarative tasks (e.g. mirror tracing or word-stem priming), with less or no hippocampal contribution, profited more from REM sleep (Plihal & Born, 1997; Rasch & Born, 2013). This dissociated involvement of SWS and REM sleep has been challenged, since non-declarative tasks also benefit from SWS and other components of NREM sleep like for example stage 2 (Smith, 1995), and declarative tasks also benefit from REM sleep (Rauchs, Desgranges, Foret, & Eustache, 2005). Another view posits that the repeated alternation of SWS and REM sleep prompts memory consolidation. This ‘sequential hypothesis’ or the ‘two-stage model’ suggests that relevant memory traces are sorted from irrelevant ones during

SWS for strengthening and integrating them into existing networks in subsequent REM episodes (Ambrosini & Giuditta, 2001; Fogel, Smith, & Beninger, 2009; Giuditta, 2014; Giuditta et al., 1995).

The two major theories for memory reprocessing during sleep, the 'active system consolidation hypothesis' and the 'synaptic downscaling hypothesis', mainly elaborate on the contribution of SWS. The active system consolidation hypothesis is based on the standard model of systems consolidation and applies primarily to the declarative memory system. It elaborates on the mechanistic contribution of brain oscillations like slow oscillations, sleep spindles and hippocampal ripples (see mechanisms below) to the reprocessing of memories during sleep. This reprocessing not only allows for the quantitative preservation of new memory traces for long-term storage (Rasch & Born, 2013; Walker & Stickgold, 2006), but also enables qualitative changes within memory networks (Landmann et al., 2014) such that the extraction of a gist is facilitated (Lutz, Diekelmann, Hinse-Stern, Born, & Rauss, 2017), rules are generalized (Batterink & Paller, 2017; Fenn, Nusbaum, & Margoliash, 2003), relational inferences can be drawn (Ellenbogen, Hu, Payne, Titone, & Walker, 2007), new insights can be gained (Wagner, Gais, Haider, Verleger, & Born, 2004) and complex problems are more likely to be solved (Beijamini, Pereira, Cini, & Louzada, 2014; Sio, Monaghan, & Ormerod, 2013). The synaptic downscaling hypothesis posits that synaptic strength accumulates throughout episodes of wakefulness due to experience-dependent plastic processes at synapses which are involved during encoding of information. During SWS, these potentiated synapses are renormalized in order to counteract saturation of the brain. The downscaling of synaptic strength allows for reprocessing of encoded information, for efficient encoding of new information and for smooth functioning of the brain in the subsequent period of wakefulness.

Active systems consolidation and synaptic downscaling mechanisms are not necessarily mutually exclusive (Feld & Diekelmann, 2015; Schouten, Pereira, Tops, & Louzada, 2016; Tononi & Cirelli, 2014). An integrative view suggests that downscaling might occur on a global level, in order to normalize synaptic strength, while selected new and relevant synapses might be spared for local reprocessing and for stabilization and integration into pre-existing networks (Tononi & Cirelli, 2014).

Mechanisms of sleep-dependent memory consolidation

Within the framework of the active system consolidation, one core mechanism is the repeated activation of new memory traces during SWS. As described by Wilson & McNaughton (1994), place cells in the hippocampus, which were co-firing during the exploration of a maze, showed a higher probability for repeated co-firing during SWS, speaking in favor of a *replay* of these traces. Such replay can also occur in different brain areas, like for example in the neocortex, thalamus, the striatum, and in motor areas (Euston, Tatsuno, & McNaughton, 2007; Gulati, Ramanathan, Wong, & Ganguly, 2014; Ji & Wilson, 2007; Lansink, Goltstein, Lankelma, McNaughton, & Pennartz, 2009; Lansink et al., 2008; Ribeiro et al., 2004). Replay can be triggered by external cues like odors and tones, if these cues are associated with the newly encoded information and re-applied during sleep, a technique termed cued reactivation or 'targeted memory reactivation' (TMR) (Rasch, Büchel, Gais, & Born 2007, for a recent review see Schouten, Pereira, Tops, & Louzada, 2016). Slow oscillations during SWS act as a pacemaker for this repeated reactivation (Ngo, Martinez, Born, & Mölle, 2013) by grouping spindles and ripples to a functional entity (Latchoumane, Ngo, Born, & Shin, 2017; Mölle, Marshall, Gais, & Born, 2002; Staresina et al., 2015; Wierzynski, Lubenov, Gu, & Siapas, 2009) such that ripples, generated in hippocampus, reach multiple cortical areas for further processing of new memory representations. This fine temporal coordination for a dialogue between hippocampus and neocortical sites seems to be interrupted during periods which lack sleep spindles (Antony et al., 2018). During such periods, memory traces at multiple sites are probably reprocessed locally, without interference from other episodes of reactivation (Antony, Schönauer, Staresina, & Cairney, 2019). Altogether, these mechanisms allow new memory traces to be stored and integrated into pre-existing networks (Rasch & Born, 2013).

Modulators of sleep-dependent memory consolidation

From the conscious stream of incoming experiences, some information will be retained in memory for later use. According to the active systems consolidation theory, the consolidation of these to-be retained memories should occur in a selective way for a parsimonious and efficient functioning of the brain (Rasch & Born, 2013), since the capacity for sleep-dependent consolidation might be limited (Feld, Weis, & Born, 2016; Ngo et al., 2015). Wilhelm and colleagues (Wilhelm, Metzkow-Mészàros, Knapp, & Born, 2012) showed that encoding strength is one modulator of sleep-dependent memory consolidation. While memory traces after medium training intensity are preferentially consolidated during sleep, both shallow and very deep traces (little training vs. very intense training) seem to fail to benefit from consolidation. The emotionality of a stimulus is a second modulator of memory consolidation, which has been shown by a wealth of studies, with memories of high and often negative affective tone being consolidated preferentially over neutral memories (Groch, Wilhelm, Diekelmann, & Born, 2013; Hu, Stylos-Allan, & Walker, 2006; Payne, Chambers, & Kensinger, 2012; Payne et al., 2015; Payne & Kensinger, 2010). Additionally, the explicit encoding of information favors access to memory consolidation during sleep, compared to implicitly encoded information (Robertson, Pascual-Leone, & Press, 2004), which is inherently the case for declarative memories, showing that top-down controlled processes are involved in memory consolidation. Along the same lines, subjects expecting to be rewarded for a specific finger tapping sequence were more efficient in typing this sequence compared to a sequence which was not announced to be rewarded after a period of sleep (Fischer & Born, 2009). The announcement of retrieval alone can act as a modulator of memory consolidation. Subjects remembered a series of words which was expected to be tested after sleep, better than a series of not expected words (Van Dongen, Thielen, Takashima, Barth, & Fernández, 2012; Wilhelm et al., 2011). A recent study investigated the interaction effect of several co-occurring modulators. Bennion, Payne and Kensinger (2016) manipulated, whether information was encoded intentionally (vs. non-intentionally), whether it was rewarded (or not rewarded) and whether it was emotional (vs. neutral). Interestingly, information seems to be prioritized during sleep for consolidation such that intentionally learned and to a lesser degree rewarded information seem to access consolidation more easily than emotional information. How these modulators precisely act in selecting specific memories for consolidation remains not fully understood.

Coherent firing in the theta band during memory encoding in prefrontal and hippocampal areas has been shown to be one possible mechanism underlying the selective consolidation of memories related to expectancy and relevance. Theta coherence might be involved in tagging specific memory representations for later replay during sleep (Benchenane et al., 2010; Rasch & Born, 2013). Similarly, the involvement of the amygdala and the ventral tegmental area during the encoding of emotional and reward-related memories might drive reactivation of these regions during sleep (Paré, Collins, & Pelletier, 2002; Rasch & Born, 2013).

Consolidation of future-directed memories during sleep

Not only rewarded or expected-to-be-tested memories (both declarative and non-declarative forms) benefit from sleep, but also future-directed memories, like for example prospective memory, are consolidated during sleep. Simple intentions benefitted from sleep, such as the intention to remind the experimenter of a specific tasks if he/she forgets the task (Diekelmann et al., 2013b), the intention to detect specific cue words in an ongoing semantic categorization task (Scullin & McDaniel, 2010) or the intention to realize specific actions like switching on an alarm on encountering the word ‘clock’ in an ongoing task (Leong, Koh, et al., 2019). In another study, participants were asked to complete a prospective memory task which entailed both a prospective component and a retrospective component (Diekelmann et al., 2013a). Participants had to detect 20 previously encoded words within an ongoing task, indicating detection by pressing a specific button on the keyboard. This kind of task requires a considerable contribution of the prospective component of prospective memory, i.e. remembering *that* something has to be done. Whenever one word was detected, participants were asked to remember the word which had been learned as an associated word, which covers the retrospective component of prospective memory, i.e. remembering *what* has to be remembered. Participants detected more words and remembered more associated words after a period of sleep, compared to after a period of wakefulness, indicating that not only the retrospective component of prospective memory, which entails a huge declarative memory component, benefits from sleep, but also the prospective component of prospective memory benefits from sleep. The finding that better performance in the prospective component of the task occurred particularly when participants were distracted from the tasks by another side task, hints at the notion that consolidation facilitates memory-driven retrieval of the intentions (Diekelmann et al., 2013a). The finding that particularly semantically related cue-actions are consolidated during sleep, further supports the idea that sleep strengthens the memory for intentions (Leong, Koh, et al., 2019).

The distinguished role of SWS in memory consolidation stated by the active system consolidation hypothesis refers mainly to memories of the declarative system. Recent work showed that future-directed intentions were realized more successfully after SWS-rich sleep than after REM-rich sleep (Diekelmann et al., 2013b) and performance at an announced retrieval test correlated with the amount of SWS (Leong, Koh, et al., 2019; Wilhelm et al., 2011). These findings hint at the notion that SWS-related mechanisms might act on future-directed memories, maybe due to the contribution of the declarative memory system in future-directed cognition (Szpunar et al., 2014). One could speculate that behavioral tagging might be involved in interaction with sleep. Memory representations might be tagged by specific characteristics like reward, emotionality, intentionality or future directedness such that tagged representations would be further processed during sleep by reactivation (according to the active systems consolidation account) and/or by down selection mechanisms (according to the synaptic downscaling account).

Whether other forms of future-directed memory, for example the memory for simulations, predictions and plans, are consolidated during sleep has not been investigated thoroughly. A recent study (Nielsen et al., 2014) showed that planning on the Tower of Hanoi benefits from sleep. Improvements from before to after a night of sleep were greater compared to before to after a period of wakefulness. These changes from before to after sleep were associated with sleep stage S2. Another study by Smith (1995) showed that total sleep deprivation and REM sleep deprivation impaired improvements on the Tower of Hanoi from before a night of sleep to one week later, while awakenings during SWS or an undisturbed night of sleep did not. However, whether planning capabilities benefitted from sleep because the implicit procedural component (non-declarative memory) was consolidated during sleep, whether the memory for the planned activities (future-directed memory with declarative/procedural memory contribution) was consolidated during sleep, or whether another option is true, cannot be disentangled in these studies.

Study 1 and 2 of this thesis will assess the role of sleep in future-directed memory. Study 1 will specifically elaborate on the conditions under which consolidation of prospective memory will occur, i.e. whether the activation state of an intention determines consolidation. Study 2 will specifically focus on memory for plans and whether they are consolidated during sleep.

Time-of-day fluctuations and cognitive functions

Throughout a 24 hour period, the activity of most organisms underlies circadian fluctuations. The bean plant, for example, opens and closes its leaves rhythmically according to daytime and night time hours (Hennessey & Field, 1992), simple animals like for example the fruit fly change their amounts of movements accordingly (Konopka & Benzer, 1971) and more complex animals like squirrel monkeys show rhythmic sleep-wake alternation (Edgar, Dement, & Fuller, 1993). Circadian rhythmicity keeps time for many functions of the organism, including sleep-wake regulation, body temperature, cortisol and melatonin (Moore-Ede, Czeisler, & Richardson, 2010a, 2010b) and even the onset of labor underlies circadian modulation (Jolly, 1972). This adjustment to a near to 24 hour cycle enables organisms to live in their niches, be it a day-active or night-active animal. Cognitive functions in human beings underlie circadian fluctuations in an adaptive way with generally better performance during daytime and reduced functioning throughout the night (Schmidt et al., 2007; Valdez, Ramírez, & García, 2012). Throughout a normal day of wakefulness, cognitive performance increases to a peak approximately in the late morning and declines towards the night (Valdez et al., 2012). These fluctuations in performance are called the ‘time-of-day effect’.

If cognitive performance is required at non-optimal times of the day, this might lead to impaired functioning. Indeed, accidents and injuries are most frequent during night shifts and still increased during afternoon shifts compared to the morning shift (Folkard & Tucker, 2003).

Mechanisms underlying time-of-day effects

The time-of-day effects in psychological measures like attention, executive functions or memory, emerge as a result of a complex interplay between endogenous rhythms and exogenous factors. Endogenous rhythms are driven by a master clock, the suprachiasmatic nucleus (SCN) in the diencephalon, which, using both feed-forward and feed-backward loops builds up and down regulate clock genes throughout a one day cycle (Huang, 2018). This cyclic activity is thought to regulate cyclic activation in all organs and cells of the body (Rosenwasser, 2003, 2009). The most distinct markers of circadian physiology are argued to be the peak, amplitude and period of melatonin levels, core body temperature (Bailey & Heitkemper, 2001; Benloucif et al., 2005) and cortisol levels (Bailey & Heitkemper, 2001). Individual differences in these endogenous rhythms are synchronized to a mean period length close to 24 hours (Czeisler et al., 1999) through the influence of external factors like light, food intake and activity (time cues, originally called 'Zeitgeber' in German). The entrainment of sleep and wakefulness to an about 24-hour rhythm allows most individuals to live in synchrony with the majority of members in a society with optimal performance during daytime and stable sleep episodes during the night. According to the two-process model of sleep-wake regulation (Borbély, 1982; Daan, Beersma, & Borbely, 1984), the cyclic variations in sleep and wakefulness including alternations in sleep propensity are called 'circadian factor' or 'process C'. A second factor influencing sleep-wake regulation constitutes the 'homeostatic factor'. Throughout a period of wakefulness, sleep pressure builds up continuously, increasing the propensity to fall asleep, until a period of sleep - particularly NREM sleep (Achermann, Dijk, Brunner, & Borbély, 1993) - reduces sleep pressure again (Borbély, 1982; Daan et al., 1984). Homeostatic and circadian factors interact as two opponent processes. An increase in sleep pressure throughout the day is counteracted by increasing circadian arousal for maintenance of wakefulness until both processes invert for promoting sleep (Dijk & Czeisler, 1994; Edgar et al., 1993).

Along the lines of sleep-wake regulation, circadian and homeostatic factors (counter-) act on neuropsychological functions like attention, working memory, executive functions and memory (Schmidt et al., 2007). On the one hand, increasing sleep pressure (homeostatic factor) dampens cognitive functions throughout the course of a day (Graw, Kräuchi, Knoblauch, Wirz-Justice, & Cajochen, 2004; Johnson et al., 1992; Wyatt, Ritz-de Cecco, Czeisler, & Dijk, 1999); on the other hand, increasing circadian arousal counteracts this decline and rescues performance levels during daytime (Cajochen, Khalsa, Wyatt, Czeisler, & Dijk, 1999; Johnson et al., 1992; T. Monk et al., 1997; Wyatt et al., 1999). In sum, many neurobehavioral functions oscillate in parallel with the endogenous circadian system. Typically, body temperature and neuropsychological performance increase in synchrony during the morning, peak in the late morning and decline towards the evening with a trough in the night around the nadir of body temperature (Blatter & Cajochen, 2007; Schmidt et al., 2007; Valdez et al., 2012). Synchrony has been shown for instance in attention (Wyatt et al., 1999), in vigilance (Colquhoun, 1971; Kleitman, Titelbaum, & Feiveson, 1938), in working memory (Johnson et al., 1992; Kleitman, 1933; Ramírez et al., 2006) in declarative memory (Cajochen et al., 1999; Krishnan & Lyons, 2015; Wright, Hull, & Czeisler, 2002; Wright, Lowry, & LeBourgeois, 2012; Wyatt et al., 1999) and in procedural memory (Cleeremans & McClelland, 1991). A few studies show that cognitive flexibility, an executive function involved in the execution phase of prospective memory (Kliegel et al., 2002), shows such parallel fluctuations (García, Ramírez, Martínez, & Valdez, 2012; Ramírez, García, & Valdez, 2012). However, the executive function inhibition shows this parallelism only in some studies (García et al., 2012; Ramírez et al., 2012), while others show a more complex and asynchronous pattern (Harrison, Jones, & Waterhouse, 2007). And despite a parallelism, for the phonological and visuospatial components of working memory, a phase delay can be observed in relation to the core body temperature of the endogenous circadian system. The nadir of phonological performance is delayed by about one hour and visuospatial performance is delayed by about three hours, with respect to the nadir of the core body temperature (Ramírez et al., 2006).

Theories explaining fluctuations in cognitive functions focus mainly on fluctuations in circadian arousal. They basically arose from studies on the Psychomotor Vigilance Task (PVT) (Dinges & Powell, 1985), a measure for sustained attention, which requires participants to react to sparse stimuli by pressing a button. The ‘arousal model’ (Colquhoun, 1971; Monk, 1982) argues that arousal levels fluctuate in covariation with cognitive performance throughout a day. Better performance is achieved when arousal is higher and errors occur when arousal is lower, e.g. during the night (Colquhoun, 1971; Monk, 1982). Since different types of tasks peak at different times of day, i.e. phases are shifted depending on the task applied (Valdez et al., 2012; Wright et al., 2002), it seems unlikely that circadian fluctuations in arousal alone constitute the basis of time-of-day effects in cognitive measures (Blatter & Cajochen, 2007). According to the ´lapse model´, arousal eventually breaks down with increasing wakefulness. During such short moments of alpha-wave depression, slow-wave activity emerges and these micro-sleep episodes lead to longer reaction times to stimuli, the omission errors (lapses) (Blatter & Cajochen, 2007; Williams, Lubin, & Goodnow, 1959). The third hypothesis, the ´state instability hypothesis´ (Doran, Van Dongen, & Dinges, 2001; Graw et al., 2004), steps in where the previous cannot explain that performance becomes more diverse with longer sleep deprivation. It argues that with increasing wakefulness, sleep-wake regulation becomes more and more instable, which leads to fluctuations in attention in the time frame of milliseconds to minutes (Doran et al., 2001) and causes not only omission errors (lapses) as stated by the 'lapse hypothesis', but also explains the occurrence of commission errors (reactions to other stimuli than the target stimuli) and the increased variability in performance (Blatter & Cajochen, 2007; Doran et al., 2001; Graw et al., 2004).

In order to disentangle circadian and homeostatic effects, three protocols have been frequently used. The constant routine protocol controls for external factors which potentially mask circadian rhythms during prolonged periods of wakefulness with participants remaining in a semi-recumbent position under constant light, temperature and food supply. The forced desynchrony protocol separates the endogenous rhythm from sleep-wake behavior by exposing participants to artificial day lengths of more or less than 24 hours encapsulated from external Zeitgeber. Both protocols allow for repeatedly testing basal attention measures and even more complex measures like memory retrieval, as long as repeated and frequent testing is possible. Under these two protocols, both a parallelism between the circadian system and cognitive performances and a homeostasis driven decline in performance have been confirmed (Schmidt et al., 2007; Valdez et al., 2012). A third approach, the time of day protocol, assesses performance at different times of a normal working day, e.g. in the morning and in the evening, while a normal sleep-wake rhythm is maintained. The individual circadian rhythm is often accounted for by measuring subjective circadian preference (Schmidt et al., 2007; Valdez et al., 2012). This approach allows for an ecological valid measure of time-of-day and synchrony effects in complex tasks which would suffer from repeated measurement, for example planning or memory tasks. With this protocol, heterogeneous time-of-day effects have been reported (Schmidt et al., 2007). Despite a parallelism with the circadian system (as described above), relatively stable performance levels can be maintained throughout a normal day in some measures, like vigilance (Cajochen et al., 1999; Doran et al., 2001; Graw et al., 2004), retrieval from long-term memory (Folkard & Monk, 1980) and planning performance (Blatter et al., 2005), but this balance might be deflected towards earlier or later performance peaks in some cognitive measures. Short-term memory performance, for example, declines throughout the day (Cajochen et al., 1999; Folkard & Monk, 1980; Johnson et al., 1992).

Modulators of time-of-day effects

Despite the entrainment of endogenous rhythms to approximately 24 hours and despite the parallelism of cognitive measures with the circadian system, inter-individual differences can be observed in the peaks and troughs of physiological and psychological measures during a day of wakefulness. These differences can be explained by a number of modulators like age, sex (Adan et al., 2012) and the chronotype or the circadian preference of a person (Adan et al., 2012; Blatter & Cajochen, 2007). For the early chronotypes, the so-called larks or morning-types, the endogenous rhythm and the preferred timing is shifted early, i.e. they prefer the morning hours for challenging mental or physical activities. For the so-called night owls or evening-types, the endogenous rhythm and the preferred timing is shifted late, i.e. they prefer the evening hours for such activities (Baehr, Revelle, & Eastman, 2000; Bailey & Heitkemper, 2001). Academic performance, for example, is moderated by circadian preference. Morning-type pupils and students, show higher academic performance than evening-type individuals (Enright & Refinetti, 2017; Preckel, Lipnevich, Schneider, & Roberts, 2011; Tonetti, Natale, & Randler, 2015). If cognitive performance measures peak at the optimal time of the day, i.e. in synchrony with the preferred time of the day, this is referred to as the ‘synchrony effect’**.** Inhibitory control, for example, is a measure which peaks in the morning for morning types and in the evening for evening types (May & Hasher, 1998). The same accounts for learning (Lehmann, Marks, & Hanstock, 2013) and verbal memory (Adan, 1991; Hidalgo et al., 2004; Petros, Beckwith, & Anderson, 1990). But this synchrony effect has not been shown consistently across all cognitive domains (Barclay & Myachykov, 2017; Fabbri, Mencarelli, Adan, & Natale, 2013; Matchoock & Mordkoff, 2009). Insight-related problem solving, for example, is better during non-optimal times of day. This might be due to decreased inhibitory control (Wieth & Zacks, 2011), which supports spontaneous processes and thus might facilitate insight.

Thus, the chronotype of an individual might act as an important modulator on time-of-day effects not only on cognitive performance measures but also on future-directed memory, possibly leading to different peaks for owls and larks in prospective memory.

Time-of-day effects in future-directed memory

Until now, only two studies have been published addressing time-of-day or synchrony effects in future-directed memories. These two studies applied prospective memory tasks, which are part of the ‘intention’ mode according to Szpunar et al´s. (2014) taxonomy. Tasks covering the ‘simulation’, ‘prediction’ and the ‘planning’ mode (Szpunar et al. 2014), have not been investigated, so far, to the knowledge of the author. Let alone possible mechanisms like the contribution of the circadian vs. homeostatic factor have been addressed. The assessment of time-of-day effects in more complex cognitive measures like planning or problem solving, belonging to the pool of executive functions, hold specific methodological difficulties. In classical constant routine and forced desynchrony protocols, tasks are realized repeatedly. Specifically in planning and problem solving, a practice effect would interfere with a time-of-day effect. A chronotype-based approach, which applies several measurements during a day of wakefulness while assessing circadian preference, has been applied in the two studies published so far.

One study investigating prospective memory showed a time-of-day effect in a sample of elderly. Medication intake and appointment adherence was better in the morning compared to midday and remained stable in the evening (Leirer, Tanke, & Morrow, 1994). This coincides with the preference for morning hours in the elderly. A more recent study by Rothen and Meier (2016) compared prospective memory performance (detecting words in a categorization task) in younger and older adults, taking into account the chronotype of the participants, which has been operationalized by whether testing took place at the preferred (on-peak) or the not-preferred (off-peak) time-of-day. Results for older adults showed that prospective memory was comparable at preferred and at not-preferred times of day, speaking against a synchrony effect. In contrast, prospective memory in younger participants was better on-peak, namely performance was better in the evening, the time which is usually the preferred time of day in young subjects (Adan et al., 2012). The authors interpret these results as a synchrony effect. However, the better performance in the evening could likewise be a time-of-day effect, due to imbalanced distribution of the preferred times of day. Younger participants were mostly evening types and thus the categorization ‘on-peak’ mainly overlapped with assignment to the evening group, whereas the categorization ‘off-peak’ mainly overlapped with the assignment to the morning group.

Study 3 of this thesis assesses time-of-day effects on prospective memory in a variety of tasks with different characteristics regarding the number of prospective tasks, the focality of the task, the complexity of the ongoing tasks and the type of prospective memory (event- vs. time-based). By taking into account the modulators circadian preference, and attentional resources, potential synchrony effects and retrieval strategies (attention-based vs. memory-based) can be assessed.

Objectives and expected output of the thesis

The aim of this thesis is to focus on the complex concept of future-directed memory and the effects sleep and circadian rhythmicity exert on it. Future-directed memory is operationalized by two concepts addressed in the Szpunar et al. (2014) taxonomy of prospection. The first concept is prospective memory, the memory for intentions to be completed in the future, the second concept is planning behavior (*intention* mode and *planning* mode of prospection according to Szpunar et al. (2014)).

Hypotheses	
Study 1	
Experiment 1	Completed intentions are not consolidated during sleep.
Experiment 2	Reinstated completed intentions are consolidated during sleep.
Experiment 3	Intentions that are instructed in temporal proximity to the learning situation and expected to be completed after sleep, are consolidated during sleep.
Study 2	Plans are consolidated during sleep.
Study 3	Intentions show a time-of-day effect and a synchrony effect with a benefit for evening hours specifically under reduced attention.

Since it has been shown that sleep consolidates prospective memory, the first study of this thesis is to shed light on the conditions under which these intentions are consolidated during sleep. More specifically, I ask if the activation state of an intention, i.e. whether the intention is active or no longer active, modulates the consolidation of the intention during sleep. The first of three experiments of the first study aims at answering the question, whether prospective memory, which is no longer relevant for the future, still benefits from sleep. It is expected that completed intentions do not benefit from sleep. If results show so, we ask in the second experiment, whether intentions can be activated again by a second instruction for a sleep benefit. Due to the unexpected finding that intentions cannot be re-activated for sleep consolidation (at least with the instruction we applied), we further asked, in the third experiment, if intentions benefit from sleep, when they are completed and reinstructed just like in the previous experiment, but with an additional instruction right in the beginning announcing that the intention should be completed after sleep. With this, the intention should be active throughout the whole experiment and we expect that the completion and reinstruction before sleep should not prevent the sleep effect anymore. In other words, we expect a consolidation effect in the third experiment.

Since the beneficial effect of sleep on future-directed memory has been shown for relatively simple prospective memory tasks, the second study of this thesis investigates whether more complex intentions benefit from sleep by applying a relatively complex and naturalistic planning task. It is expected that plans are consolidated during sleep just like prospective memory and many other forms of classical memory.

Circadian rhythms have been proven to affect many cognitive functions like vigilance, attention, working memory and declarative memory (Schmidt et al., 2007; Valdez et al., 2012). However, little is known about the diurnal variations in future-directed memories, which will be tackled in the third study of this thesis. More precisely, a variety of prospective memory tasks with different characteristics regarding the number of prospective tasks, the focality of the task, the complexity of the ongoing tasks and the type of prospective memory, were applied at two different times of day to investigate circadian effects. Since young and healthy subjects tend to prefer evening hours with delayed circadian arousal and later peaks in cognitive performance, we expect that future-directed memory in our young and healthy sample is more successful in the evening hours irrespective of task characteristics. In order to account for the multiple mediators and moderators affecting time-of-day effects, we manipulated the attentional resources available for completing the prospective memory task (in one of the tasks) and assessed the chronotype of participants, as two examples of such influencing factors. We expect a drop in performance especially in the evening, as soon as attention is deflected away from the prospective memory task.

STUDY I

CONSOLIDATION OF PROSPECTIVE MEMORY:

EFFECT OF SLEEP ON COMPLETED AND REINSTATED INTENTIONS

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Abstract

Sleep has been shown to facilitate the consolidation of prospective memory, which is the ability to execute intended actions at the appropriate time in the future. In a previous study, the sleep benefit for prospective memory mainly expressed as preserved prospective memory performance under divided attention as compared with full attention. Based on evidence that intentions are only remembered as long as they have not been executed yet (cf. 'Zeigarnik effect'), here we asked whether the enhancement of prospective memory by sleep vanishes if the intention is completed before sleep and whether completed intentions can be reinstated to benefit from sleep again. In Experiment 1, subjects learned cue-associate word pairs in the evening and were prospectively instructed to detect the cue words and to type in the associates in a lexical decision task (serving as ongoing task) 2 h later before a night of sleep or wakefulness. At a second surprise test two days later, sleep and wake subjects did not differ in prospective memory performance. Specifically, both sleep and wake groups detected fewer cue words under divided compared to full attention, indicating that sleep does not facilitate the consolidation of completed intentions. Unexpectedly, in Experiment 2, reinstating the intention, by instructing subjects about the second test after completion of the first test, was not sufficient to restore the sleep benefit. However, in Experiment 3, in which subjects were instructed about both test sessions immediately after learning, sleep facilitated prospective memory performance at the second test after two days, evidenced by comparable cue word detection under divided attention and full attention in sleep participants, whereas wake participants detected fewer cue words under divided relative to full attention. Together, these findings show that for prospective memory to benefit from sleep, (i) the intention has to be active across the sleep period, and (ii) the intention should be induced in temporal proximity to the initial learning session.

Introduction

Sleep facilitates the consolidation and subsequent recall of newly encoded memories (Diekelmann & Born, 2010; Paller & Voss, 2004; Rasch & Born, 2013; Stickgold, 2005). Memories which are relevant for future behavior benefit particularly from sleep. Emotional information, for example, is retained better across sleep compared to wake periods than neutral information, with some studies even reporting an additional memory boost for emotional content after sleep at the expense of reduced memory for neutral contents (Payne et al., 2012; Payne, Stickgold, Swanberg, & Kensinger, 2008; Payne & Kensinger, 2010, 2011). Others found that sleep improves memory consolidation only when subjects expect to be tested on the learned material after sleep, whereas no sleep benefit is evident for memories that are not expected to be tested again (Van Dongen et al., 2012; Wilhelm et al., 2011). When manipulating the relevance of memories by announcing a reward for good performance at testing after sleep, subjects show better performance for a task for which they expected to be rewarded than for a task for which they did not expect any reward, with this difference being only evident after sleep but not after an equivalent interval of wakefulness (Fischer & Born, 2009).

These findings suggest that sleep facilitates memory consolidation selectively if the memory content is regarded as important for the individual and as potentially useful for future actions. Prospective memory is the type of memory that is inherently future-directed, being defined as the ability to execute an intended action at the appropriate time in the future (Ellis, 1996). Scullin and McDaniel (2010) were the first to demonstrate that delayed event-based prospective memory, i.e., the ability to perform an intended action upon detection of a prospective memory cue after a longer time interval, is improved by a period of sleep during the retention interval. In this study, subjects were asked to detect two different cue words, each presented once in three different ongoing tasks after an interval of 12 hours either filled with sleep or wakefulness. After the sleep interval, subjects detected the cue words more efficiently compared to the wake period, suggesting that sleep facilitated prospective memory cue detection. In another study by Diekelmann and colleagues (Diekelmann et al., 2013b), using a more naturalistic prospective memory task, subjects were told a cover story, in which they were asked to pay attention that at the test session two days later, a vigilance task that they were required to perform was presented in a specific color, which was allegedly a sign for the correct version of the task. Subjects were told that sometimes the experimenter can make a ‘mistake’ and start the wrong task version and in this case, subjects should immediately report the mistake. For subjects who were allowed to sleep after this instruction, the probability to detect the experimenter´s ‘mistake’ at testing was twice as high as for subjects who had stayed awake after formation of the intention (Diekelmann et al., 2013b). A second experiment of this study tested whether the beneficial effect of sleep depended on a specific sleep stage. Higher probabilities to detect the ‘mistake’ were seen after an early slow wave sleep (SWS)-rich sleep period but not after a late rapid eye movement (REM) sleep-rich period, indicating that the beneficial effect of sleep for prospective memory performance is dependent on SWS rather than REM sleep (Diekelmann et al., 2013b). To date this is the only study examining the role of single sleep stages for prospective memory, and thus, these findings will have to be confirmed in future studies.

Recent evidence further suggests that sleep supports different aspects and processes of prospective remembering (Diekelmann et al., 2013a). Prospective memory includes two sub-components: the ability to remember *that* something has to be done (the prospective component or *intent*), and the ability to remember *what* has to be done (the retrospective component or *content*) (Einstein & McDaniel, 1990, 1996; Kliegel, McDaniel, et al., 2008). Moreover, prospective remembering can be accomplished applying either resource-dependent environmental monitoring strategies or automatic spontaneous retrieval processes (McDaniel & Einstein, 2000). According to the monitoring account, attentional resources are needed to keep the intention actively in mind and to search the environment for cues that indicate the correct time and place to execute the intention (Smith, 2003; Smith & Bayen, 2004). Spontaneous retrieval, on the other hand, can occur when the association between the cue and the intended action is strong enough such that the encounter of a cue in the environment automatically brings to mind the associated intention (McDaniel et al., 2004). The ‘dynamic multiprocess framework’ suggests that monitoring and spontaneous retrieval processes interact dynamically to support successful prospective remembering, with one or the other process prevailing depending on the individual, the context and the task demands (Gilbert, Hadjipavlou, & Raoelison, 2013; Scullin et al., 2013).

A study by Diekelmann and colleagues (2013a) indicated that sleep after the instruction of an intention improves both the prospective component and the retrospective component of prospective memory and facilitates the use of spontaneous associative retrieval processes to retrieve the intention. In this study, subjects learned 20 cue words, each of which was linked to a specific associated word. After a delay of two days, which was filled with a night of sleep or wakefulness and a second (recovery) night of sleep, subjects had to detect the cue words during a lexical decision task, serving as ongoing task, and to type in the associated word upon detecting a cue word. After sleep compared to wakefulness, subjects were more likely to execute the intention, by detecting at least one cue word. Sleep subjects also detected more cue words than wake subjects (prospective component) and remembered more associated words upon cue detection (retrospective component). Interestingly, higher cue detection in sleep subjects was only observed under divided attention conditions when attentional resources were reduced, suggesting that after sleep, subjects were able to rely to a larger extent on spontaneous retrieval processes rather than on attentional monitoring. These findings indicate that sleep strengthens the intentional memory trace and particularly the association between the cue and the associated intention allowing for the automatic activation of the intention upon cue detection.

Building on these findings and based on evidence that sleep preferentially benefits memories that are relevant for future behavior, here we asked whether sleep facilitates intentions only as long as they are active across the retention interval, with the sleep effect vanishing once the intended actions have been completed. In everyday life, it is highly functional to forget or even actively inhibit intentions upon their completion in order to free resources for new plans and intentions as well as to prevent commission errors, i.e. the erroneous execution of intentions that were already executed (Pink & Dodson, 2013; Scullin & Bugg, 2013; Scullin, Bugg, & McDaniel, 2012; Walser, Fischer, & Goschke, 2012). For example, inadvertently taking certain medication twice can be highly dangerous for the individual. Once an intention has been realized, the memory for the intended action vanishes, an effect known as the Zeigarnik effect (Mäntylä & Sgaramella, 1997; Zeigarnik, 1927). Upon completion of an intention, the monitoring of the environment for cues that are associated with the intended action, is discontinued (Beck, Ruge, Walser, & Goschke, 2014; Scullin, Einstein, & McDaniel, 2009), which is associated with the deactivation of brain areas that are engaged in monitoring processes during the active phase of the intention (Beck et al., 2014). Whether the reported effect of sleep on prospective memory is abolished once an intention has been completed is currently unknown. It also remains an open question, whether intentions can be reinstated for sleep-dependent consolidation after their completion. We hypothesized that intentions do no longer benefit from sleep when they are completed before the sleep interval and are thus no longer relevant for future behavior. Additionally, we expected completed intentions to benefit from sleep again when they are reinstated after completion, making them again relevant for later testing. To test these questions, we performed three consecutive experiments, all of which were based on our previously published findings described above (Diekelmann et al., 2013a; from now on called “Basic experiment”).

Experiment 1: Intention completed

Our Basic experiment (Diekelmann et al., 2013a) established that sleep facilitates the ability to execute an intended action at the appropriate time after a delay of two days (see Figure 4A for the experimental design). Most interestingly, subjects who were allowed to sleep after intention formation detected more cues in the ongoing task at the delayed test session specifically under divided attention conditions. Sleep and wake subjects performed equally well in cue detection when they had full attentional resources available. With reduced attentional resources, however, cue detection was markedly impaired in wake subjects but remained completely unaffected in sleep subjects (see Figure 5A), suggesting that sleep strengthened the cue-intention association thereby favoring spontaneous retrieval processes. However, from these data it remains unclear whether the sleep effect is specific for the memories associated with the intention or whether sleep simply non-selectively strengthens memories in the associative network that were encoded shortly before sleep. Here we manipulated the intentional status of the memories by having the intended action completed before the sleep interval. Specifically, we asked whether the beneficial effect of sleep vanishes when the intended behavior is completed before sleep and thus, the intention is no longer relevant.

Subjects performed on the same task with the same instruction as in the Basic experiment (Diekelmann et al., 2013a) (Figure 4). However, a first test session took place in the evening 2 hours after instruction of the prospective memory task, before one group of subjects went to sleep (*n* = 18) whereas the other stayed awake the following night (*n* = 15; Figure 4B). During the first test session, subjects already completed the intention. To ensure that the intention was no longer active during subsequent sleep, participants were told immediately after this test session that they *would not* have to do this task again. Nevertheless, a second test session occurred unexpected to the subjects two days later, like in the Basic experiment. Based on evidence indicating that sleep selectively strengthens memories of relevance for future behavior (Fischer & Born, 2009; Wilhelm et al., 2011), we hypothesized that the improving effect of sleep on prospective memory would disappear when the intended behavior is completed before sleep. Specifically, sleep should no longer facilitate the storage of the cue-intention association, thus, both sleep and wake subjects would be expected to rely to a larger extent on monitoring processes and should therefore to the same extent be impaired in cue detection under divided attention.

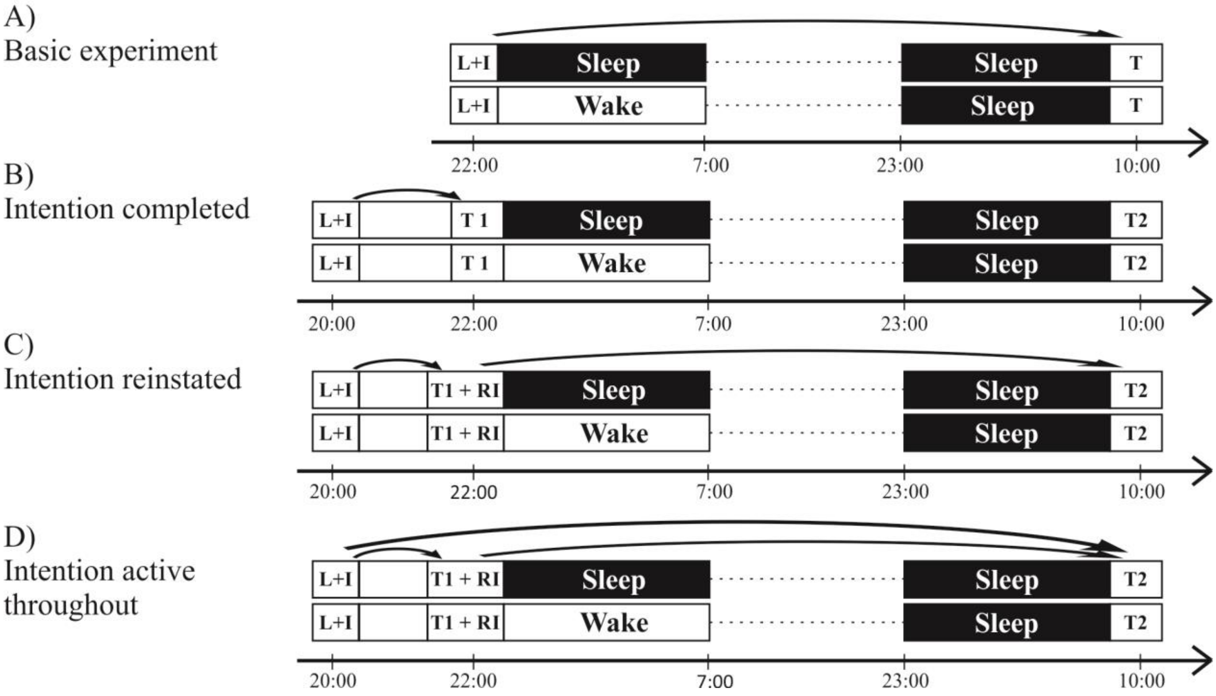


Figure 4 Experimental design **A)** In our Basic experiment (Diekelmann et al., 2013a), learning (L) and instruction of the intention (I) took place in the evening (~22.00 h), before a night of sleep (sleep group) or wakefulness (wake group). Subjects were instructed that they would be tested (T) on their prospective memory two days later after an additional night of (recovery) sleep. **B)** In Experiment 1 (Intention completed), learning took place at ~20.00 h. Thereafter, participants were instructed that they would be tested on their prospective memory two hours later (T1). Following a night of sleep or wakefulness and another recovery night, a second surprise test took place in the morning (T2). **C)** In Experiment 2 (Intention reinstated), participants learned and were instructed for the first prospective memory test (T1) two hours later, like in Experiment 1. After the first test, the intention was reinstated (RI) by instructing subjects that they would be tested on their prospective memory again two days later (T2). **D)** In Experiment 3 (Intention active throughout), learning took place like in Experiments 1 and 2. After learning, subjects were instructed that they would be tested on their prospective memory twice, once in two hours (T1) and a second time two days later (T2). Following the first test, subjects received a reminder instruction (RI) for the second test. Arrows indicate which test session(s) the different instructions are directed at.

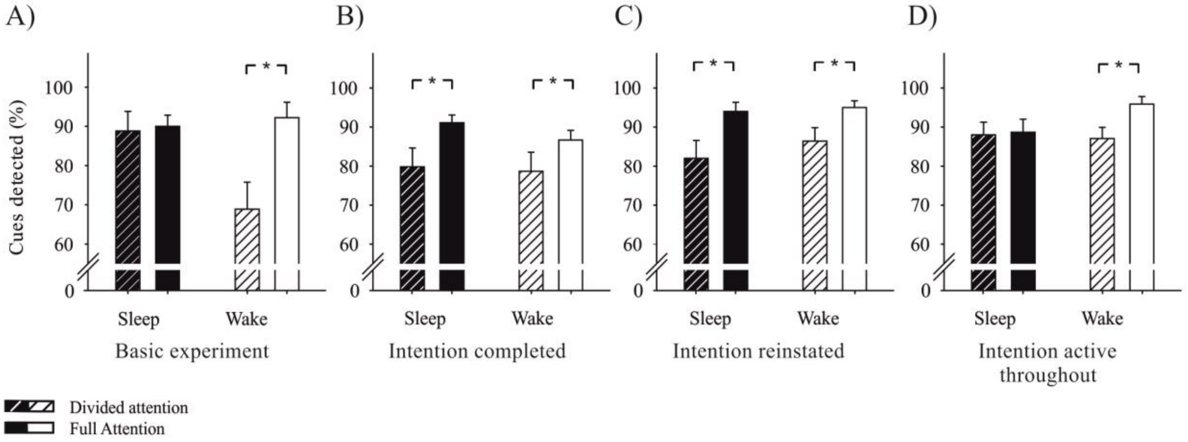


Figure 5 Effects of sleep on prospective memory. **A)** In our Basic experiment (Diekelmann et al., 2013a), sleep participants detected a comparable number of cues under full attention and under divided attention conditions, whereas wake participants were markedly impaired in cue detection under divided attention. **B)** With the intention completed before sleep in Experiment 1, both sleep and wake subjects showed impaired prospective memory performance, i.e., diminished numbers of cues detected, under divided attention. **C)** Reinstatement of the intention after its completion in Experiment 2 did not suffice to reinstate the sleep benefit. Both sleep and wake subjects were impaired in cue detection under divided attention. **D)** When the intention was active throughout the entire experimental period in Experiment 3, i.e., when subjects expected both test sessions from the beginning, sleep benefitted prospective memory despite the first completion of the intention before sleep. While wake subjects detected less cues under divided attention compared to full attention, sleep subjects were not impaired by divided attention. Means ± standard errors of the means (SEM) are shown. * $p < 0.05$

Methods

Participants

A total of 33 subjects (19 females, mean age [± standard deviation (SD)]: 21.94 ± 2.97), with regular sleep-wake cycles (≥ 6 hours sleep per night) and no shift work for at least six weeks prior to the experiments participated in Experiment 1. Subjects reported no history of any neurological, psychiatric or endocrine disorder and did not take any medication at the time of the experiments. Ingestion of caffeine and alcohol was not allowed from the day before until the end of the experiments and subjects were instructed to stay awake during the day after the sleep/wake night. Prior to the experimental night, subjects spent one adaptation night in the sleep laboratory. All subjects gave written informed consent and were paid for participation. The study was approved by the local ethics committee of the University of Lübeck.

Design and procedure

All subjects reported to the laboratory at 19:30 h, filled in questionnaires, underwent the initial learning session at 20:00 – 20:45 h and received the prospective memory instruction thereafter (Figure 4B). Subjects then watched a non-disturbing movie until they were informed about whether they were assigned to the sleep or the wake group. In the sleep condition, electrodes were attached for standard polysomnographic recordings, including EEG (at sites C3 and C4), EOG and EMG. Polysomnographic recordings were visually scored offline according to standard criteria (Rechtschaffen & Kales, 1986). The first test session took place between 22:00 – 22:30 h. In the sleep condition, subjects then went to bed for regular sleep between 23:00 – 07:00 h, whereas subjects in the wake condition stayed awake throughout the night, spending the time with reading, watching TV or playing simple games. Subjects in both conditions left the laboratory the next morning. After spending the day awake and another night of sleep at home, allowing the subjects in the wake condition to recover from their initial sleep loss, they returned to the laboratory for the second test session at 10:00 h the following day. Subjects kept record of their activities and their bedtime and wake-up time for the night of sleep at home.

Prospective memory task

The same prospective memory task as in our Basic experiment (Diekelmann et al., 2013a) was applied. Participants were required to detect cues (i.e., specific cue words) and perform associated actions (i.e., recall associated second words) in an ongoing task (i.e., lexical decision task; Figure 6). In the initial learning session, subjects first practiced the lexical decision task (serving as ongoing task later) without any prospective memory cues. Subjects were presented in a random sequence with 100 word stimuli, half of which were existing German words. The other half were 'non-words' which were derived from German words by substituting one consonant (Marsh, Hicks, Cook, Hansen, & Pallos, 2003; Marsh, Hicks, & Watson, 2002). Subjects were instructed to press as fast and as accurately as possible the right key (on a keyboard) for correct words and the left key for non-words (with the respective index finger). After practice on the lexical decision task, subjects learned 20 cue–

associate word pairs for the subsequent prospective memory task. Half of the word pairs were semantically related, e.g. *Genie – Bottle*, and half were not semantically related, e.g. *Season – Master* (however, since semantic relatedness did not affect memory measures differentially for the sleep and wake group, related and unrelated word pairs were combined in all analyses). Subjects learned the cue words first separately from the associated words. Cue words were presented successively for 5 sec each with 1-sec breaks in between. After presentation of all cue words, subjects recalled the words in a free recall test. Presentation and free recall was repeated to a criterion of 90% (i.e., 18) correctly recalled cue words to ensure that all subjects would perfectly recognize the cue words in a recognition test and prospective memory retrieval would not depend on how well cue words had been learned (see also Diekelmann et al., 2013a). The 90% criterion in the free recall test was chosen based on pilot studies indicating that this criterion produced practically perfect performance on the word recognition test. After learning of cue words, subjects learned the respective associated words for each cue word. Word pairs were presented successively for 5 sec each with a 1-sec break in between. For each word pair, the cue word was presented on the left side of the screen and the associated word on the right side of the screen. After all word pairs had been presented once, a cued recall test followed in which subjects upon presentation of each cue word were required to press first the ‘space’ bar, then a field opened on the screen where they should type in the corresponding associated word. After pressing ’enter’, the next cue word appeared without feedback about the correctness of the previous response. If subjects did not achieve the criterion of 60% (i.e., 12) correctly recalled associated words, all word pairs were presented again for re-learning, followed by another cued recall test. Presentation of the word pairs and cued recall was repeated until subjects met the 60% learning criterion. The 60% criterion was chosen based on previous studies indicating maximal effects of sleep on consolidation of word pair memories at this criterion (Drosopoulos, Schulze, Fischer, & Born, 2007).

The prospective memory instruction was given after the learning phase. Subjects were informed that, apart from testing their lexical discrimination abilities, we were also interested in their ability to remember to do something in the future. For this purpose, some of the cue words they had just learned would occasionally appear within the lexical decision task when they would be tested again. Subjects were instructed that the test would take place 2 h later that same evening. They were instructed that when they detected a cue word within the lexical decision task at this test they should press the 'space' bar and then a field would open where they should type in the associated word, confirm with 'enter' and continue with the lexical decision task. Subjects had to repeat this instruction in their own words to ensure full understanding. They were explicitly instructed to memorize this instruction because at the test session the experimenter would *not* remind them of what to do.

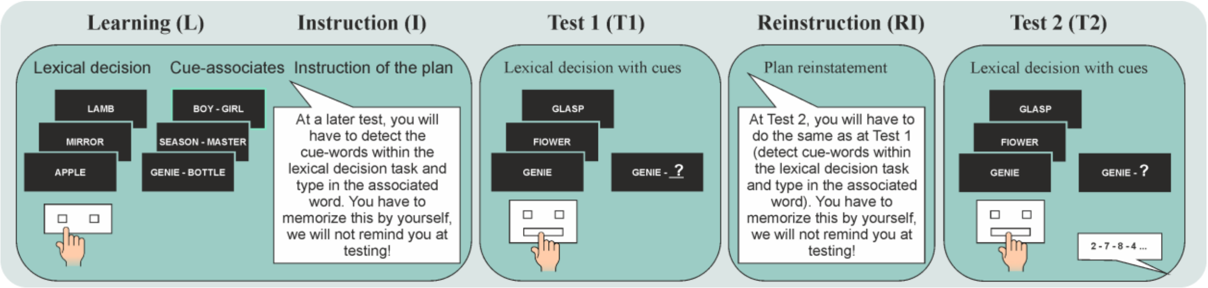


Figure 6 Prospective memory task. In all experiments, subjects took part in a learning session, during which they practiced on the lexical decision task and learned 20 cue-associate word pairs. The instruction of prospective memory (I) differed for the different experiments. In Experiment 1 (Intention completed), subjects were instructed that at a test session in 2 h (Test 1), some of the 20 cue words could occur within the lexical decision task and if they recognized a cue word they should press the 'space' bar and type in the respective associated word. Subjects were explicitly told that they need to memorize this instruction because the experimenter would not remind them of what to do at the test session. After Test 1, subjects did not receive another reinstruction (RI) but Test 2 took place 2 days later as a surprise test. Test 2 was identical to Test 1, except that in order to manipulate available attentional resources, subjects performed a secondary task in parallel (monitoring spoken digits for two consecutive even digits) either during the first or second half of the lexical decision task. In Experiment 2 (Intention reinstated), participants followed the same protocol as in Experiment 1 (Intention completed), with the only difference that after Test 1, subjects received a reinstruction of the intention (RI) in which they were told that they would have to perform on the task again in a second test session 2 days later (Test 2). In Experiment 3 (Intention active throughout), the protocol was identical to that of Experiment 2 (Intention reinstated), with the only exception that during the initial instruction (I), subjects were told that they would have to perform on the task twice, in test session 1 after 2 h and in test session 2 after 2 days. Like in Experiment 2 (Intention reinstated), they received an additional reinstruction (RI) for Test 2 after completion of Test 1. In our Basic experiment (Diekelmann et al., 2013a), participants were tested for their prospective memory only once after 2 days (Test 2), with this test being instructed (I) immediately after the learning session

In the test session 2 h later, subjects performed the lexical decision task without being reminded of the instructed intention. The lexical decision task during testing contained 390 word stimuli, i.e., 185 real words, 185 non-words, and the 20 learned cue words. Cue words were presented every 16th to 20th word (mean: 18th). A break was made after half of the words had been presented. After this first test session subjects were told that during the second test session after two days they would have to perform on completely different tasks for another part of the study. Thus, they would not have to do the prospective memory task again. The second test session, however, was basically identical to the first test session. Yet, subjects were explicitly instructed in the second test session to detect the cue words and type in the associated words, as they did not expect another test of the previous task. Note that this procedure in fact corresponds to the standard assessment of prospective memory where subjects are explicitly instructed before testing and prospective memory performance is quantified by the subject's ability to detect cues during a distracting ongoing task. In order to test whether subjects used a relatively resource-demanding monitoring strategy or a relatively resource-independent spontaneous-associative retrieval strategy, we directly manipulated available attentional resources during the second test session: during one of the halves of the task (balanced across subjects) the subjects performed in parallel an auditory attention task in which spoken digits were presented via loudspeakers at a rate of one digit every two seconds. The subjects were required to press a separate key whenever two even digits occurred consecutively.

Control tasks

In the end of the two test sessions, i.e., after the first test in the evening as well as after the second test two days later, memory for the cue words was tested in a recognition test. The 20 cue words were presented randomly mixed with 40 distractor words (not presented before) and subjects had to indicate for each word if it was a cue word or new. Additionally, memory for the associated words was tested in a cued recall. Each cue word was presented on the screen and subjects had to recall the respective associated word. No feedback was given on whether or not their response was correct. To control for general alertness and vigilance, all subjects performed on a vigilance task for the duration of five minutes before learning and after the two test sessions. In this task, a dot randomly appeared at the left or right side of a computer screen every 2–10 seconds and participants had to respond as quickly as possible by pressing the corresponding left or right button. Because vigilance data were missing for two subjects in the wake group and from one subject in the sleep group, the available sample size added up to $n = 17$ (sleep group) and $n = 13$ (wake group) for the analyses of this task. Subjects also rated their subjective sleepiness on the Stanford Sleepiness Scale before learning and after the test sessions, ranging from 1 ("feeling active, vital, alert, or wide awake") to 7 ("no longer fighting sleep, sleep onset soon; having dream-like thoughts") (Hoddes, Zarcone, Smythe, Phillips, & Dement, 1973). Furthermore, after the second test session, all subjects completed a questionnaire to assess rehearsal of the prospective memory instruction and rehearsal of the cue-associate pairs during the retention interval as well as the use of strategies to remember the instruction and the cue-associates. For the final cue recognition test and the cued recall of the associated words, one data set of the wake group was missing, thus analyses included $n = 14$ participants in the wake group and $n = 18$ participants in the sleep group.

Statistical analysis

All variables were analyzed using analyses of variance (ANOVA) and post-hoc *t*-tests. Additionally, non-parametric post-hoc tests (i.e., Mann-Whitney U-Test and Wilcoxon-Test) were used when deviations from the normal distribution occurred. Level of significance was set to $p = .05$. Greenhouse-Geisser correction for degrees of freedom was applied where appropriate.

Results

Prospective memory task performance

With the intention completed before sleep, sleep did no longer improve the prospective component of prospective memory at testing after two days. At the second test session, subjects in the sleep group detected 91.11 ± 1.96% of the cue words without the secondary task and 80.00 ± 4.64% with the secondary task to be performed in parallel ($z = 2.55$, $p = 0.01$, $d = 0.76$). Wake subjects detected 86.67 ± 3.47% and 78.67 ± 4.87% ($z = 2.39$, $p = 0.02$, $d = 0.51$) of the cue words without and with the secondary task, respectively (main effect 'with/without secondary task': $F(1, 31) = 14.00$, $p < 0.001$, $\eta_p^2 = 0.31$; main effect 'sleep/wake': $F(1, 31) = 0.35$, $p = 0.56$; 'sleep/wake' x 'with/without secondary task' interaction: $F(1, 31) = 0.37$, $p = 0.55$;

Figure 5B). Thus as expected, divided attention by the secondary task during the second test session impaired cue detection in the sleep group to the same extent as in the wake group.

Completing the intention before sleep also prevented the beneficial effect of sleep on the retrospective component of prospective memory. Relative to the number of cues detected, sleep subjects remembered 63.90 ± 3.89% of the associated words and wake subjects remembered 68.51 ± 4.26%, $F(1, 31) = 0.64$, $p = 0.43$ (for main effect 'sleep/wake', Supplementary Figure S1B) at the second test, which was independent of attentional resources available, $F(1, 31) = 0.01$, $p = 0.92$, for the interaction 'sleep/wake' x 'with/without secondary task'; $F(1, 31) = 0.46$, $p = 0.50$, for main effect 'with/without secondary task'.

Initial learning performance of cue words and associated words was comparable between the sleep and wake group. Subjects in the sleep and wake group remembered 19.00 ± 0.20 and 18.73 ± 0.18 cue words in the criterion learning trial, $U = 111.00$, $z = -.93$, $p = .38$, and needed on average 2.33 ± 0.20 and 2.33 ± 0.19 trials to reach the criterion, $U = 131.50$, $z = -.14$, $p = .92$. Recall of associated words was 15.83 ± 0.54 and 15.67 ± 0.60 in the criterion learning trial, $t(31) = 0.21$, $p = 0.84$, with a mean of 1.22 ± 0.13 and 1.13 ± 0.09 learning trials, $U = 129.50$, $z = -.32$, $p = .86$, in the sleep and wake group, respectively. Likewise, performance during the first completion of the prospective memory task in the evening was comparable between the sleep and wake group. Sleep and wake participants detected 84.72 ± 4.84% and 86.67 ± 2.87% of cue words, $U = 128.50$, $z = -.24$, $p = .82$, and they remembered 69.25 ± 3.79% and 64.90 ± 3.86% of associated words relative to the number of correctly detected cue words, $t(31) = .80$, $p = 43$.

Ongoing task performance

Sleep and wake subjects did not differ in lexical decision task performance at learning, at the first test in the evening and at the second test after two days (Table 1; trials without the secondary task for reaction time: main effect 'sleep/wake': $F(1,31) = .00$, $p = .97$, main effect 'learning/test1/test2': $F(1.66,51.54) = 5.75$, $p = .008$, interaction 'sleep/wake' x 'learning/test1/test2': $F(1.66,51.54) = 0.28$, $p = .72$; for error rate: main effect 'sleep/wake': $F(1,31) = .92$, $p = .35$, main effect 'learning/test1/test2':

$F(1.62,50.06) = 2.48$, $p = .11$, interaction ‘sleep/wake’ x ‘learning/test1/test2’: $F(1.62, 50.06) = 3.19$, $p = .06$). Sleep and wake subjects both responded significantly faster at the second test in comparison to the learning session and the first test in the evening (learning vs. second test: $t(32) = 2.50$, $p = .02$, $d = 0.25$; first test vs. second test: $t(32) = 3.29$, $p < .01$, $d = 0.34$; learning vs. first test: $t(32) = -1.25$, $p = .22$), while the error rate did not change over time.

Table 1. Ongoing task performance

	Intention completed		**Intention reinstated**		**Intention active throughout**	
	Sleep	**Wake**	**Sleep**	**Wake**	**Sleep**	**Wake**
Reaction time						
Learning	1215 ± 71	1238 ± 52	1081 ± 47	1006 ± 59	979 ± 55	1229 ± 66
Test 1	1285 ± 67	1294 ± 64	1200 ± 48	1064 ± 53	1090 ± 55	1279 ± 75
Test 2						
Full attention	1159 ± 64	1119 ± 73	1109 ± 52	1021 ± 58	1016 ± 54	1222 ± 59
Divided attention	1580 ± 70	1537 ± 70	1367 ± 33	1421 ± 74	1420 ± 84	1610 ± 66
Error rate						
Learning	4.83 ± 0.57	6.07 ± 1.26	4.54 ± 1.03	4.86 ± 0.86	5.80 ± 1.01	4.36 ± 0.75
Test 1	4.74 ± 0.63	3.73 ± 0.44	3.90 ± 0.72	4.45 ± 0.41	5.11 ± 0.71	4.39 ± 0.72
Test 2						
Full attention	3.23 ± 0.47	5.28 ± 1.01	3.65 ± 0.60	4.33 ± 0.71	4.94 ± 1.04	3.66 ± 0.80
Divided attention	4.51 ± 0.42	6.27 ± 1.21	5.48 ± 0.77	6.30 ± 1.07	5.39 ± 0.85	5.75 ± 1.23

Reaction times (in ms) and error rates (in %) in the lexical decision task during learning, test 1, and test 2. For test 2, measures are provided separately for full attention and divided attention. Means ± SEM are shown.

In the second test session, performing the secondary auditory attention task in parallel slowed down reaction times for lexical decisions in both sleep subjects and wake subjects (for main effect ‘with/without secondary task’: $F(1,31) = 198.20$, $p < .001$, $\eta_p^2 = 0.87$, for ‘sleep/wake’ main effect: $F(1,31) = .20$, $p = .66$, for ‘sleep/wake’ x ‘with/without secondary task’: $F(1,31) = .00$, $p = .97$), and increased error rates (for main effect ‘with/without secondary task’: $F(1,31) = 6.89$, $p = .013$, $\eta_p^2 = 0.18$, for main effect ‘sleep/wake’: $F(1,31) = 3.37$, $p = .08$, for ‘sleep/wake’ x ‘with/without secondary task’: $F(1,31) = .10$, $p = .75$), confirming that the secondary auditory attention task put a high load on attentional resources.

Control tasks

The final cue recognition test at the end of the second test session confirmed that both sleep and wake participants had almost perfect retrospective memory for the cue words (recognition accuracy: sleep, 99.07 ± 0.34%; wake, 97.86 ± 0.77%; $U = 97.00$, $z = -1.25$, $p = .24$). Moreover, sleep and wake participants did not differ in cued recall of the associated words (sleep: 64.44 ± 3.61%, wake: 67.86 ± 4.15%; $t(30) = -.62$, $p = .54$). Sleep and wake subjects were overall comparable in their performance on the vigilance task regarding reaction time (for main effect ‘sleep/wake’ $p = .78$, for interaction ‘sleep/wake’ x ‘learning/test1/test2’ $p = .97$, for main effect ‘learning/test1/test2’ $p < .01$, $\eta_p^2 = .23$) and error rate (for main effect ‘sleep/wake’ $p = .78$, for interaction ‘sleep/wake’ x ‘learning/test1/test2’ $p = .26$, for main effect ‘learning/test1/test2’ $p = .80$) as well as in subjective sleepiness (for main effect 'sleep/wake' $p = .13$, for main effect ‘learning/test1/test2’ $p < .001$, $\eta_p^2 = .44$, for interaction ‘sleep/wake’ x ‘learning/test1/test2’ $p = .21$), despite generally lower vigilance performance (all $p < .04$) and higher sleepiness ratings at the first test in the evening ($p < .001$) for all subjects irrespective of group (Table 2). Subjects in the sleep group also displayed normal sleep patterns during the night following the first test session (Table 3).

Table 2. Vigilance and subjective sleepiness

	Intention completed		Intention reinstated		Intention active throughout	
	Sleep	**Wake**	**Sleep**	**Wake**	**Sleep**	**Wake**
			Vigilance performance			
Reaction time						
Learning	348 ± 12	345 ± 10	412 ± 13	418 ± 11	420 ± 12	426 ± 9
Test 1	359 ± 13	355 ± 11	421 ± 14	446 ± 13	419 ± 12	434 ± 8
Test 2	337 ± 11	331 ± 10	406 ± 10	424 ± 11	405 ± 12	426 ± 7
Error rate						
Learning	4.41 ± 0.73	4.62 ± 0.84	3.5 ± 0.64	3.93 ± 0.63	1.83 ± 0.45	2.03 ± 0.57
Test 1	3.82 ± 0.94	4.42 ± 0.58	3.5 ± 0.64	3.57 ± 0.97	2.50 ± 0.65	2.34 ± 0.66
Test 2	5.00 ± 0.91	3.46 ± 0.67	3.17 ± 0.57	3.04 ± 0.54	2.33 ± 0.86	2.50 ± 0.82
			Subjective Sleepiness			
Learning	2.33 ± 0.20	2.00 ± 0.20	2.93 ± 0.23	2.21 ± 0.30	2.53 ± 0.26	2.47 ± 0.15
Test 1	3.56 ± 0.25	2.87 ± 0.26	3.93 ± 0.25	5.50 ± 1.50	4.07 ± 0.25	3.29 ± 0.22
Test 2	2.11 ± 0.21	2.07 ± 0.18	2.27 ± 0.21	2.86 ± 0.29	1.93 ± 0.12	3.00 ± 0.27

Vigilance performance (reaction times in ms and error rates in % of all trials) and subjective sleepiness (Stanford Sleepiness Scale) during learning, test 1 and test 2. There were no significant differences between respective groups in both experiments. Means ± SEM are shown.

Table 3. Sleep parameters

Sleep stage	Intention completed	Intention reinstated	Intention active throughout
Sleep time	447.81 ± 8.03	446.43 ± 10.69	439.33 ± 8.60
W	6.94 ± 1.50	8.60 ± 3.07	13.37 ± 2.60
S1	19.69 ± 2.61	20.85 ± 2.45	27.87± 4.12
S2	233.89 ± 6.20	240.30 ± 8.75	237.70 ± 8.69
SWS	79.50 ± 6.71	76.93 ± 5.84	72.03 ± 7.60
REM	104.56 ± 4.16	108.30 ± 6.19	101.03 ± 6.09

Sleep time (total sleep time), W (wake), S1 (sleep stage 1), S2 (sleep stage 2), SWS (slow wave sleep, i.e., the sum of sleep in stages 3 and 4 sleep) and REM (rapid eye movement sleep) in minutes. Means ± SEM are shown.

Discussion

As expected, Experiment 1 showed that a period of sleep following an already completed intention does not improve the ability to implement the behavior when participants are asked to perform the prospective memory task again two days later. As hypothesized, participants in both the sleep and wake group detected significantly less cues when their attention was reduced by a secondary auditory task compared to the full attention condition, supporting the notion that both sleep and wake subjects relied to a greater extent on resource-intensive monitoring rather than spontaneous retrieval for cue detection. We suggest that after completing the intention, with the knowledge that the intended actions do not have to be performed again, sleep no longer fosters the storage of the associations between the cues and the intended actions in the associative memory network, such that after sleep, subjects rely to a lesser extent on automatic activation of the intention upon encounter with the cues. These findings are consistent with the Zeigarnik effect demonstrating that memories of uncompleted actions are better retained than memories of already completed actions (Mäntylä & Sgaramella, 1997; Zeigarnik, 1927). In combination with our Basic experiment, which showed a sleep effect for uncompleted intentions (Diekelmann et al., 2013a), these results indicate that an intention, for profiting from sleep, needs to be active over the sleep period and thus, needs to be relevant for future behavior.

Experiment 2: Intention reinstated

Experiment 1 showed that sleep no longer facilitates the ability to execute an intended action after a delay of two days when the intention has already been completed before the night of sleep or wakefulness. In everyday life, however, completed intentions can become relevant again. For example, a person might form the intention to water the flowers in her flat. After completing this intention, she might renew the intention to water the flowers again two days later. This raises the question, whether it is possible to reinstate a completed intention to make it sensitive for sleep-dependent consolidation processes again. In Experiment 2, we examined the effect of sleep on intentions that were completed and then reinstated before sleep or wakefulness.

Subjects performed on the same task with the same instruction as in Experiment 1, i.e., subjects completed the intention 2 h after the initial intention formation. However, after the first test session the intention was reinstated by instructing the subjects that they would have to do the task again at a second test session two days later (Figure 4C, Figure 6). Following this instruction, one group of subjects went to sleep (*n* = 15) whereas the other group stayed awake (*n* = 14) the following night like in Experiment 1. We hypothesized that the improving effect of sleep on prospective memory performance would reappear with the intention being reinstated before sleep. Specifically, sleep should again facilitate the storage of the cue-intention associations, such that after sleep, subjects would be expected to rely to a larger extent on spontaneous retrieval and should be less impaired in cue detection under divided attention compared to wake subjects.

Methods

Participants

A total of 29 healthy young adults (19 females, mean age [± SD]: 22.69 ± 2.98), were included in the analysis of Experiment 2. Criteria for subjects to participate in the study were as in Experiment 1. In total, 4 sleep subjects and 9 wake subjects had to be excluded. Nine participants were excluded due to problems with the protocol (3 participants talked about the experiment, 3 participants did not detect any of the cue words in the first test session, one participant slept for 2.5 hours during the day after the experimental night, one participant got sick during the experimental night, and one participant exceeded the pre-defined body-mass-index cut-off of 25). Four outliers had to be excluded due to very poor prospective memory performance during the second test (more than 2 SD below the overall mean). All subjects gave written informed consent and were paid for participation. The study was approved by the local ethics committee of the University Tübingen.

Design and procedure

The experimental design and procedure was identical to Experiment 1, with the only exception that after the first test session in the evening, subjects were instructed, that they would have to complete the task again two days later and that they would have to keep this instruction in mind because the experimenter would not remind them of what to do at the second test session (Figure 4C).

Prospective memory task

Tasks and materials were identical to Experiment 1 (intention completed) except that subjects after the first test session were instructed about the second test two days later (Figure 6). Although subjects expected the second test by then, they were still explicitly instructed before the second test session to detect the cue words and to type in the associated words in the lexical decision task, in order to ensure comparable conditions with Experiment 1.

Control tasks and statistical analyses were as for Experiment 1.

Results

Prospective memory task performance

Reinstating the intention after completion of the task before sleep did not suffice for sleep to improve cue detection in the prospective memory task. Subjects in the sleep group detected 94.00 ± 2.35% of the cue words without the secondary task and

82.00 ± 4.60% with the secondary task to be performed in parallel ($z = -2.57$, $p = .01$, $d = 0.88$). Wake subjects detected 95.00 ± 1.74% and 86.43 ± 3.41% ($z = -2.17$, $p = .03$, $d = 0.88$) of cue words without and with the secondary task, respectively (main effect ´with/without secondary task´: $F(1,27) = 16.51$, $p < .001$, $\eta_p^2 = .38$; main effect ´sleep/wake´: $F(1,27) = .50$, $p = .49$; ´sleep/wake´ x ´with/without secondary task´ interaction: $F(1,27) = .46$, $p = .50$; Figure 5C). Thus, divided attention impaired cue detection in the sleep group to the same extent as in the wake group, similar to Experiment 1, suggesting that reinstating the intention before sleep did not make the intention subject to sleep-dependent consolidation processes again.

Reinstating the completed intention also did not affect the sleep benefit on the retrospective component of prospective memory. Relative to the number of cues detected, sleep subjects at the second test remembered 71.61 ± 4.42% of the associated words and wake subjects remembered 74.56 ± 4.58%, $F(1,27) = .22$, $p = .65$ (for main effect ´sleep/wake´, Supplementary Figure S1C), which was independent of attentional resources available, $F(1,27) = .01$, $p = .94$ for the interaction ´sleep/wake´ x ´secondary task´ and $F(1,27) = .16$, $p = .69$ for main effect ´with/without secondary task´.

As in Experiment 1, learning performance of cue words and associated words was comparable between groups. Subjects in the sleep and wake group remembered 18.47 ± .17 and 18.71 ± .22 cue words in the criterion learning trial ($U = 89.00$, $z = -.78$, $p = .45$), and needed on average 2.53 ± .19 and 2.71 ± .30 trials to reach the criterion ($U = 96.00$, $z = -.39$, $p = .72$). Recall of associated words was 15.93 ± .71 and 17.00 ± .55 in the criterion learning trial, $t(27) = -1.18$, $p = .25$, with a mean of 1.27 ± .12 and 1.36 ± .13 learning trials, $U = 95.50$, $z = -.52$, $p = .70$, in the sleep and wake group, respectively. During the first completion of the task in the evening, subjects were comparable in prospective memory task performance. Sleep participants detected 82.33 ± 2.84% of cue words and wake participants detected 85.36 ± 3.53% ($U = 79.00$, $z = -1.16$, $p = .26$). Relative to the number of correctly detected cue words, both groups were also comparable in the number of remembered associated words (sleep: 67.58 ± 4.81%, wake: 75.50 ± 3.44%; $t(27) = -1.32$, $p = .20$).

Ongoing task performance

Sleep and wake subjects did not differ in lexical decision performance at learning, at the first test as well as at the second test (Table 1; without the secondary task: main effect ‘sleep/wake’ for reaction time $F(1,27) = 2.13$, $p = .16$, for error rate $F(1,27) = 0.33$, $p = .57$, interaction ‘sleep/wake’ x ‘learning/test1/test2’ for reaction time $F(1.54, 41.57) = 0.76$, $p = .44$, for error rate $F(1.50, 40.49) = 0.07$, $p = .89$). Like in Experiment 1, reaction times changed across time, independent of sleep and wake conditions (main effect ‘learning/test1/test2’ $F(1.54, 41.57) = 6.08$, $p = .009$, $\eta_p^2 = .18$). All subjects slowed down responses from the learning to the first test session and accelerated their reaction time again from the first to the second test session (learning vs. first test: $t(28) = -4.84$, $p < .001$, $d = 0.45$; first test vs. second test: $t(28) = 2.35$, $p = .03$, $d = 0.34$; learning vs. second test: $t(28) = -0.72$, $p = .48$). Error rates did not change over time (main effect ‘learning/test1/test2’ $F(1.50, 40.49) = 1.12$, $p = .32$).

Performing the secondary auditory attention task in parallel during the second test session slowed down reaction times for lexical decisions in both sleep subjects and wake subjects (for main effect ´with/without secondary task´: $F(1,27) = 76.28$, $p < .001$, $\eta_p^2 = 0.74$; for ´sleep/wake´ main effect: $F(1,27) = .06$, $p = .80$, for interaction ´with/without secondary task´ x ´sleep/wake´: $F(1,27) = 3.49$, $p = .07$), and increased error rates (for main effect ´with/without secondary task´: $F(1,27) = 31.07$, $p < .001$, $\eta_p^2 = 0.54$; for main effect ´sleep/wake´: $F(1,27) = .49$, $p = .49$, for interaction ´with/without secondary task´ x ´sleep/wake´: $F(1,27) = .05$, $p = .83$).

Control tasks

The final cue recognition test after the second test session confirmed, like in Experiment 1, that sleep and wake participants almost perfectly recognized all of the cue words (recognition accuracy: sleep 99.00 ± 0.56%, wake 99.52 ± .21%, $U = 98.00$, $z = -.38$, $p = .87$). Memory for the associated words in the cued recall was also comparable in the sleep and wake group (sleep 72.33 ± 4.28%, wake 78.57 ± 3.69%, $t(27) = 1.10$, $p = .28$). Like in Experiment 1, sleep and wake subjects were also comparable in performance on the vigilance task (reaction times and error rates) as well as in reported sleepiness during learning and both test sessions (for main effect ‘sleep/wake’ and interaction ‘sleep/wake’ x ‘learning/test1/test2’: all $p > .10$, Table 2), despite generally slower reaction times and higher sleepiness ratings at the first test in the evening for all subjects (for main effect ‘learning/test1/test2’: reaction time $p < .001$, $\eta_p^2 = 0.29$; sleepiness $p = .003$, $\eta_p^2 = 0.27$; error rate $p = .60$). Subjects in the sleep group also displayed normal sleep patterns during the night following the first test session (Table 3).

Discussion

Experiment 2 examined the possibility to reinstate completed intentions for a sleep-dependent improvement. Contrary to our hypothesis, a period of sleep following intention reinstatement did not facilitate the ability to execute the intended action after a delay of two days. Like in Experiment 1, participants in both the sleep group and the wake group detected less cues in the ongoing task when their attention was reduced by the secondary auditory attention task, suggesting that both groups relied to a larger extent on monitoring and sleep subjects were not able to recruit on less resource-dependent spontaneous retrieval processes to detect cue words.

This finding indicates that reinstating an intention after its completion does not make the intentional memory trace gain access to sleep-dependent memory processing. Instructing participants to do the task again two days later, with this instruction being provided only after having completed the task, does not seem to be sufficient to reinstate the intention for the enhancing effects of sleep. One possible explanation for this failure is that the reinstatement took place too long after the original learning experience. The execution of intentions has been suggested to depend on a link formed between the intention and the context in which the intention is expected to be executed (Marsh, Hicks, & Cook, 2006), with this context effect being most evident when the intention-context link is formed during initial encoding of the intention (Nowinski & Dismukes, 2005). Similarly, Scullin and colleagues (2010) observed a sleep effect on prospective memory only in the context, i.e., the ongoing task, which was temporally paired with the prospective memory instruction during the learning session. Scullin and colleagues (2010) argued that the intention-context association is strengthened by consolidation processes during sleep, which then facilitates subsequent spontaneous retrieval processes. Based on this evidence, it can be speculated that in the present paradigm the intention must be formed in close proximity to the initial learning session in order for sleep to strengthen the memory representations of the cue-associate relations.

Experiment 3: Intention active throughout

Experiments 1 and 2 established that (i) sleep no longer benefits the execution of intentions when these intentions are already completed before sleep, and (ii) instructing subjects for the second test session after completion of the intention in the first test session is not sufficient to reinstate the sleep benefit. Importantly, in Experiments 1 and 2, the prospective memory instruction given after the learning session was only directed at the first test session 2 h after learning, but this instruction never included the second test session two days later. In Experiment 2, the reinstatement of the intention took place after the first test session, that is, about 2 h after the end of the initial learning session and the initial prospective memory instruction. Considering that sleep might act to strengthen the intentional cue-associate connection that is formed in the learning context, 2 h of time difference between the reinstatement of the intention and the initial encoding of the cue-associates might have been too long in order to link the renewed intention to the previously learned cue-associate word pairs. Accordingly, in Experiment 3 we tested whether completed intentions benefit from sleep if the subjects are instructed about both test sessions (the first one after 2 h and the second one after 2 days) immediately after the learning session, such that the intention for the second delayed test is formed in temporal proximity to the cue-associate learning context and is active throughout the entire experimental period.

The same task and setup was used as in Experiments 1 and 2. However, after the learning session, subjects were instructed that they would have to do the task two days later, with this delayed test session being introduced as the main part of the experiment. In addition, subjects were told that they would have to complete the task once already in 2 h, for practice purposes. After the first test session, the instruction for the second test session was repeated to keep the procedure comparable with Experiment 2 (Figure 4D). After this instruction, one group of subjects went to sleep (*n* = 15) whereas the other stayed awake the following night (*n* = 17). We expected that with the intention active across the entire retention interval and the intention being formed in close proximity to the initial learning, sleep would strengthen the intentional association between the cues and the associated actions. Therefore, we hypothesized that after sleep, subjects would rely to a larger extent on spontaneous retrieval and would be less impaired in cue detection under divided attention conditions compared to wake subjects.

Methods

Participants

A total of 32 healthy young adults (16 females, mean age [± SD]: 22.91 ± 2.72) were included in the analysis of Experiment 3. Inclusion and exclusion criteria were identical to Experiments 1 and 2. Overall 4 participants of the sleep group and 2 participants from the wake group had to be excluded. One participant showed pathological sleep with a REM sleep-onset latency of 5.5 min and one participant slept for 2 h during the day after the experimental night. Four outliers had to be excluded due to poor prospective memory performance during the second test session (more than 2 SD below the overall mean). All subjects gave written informed consent and were paid for participation. The study was approved by the local ethics committee of the University Tübingen.

Design and procedure

The experimental design and procedure were identical to Experiment 1, with the only exception that this time, immediately after the learning session, subjects were instructed that there would be two test sessions during which they would have to complete the instructed intention (Figure 4D).

Prospective memory task

Tasks and materials were identical to Experiments 1 and 2, except that subjects after the learning session were instructed about both test sessions (Figure 6). With this instruction, they were told that they would have to detect the cue words and type in the associated words at the test session in 2 days and for practice purposes also in 2 h before the night of sleep or wakefulness. They were instructed that for both test sessions they would have to keep this instruction in mind because the experimenter would not remind them of what to do. Although subjects expected the second test, they were still explicitly instructed before the second test session to detect the cue words and type in the associated words in the lexical decision task, in order to ensure comparable conditions with Experiments 1 and 2.

Control tasks

Control tasks were identical to Experiments 1 and 2. Because vigilance data were missing for one subject in the wake group, the available sample size was $n = 15$ (sleep group) and $n = 16$ (wake group) for the analyses of the vigilance task. For the final cue recognition test and the cued recall of the associated words, data of one subject in the sleep group was missing, thus analyses included $n = 14$ participants in the sleep group and $n = 17$ participants in the wake group for these data.

Statistical analyses were as in Experiments 1 and 2.

Results

Prospective memory task performance

As expected, with the intention instructed immediately after the learning session, sleep improved the detection of cued words in the lexical decision task under divided attention conditions. Subjects in the sleep group detected 88.67 ± 3.36% of cue words without the secondary task and 88.00 ± 3.27% with the secondary task to be performed in parallel ($z = -.38$, $p = 1$). Wake subjects, on the other hand differed in cue detection when they had to perform the secondary task in parallel. They detected 95.88 ± 1.93% of cues without and 87.06 ± 2.68% with the secondary task ($z = -2.28$, $p = .02$; ´sleep/wake´ x ´with/without secondary task´ interaction: $F(1,30) = 4.58$, $p = .04$, $\eta_p^2 = 0.13$; main effect ´sleep/wake´: $F(1,30) = .81$, $p = .38$; main effect ´with/without secondary task´: $F(1,30) = 6.21$, $p = .02$, $\eta_p^2 = 0.17$; Figure 5D).

Although descriptively on a higher level, the retrospective component of prospective memory was not significantly improved by the sleep manipulation. Relative to the number of cues detected, sleep subjects at the second test remembered 71.01 ± 3.97% of the associated words and wake subjects remembered 66.55 ± 3.73%,

$F(1,30) = .67$, $p = .42$ (for main effect ´sleep/wake´, Supplementary Figure S1D), which was independent of attentional resources available, ($F(1,30) = 2.54$, $p = .12$ for the interaction ´sleep/wake´ x ´secondary task´ and $F(1,30) = .02$, $p = .90$ for the main effect ´with/without secondary task´).

As in Experiments 1 and 2, learning performance of cue words and associated words was comparable between groups. Subjects in the sleep and wake group remembered 19.00 ± .22 and 18.59 ± .21 cue words in the criterion learning trial ($U = 92.00$, $z = -1.44$, $p = .175$), and needed on average 2.33 ± .19 and 2.71 ± .29 trials to reach the criterion ($U = 105.00$, $z = -.96$, $p = .35$). Recall of associated words was 15.73 ± .67 and 15.00 ± .66 in the criterion learning trial ($U = 104.00$, $z = -.90$, $p = .38$) with a mean of 1.27 ± .12 and 1.35 ± .12 learning trials ($U = 116.50$, $z = -.52$, $p = .71$) in the sleep and wake group, respectively. During the first completion of the task in the evening, sleep and wake participants did not differ in prospective memory performance. Sleep subjects detected 84.00 ± 3.69% of cue words and wake subjects detected 87.65 ± 4.87% ($U = 96.00$, $z = -1.22$, $p = .23$). Relative to the number of correctly detected cue words, sleep and wake subjects remembered 68.82 ± 3.69% and 68.25 ± 3.83% of the associates, $t(30) = .11$, $p = .92$.

Ongoing task performance

In the lexical decision task, subjects in the sleep group showed overall faster reaction times than the wake group (Table 1; main effect ‘sleep/wake’: $F(1, 30) = 6.94$, $p = .01$, $\eta_p^2 = 0.19$), which was consistent across learning and both test sessions (interaction ‘learning/test1/test2’ x ‘sleep/wake’: $F(2,60) = 0.89$, $p = .42$). Additionally, independent of sleep and wake conditions, subjects slowed down in their reaction time from the learning to the first test session ($t(31) = -3.48$, $p < .01$) and showed faster reaction times again from the first to the second test session ($z = -2.67$, $p < .01$), while the learning session and the second test session did not differ ($z = -.69$, $p = 50$; main effect ‘learning/test1/test2’: $F(2,60) = 6.59$, $p = .003$, $\eta_p^2 = 0.18$). Error rates in the lexical decision task did not differ between groups (for main effect ‘sleep/wake’: $F(1,30) = 1.26$, $p = .27$; for main effect ‘learning/test1/test2’: $F(1.39, 41.80) = 1.08$, $p = .33$; for interaction ‘sleep/wake’ x ‘learning/test1/test2’: $F(1.39, 41.80) = .26$, $p = .69$).

Performing the secondary auditory attention task in parallel during the second test session slowed down reaction times for lexical decisions in both sleep subjects and wake subjects (for main effect ´with/without secondary task´: $F(1,30) = 182.12$, $p < .001$, $\eta_p^2 = 0.86$; for interaction ´with/without secondary task´ x ´sleep/wake´: $F(1,30) = .07$, $p = .79$), again with sleep subjects overall responding faster (main effect ´sleep/wake´: $F(1,30) = 4.90$, $p = .04$, $\eta_p^2 = 0.14$). Divided attention by the secondary task also increased the error rates in the sleep group as well as in the wake group (for main effect ´with/without secondary task´: $F(1,30) = 8.03$, $p < .01$, $\eta_p^2 = 0.21$, for main effect ´sleep/wake´: $F(1,30) = .12$, $p = .74$, for interaction ´with/without secondary task´ x ´sleep/wake´: $F(1,30) = 3.31$, $p = .08$).

Control tasks

Like in Experiments 1 and 2, the final cue recognition test at the second test session confirmed that sleep and wake participants almost perfectly remembered all of the cue words (recognition accuracy: sleep 99.81 ± 0.41%, wake 99.41 ± .20%, $U = 95.50$, $z = -1.07$, $p = .32$). Sleep and wake participants were also comparable in final cued recall of the associated words (sleep 73.21 ± 3.65%, wake 70.29 ± 3.22%, $t(29) = -.60$, $p = .55$). Likewise, sleep and wake subjects did not differ in their performance in the vigilance task (for reaction time and error rate: main effects 'sleep/wake' and interactions 'sleep/wake' x 'learning/test1/test2' $p > .30$, Table 2), despite generally slower reaction times for all subjects at the first test session in the evening, like in Experiments 1 and 2 (main effect 'learning/test1/test2': for reaction time $p = .03$, $\eta_p^2 = 0.21$; for error rate $p = .61$). The sleep and wake groups differed in subjective sleepiness at the first test session ($U = 72.00$, $z = -2.19$, $p = .03$) and the second test session ($U = 52.00$, $z = -3.11$, $p < .01$), with the sleep participants being more sleepy at test 1 (sleep: 4.07 ± .24, wake: 3.29 ± .23) and less sleepy at test 2 (sleep: 1.93 ± .23, wake: 3.00 ± .21). Sleepiness levels at learning were comparable between groups ($U = 125.50$, $z = -.09$, $p = .93$; interaction: ´learning/test1/test2´ x ´sleep/wake´: $F(2,60) = 12.68$, $p < .001$, $\eta_p^2 = 0.30$; main effect: ´learning/test1/test2´: $F(2,60) = 28.14$, $p < .001$, $\eta_p^2 = 0.48$; main effect: ´sleep/wake´: $F(1,30) = .12$, $p = .74$). Finally, subjects in the sleep group displayed normal sleep patterns during the night following prospective memory instructions (Table 3).

Discussion

In accordance with our hypothesis, Experiment 3 showed that sleep benefits the ability to execute an intention that has been completed once before sleep, when subjects are instructed about the delayed prospective memory test immediately after the initial learning session. Thus, sleep facilitates the delayed execution of the intention if the intention is formed in close temporal proximity to the learning of the cue-associates and if subjects know from the beginning that they have to execute the intention again two days later. In this case, relative to performance under full attention, sleep subjects were not impaired in cue detection under divided attention conditions. Wake subjects, on the other hand, differed in performance under divided attention and full attention, with a relatively lower performance when the attention was reduced. This pattern of results suggests that sleep subjects were able to rely to a larger extent on spontaneous retrieval processes to detect the cues, while wake subjects depended more on attention-based monitoring strategies. With the intention being formed in close proximity to the learning session, sleep presumably strengthened the link between the intention and the cue-associate representations in the memory network allowing for an automatic activation of the intention upon encountering the cue words.

The finding that wake participants generally showed slower reaction times in the lexical decision task was unexpected. Importantly, this difference was evident across all sessions, i.e., wake subjects already performed slower during the learning session and the first test session in the evening, excluding the possibility that slower reaction times were due to the wakefulness manipulation. Sleepiness is unlikely to explain the differences in lexical decision reaction times because wake subjects showed slower reaction times throughout all sessions but only displayed lower sleepiness than the sleep group at the first test session and higher sleepiness at the second test session. Moreover, sleepiness was not significantly correlated with reaction times in the lexical decision task, neither at test 1 (sleep: *r* = .43, *p* = .11, wake: *r* = -.30, *p* = .25) nor at test 2 (sleep: full attention, *r* = .03, *p* = .91, divided attention, *r* = -.15, *p* = .61; wake: full attention, *r* = .07, *p* = .79, divided attention, *r* = .15, *p* = .58). Importantly, sleepiness at the second test session did also not significantly correlate with the number of cues detected under full attention (sleep: *r* = -.50, *p* = .06, wake: *r* = .21, *p* = .42) as well as under divided attention (sleep: *r* = -.40, *p* = .15, wake: *r* =

.25, p = .33). Finally, reaction times in the lexical decision task were not associated with the number of cues detected at test 1 (sleep: r = -.04, p = .90, wake: r = .09, p = .73) and at test 2 (sleep: full attention, r = .32, p = .24, divided attention: r = .48, p = .07; wake: full attention, r = .43, p = .09, divided attention, r = -.17 p = .52), indicating that sleepiness and reaction times in the lexical decision task did not affect the number of cues detected.

On a descriptive level, wake subjects in Experiment 3 overall performed very well in cue detection, such that in the full attention condition their performance was above the average of around 90%, and in the divided attention condition they performed on a level comparable with the sleep participants. Although this difference was not significant (all p > .07), it is in contrast to our Basic experiment (Diekelmann et al., 2013a) where under divided attention wake participants performed significantly worse than sleep participants. It could be speculated that this high performance level in wake subjects was due to subjectively higher sleepiness in these participants, which might have led to overcompensation with regard to the detection of the cue words, with wake subjects focusing all available attentional resources on the prospective memory task. However, subjective sleepiness was not correlated with the number of cues detected, speaking against this possibility. Moreover, objective alertness levels as measured by reaction times and error rates in the vigilance task were not different in wake subjects compared to sleep participants. Vigilance task performance was also not correlated with cue detection in the prospective memory task (all p > .05), speaking against the possibility that prospective memory performance was affected by general alertness levels. Alternatively, higher overall performance in wake participants might be interpreted in light of recent findings showing that sleep deprivation can be a state of heightened plasticity due to prefrontal disinhibition (Sprenger et al., 2015). In the wake group, disinhibition under sleep deprivation following the first test session might have triggered plastic changes during subsequent recovery sleep, leading to overall higher performance levels at the second test two days later.

Cross-experiment comparison

For a post-hoc comparison of cue detection across all four experiments, an ANOVA with the between-subjects factors 'experiment' (Basic experiment/ Experiment 1 (Intention completed)/ Experiment II (Intention reinstated)/ Experiment III (Intention active throughout)) and 'sleep/wake' and the within-subject factor 'with/without secondary task' was conducted. This overall comparison confirmed that cue detection for sleep and wake participants differed depending on the instructed intention and on whether participants had to perform the prospective memory task under full attention or divided attention conditions (interaction 'experiment' x 'sleep/wake' x 'with/without secondary task': $F(3,112) = 3.65$, $p = .02$, $\eta_p^2 = .09$).

When analyzing all sleep groups separately, the beneficial effect of sleep on cue detection differed across experiments (interaction 'experiment' x 'with/without secondary task': $F(3,61) = 2.60$, $p = .06$, $\eta_p^2 = .11$; main effect 'experiment': $p = .80$, main effect 'with/without secondary task': $p < .01$): the sleep effect, as reflected in comparable cue detection under full attention and divided attention, was evident only when the intention was induced together with the previous encoding of cue-associates and when the intention was active throughout the entire retention period (comparison of the Basic experiment and Experiment 3: $p > .70$ for interaction 'experiment' x 'with/without secondary task' and main effect 'with/without secondary task'). No such sleep effect was evident when participants completed the intention before sleep and when the intention was simply reinstated after completion, as reflected in decreased cue detection when participants performed the task under divided attention compared to full attention (comparison of Experiment 1 and Experiment 2: $F(1,31) = 17.33$, $p < .001$, $\eta_p^2 = .36$, for main effect 'with/without secondary task', $F(1,31) = 0.03$, $p = .87$, for interaction 'experiment' x 'with/without secondary task'). Comparing the sleep groups of the intention active throughout experiment (Experiment 3, sleep effect) with the sleep groups of the intention completed and the intention reinstated experiments (Experiments 1 and 2, no sleep effect), confirmed a significantly better cue detection under divided attention with the intention active throughout the retention period (interaction 'experiment' x 'with/without secondary task': $F(1,31) = 4.88$, $p = .04$, $\eta_p^2 = .14$ for Experiment 3 vs. Experiment 1, and $F(1,28) = 7.63$, $p = .01$, $\eta_p^2 = .21$ for Experiment 3 vs. Experiment 2). Similarly, the sleep groups of the Basic experiment tended to perform better in cue detection under divided attention than the sleep groups of the intention completed and the intention reinstated experiments (interaction 'experiment' x 'with/without secondary task': $F(1,33) = 2.65$, $p = .11$, $\eta_p^2 = .07$ for Basic experiment vs. Experiment 1, and $F(1,30) = 3.25$, $p = .08$, $\eta_p^2 = .10$ for Basic experiment vs. Experiment 2).

Separate analyses of all wake groups across the four experiments showed a decrease in cue detection under divided attention compared to full attention in all experiments (comparison across all experiments and when comparing single experiments with each other: all $p < .005$ for main effects 'with/without secondary task', all $p > .11$ for interaction effects 'experiment' x 'with/without secondary task'). Overall performance in cue detection also differed across experiments ($p = .03$ for main effect ´experiment´), with post-hoc tests, comparing the single experiments, showing that wake subjects in Experiment 3 performed better than in the Basic experiment and in Experiment 1 ($p = .01$ and $p = .04$) and wake subjects in Experiment 2 performed better than in the Basic experiment and in Experiment 1 ($p = .03$ and $p = .09$; all other $p > .70$).

Despite these differences between experiments in the wake groups, the cross-experiment comparisons are in line with the reported findings of the single experiments and confirm the beneficial effect of sleep for intentions selectively and only when the intention is active during sleep and when it is induced in temporal proximity to the learning session.

General discussion

Based on the previous finding from our Basic experiment that sleep benefits prospective memory (Diekelmann et al., 2013a), here we investigated in three experiments, whether this beneficial effect of sleep depends on the relevance of prospective memories for actions to be performed in the future. Particularly, we asked whether the sleep effect is abolished when the intended action is completed before sleep and whether an intention can be reinstated for a sleep benefit after its completion. We show in Experiment 1 that once an intention is completed before sleep, the subsequent execution of prospective memory is no longer facilitated by a night of sleep. In Experiment 2, we found that contrary to our hypothesis, reinstructing the intention after its completion is not sufficient to reinstate the intention for a sleep benefit. Experiment 3 finally demonstrates that sleep improves intention execution if the intention for both test sessions is formed in temporal proximity to the initial learning session and thus, subjects expect right from the start to be tested on the prospective memory task again after its first completion.

These findings are in line with previous evidence indicating that sleep-dependent memory consolidation is selective in the way that it particularly fosters memories that are relevant for future behavior. Sleep has been shown to favor the consolidation of memories that are expected to be rewarded at testing as compared with memories for which reward was not expected (Fischer & Born, 2009) . Likewise, emotionally charged memories benefit to a larger extent from sleep than neutral memories (Payne et al., 2012, 2008; Payne & Kensinger, 2010, 2011), and sleep selectively consolidates memories for which subjects expect to be tested after sleep, whereas memories that are not expected to be tested do not benefit from sleep (Van Dongen et al., 2012; Wilhelm et al., 2011). In accord with this evidence, Experiment 1 demonstrates for the first time that completing an intention before sleep abolishes the previously shown beneficial effect of sleep on the subsequent execution of the intention. These findings are reminiscent of the Zeigarnik effect in suggesting that sleep improves prospective memories only as long as they still have to be executed in the future, i.e. as long as they are relevant for future behavior, with sleep's supportive effect vanishing once the intention has been completed. They corroborate the concept of prospective memory as a fundamentally dynamic type of memory existing only in the presence of specific (driving) intentions.

Based on our Basic experiment (Diekelmann et al., 2013a) we suggest that sleep improves prospective remembering by strengthening the association between the prospective memory cue and the associated intended action, thereby favoring spontaneous associative retrieval processes upon encountering the prospective memory cue after sleep (Diekelmann et al., 2013a; McDaniel et al., 2004; Scullin & McDaniel, 2010). Experiment 1 indicates that this proposed strengthening of the cue-action association is dependent on the intention being active across the sleep period. Considering the results of our Basic experiment (Diekelmann et al., 2013a), it could be argued that sleep did not specifically improve the intentional aspect of prospective memory but rather non-specifically strengthened the associations encoded prior to sleep, thereby indirectly facilitating spontaneous retrieval of the intention as a by-product of 'simple' retrospective associative memory consolidation. However, if this was true, we would have expected a beneficial effect of sleep also for completed intentions, considering that the cue-associates were encoded similarly prior to sleep with and without completion of the intention. The finding that, despite similar retrospective memory encoding, sleep did not benefit completed intentions suggests that – similar to the Zeigarnik effect – the effect of sleep for prospective memory critically depends on the intention being active across sleep, i.e., the intention being relevant for the successful execution of future actions.

There are different possible explanations for the abolished sleep effect after intention completion. Zeigarnik attributed better memory for uncompleted intentions on the 'tension' that is generated when a task is interrupted or not yet completed (Zeigarnik, 1927). According to this assumption, uncompleted intentions in the present study might have existed in a state of increased tension, with this tension possibly signaling importance of the memory, similar to an emotional charge, which then leads to a preferential access to sleep-dependent memory consolidation. With the intention completed before sleep, the tension might be released and, with it, the relevance signal for consolidation during sleep.

More contemporary theories suggest that intentions that are to be executed in the future show a privileged status of heightened activation over information that is simply to be remembered (Goschke & Kuhl, 1993; Marsh et al., 1998), an effect known as the 'intention superiority effect'. In this vein, uncompleted intentions that are still to be executed might show heightened activation making these intentions relevant and susceptible to sleep-dependent consolidation, whereas reduced or abolished activation after intention completion might in turn reduce their sensitivity to consolidation processes during sleep. It has been shown that finished intentions no longer elicit longer reaction times when cues are presented again, whereas cues of suspended intentions that are still relevant for later execution elicit slower responses (Scullin, Bugg, McDaniel, & Einstein, 2011; Scullin et al., 2009). Likewise, subjects can more efficiently deactivate intentions and thereby avoid commission errors when the intention is completed than when it is not yet completed (Bugg & Scullin, 2013). However, the exact mechanisms of this process, e.g., whether the heightened activation of intentions passively fades after their completion or whether completed intentions become actively inhibited, are not yet fully understood (see for example Bugg & Scullin, 2013; Bugg, Scullin, & McDaniel, 2013; Pink & Dodson, 2013; Walser, Plessow, Goschke, & Fischer, 2013).

An alternative explanation is based on the idea that the intentional memory does not only comprise the cue-action association but additionally includes a link to a (separate) intention representation that together with the cue-action association forms an intentional memory network. The intention representation, by signaling future relevance, might tag the cue-action association for consolidation processes during sleep. In order for the intentional network to be efficiently established, the intention representation might have to be encoded together with the cue-action association in order to tag this association for subsequent consolidation. This idea is in line with evidence suggesting that a link formed between the intention and the context in which the intention has to be executed determines subsequent prospective memory performance in that same context (Marsh et al., 2006; Nowinski & Dismukes, 2005). Moreover, it has been shown that sleep particularly facilitates intention execution in the context that was temporally paired with the encoding of the intention (Scullin & McDaniel, 2010). Thus, in Experiment 1, the initial encoding of the cue-action associations might have been specifically linked to the expected execution of the intention at the first retest 2 h later, with this link therefore not being subject to subsequent sleep-dependent consolidation processes.

The findings of Experiment 2 and Experiment 3 are in line with this latter explanation. Experiment 2 shows that it is not possible to reinstate a completed intention for sleep-dependent consolidation simply by announcing, after completion of the intention, that subjects would have to execute the task again two days later. While a renewed tension according to the Zeigarnik effect as well as a renewed activation according to the 'intention superiority effect' could be expected to be achieved relatively easy with a reinstruction of the intention, it might be hard or even impossible to connect the intention to the original cue-action associations after the completion of the intention. With the reinstruction of the intention taking place about 2 h after the initial encoding of the cue-action associations, the reinstructed intention representation might not be effectively connected to the cue-action associations, thus failing to tag these associations for consolidation processes during sleep. Experiment 3 shows that the sleep effect reappears when subjects are instructed right after the initial learning of the cue-action associations that they would be tested on their prospective memory twice. This finding suggests that the temporal proximity between intention formation and encoding of the cue-action associations is a key factor for the sleep benefit to emerge, which is in line with evidence from Scullin and colleagues (2010) showing that intentions benefit from sleep particularly when they are temporally paired with the context in which they have to be executed later on, but not when there is a temporal gap between the intention instruction and the context encounter.

On a neurophysiological level, it can be speculated that the intention instruction given shortly after initial learning, i.e., in the learning context, recruits neuronal plastic processes that are initiated during encoding, such that the cue-action associations can be tagged by the intention for further processing during sleep. There is ample evidence that newly encoded retrospective memories become reactivated during periods of subsequent sleep (for review see (Abel, Havekes, Saletin, & Walker, 2013; Rasch & Born, 2013). Neuronal network activity that is evident during the encoding of new experiences is re-expressed ('replayed') in a similar way during sleep following the learning experience (Ji & Wilson, 2007; Nádasdy, Hirase, Czurkó, Csicsvari, & Buzsáki, 1999; Wilson & McNaughton, 1994). Such replay events are assumed to strengthen the underlying neuronal connections and have mainly been observed during SWS. A recent study found sleep-dependent improvements of prospective memory specifically after SWS-rich sleep periods (Diekelmann et al., 2013b), suggesting that similar replay mechanisms might be involved in the reprocessing of prospective memories during sleep. In the wake state, successful prospective memory has been shown to rely mainly on activations in prefrontal cortical areas (Burgess, Dumontheil, & Gilbert, 2007; Burgess, Scott, & Frith, 2003), and there is evidence that sleep-associated memory reactivation extends from hippocampal to cortical areas including prefrontal cortex (Euston et al., 2007; Igloi, Gaggioni, Sterpenich, & Schwartz, 2015; Peyrache, Khamassi, Benchenane, Wiener, & Battaglia, 2009). Reactivations in prefrontal areas during sleep might be specifically linked to intentional memory networks to support prospective memory and planning (Buhry, Azizi, & Cheng, 2011; Schwindel & McNaughton, 2011). In the present study, the intention instruction given shortly after the initial learning experience might have tagged the newly encoded intentional memory networks for subsequent reactivation during sleep, and presumably during SWS, to strengthen the intentional cue-action associations. The execution of the intention during the expected completion of the task, on the other hand, might not (or to a lesser extent) induce the plastic processes on which a reinstatement of the intention/tag could build. With no (or a weaker) reinstatement of the intention, the intentional memory network might not be tagged for subsequent replay during sleep, or alternatively, the replay might not be strong enough to induce sufficient strengthening of the underlying connections. Future studies should scrutinize potential neurophysiological mechanisms of intention formation and intention reinstatement systematically.

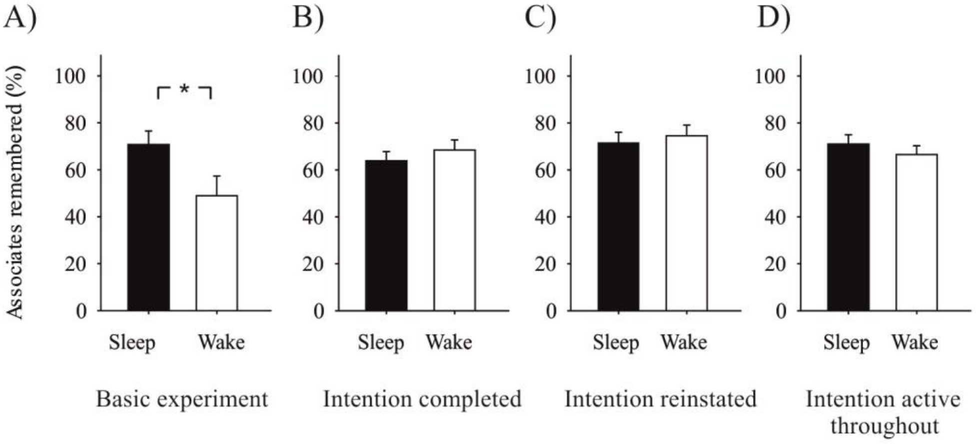
Importantly, Experiment 3 excludes the possibility that the mere execution of the task before sleep abolishes the sleep effect. The fact that Experiment 3 shows a beneficial effect of sleep on prospective remembering despite prior task execution strongly argues against the possibility that simply performing on the task before sleep explains the lacking sleep effect in Experiment 2. In showing a beneficial sleep effect on prospective memory, Experiment 3 also replicates and extends findings from our Basic experiment (Diekelmann et al., 2013a) using an identical relatively complex prospective memory task including 20 different cue words. Together with earlier findings reporting sleep benefits for a simple one-item prospective memory task in a more real world-like setting (Diekelmann et al., 2013b) and a more typical laboratory prospective memory task using two cue words (Scullin & McDaniel, 2010), there is now convincing evidence that sleep facilitates prospective remembering in a range of different tasks and settings.

Overall performance levels of cue detection were higher in the experiments of the present study compared to our Basic experiment (Diekelmann et al., 2013a), with this effect being most pronounced in the wake groups. The overall higher performance levels can be explained by the additional test session before sleep introduced in all three experiments. Detecting the cue words and remembering the associates during the first test session before sleep might have served as an additional practice of the cue-associate pairs. The observation that overall cue detection further increased across experiments in the wake groups could be explained by the increasing number of intention instructions and execution of the task. Previous evidence indicates that the perceived importance of the prospective memory task affects cue detection performance, with higher importance typically leading to better cue detection (McDaniel & Einstein, 2000; Walter & Meier, 2014, 2017). Considering that in the present study, additional (re-)instructions were introduced in each of the successive experiments, this might have inadvertently added further importance to the prospective memory task, increasing relevance in the intentional memory network. We can only speculate why this increase in overall cue detection across experiments was more pronounced in wake subjects. Sleep possibly supports different mechanisms of prospective memory performance, such as memory consolidation and reactivation, which might ‘overwrite’ processes otherwise affecting prospective memory performance in the wake state, such as additional practice and repeated intention instructions. By strengthening the intentional memory connections, we assume that sleep favors spontaneous-associative retrieval processes (Diekelmann et al., 2013a), whereas wake participants rely to a larger extent on monitoring strategies, with the latter possibly being more susceptible to the manipulation of task importance (McDaniel & Einstein, 2000). Future studies should directly test these ideas.

While the generally enhanced performance level might have been still sufficient to yield a sleep benefit for the prospective component of prospective memory, i.e. cue detection, the intentional memories might have been too strong for a sleep benefit on the retrospective component to occur. At first glance, this is surprising considering that a successful sleep effect on prospective memory could be expected to entail a benefit for both the prospective component to detect the cue words and the retrospective component to remember the associated words, as was evident in our Basic experiment (Diekelmann et al., 2013a). However, even though subjects did not receive any feedback on their performance during the first test session, there is evidence that memory retrieval per se can strengthen retrospective memories (Karpicke & Roediger, 2008; Roediger & Karpicke, 2006; Smith, Roediger, & Karpicke, 2013). Moreover, it has been suggested that sleep benefits retrospective memory optimally when memories are encoded with medium strength, whereas memories that are too strong or too weak do not benefit from sleep (Stickgold, 2009; Wilhelm et al., 2012). Thus, stronger cue-action associations following the first prospective memory test in the evening before sleep might have hindered the emergence of an improving effect of sleep on the retrospective component. Additionally, the retrospective component was not affected by divided attention in any of the experiments – other than the prospective component, which was impaired under divided attention conditions. This pattern of results replicates the findings from our Basic experiment (Diekelmann et al., 2013a) and is in line with evidence indicating that retrospective memory recall is less dependent on attentional resources (Craik, Govoni, Naveh-Benjamin, & Anderson, 1996; Iidaka, Anderson, Kapur, Cabeza, & Craik, 2000), particularly with the retrospective component (word recall) and the secondary task (digit monitoring) relying on different processing systems in our paradigm (i.e., verbal vs. numerical) (Fernandes & Guild, 2009; Skinner, Fernandes, & Grady, 2009).

Altogether, our four experiments show that prospective memory benefits from a night of sleep only if the intention is active throughout the entire experimental period, suggesting that sleep facilitates prospective memory only as long as the intention is relevant for future actions and if the intention is formed in close proximity to the initial learning session. The sleep effect on prospective memory is abolished once the intention has been completed before sleep and cannot be reinstated by simply reinstructing the intention after its completion. Future studies will have to examine the neuronal mechanisms underlying these effects, including the potential role of different sleep stages and sleep parameters.

Supplementary Material



Supplementary Figure S1 Percentage of associated words relative to the number of correctly detected cue words (measuring the retrospective component) in **A)** the Basic experiment (Diekelmann, 2013a) and the three experiments of the present study: **B)** Intention completed, **C)** Intention reinstated, and **D)** Intention active throughout. Sleep and wake participants´ performance were comparable in the three experiments of the present study, whereas sleep subjects remembered more associates than wake subjects in the Basic experiment (Diekelmann et al., 2013a). * $p < 0.05$

STUDY Ⅱ

EFFECTS OF SLEEP ON THE REALIZATION OF COMPLEX PLANS

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Abstract

Sleep consolidates newly encoded memories, particularly those memories that are relevant for future behavior. This study explored whether sleep facilitates the successful execution of relatively complex plans in the future. We applied the Dresden Breakfast Task, in which subjects are instructed to prepare a virtual breakfast comprising several tasks (e.g. table setting, preparing eggs). After forming a detailed plan how to realize these tasks, the sleep group (n = 17) spent a night of sleep at home, monitored by polysomnography, and the wake group (n = 19) spent a normal day awake, monitored by actigraphy. After a 12-hour interval, all participants were asked to prepare the virtual breakfast. Contrary to our hypothesis, overall performance in breakfast preparation did not differ significantly between the sleep and wake groups. However, sleep participants performed better in one of six tasks, specifically the task 'Table setting' ($p < .01$), which was driven by higher scores in a subtask measuring the correct position of the tableware ($p < .01$). Additional exploratory analyses revealed that a significant number of wake participants performed below the minimal score of the sleep group ($p < .01$); and sleep participants achieved the maximal score in significantly more subtasks than wake participants (57% vs. 27%; $p = .018$). Plan adherence, assessing how well participants adhered to their own previously developed plan, did not differ between the sleep and wake groups. These findings provide first evidence that sleep may support some aspects of the realization of complex, rather naturalistic plans.

Introduction

Sleep is well-known to benefit the consolidation of newly acquired memories. Sleep following learning facilitates the stabilization of memories as well as their redistribution from short-term to long-term stores (Nieuwenhuis et al., 2013; Rasch & Born, 2013). Recent evidence suggests that this process is not ubiquitous, but selectively favors those contents that are in any way relevant for future behavior (Bennion et al., 2016). Sleep preferentially benefits memories for which subjects expect to be rewarded (Fischer & Born, 2009), for which they expect to be tested after sleep (Van Dongen et al., 2012) or if memories are emotionally salient (Groch et al., 2013; Payne et al., 2008).

In everyday life, future-directed memories[1] are particularly important for the successful formation and realization of plans and intentions (Szpunar et al., 2014). Planning is a central cognitive ability that is essential for everyday functioning, from preparing breakfast in the morning to writing a scientific paper (Owen, 1997; Tanji & Hoshi, 2001). Complete or partial sleep deprivation was found to impair the ability to make and revise plans strategically (Harrison & Horne, 2000) as well as to execute them successfully (Grundgeiger et al., 2013). A recent study tested the effect of normal undisturbed sleep on the implementation of a relatively simple plan. Participants who had slept after plan instruction, realized the plan twice as often as wake participants after a delay of two days (Diekelmann et al., 2013b). This effect was selective for subjects who obtained high amounts of slow wave sleep (SWS) during the night and was not evident in subjects who had high amounts of rapid eye movement (REM) sleep. In two similar studies, participants who were instructed to detect specific words in an ongoing task, realized their planned actions more successfully (i.e.

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[1] By ‘future-directed memories’, we mean any type of memory that is related to future behavior, including memory for simulations and predictions, prospective memory, as well as memory for plans and intentions.

detected more words correctly) if they were allowed to sleep after the instruction than participants who stayed awake (Diekelmann et al., 2013a; Scullin & McDaniel, 2010).

Together, these studies indicate that sleep is beneficial for the realization of simple plans. However, it remains unclear whether sleep likewise supports the realization of more complex everyday-like plans. Real-life planning often incorporates several complex intentions, with different overlapping sub-intentions and sometimes one intention being nested in the realization of another. When preparing breakfast, for example, you may start by turning on the kettle to prepare water for the tea, then you may start boiling eggs and have to remember to take them out after about 7 min, while in the meantime you may set the table etc.

In the present study, we applied a complex and rather naturalistic planning task – the Dresden Breakfast Task (Altgassen, Kretschmer, & Kliegel, 2014), which requires participants to plan and prepare a virtual breakfast in a pre-defined way. We expected better breakfast preparation performance if participants were allowed to sleep after encoding of the plan compared to participants that stayed awake.

Methods

Participants

A total of 38 young and healthy participants (25 females, mean age [± *SD*]: 24.34 ± 2.59) took part in the experiment. To exclude gender as a possible confounding factor, participants were allocated to the sleep or wake group based on a covariate adaptive randomization strategy (Suresh, 2011), ensuring roughly equal distribution of female and male participants across groups. Two participants (one from each group) were excluded from the final analyses because they did not adhere to the experimental instructions and talked to their roommates about the task after encoding (Note that all results remain the same when these participants are included in the analyses). Final analyses were based on data from 36 participants (sleep: *n* = 17, 10 females, mean age [± *SD*]: 24.35 ± 2.81 years; wake: *n* = 19, 13 females, mean age [± *SD*]: 24.05 ± 2.35). All participants reported regular sleep-wake cycles (≥ 6 hours sleep per night, within the time window 11:00pm – 6:00am), no shift work for at least 6 weeks prior to the experiment and no regular night shifts in the past. During the experiment, subjects were instructed not to take any exams and to refrain from other stressful activities. Subjects reported no history of any neurological, psychiatric or endocrine disorder and did not take any medication except for hormonal contraception and thyroid hormones during the time of the experiment. Consumption of caffeine and alcohol was not allowed during the experimental period. All subjects gave written informed consent and were paid for participation. The study was approved by the local ethics committee of the Medical Faculty of the University of Tübingen, Germany.

Design and procedure

In a between-subject design, encoding of the plan took place in the evening for the sleep group (9:30pm ± 1h) and in the morning for the wake group (9:30am ± 1h; Figure 7A). For the plan encoding session, all participants reported to the lab to perform the Dresden Breakfast Task (see below for task description). After the encoding session, in the sleep group the electrodes for portable polysomnographic recordings were attached to the subject's head, and subjects in the wake group were equipped with an actigraphy device (Actiwatch 2, Philips Respironics), which was attached to their non-dominant wrist. Then all subjects left the lab and either had an 8 hour period of normal sleep at home (sleep group) or went about their daily activities (wake group). After a retention interval of 12 hours, all participants returned to the lab and were tested for plan realization in the Dresden Breakfast Task (at ~ 9:30am and 9:30pm for the sleep and wake group, respectively).

Dresden Breakfast Task

The Dresden Breakfast Task is a complex naturalistic memory task with a strong planning component (Altgassen et al., 2014, 2015). The task version that was applied in the present study was identical to the version developed by Altgassen et al. (2014), including the same virtual layout, the same breakfast preparation tasks and subtasks and the same instructions; however, here we report slightly adapted performance measures according to our research questions (see below).

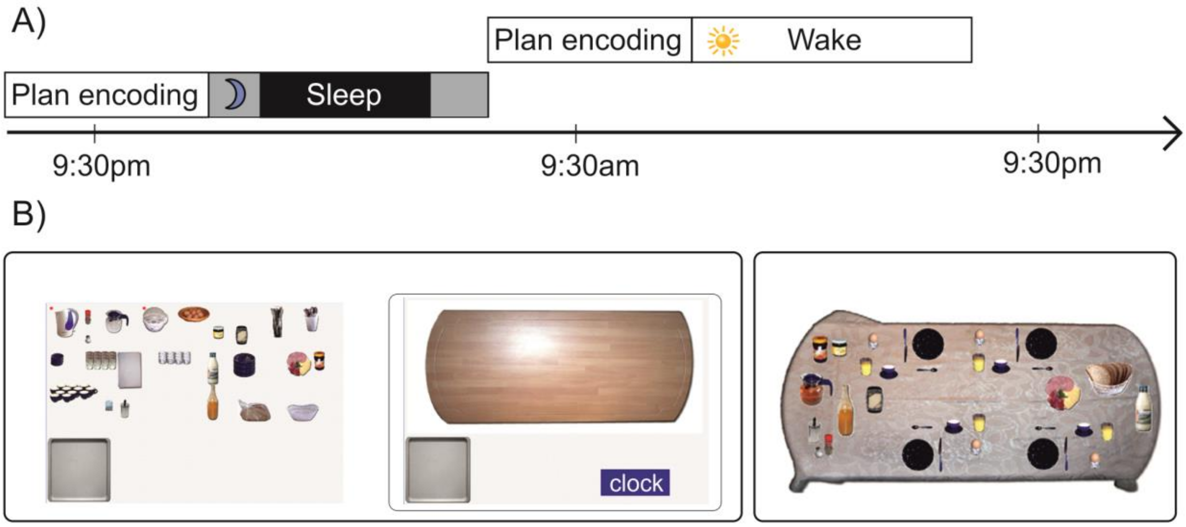

Figure 7 Experimental design and layout of the Dresden Breakfast Task. **A)** Sleep and wake participants encoded a detailed plan of how to prepare breakfast in the evening or morning, respectively. The plan encoding session was followed by an interval of 12 h consisting either of a whole night of ~8 h of sleep (sleep group) or a normal day of wakefulness (wake group). Participants had to prepare the virtual breakfast during the plan realization session. **B)** In the Dresden Breakfast Task, participants are asked to set the table within 7 min with the help of a tray and by switching back and forth from the kitchen display to the dining room display. The 'kitchen' (left) contains tableware, tablecloth, food and tools for preparing tea and cooking eggs, as well as a tray for moving the items to the table. The table that is to be laid is located in the 'dining room' (middle). The optimal 'final table layout' for four people according to the task specifications is

shown on the right. Whenever participants click on the blue field located in the dining room, the virtual time appears

In the Dresden Breakfast Task, participants are asked to prepare a virtual breakfast for four persons within seven minutes (Figure 7B). Breakfast preparation consists of six pre-defined tasks: 1) Table setting, 2) Placing food, 3) Preparing eggs, 4) Preparing bread, 5) Preparing tea, and 6) Placing butter on the table. These six tasks differ in complexity and the number of subtasks needed to complete the task (Table 4). For example, in order to complete the task 'Table setting', participants are required to perform eight subtasks, for which they receive a maximum of 49 points: placing four plates (4 points), four cups (4 points), four saucers (4 points), four glasses (4 points), four knifes (4 points), four spoons (4 points) and the table cloth (1 point) on the table, and additionally all of the pieces of the tableware have to be placed at the correct position (24 points). Accordingly, participants can miss points if they do not place all pieces of the tableware and cutlery on the table (e.g. only 3 points for three plates in the subtask 'Plates') or if they place all the items on the table but not in the correct position (e.g. 0 points for the subtask 'Correct positions' if none of the tableware and cutlery is at its correct location). The scores for each of the six tasks are obtained by adding the scores of the respective subtasks (e.g. 49 points for 'Table setting'). Overall performance is measured as the sum of all completed subtasks (max. 90 points, see Table 4). In the instruction for participants, some tasks were prioritized over others as in Altgassen et al. (2014), e.g. having the table ready when the guests arrive, having the tea and eggs just ready before the guests arrive, as well as following rules according to common sense (e.g. putting the table cloth first, then placing the tableware).

During the plan encoding session, participants were introduced to the six tasks and their subtasks and were explained that they would have to complete them within seven minutes. After the introduction to the task, they were familiarized with the functions of the computer program. In the following 10-minute planning phase, participants had to elaborate on how exactly they were planning to realize all the tasks. Participants wrote down their plan and also verbalized it for digital recording. During the plan realization session, participants were asked to prepare the breakfast. In addition to the scores for the six tasks, the single subtasks, and the overall performance score, we also assessed the overall number of actions participants carried out (i.e. the number of automatically recorded mouse clicks). The number of mouse clicks in relation to performance in the plan realization session can be considered a measure of plan efficiency, since each single movement in the task environment counts as a mouse click and participants with a well-developed plan, arguably, need less going back and forth between rooms as well as less re-positioning of pieces (see Figure 7B). Moreover, plan adherence was assessed by two independent raters as the correspondence (in %) between the individual plan that participants developed in the plan encoding session and their actual course of action in the plan realization session (inter-rater reliability: $r = .86$, $p < .001$).

Control tasks

Before plan encoding as well as after plan realization, a 5-minute vigilance task (Diekelmann et al., 2013a), measuring reaction times (in ms) and error rates (in %) and the Stanford Sleepiness Scale (Hoddes et al., 1973) were applied to control for general alertness.

The polysomnography setup for sleep subjects included EEG (at positions C3 and C4), EMG (at the chin) and EOG (below and above the eyes). Recordings were visually scored offline according to standard criteria (Rechtschaffen & Kales, 1986). One sleep data set could not be formally analyzed due to artefacts in the EMG channel, but EEG and EOG quality sufficed to confirm sufficient sleep, therefore this subject was not excluded from analyses of the Dresden Breakfast Task. Wake participants were monitored by actigraphy during the retention interval and were asked to report their daytime activities in a questionnaire, in order to exclude that subjects slept during the day. One actigraphy dataset could not be analyzed due to technical failure, but the questionnaire report did not hint at any sleep episodes.

Statistical analysis

Performance in the Dresden Breakfast Task during the plan realization session was analyzed using Mann-Whitney U-tests because data were not normally distributed (for overall performance, the six tasks and their subtasks, as well as for mouse clicks). Plan adherence was analyzed with t-tests given that these data were normally distributed. Means (*M*) ± SEM as well as the median (*Md*) are reported, due to skewness of the data. In order to account for this skewness, we compared the variances of the sleep and wake group for overall performance and tested in an exploratory analysis how many participants of the wake group performed below the minimum score of the sleep group by means of χ^2-test. Additionally, we counted the number of subtasks in which all sleep participants vs. all wake participants achieved the highest possible score, and compared groups by means of χ^2-test. Correlations were calculated as Pearson´s product moment correlations (r), or Spearman´s rank correlation coefficient (r_s) when assumptions of normal distribution were not met.

For analysis of vigilance and subjective sleepiness, we applied a mixed ANOVA with ‘sleep/wake’ as between-subject factor and ‘plan encoding/realization’ as within-subject factor, as well as non-parametric post-hoc comparisons (since normal distribution was not given). Since groups differed in sleepiness during the plan realization session, a bootstrapped hierarchical regression analysis tested whether sleepiness predicted the observed differences between the sleep and wake groups (applying a bias corrected and accelerated method). To test for time-of-day effects, we computed a mixed ANOVA with the between-subject factor ‘sleep/wake’ and the within-subject factor ‘morning/evening’ for sleepiness and vigilance. The level of significance was set to $p = .05$ and was Bonferroni-corrected for multiple testing, resulting in a level of significance of $p = .05/6 = .008$ for the six single tasks of the Dresden Breakfast Task, $p = .05/8 = .006$ for the eight subtasks of ‘Table setting’, $p = .05/2 = .025$ for the number of wake participants scoring below the minimum of sleep participants as well as the percentage of subtasks with maximal score by the whole group, and $p = .05/12 = .004$ for the correlations of performance measures (overall performance, ‘Table setting’, ‘Correct positions’, plan adherence) with sleep measures (minutes in S2, SWS, REM). All statistical analyses were run with IBM SPSS 21.

Results

Dresden Breakfast Task

Contrary to our hypothesis, the sleep and wake groups did not differ significantly in the main measure of breakfast preparation. Although on a descriptive level, participants performed slightly better if they had slept after planning compared to participants who had stayed awake, the difference between groups did not reach significance in the overall performance measure (sleep: *M* = 81.53 ± 0.94, *Md* = 81.00; wake: *M* = 76.89 ± 2.44, *Md* = 79.00; *U* = 111.50, *z* = -1.59, *p* = .11, Figure 8A). When looking more closely into performance of the single tasks and subtasks, a difference in the task ‘Table setting’ was evident, showing that sleep participants (*M* = 48.00 ± 0.45, *Md* = 49.00) performed significantly better than wake participants (*M* = 43.05 ± 1.39, *Md* = 45.00; *U* = 65.00, *z* = -3.19, *p* = .001; Figure 8B). Better performance of sleep participants in the task ‘Table setting’ was primarily driven by the subtask ‘Correct positions’, a score measuring to which extent the single sets of plates, cutlery, glasses and cups were placed at the correct position on the table (sleep: *M* = 23.35 ± 0.32, *Md* = 24.00; wake: *M* = 19.63 ± 0.93, *Md* = 20.00; *U* = 62.00, *z* = -3.38, *p* < .001; Figure 8C).

Sleep participants also tended to perform better than wake participants in the task ‘Placing food’, although this difference failed to reach significance (sleep: *M* = 11.88 ± 0.12, *Md* = 12.00; wake: *M* = 11.32 ± 0.25, *Md* = 12.00; *U* = 119.50, *z* = -1.93, *p* = .08). In all other tasks, participants of the sleep and wake groups performed comparably well (all *p* > .25; Table 4).

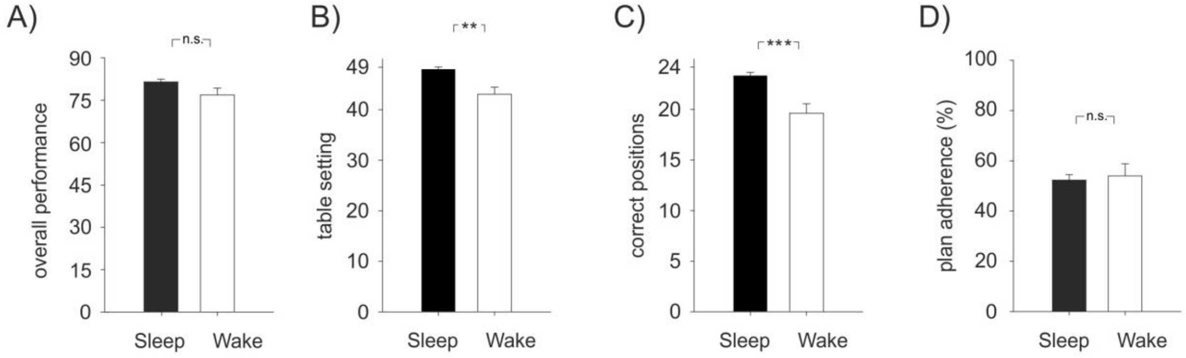

Figure 8 Performance on the Dresden Breakfast Task after sleep and wakefulness. **A)** Sleep and wake participants did not differ significantly in the overall performance measure (max. 90 points). **B)** Sleep participants outperformed wake participants in one of six tasks, i.e. the task 'table-setting' (max. 49 points) (note that the effect remains significant after Bonferroni correction for six comparisons). **C)** The difference in 'table-setting' was based mainly on sleep participants showing better performance in the subtask 'correct positions', one of eight subtasks of the task 'table-setting', measuring how well the tableware was placed in the correct position on the table (max. 24 points) (note that the effect remains significant after Bonferroni correction for eight comparisons). **D)** Sleep and wake groups were comparable in how well they adhered to their own previously developed plan during plan realization (in %). Means and standard errors of the means (SEM) are displayed. NS: not significant; **P < 0.01; ***P < 0.001.

Table 4. Performance on the six tasks of the Dresden Breakfast Task

	Sleep group	Wake group	Maximal score	*n° Sub-tasks*	*p*
Table setting	48.00 ± 0.45	43.05 ± 1.39	49	8	.001**
Placing food	11.88 ± 0.12	11.32 ± 0.25	12	9	.08
Preparing eggs	7.82 ± 0.99	9.37 ± 0.99	14	5	.27
Preparing bread	9.00 ± 00	8.16 ± 0.58	9	2	.49
Preparing tea	3.29 ± 0.17	3.42 ± 0.12	4	4	.71
Placing butter on the table	1.53 ± 0.13	1.58 ± 0.12	2	2	> .99

Performance on the six tasks is indicated as Means ± SEM for the sleep and wake groups, respectively. Maximal score: The highest possible score of each task, n° subtasks: the number of subtasks that each task comprises; *p, p*-values; ** *p* < .01, based on group comparisons by Mann-Whitney U tests. Note that the effect in 'Table setting' remains significant after Bonferroni correction for six comparisons.

Interestingly, overall performance in both the sleep group and the wake group was very good, with almost all subjects scoring in the highest quartile of the scale (Figure 9A). Despite this ceiling effect, variances in the sleep and wake group differed significantly ($F(1,34) = 6.27$, $p = .017$). To examine this difference in variances more closely, we ran an additional exploratory analysis. This analysis revealed that a significant number of participants in the wake group (*n* = 8) scored below the minimum score of the sleep group (χ^2 = 9.20, df = 1, *p* = .002; Figure 9A). Moreover, all sleep participants achieved the maximum score in 57% (17 subtasks) out of all 30 subtasks, whereas all wake participants reached the maximal score in only 27% of subtasks (8 subtasks) (χ^2 = 5.55, df = 1, *p* = .018; Figure 9B). Since one participant performed extremely low in the wake group, we excluded this outlier for a more conservative analysis. All significant results as mentioned above remained significant after exclusion of the outlier, except for the number of sleep participants achieving the maximal score in more subtasks than wake participants (*p* = .20 after outlier exclusion; see Supplementary Table S1 for comparison with and without the outlier for all measures).

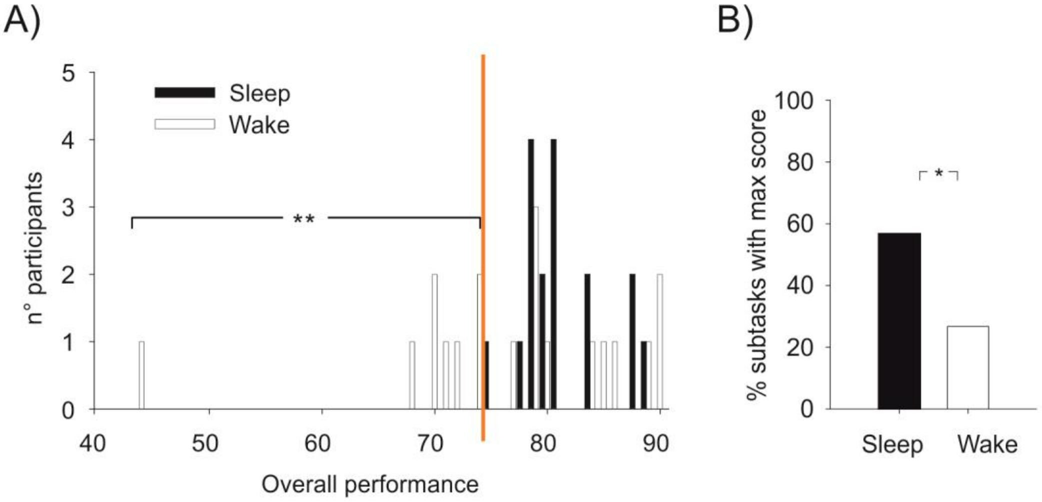

Figure 9 Exploratory analyses of overall performance on the Dresden Breakfast Task. **A)** Frequency distribution of the number of participants reaching the respective overall performance scores in the sleep and wake groups. A significant number of wake participants performed below the minimum score of the sleep group, even after exclusion of the wake participant with the lowest performance (44 points, included in the graph). The yellow line indicates the cut-off for the lowest performance score of the sleep group. **B)** Percentage of subtasks (of 30 subtasks) in which the whole sleep group and the whole wake group reached the maximal score. *P < 0.05 (note that both effects remain significant after Bonferroni correction for two comparisons).

Importantly, sleep and wake participants did not differ in the overall number of actions, measured by the number of mouse clicks within the 7-minute breakfast preparation time (sleep: *M* = 639.35 ± 18.09, *Md* = 630.00, wake: *M* = 645.74 ± 18.38, *Md* = 632.00; *U* = 152.00, *z* = -0.30, *p* = .76). Finally, sleep and wake participants did not differ in the extent to which they realized their own plans that they had developed in the plan encoding session. Sleep and wake participants realized on average 52 ± 2% and 54 ± 5% of their plans, respectively (plan adherence: $t(24.70) = .31$, $p = .76$) (Figure 8D).

Sleep data and control tasks

Sleep participants slept on average 465.5 ± 11.7 min. They spent on average 24.8 ± 6.8 min in wake, 21.7 ± 1.4 min in stage 1, 238.1 ± 9.2 min in stage 2, 69.8 ± 4.0 min in SWS (i.e. the sum of stage 3 and stage 4) and 103.7 ± 6.2 min in REM sleep. The first epoch of SWS occurred on average after 15.6 ± 1.4 min and the first epoch of REM sleep occurred on average after 98.7 ± 10.8 min. None of the measures of the Dresden Breakfast Task correlated significantly with any of the sleep variables after correction for multiple comparisons. From actigraphy recordings and daytime activity reports we ensured that none of the wake subjects slept during the day.

The sleep and wake groups did not differ in reaction times ([in ms] plan encoding, sleep: 464.58 ± 10.88, wake: 456.15 ± 9.69; plan realization, sleep: 463.27 ± 14.25, wake: 459.31 ± 10.23) and error rate ([in %] plan encoding, sleep: 2.50 ± 0.71, wake: 2.90 ± 0.88; plan realization, sleep: 2.65 ± 0.62, wake: 3.16 ± 0.54) of the vigilance task (all $p > .55$). Subjective sleepiness did not differ between sleep and wake participants during plan encoding (sleep: $M = 2.77 \pm 0.21$, wake: $M = 2.37 \pm 0.14$; $U = 128.00$, $z = -1.18$, $p = .25$), but sleep participants felt subjectively more alert than wake participants during plan realization (sleep: $M = 1.94 \pm 0.16$, wake: $M = 2.58 \pm 0.19$; $U = 96.00$, $z = -2.27$, $p = .025$; interaction 'plan encoding/realization' x 'sleep/wake': $F(1,34) = 9.16$, $p = .005$; main effects: $p > .08$). Importantly, sleepiness scores during plan realization did not correlate with performance on the Dresden Breakfast Task (for overall performance, 'Table setting', 'Correct positions' and plan adherence), neither in wake participants nor in sleep participants (all $p > .06$). Subjective sleepiness did also not add substantially to explain group differences in 'Table setting' (change in $R^2 = .03$, $p = .23$) and 'Correct positions' (change in $R^2 = .72$, $p = .06$) in a hierarchical regression analysis. Although sleepiness significantly predicted performance in the subtask 'Correct positions' in a group + sleepiness model ($b_{\text{group + sleepiness model}} = 1.30$, $p = .041$), sleepiness did not diminish the influence of group ($b_{\text{group-only model}} = 3.72$, $p = .005$, $\mathrm{b}_{\text{group + sleepiness model}} = 4.55$, $p = .003$) (for all results see Supplementary Table S2/S3). With regard to time of day, subjective sleepiness was generally lower in morning sessions compared to evening sessions, irrespective of group assignment (main effect ‘time-of-day’: $p = .005$, interaction ‘time-of-day’ x ‘sleep/wake’: $p > .08$). Such a time-of-day difference was not evident in objective reaction times and in error rates in the vigilance task (all p > .57).

Discussion

This study asked whether sleep supports the realization of a complex plan in a naturalistic everyday-like setting. We expected that participants would execute their plan to prepare a virtual breakfast according to predefined task specifications more successfully if they had slept after planning breakfast preparation in comparison to participants that stayed awake after planning. Contrary to our hypothesis, sleep participants were not superior to wake participants in overall performance of breakfast preparation. However, in line with our hypothesis, sleep participants outperformed wake participants in one of six tasks (‘Table setting’), which was based on better performance of the sleep group in one of eight subtasks (‘Correct positions’), indicating that sleep may support some aspects of complex plan execution. Plan adherence, on the other hand, was comparable after sleep and wakefulness, suggesting that sleep participants did not adhere to their previously developed plans more closely than wake participants.

The primary finding that sleep and wake participants did not differ in overall performance of breakfast preparation contradicts previous evidence showing that future-relevant memory is preferentially consolidated during sleep (Diekelmann et al., 2013b; Fischer & Born, 2009; Scullin & McDaniel, 2010; Van Dongen et al., 2012). It is surprising that, although sleep has been shown to benefit future-directed memory in relatively simple laboratory tasks, it does not seem to enhance overall performance in a naturalistic version of a rather complex everyday-like planning task. We suggest two possible explanations for this finding. First, complex plans may not be as sensitive to sleep-dependent consolidation processes as more simple plans and intentions. So far, only memories for rather simple plans and intentions have been reported to benefit from sleep, such as detecting single cue words in an ongoing task or reminding the experimenter of a previously instructed task (Diekelmann et al., 2013a, 2013b; Fischer & Born, 2009; Scullin & McDaniel, 2010; Van Dongen et al., 2012). It is possible that more complex plans require additional processes and abilities, like executive functions (Dehaene & Changeux, 1997; Tanji & Hoshi, 2008), that are not or to a lesser extent dependent on sleep and/or can be compensated for

(Harrison & Horne, 2000). A second possible explanation relates to the characteristics of the Dresden Breakfast Task applied in the present study. This task has originally been developed for clinical studies in older people and patients with autism spectrum disorders (Altgassen et al., 2012, 2014). Accordingly, the task may have been too easy for the healthy young subjects in the present study, a speculation that is supported by our observation of a ceiling effect in overall performance as well as in most of the single tasks and subtasks. This ceiling effect may have prevented the detection of smaller effects of sleep on the consolidation of complex plans. Future studies should apply tasks that allow for more fine-grained performance measures in healthy young individuals in larger samples.

Despite this ceiling effect and the non-significant group difference in overall performance, sleep participants realized breakfast preparation more successfully than wake participants on some sub-measures of overall performance. Sleep participants showed better performance in laying the table, especially in adhering to the correct placement of plates, cups, glasses and cutlery. It can be speculated that sleep specifically consolidated the memory for the correct layout of the table, which is in line with studies showing sleep-dependent consolidation of picture-location associations (Rasch et al., 2007; Van Dongen et al., 2012). In addition to better table setting performance, exploratory analyses showed that sleep participants completed more subtasks to perfection than wake participants, and a significant number of wake participants scored below the lowest performance of the sleep participants. Together, these observations provide first hints that sleep may support the execution of complex real life-like plans in at least some more exploratory performance measures. Importantly, the better performance of sleep participants in these measures was achieved with a comparable number of actions (mouse clicks) carried out, excluding that sleep subjects were simply more active during plan execution. The finding that the sleep group achieved better results than the wake group despite the same number of actions within a limited amount of time suggests that the seep group acted more efficiently and possibly also in a more goal-oriented manner to realize their plans. This speculation is further supported by the finding that the sleep and wake groups showed comparable plan adherence. Both groups seemed to have remembered and adhered to their own previously developed plan equally well, but still sleep participants showed superior plan realization in some measures. It can be speculated that sleep does not simply strengthen the memory traces for single pieces of information (e.g. the exact plan) but rather acts on a higher level of organization by structuring the large number of single steps of the action plan and shaping it for more efficient execution. This idea is corroborated by previous findings indicating that sleep can reorganize newly encoded memories (Landmann et al., 2014) such that the extraction of gist is facilitated (Lutz et al., 2017), relational inferences can be drawn (Ellenbogen et al., 2007) and even complex problems are more likely to be solved (Beijamini et al., 2014; Sio et al., 2013). Interestingly, the mental simulation of future scenarios, which is an essential component of planning complex behaviors, activates among others hippocampal and prefrontal cortical areas (Andrews-Hanna, Smallwood, & Spreng, 2014; Schacter et al., 2012), which are regarded as key candidate brain areas involved in the reorganization of information during sleep. This reorganization is assumed to originate from repeated neural reactivations of newly encoded information in hippocampal-neocortical circuits, which strengthens and integrates relevant memories into pre-existing networks (Landmann et al., 2014), possibly in combination with a down-selection process that reduces overall synaptic weight by weakening irrelevant connections (Tononi & Cirelli, 2014).

Some caveats should be considered when interpreting our findings. Sleep participants reported less subjective sleepiness during plan realization than wake participants, which might have affected their performance levels. Although we cannot fully exclude this possibility, we consider it unlikely since both groups did not differ in objective alertness measures in the vigilance task as well as in the overall number of performed actions (i.e. mouse clicks) during the breakfast preparation task. Moreover, subjective sleepiness ratings were not associated with any of the performance measures in the breakfast preparation task and did not provide incremental prediction of group differences in breakfast preparation. Another possible caveat relates to circadian factors. Sleep and wake participants performed the breakfast task at different circadian times, which might have influenced encoding and/or execution of the plan (Schmidt et al., 2007). Speaking against this possibility is evidence indicating that prospective memory performance in young subjects is better during peak performance time (i.e. during evening hours) (Rothen & Meier, 2017). In the present study, sleep subjects did not show impaired performance in the morning (i.e. during low performance time at plan realization), but performed equally well or even better than participants in the evening, suggesting that circadian factors are unlikely to have affected plan realization as a strong confounding factor. Moreover, previous studies comparing 12 hour intervals of nocturnal sleep and diurnal wakefulness, have shown that sleep-dependent memory consolidation is not affected by circadian variations (Payne et al., 2008; Wagner et al., 2004). On the other hand, participants were less sleepy in the morning than in the evening, irrespective of group assignment. Lower sleepiness in the morning might have eased plan encoding in wake participants and plan realization in sleep participants. However, since the effect of sleepiness on encoding and realization of the plans cannot be disentangled in the present study and we did not assess circadian typology, these questions will have to be addressed systematically in future studies. Another caveat relates to the fact that breakfast preparation per se is a typical morning activity; performing this task in the morning might have eased plan execution in the sleep group. Cultural differences in breakfast traditions as well as individual breakfast habits and automatic behaviors might further affect performance on the Dresden Breakfast Task. Future studies should test these possibilities and directly assess measures of participants’ typical breakfast behaviors.

Our finding of a beneficial effect of sleep on some aspects of complex everyday-like plan realization may have important implications for clinical applications. Failures in the realization of plans are a common complaint in a number of disorders such as mild cognitive impairment (MCI), Alzheimer’s disease and Parkinson’s disease (Ramanan & Kumar, 2013; Van den Berg, Kant, & Postma, 2012), with these diseases also being characterized by pronounced sleep disturbances (Mander, Winer, Jagust, & Walker, 2016; Suzuki, Miyamoto, Miyamoto, & Hirata, 2015). The present findings may stimulate further research into this question, potentially leading to the development of novel sleep interventions to treat these symptoms as well as to counter planning impairments at early stages of the diseases to prevent the progression of memory decline and to retain patients’ everyday life functioning for as long as possible.

Supplementary Material

Table S1. Impact of outlier exclusion on measures of the Dresden Breakfast Task

	Sleep group	Wake group complete data	Wake group outlier excluded	*p* complete / excluded
Table setting	48.00 ± 0.45	43.05 ± 1.39	44.00 ± 1.08	.001** / .002**
Correct positions	23.35 ± 0.32	19.63 ± 0.93	20.17 ± 0.81	<.001*** / .001**
Max. score (% of 30 subtasks)	57%	27%	40%	.018* / .20
Below min. score of sleep group		*n* = 8	*n* = 7	.002** / .004**

Sleep and wake participants´ performance on the Dresden Breakfast Task indicated as Means ± SEM for the task 'Table setting' and the subtask 'Correct positions', as well as the percentage of all 30 subtasks in which the whole group achieved the maximum score (Max. score) and the number of wake participants that performed below the min. score of the sleep group. *p* values are presented for non-parametric sleep vs. wake comparisons (separately for complete data set and with outlier excluded from the wake group). Significant results remain significant after Bonferroni correction for 6 comparisons for the task 'Table setting', for 8 comparisons for the subtask 'Correct positions' and for 2 comparisons for the Max. score (% of 30 subtasks) and Below min. score of sleep group. * *p* < .05, ** *p* < .01, *** *p* < .001.

Table S2. Predicting the task ‘Table setting’ by group (sleep/wake) and sleepiness during the plan realization session, bootstrapped hierarchical regression

	b	**SE *b*^{a}**	***p*^{a}**	**BCa 95% CI^a**		**Change**	***p***
				Lower limit	**Upper limit**	**in R²**	**(change in R²)**
Step 1						.25	**.002**
Constant	43.05	1.37	.000	39.84	45.75		
Group	5.18	1.43	**.012**	2.72	7.91		
Step 2						.03	.23
Constant	39.80	3.25	.000	31.59	45.50		
Group	5.99	1.74	**.013**	3.14	9.44		
Sleepiness	1.26	.95	.12	-.25	3.23		

Note: R² = .25 for Step 1, R² = .29 for Step 2, ^{a} = bootstrapped parameters, BCa 95% CI: confidence interval of 95%, bias corrected and accelerated method, bold: significant *p*-value ($p < .05$)

Table S3. Predicting the subtask ‘Correct positions’ by group (sleep/wake) and sleepiness during the plan realization session, bootstrapped hierarchical regression

	b	**SE *b*^{a}**	***p*^{a}**	**BCa 95% CI^a**		**Change**	***p***
				Lower limit	**Upper limit**	**in R²**	**(change in R²)**
Step 1						.28	**.001**
Constant	19.63	.93	<.001	17.57	21.47		
Group	3.72	.99	**.005**	1.94	5.69		
Step 2						.07	.06
Constant	16.28	2.02	<.001	11.65	19.84		
Group	4.55	1.11	**.003**	2.65	6.91		
Sleepiness	1.30	.61	**.041**	.22	2.62		

Note: R² = .28 for Step 1, R² = .35 for Step 2, ^{a} = bootstrapped parameters, BCa 95% CI: confidence interval of 95%, bias corrected and accelerated method, bold: significant *p*-value ($p < .05$)

STUDY Ⅲ

TIME-OF-DAY EFFECTS ON PROSPECTIVE MEMORY

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Keywords: prospective memory; time-of-day effect; synchrony effect; circadian preference; chronotype; morningness-eveningness

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Abstract

Cognitive performance fluctuates during the course of a day. Different cognitive functions show optimal performance at different times of the day, known as the 'time-of-day effect'. While this effect has been observed for a number of cognitive domains including declarative memory, it is presently unclear whether performance fluctuations are also seen in prospective memory, i.e. memory for intentions to be realized in the future. The present study examined time-of-day effects in four different prospective memory tasks with varying degrees of complexity, taking into account circadian preference (i.e. morningness-eveningness/chronotype) and attentional resources (in one of the tasks). In a pilot study (n = 48) and a main experiment (n = 39), prospective memory was compared between morning groups (~09:00) and evening groups (~21:00) of young adults. We found time-of-day effects, with better performance in the evening than in the morning, in a simple one-item prospective memory task (Red Pencil Task, p = .02), a classical event-based prospective memory task including the detection of cue syllables in a lexical decision ongoing task (Syllable Detection Task, p < .048), and a rather naturalistic complex planning task for breakfast preparation (Dresden Breakfast Task, including time-based prospective memory (p = .026) and event-based prospective memory (p = .054)). These time-of-day effects were neither modulated by circadian preference nor by attentional resources. Another simple one-item prospective memory task was not affected by time of day (Color Task, p = .14). Ongoing task performance in the Syllable Detection Task and the Dresden Breakfast Task, overall, did not differ significantly between morning and evening groups. These findings provide tentative evidence for time-of-day effects in prospective memory of young adults, with better performance in the evening hours.

Introduction

Prospective memory (PM) refers to the ability to realize planned intentions at an appropriate time in the future. The appropriate moment to realize an intention can be at a specific time (time-based prospective memory, e.g. taking medication at 08:00 in the morning) or is signaled by a cue in the environment (event-based prospective memory, e.g. taking the cake out of the oven when the timer rings). According to the (dynamic) multiprocess framework, both types of prospective memory can be accomplished using different strategies, either attention-based strategies that allow for the constant monitoring of the elapsed time or the environment for cues, or spontaneous memory-based retrieval strategies when the appropriate timing or the environmental cue automatically brings the intention to mind (Einstein et al., 2005; Kliegel, McDaniel, et al., 2008; McDaniel & Einstein, 2000, 2007; Scullin et al., 2013). On a neurophysiological level, prospective memory is supported by different brain areas, most prominently the anterior prefrontal cortex (Burgess et al., 2007, 2003). Attention-based monitoring strategies additionally rely on activity in a dorsal frontoparietal network (including the dorsolateral prefrontal cortex, pre-supplementary motor area, superior parietal lobule and precuneus), which is assumed to mediate the top-down control of attention towards environmental cues as well as towards keeping the intention active in mind (Cona et al., 2015). Memory-based spontaneous retrieval strategies, on the other hand, are mainly associated with activity in a ventral frontoparietal network (including mid-ventrolateral prefrontal regions, inferior parietal lobule and supramarginal gyrus), which is assumed to mediate the bottom-up capture of attention by environmental cues, reflexively directing the attention towards the associated intention (Cona et al., 2015).

Prospective memory performance is influenced by a number of different factors (Einstein et al., 2005; Scullin et al., 2013). Studies on circadian rhythmicity have shown that cognitive performance in various domains fluctuates across the course of a day in synchrony with endogenous circadian rhythms (Schmidt et al., 2007; Valdez et al., 2012). Attention capacities, for example, co-vary with core body temperature and melatonin levels, two important markers of circadian rhythmicity (Blatter &

Cajochen, 2007; Schmidt et al., 2007; Wyatt et al., 1999). Similar effects have been observed for memory functions, including working memory and declarative memory (Krishnan & Lyons, 2015; Wright et al., 2012). According to the arousal hypothesis, fluctuations in cognitive functions are driven by higher or lower basal arousal levels at different times of day (Colquhoun, 1971; Monk, 1982). A key role in the regulation of circadian rhythmicity of arousal is assigned to the suprachiasmatic nucleus (SCN) and the locus coeruleus (LC), collectively triggering the ascending arousal system, which in turn activates cortical areas, especially prefrontal areas (Aston-Jones, 2005; Blatter & Cajochen, 2007; Saper, Chou, & Scammell, 2001; Saper, Scammell, & Lu, 2005). Changes in arousal across the day may modulate activity in task-specific brain areas (Byrne, Hughes, Rossell, Johnson, & Murray, 2017; Lara, Madrid, & Correa, 2014; Marek et al., 2010), such that during times with generally low arousal levels, it may be more difficult to direct resources to brain regions needed for specific task demands (Blatter & Cajochen, 2007). Tasks that rely on the engagement of the pre-frontal cortex, i.e. a brain area that is critically involved in prospective memory, seem to be particularly vulnerable to fluctuations in arousal levels (Harrison & Horne, 2000; Schmidt et al., 2015).

The optimal time of day at which performance reaches peak levels thereby differs across cognitive domains, a phenomenon known as the ‘time-of-day effect’ (Blatter & Cajochen, 2007). For simple attention tasks like the PVT, optimal performance levels are mostly observed in the late morning (Kraemer et al., 2000; Wyatt et al., 1999), whereas for more complex tasks like declarative memory (e.g. word pair learning), some studies found better performance in the evening hours (Hidalgo et al., 2004; Koulack, 1997). However, this pattern is rather inconsistent across studies using various different tasks, indicating that time-of-day effects may also depend on specific task characteristics such as complexity, difficulty and cognitive load (Blatter & Cajochen, 2007). Apart from task characteristics, fluctuations of cognitive performance across the day are also related to inter-individual differences, such as circadian preference. Circadian preference describes an individual’s preference for morning times or evening times, also known as morningness-eveningness (Horne & Östbeg, 1976) or chronotype (Roenneberg et al., 2004). Morning types usually achieve better performance in the morning, whereas evening types perform better in the evening in some cognitive functions like inhibitory control (May & Hasher, 1998), learning (Lehmann et al., 2013) and declarative memory (Adan, 1991; Petros et al., 1990). This so-called ‘synchrony effect’ (i.e. better performance at individually optimal times) was found to be most strongly pronounced for more complex and difficult aspects of a task (Petros et al., 1990) and for tasks with an associative memory component (Maylor & Badham, 2018). However, like the time-of-day effect, the synchrony effect has not been shown consistently across all studies and in all cognitive domains (Fabbri et al., 2013; Matchoock & Mordkoff, 2009). Moreover, it remains unclear why different cognitive functions show optimal performance at different times of day for different chronotypes. From a theoretical point of view, prospective memory is particularly interesting in this regard as it relies on elements of different cognitive functions like attention, response inhibition, working memory, planning and episodic memory, depending on the specific task requirements (McDaniel & Einstein, 2000; Scullin et al., 2013). Although time-of-day and synchrony effects have been studied in these functions separately, it is not clear how they interact to support (or not) optimal prospective remembering.

For prospective memory, both time-of-day effects and the synchrony effect have rarely been investigated despite their importance for everyday life functioning and safety in work environments (Dismukes, 2012). In fact, industrial accidents and injuries are most frequent during non-optimal times of the day (like at night) and increase during afternoon hours compared to morning hours (Folkard & Tucker, 2003). For example, the serious incident at the Three Mile Island power plant in Pennsylvania in 1979 has been related to the failure to notice a lack of coolant water (Mitler et al., 1988), which can be considered an omission error in event-based prospective memory. One early study by Leirer et al. (Leirer et al., 1994) assessed prospective memory in simulated real life-like tasks, like medication intake and appointment adherence, in older adults at different times across the day, i.e. in the morning, at midday and in the evening. Performance was found to be better in the morning compared to midday, but did not consistently change towards the evening. A more recent study by Rothen and Meier (Rothen & Meier, 2017) applied a laboratory event-based prospective memory task (i.e. detecting cue words in a word categorization task) in older and younger adults. Testing took place in the morning and in the evening, also considering circadian preference according to different chronotypes. Prospective memory was found to be better at individually optimal times of the day for younger adults but not for older adults. Rothen and Meier (Rothen & Meier, 2017) suggested that younger adults might rely to a larger extent on attention-based prospective memory strategies, which may benefit from higher arousal and attentional capacities at the individual's optimal time of day. Interestingly, in the study by Rothen and Meier, younger adults were mostly evening types, such that the optimal time of day was mostly during the evening, speaking for both time-of-day and synchrony effects.

In the present study, we applied a time of day design to compare prospective memory performance of healthy young adults in the morning and in the evening. In order to test whether a putative time-of-day effect is modulated by circadian preference, i.e. a synchrony effect, we additionally assessed morningness-eveningness preferences and chronotype. We first conducted a pilot study, in which we applied a simple one-item prospective memory task as part of another study (Barner, Altgassen, Born, & Diekelmann, 2018). The main experiment then compared three different prospective memory tasks that varied in the complexity of the prospective memory instruction, the complexity of the ongoing task, the type of prospective memory (event-based vs. time-based), the manipulation of attentional resources (in one of the tasks) and the time interval between instruction and realization. Based on previous evidence and the observation that young adults are mostly evening types, we expected overall better performance in the evening for all prospective memory tasks (time-of-day effect), with this effect being particularly pronounced in evening types (synchrony effect). Furthermore, we expected that attention modulates the time-of-day effect and the synchrony effect, such that prospective memory performance is impaired under divided attention conditions especially in the evening and especially for evening types.

Methods

Pilot study – Red Pencil Task

Data for the pilot study was collected partly together with a previous study, testing sleep-dependent consolidation of complex plans, which has been published elsewhere (Barner et al., 2018). Overall, data for 48 young and healthy participants was available for the pilot study (31 female, mean age [± SD]: 23.79 ± 2.78), with data of 39 of these participants taken from the previous study and data of nine participants collected separately. Subjects participated either in the morning group (tested at 09:00 ± 1h, n = 25) or in the evening group (tested at 21:00 ± 1h, n = 23). All participants were examined on a simple one-item prospective memory task, the 'Red Pencil Task' (Hering, Cortez, Kliegel, & Altgassen, 2014). Specifically, participants were instructed to say the expression 'red pencil' aloud as soon as the experimenter would mention this exact expression later in the course of the experiment (Figure 10A). About 30 min after this instruction, the experimenter handed a paper and a red pencil to the participants for taking notes, saying "You can write down your notes with this red pencil". It was recorded whether the participants repeated the expression 'red pencil'.

Main experiment

Participants

A total of 42 young and healthy participants (29 females, mean age [± SD]: 23.29 ± 2.81) took part in the main experiment. Three participants were excluded from the final analyses. Two participants of the morning group did not adhere to the experimental instructions (they took medication) and one participant of the evening group displayed very low habitual sleep quality (PSQI = 12, for all other participants PSQI ≤ 8). Final analyses were based on data from 39 participants (morning group: n = 20, 14 females, mean age [± SD]: 22.65 ± 2.72 years; evening group: n = 19, 14 females, mean age [± SD]: 23.79 ± 2.80; with age being comparable between groups: U = 145.50, z = -1.27, p = .21). All participants reported regular sleep-wake cycles (at least 6 hours sleep per night, going to bed latest at 01:00 and waking up earliest at

06:00), no shift work for at least 6 weeks prior to the experiment and no regular night shifts in the past. During the experiment, subjects were instructed not to take any exams and to refrain from other stressful activities. Subjects reported no history of any neurological, psychiatric or endocrine disorder and did not take any medication except for hormonal contraception and thyroid hormones during the time of the experiment. Consumption of caffeine and alcohol was not allowed during the experimental period. All subjects provided written informed consent and were paid for participation. The study was approved by the local ethics committee of the Medical Faculty of the University of Tübingen, Germany.

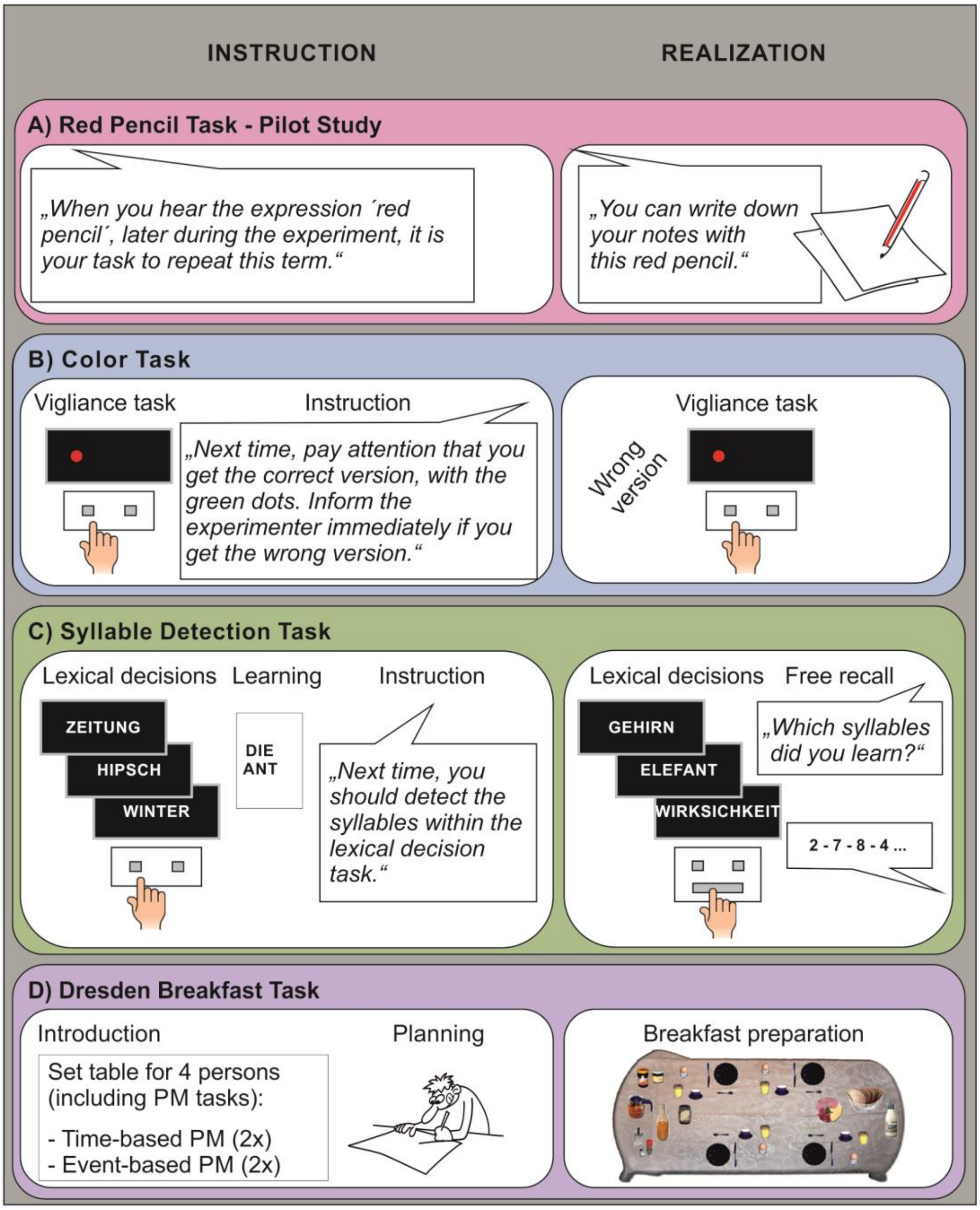

Figure 10 Experimental tasks. **A)** Red Pencil Task. In the pilot study, participants were instructed to repeat the expression ‘red pencil’ as soon as they heard this expression later in the experiment. It was recorded whether they repeated the expression during the realization phase when the experimenter mentioned a ‘red pencil’. The pilot study was part of another study published elsewhere (Barner et al., 2018). **B)** Color Task. During the instruction phase, participants performed on a vigilance task with specifically colored dots (e.g. red). They were then instructed that they would have to perform on the same task again later in the experiment but on a version with different colors (e.g. green). They were told to notify the experimenter immediately if they received the version with the wrong color. It was recorded whether they informed the experimenter during the realization phase when they were presented with the allegedly wrong version. **C)** Syllable Detection Task. During the instruction phase, subjects practiced on the lexical decision task first, which required them to press one of two buttons indicating whether the presented word was a real word or not. They then learned two German syllables (‘die’ and ‘ant’) and were instructed that at a later test, the syllables may occur within the lexical decision task (serving as ongoing task), and if they detected one of the syllables they should press the ‘space’ bar. To manipulate attentional resources during the realization phase, participants performed an auditory attention task (monitoring spoken digits for two consecutive even digits) in parallel either during the first or second half of the lexical decision task (including the cue syllables). **D)** Dresden Breakfast Task. During the instruction phase, participants were familiarized with the different tasks and subtasks of the virtual breakfast preparation task. The task included two time-based and two event-based prospective memory tasks (e.g. let tea soak for 4 min, switch off egg boiler upon signal). After the instruction, participants were allowed 10 min to plan how to realize the different tasks. In the realization phase, the number of successfully executed prospective memory tasks was assessed within the ongoing breakfast preparation task.

Design and procedure

Subjects participated either in the morning group, for which testing started at 08:30, or in the evening group, for which testing started at 19:00. Upon arrival in the lab, participants provided information about their health, their sleep in the preceding night and their alcohol and caffeine consumption in an introductory interview and then filled out the Stanford Sleepiness Scale (SSS). Afterwards, the INSTRUCTION phase started, during which participants practiced the ongoing tasks of the three prospective memory tasks (‘Color Task’, ‘Syllable Detection Task’ and ‘Dresden Breakfast Task’). This constituted the ‘baseline/ongoing phase’ without any prospective memory cues. After each ongoing task, participants received the respective prospective memory instruction (Figure 11, INSTRUCTION phase). For each of the tasks, they were instructed to perform the ongoing task continuously, but to stop the ongoing task whenever they encountered a prospective memory cue. They should then respond to the cue with the instructed response and after that, continue with the ongoing task until they detect the next prospective memory cue. The three tasks varied in the complexity of the prospective memory instruction, the type of prospective memory (event-based or time-based), and the complexity of the ongoing task (see below for detailed task description). The order of tasks was fixed for all participants. Immediately after the INSTRUCTION phase, the REALIZATION phase started, during which all subjects were required to execute the intentions (Figure 11, REALIZATION phase). The REALIZATION phase contained the ongoing tasks together with the prospective memory cues that had been instructed earlier, i.e. this constituted the 'ongoing+PM phase'. Participants were not reminded about the instructed intentions but were simply asked to perform all tasks as instructed earlier. This phase started with the 'Syllable Detection Task', followed by the 'Dresden Breakfast Task' and the 'Color Task', again in fixed order for all participants.

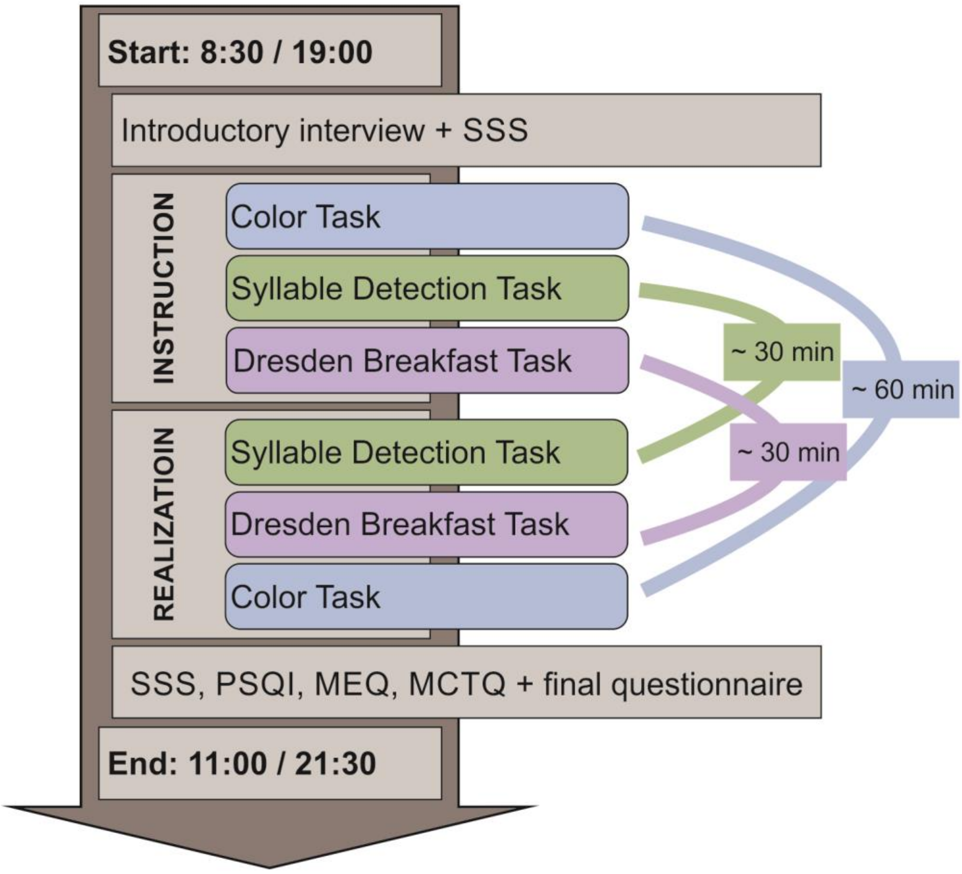

Figure 11 Experimental procedures of the main experiment. Testing took place between 08:30 – 11:00 for the morning group and between 19:00 – 21:30 for the evening group. Participants started and ended the session with different control tasks. During the INSTRUCTION phase, participants received instructions for three prospective memory tasks, the 'Color Task', the 'Syllable Detection Task' and the 'Dresden Breakfast Task'. The REALIZATION phase started immediately thereafter, resulting in different time intervals between instruction and realization for the three tasks (indicated by the curved lines and times). The order of tasks was fixed for all participants. SSS: Stanford Sleepiness Scale, PSQI: Pittsburgh Sleep Quality Index, MEQ: Morningness-Eveningness-Questionnaire, MCTQ: Munich ChronoType Questionnaire.

The different durations of the single tasks resulted in different delays between instruction and realization. Testing of the ‘Syllable Detection Task’ and the ‘Dresden Breakfast Task’ started ~30 min after their respective instruction, and testing of the ‘Color Task’ started ~60 min after the instruction. The testing session ended with participants filling out the Stanford Sleepiness Scale again as well as the Pittsburgh Sleep Quality Index (PSQI), the Morningness-Eveningness Questionnaire (MEQ), the Munich ChronoType Questionnaire (MCTQ), and a final questionnaire assessing general aspects of the experiment (see below).

Color Task

The Color Task is a simple one-item event-based prospective memory task developed by Diekelmann et al. (Diekelmann et al., 2013b). During the INSTRUCTION phase, the Color Task was introduced to the subjects as a vigilance task, which served as the ongoing task. Participants were asked to respond to a colored dot appearing on the left or right side of a computer screen by pressing the left or right button on a keyboard as fast and as accurately as possible (Figure 10B). Importantly, the dot was in a specific color (red or green, balanced across subjects) throughout the task. The color of the dot stayed the same for the entire duration of the task. The task included 40 trials with the dot appearing every 2-10 sec, with 20 trials on the left side and 20 trials on the right side (task duration approximately 5 min). Participants completed this task as ongoing task once during the INSTRUCTION phase. After completion of the task, participants received the prospective memory instruction: they were told that they would be tested again on this task later in the session, but on a slightly different version with the dot in another color (i.e., green or red, respectively). The experimenter emphasized that the participant should pay attention that the correct version, with the dot in the new color, would be presented at testing, because

completed this task as ongoing task once during the INSTRUCTION phase. After completion of the task, participants received the prospective memory instruction: they were told that they would be tested again on this task later in the session, but on a slightly different version with the dot in another color (i.e., green or red, respectively). The experimenter emphasized that the participant should pay attention that the correct version, with the dot in the new color, would be presented at testing, because

sometimes an error may occur when starting the task. If the participants noticed that they got the wrong version (i.e. the version with the dot in the same color), they should immediately inform the experimenter.

During the REALIZATION phase (about 60 min after the instruction), all participants were presented with the ongoing task (the vigilance task) again, but with the supposedly wrong version, i.e. with the dot in the same color as during the INSTRUCTION phase. Throughout the task, the dot stayed in the very same color as during the INSTRUCTION phase, i.e. the color of the dot actually never changed. Participants were not reminded of the supposedly different versions and the prospective memory instruction to detect the mistake, but it was recorded whether they approached the experimenter to ask for the correct version. During the REALIZATION phase, the vigilance task (with the 'wrong' color) contained twice as many trials (i.e. 80 trials) and lasted longer (approximately 10 min) in order to provide more time and more possibilities to detect the mistake. If subjects realized the mistake and notified the experimenter, the 'correct' version of the vigilance task with the other color was started (including 40 trials, like in the INSTRUCTION phase).

Syllable Detection Task

The Syllable Detection Task is a classical eight-item event-based prospective memory task, embedded in a lexical decision task that serves as ongoing task (Figure 10C). During the INSTRUCTION phase, subjects first practiced on the lexical decision task without any prospective memory cues. Subjects were presented with 100 word stimuli in a fixed pseudo-random sequence, half of which were real German words. The other half were 'non-words' which were derived from German words by substituting one consonant (Marsh et al., 2003, 2002). Subjects were instructed to press the right key (on a keyboard) for real words and the left key for non-words as fast and as accurately as possible with their respective index fingers. After practice on the lexical decision task, subjects learned two German syllables ('die' and 'ant'), which served as non-focal prospective memory cues for the subsequent prospective memory task. During learning, syllables were presented successively in random order for 5 sec each with 1 sec breaks in between. After both syllables had been presented twice, subjects were asked to write them down in a free recall test. All participants were able to recall both syllables correctly. After learning and recall of the syllables, participants were given the prospective memory instruction. They were informed that, apart from testing their lexical discrimination abilities, we were also interested in their ability to remember to do something in the future. For this purpose, they would be tested again on the lexical decision task later during the same session, but then, the syllables they had just learned may occasionally appear within the lexical decision task. They were instructed that they should interrupt the lexical decisions and press the 'space' bar instead, whenever they detected one of the syllables within a word or a non-word of the lexical decision task. Subjects had to repeat this instruction in their own words to ensure full understanding. They were explicitly instructed to memorize this instruction because during the REALIZATION phase, the experimenter would not remind them of what to do.

During the REALIZATION phase (about 30 min after the instruction), subjects performed the lexical decision task including the prospective memory cues (i.e. the syllables), without being reminded of the instructed intention. This time, the lexical decision task contained 378 word stimuli, including 189 real words and 189 non-words. A break was introduced after half of the words had been presented. Syllables were presented only in the second part of each half (93th, 122nd, 154th and 185th word in one half; 91st, 124th, 153rd and 184th word in the other half, with the order of the two halves balanced across subjects) in order to increase the difficulty to detect the syllables. In each half, both syllables were incorporated twice in words, and twice in non-words, resulting in eight syllable presentations in total. Both syllables could appear as first syllables or in the middle of a word/non-word of the lexical decision task. Additionally, in this task, we were interested in the role of attention for the detection of prospective memory cues. In order to test the extent to which subjects relied on attentional resources to detect the cues, we directly manipulated available attentional resources during the REALIZATION phase. During one of the halves of the lexical decision task (balanced across subjects), participants performed on an auditory attention task in parallel (i.e. divided attention). In this task, spoken digits were presented via loudspeakers at a rate of one digit every 2 sec and subjects were required to press a separate key whenever two even digits occurred consecutively.

Prospective memory performance was analyzed as the number of participants that detected at least one syllable in the lexical decision task as well as the mean number of detected syllables, with and without divided attention, respectively. Ongoing task performance was measured as reaction times (in ms) and error rates (in %) of lexical decisions. Costs of prospective memory were measured as changes in reaction times in the lexical decision task during the INSTRUCTION phase (without prospective memory cues) compared to the REALIZATION phase (with prospective memory cues) in the half of the task with full attention (i.e. without the divided attention task).

Dresden Breakfast Task

The ‘Dresden Breakfast Task’ is a complex and relatively naturalistic task with a strong planning component, which includes two event-based and two time-based prospective memory tasks (Altgassen et al., 2014, 2015) (Figure 10D). The task version that was used in the present study was identical to the version developed by Altgassen et al. (Altgassen et al., 2014), including the same virtual layout, the same breakfast preparation tasks and subtasks, and the same instructions. During the INSTRUCTION phase, participants were introduced to the Dresden Breakfast Task and were explained that they would have to prepare a virtual breakfast for four persons within seven minutes at a later time in the same session. Participants were introduced to six different tasks of breakfast preparation, including 1) Table setting, 2) Placing food, 3) Preparing eggs, 4) Preparing bread, 5) Preparing tea, and 6) Placing butter on the table. Each of these tasks comprised a number of pre-defined subtasks (overall 26 subtasks) and participants received points for the realization of these subtasks (overall 86 points). Participants were also told that there were certain rules that they would have to follow, for example, the four sets of plate, knife, teaspoon, saucer, cup and glass were supposed to be placed vis-á-vis to each other. Additionally, some of the tasks were prioritized over others, like having the table ready when the guests arrive, having the tea and eggs just ready before the guests arrive, as well as rules according to common sense (e.g. putting the table cloth first, then placing the tableware) (Altgassen et al., 2014). During these general instructions, participants were also introduced to the prospective memory tasks as part of breakfast preparation. In order to realize the two time-based prospective memory tasks, participants were asked to place the butter on the table exactly 5 min before the guests arrive (± 60 sec), and let the tea bag soak for exactly four minutes (± 60 sec). For completing the two event-based prospective memory tasks, participants were asked to pour the hot water into the teapot right after it had boiled (± 20 sec), and to switch off the egg boiler right after it had indicated by a sound that the eggs are ready (± 20 sec). After the instructions, participants were familiarized with the functions of the computer program. They were explained how to move items from the kitchen to the dining room by using a tray, and how to prepare the tea, the eggs and the bread in the kitchen. Participants were informed that the virtual time for the task started at 09:53, with the guests arriving at 10:00, and they would be allowed to check the time as often as they wished by clicking on the display of the clock. In the following 10-minute planning phase, participants had to elaborate on how they were planning to realize all the tasks and had to write down their plans.

During the REALIZATION phase (about 30 min after the instruction), participants were asked to prepare the breakfast as instructed. The different tasks of breakfast preparation (i.e. all 26 subtasks) served as the ongoing task for the four prospective memory tasks. Prospective memory was measured as the mean number of successfully executed prospective memory (PM) tasks for overall PM (4 tasks, event-based and time-based combined), event-based PM (2 tasks) and time-based PM (2 tasks). Additionally, the number of good performers was analyzed as the percentage of participants successfully completing at least 1 of 4 tasks for overall PM, at least 1 of 2 tasks for time-based PM, and 2 of 2 tasks for event-based PM (because all participants completed at least 1 event-based PM task, see below). Ongoing task performance of breakfast preparation was measured as the mean number of points achieved in the 26 subtasks (max. 86 points) as well as the mean number of points in each of the six different tasks, separately. Additionally, we assessed how many of these six tasks were realized completely (task completion in % out of six), and in how many out of the 26 subtasks the whole morning group and the whole evening group achieved the maximal score (subtasks with max score, % out of 26). As measures of general activity, we analyzed room switching (mean number of transitions from the dining room display to the kitchen display and back), task switching (mean number of interruptions of one of the six tasks in order to continue another task), time monitoring (mean number of klicks on the virtual clock), and the overall number of actions participants carried out as a measure of performance speed (mean number of automatically recorded mouse clicks).

Circadian preference

Circadian preference was assessed by a German version of the Morningness-Eveningness Questionnaire (D-MEQ, Griefahn et al. (Griefahn, Kunemund, Brode, & Mehnert, 2001)) and by the Munich ChronoType Questionnaire (MCTQ), developed by Roenneberg et al. (Roenneberg, Wirz-Justice, & Merrow, 2003). The MEQ assesses the preferred diurnal time of day for activities and sleep, with the overall MEQ score ranging from 16 to 86 with higher scores for morning types. The MCTQ assesses sleep schedules on work days and work-free days for calculating the MSFsc score, reflecting the midpoint of sleep on work-free days corrected by the sleep dept participants build up during working days compared to work-free days (Roenneberg et al., 2004). MSFsc scores ranged from 2.63 to 6.87 in the present study, with higher scores reflecting evening preference.

Control tasks

To control for general alertness, all subjects rated their subjective sleepiness on the Stanford Sleepiness Scale (SSS) (Hoddes et al., 1973), once before and once after the experimental tasks (Figure 11). After the experimental tasks, participants additionally provided information about their habitual sleep quality on the Pittsburgh Sleep Quality Index (PSQI by Buysse et al. (Buysse, Reynolds, Monk, Berman, & Kupfer, 1989)) and about their circadian preference (MEQ and MSFsc, see above). A final questionnaire assessed participants' general beliefs about the experiment, e.g. how much they liked the experiment and which hypothesis they thought was tested. Additionally, in order to control for general vigilance, reaction times (ms) and error rates (% of wrong button presses) were extracted from the vigilance task that was part of the Color Task during the INSTRUCTION phase (i.e. before prospective memory instructions, Figure 10B) (Diekelmann et al., 2013b).

Statistical analysis

Red Pencil Task and Color Task

The number of participants that performed the Red Pencil Task and the Color Task successfully was compared by means of Chi² test.

Syllable Detection Task.

The number of participants that detected at least one syllable in the Syllable Detection Task was compared by means of Chi² test. The mean number of detected syllables was compared by a Mann-Whitney-U test because the data were not normally distributed. Analysis of covariance (ANCOVA) was applied for testing the effect of the covariate ‘circadian preference’ (MEQ and MSFsc). To follow up on an effect of circadian preference, we applied a median split of the MEQ and MSFsc data and calculated ANOVAs with the group factor ‘morning/evening’ and the additional subgroup factor ‘circadian preference’ (morning preference vs. evening preference). Because analyses of the MEQ and MSFsc revealed very similar results, only the results of the MEQ are reported (as this measure has been most frequently used in the literature). The effect of divided attention was analyzed with the additional within-subject factor ‘attention’ (full attention vs. divided attention). Performance on the lexical decisions (i.e. the ongoing task) was compared by means of Mann-Whitney-U tests during the INSTRUCTION phase (due to skewness of the data) and ANOVAs with the group factor ‘morning/evening’ during the REALIZATION phase. Costs in the ongoing task were analyzed with an ANOVA with the within-subject factor ‘instruction/realization phase’ and the group factor ‘morning/evening’.

Dresden Breakfast Task

The mean number of successfully completed prospective memory tasks was compared by Mann-Whitney-U tests (because the data were not normally distributed). The number of good performers (completing at least 1 or 2 PM tasks successfully) was compared by means of Chi² tests. Like for the Syllable Detection Task, an ANCOVA was applied for testing the effect of the covariate ‘circadian preference’ (MEQ and MSFsc). Additional ANOVAs with the subgroup factor ‘circadian preference’ (morning preference vs. evening preference based on MEQ and MSFsc median splits) were calculated, but again, only the results of the MEQ are reported (as both analyses revealed very similar results). Ongoing task performance measures were analyzed using t-tests or Mann-Whitney-U tests, depending on whether the data were normally distributed. Additionally, the number of subtasks in which all participants achieved the highest possible score was compared by means of a Chi² test. Note that one data set (from the evening group) was excluded from analysis because the participant started the task only when the experimental time was running already for ~30 seconds.

Control tasks

Reaction times (ms) and error rates (%) in the vigilance task as well as data of the PSQI were compared by means of Mann-Whitney-U tests. MEQ and MSFsc scores were compared by means of ANOVA with the group factor 'morning/evening' and the subgroup factor 'circadian preference' (based on median splits as above). Subjective sleepiness (SSS) was analyzed with an ANOVA with the group factor 'morning/evening' and the within-subject factor 'start/end' (referring to the two testing time points at the beginning and the end of the experimental session).

Spearman´s correlation coefficient was used as a measure for correlations, due to not normally distributed data. Correlations were corrected for multiple comparisons with Bonferroni correction. For the lexical decision task and the vigilance task, very long reaction times (> 5000 ms) were excluded from data analyses. The level of significance was set to $p = .05$ and effect sizes are reported as partial eta squared (η_p^2).

Results

Pilot study – Red Pencil Task

In the Red Pencil Task, participants showed better performance in the evening than in the morning. In the evening group, 69.6% of participants (16 of 23) successfully repeated the expression ‘red pencil’ when the experimenter said these words, while only 36.0% of participants (9 of 25) in the morning group succeeded in this task ($Chi^2(1) = 5.41$, $p = .02$; Figure 12A).

Color Task

Performance in the Color Task did not differ between evening and morning groups. In the evening group, 89.5% participants (17 of 19) noticed that they were given the wrongly colored version of the vigilance task. In the morning group, all participants (20 of 20) noticed the mistake ($Chi^2(1) = 2.22$, $p = .14$, Figure 12B).

Syllable Detection Task

Prospective memory performance

Overall, participants in the evening group showed better performance in syllable detection than participants in the morning group. In the evening group, 84.2% of participants detected at least one syllable in the ongoing lexical decision task (16 out of 19 participants), while only 55.0% of the participants in the morning group detected at least one syllable (11 out of 20 participants, $Chi^2(1) = 3.90$, $p = .048$, Figure 12C). Likewise, evening participants ($M = 34.21 \pm 5.39$) detected significantly more syllables than morning participants ($M = 16.25 \pm 4.54$, $U = 104.00$, $z = -2.47$, $p = .013$, Figure 12C). Syllable detection was also significantly better in the evening when taking into account that attention was reduced during half of the lexical decision task by an auditory attention task (main effect ‘morning/evening’: $F(1,37) = 6.54$, $p = .015$, $\eta_p^2 = .15$). Attention itself did not significantly modulate syllable detection (main effect ‘attention’: $F(1,37) = 2.72$, $p = .11$, interaction ‘morning/evening x attention’: $F(1,37) = .14$, $p = .71$). Of note, the difference between the evening and morning groups became non-significant when only those participants that detected at least one syllable were analyzed (main effect 'morning/evening': (F1,25) = 2.15, p = .16, main effect 'attention': F(1,25) = 2.59, p = .12, interaction 'morning/evening x attention': F(1,25) = .001, p = .98), which however, may have been due to overall lower power (n = 16 and n = 11 in the evening and morning groups, respectively).

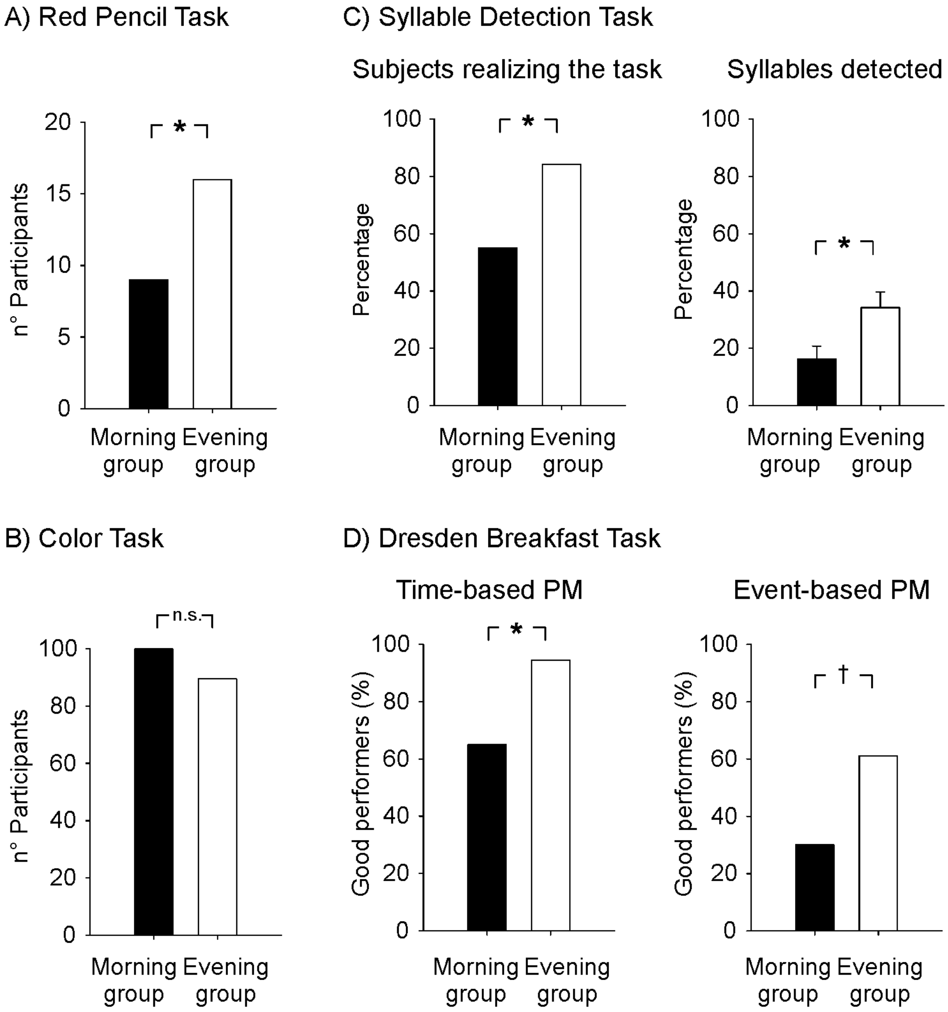

Figure 12 Prospective memory performance **A)** Red Pencil Task of the pilot study. More participants executed the task successfully in the evening than in the morning. **B)** Color Task. The number of participants that executed the task successfully did not differ in the evening and in the morning. **C)** Syllable Detection Task. Significantly more participants detected at least one cue syllable in the evening than in the morning (left panel), and overall participants detected more cue syllables in the evening than in morning (right panel). **D)** Dresden Breakfast Task. Significantly more participants in the evening group compared to the morning group were good performers in time-based prospective memory (PM) (good performers defined as executing at least 1 out of 2 tasks) (left panel). A trend towards more good performers in the evening was also evident in event-based prospective memory (PM) (good performers defined as executing 2 out of 2 tasks) (right panel). * p < .05, † p < .10.

When testing for the influence of circadian preference, by introducing morningness-eveningness (MEQ) scores as a covariate, participants in the evening group still detected more syllables than in the morning group, suggesting that higher performance in the evening was independent of circadian preference (main effect 'morning/evening': $F(1,35) = 8.50$, $p = .006$, $\eta_p^2 = .20$). Unexpectedly, participants detected more syllables, the more they prefer morning hours as their preferential time of day (main effect of the covariate 'circadian preference': $F(1,35) = 4.66$, $p = .038$, $\eta_p^2 = .12$). To follow up on a potential association of syllable detection performance with circadian preference, we separated participants into 'morning preference' and 'evening preference' subgroups based on a median split of the MEQ (Table 5). This analysis confirmed that the effect of better syllable detection in the evening was independent of circadian preference, i.e. participants performed better in the evening irrespective of whether they preferred evening or morning hours (main effect 'morning/evening': $F(1,35) = 6.50$, $p = .015$, $\eta_p^2 = .16$, 'morning/evening x circadian preference' interaction: $F(1,35) < 0.01$, $p = .98$). Interestingly though, participants with a morning preference performed marginally better than participants with an evening preference (main effect 'circadian preference': $F(1,35) = 3.19$, $p = .083$). This finding was confirmed by a significant correlation between morningness-eveningness ratings in the MEQ and the number of detected syllables, with higher morningness being associated with better syllable detection ($r_s = .33$, $p = .045$).

Table 5. Circadian preference

	Morning group[a]		**Evening group**	
	Morning preference	Evening preference	Morning preference	Evening preference
MEQ	59.83 ± 1.99[b]	45.20 ± 1.94	58.75 ± 1.44	45.83 ± 3.11
MSFsc	3.82 ± 0.19	5.44 ± 0.18	3.92 ± 0.13	5.36 ± 0.24

Means and standard error of the means are indicated for participants with a morning preference and an evening preference according to a median split in MEQ (Md = 53.25) and MSFsc (Md = 4.58) in the morning and evening groups, respectively. [a]Data for one subject not included in mean for MSFsc (value equals median), [b]Data for one subject missing for MEQ.

Syllable detection did not correlate significantly with the time participants spent in bed the night before the experiment, nor with the starting time of the experiment, the time participants got up in the morning, and the time between getting up in the morning and the start of the experiment (all $p > .15$). In the end of the experiment, all participants remembered both syllables correctly in a free recall test (data available for 32 of 39 participants), indicating that retrospective memory for the syllables was perfect in both the morning and evening groups.

Ongoing task performance

Morning and evening participants did not differ in lexical decision performance (Table 6), neither during the INSTRUCTION phase (mean reaction times in the morning: 1042.50 ± 54.94 ms vs. evening: 971.74 ± 60.91 ms, U = 153.00, z = -1.04, p = .30; error rate in the morning: 5.40 ± 0.65% vs. evening 6.53 ± 0.85%, U = 163.50, z = -0.75, p = .45) nor during the REALIZATION phase (averaged across trials with and without divided attention, reaction times in the morning: 1495.91 ± 76.60 ms vs. evening: 1485.56 ± 96.65 ms, main effect 'morning/ evening': F(1,37) = .01, p = .93; error rate in the morning: 4.93 ± 0.75% vs. evening: 5.71 ± 1.21%, F(1,37) = .31, p = .58). During the REALIZATION phase, the divided attention task slowed down reaction times (main effect of 'attention': F(1,37) = 26.23, p < .001, η_p^2 = .42) and increased error rates (main effect of 'attention': F(1,37) = .11.79, p = .001, η_p^2 = .24) to the same extent in the morning group and in the evening group (interaction 'attention x morning/evening', reaction times: F(1,37) = 1.78, p = .19, error rate: F(1,37) = 2.75, p = .11). Introduction of the prospective memory task produced significant costs in the ongoing lexical decision task. Reaction times slowed down, on average, from 1007.12 ± 40.93 ms during the INSTRUCTION phase (without PM cues present) to 1378.86 ± 59.69 ms during the REALIZATION phase (with PM cues present and full attention, main effect 'instruction/realization phase': F(1,37) = 55.50, p < .001, η_p^2 = .60). These costs were comparable between the morning group and the evening group (main effect 'morning/evening': F(1,37) = .63, p = .43, interaction 'instruction/realization phase' x 'morning/evening': F(1,37) < .001, p > .99). Higher costs were correlated with better performance in syllable detection (r_s = .38, p = .02). Error rates in the lexical decision task decreased from 5.96 ± 0.53% during the INSTRUCTION phase (without PM cues present) to 4.40 ± 0.75% during the REALIZATION phase (PM cues present, F(1,37) = 7.37, p = .01, η^2 = .17), with this reduction, again, being comparable between morning and evening groups (main effect 'morning/evening': F(1,37) = 1.45, p = .24, interaction 'instruction/realization phase' x 'morning/evening': F(1,37) = 0.22, p = .64).

Table 6. Ongoing task performance in the Syllable Detection Task

	Morning group	**Evening group**
INSTRUCTION phase		
Reaction time (ms)	1042.50 ± 54.94	971.74 ± 60.91
Error rate (%)	5.40 ± 0.65	6.53 ± 0.85
REALIZATION phase		
Reaction time (ms)		
Full attention	1409.50 ± 73.99	1338.21 ± 94.56
Divided attention	1582.33 ± 95.28	1632.91 ± 104.87
Error rate (%)		
Full attention	3.56 ± 0.65	5.23 ± 1.37
Divided attention	6.30 ± 1.00	6.19 ± 1.15

Means and standard error of the means are shown.

Dresden Breakfast Task

Prospective memory performance

The Dresden Breakfast Task includes four prospective memory (PM) tasks, i.e. two time-based PM tasks and two event-based PM tasks. Although for overall PM, the evening group performed better than the morning group on a descriptive level, this difference did not reach significance (evening: 2.94 ± 0.22, morning: 2.35 ± 0.25, U = 125.50, z = -1.65, p = .109). The same pattern of a descriptive but non-significant advantage for the evening group compared to the morning group was evident for event-based PM (evening: 1.61 ± 0.12, morning: 1.30 ± 0.11, U = 124.00, z = -1.90, p = .101) and time-based PM separately (evening: 1.33 ± 0.14, morning: 1.05 ± 0.20, U = 149.50, z = -0.96, p = .38).

To explore the descriptive difference between evening and morning groups in more detail, we analyzed the number of good performers for overall PM performance, defined as participants completing at least one out of four PM tasks (event-based and time-based combined). This analysis revealed that there were significantly more good performers in the evening group compared to the morning group ($\text{Chi}^2(1)$ =

4.94, $p = .026$). In the evening group, 94% of participants (17 out of 18) were good performers, whereas only 65% of participants (13 out of 20) were good performers in the morning group, supporting the idea that prospective memory performance was slightly better in the evening than in the morning. This difference was mainly driven by the time-based PM task, in which participants reached values from 0 to 2, resulting in the same distribution of 94% of good performers (who completed at least 1 out of 2 tasks) in the evening group and 65% of good performers in the morning group (Figure 12D, $Chi^2(1) = 4.94$, $p = .026$). For event-based PM, all participants reached values from 1 to 2, indicating that event-based PM might have been slightly easier than time-based PM. Since there were no participants with values of 0, we calculated how many participants successfully completed both event-based PM tasks as compared to only one. This analysis showed a trend for better event-based PM in the evening group (61% of participants completing 2 of 2 tasks, 11 out of 18) compared to the morning group (30% of participants (6 out of 20), $Chi^2 = 3.71$, $p = .054$, Figure 12D).

When testing for the influence of circadian preference, with morningness-eveningness (MEQ) scores as covariate, participants in the evening group showed marginally better performance than participants in the morning group in mean overall PM (main effect ‘morning/evening’: $F(1,34) = 3.40$, $p = .074$, $\eta_p^2 = .09$) as well as in mean event-based PM (main effect ‘morning/evening’: $F(1,34) = 3.82$, $p = .059$, $\eta_p^2 = .10$), with no significant difference in time-based PM (main effect ‘group’: $F(1,34) = 1.03$, $p = .20$). Circadian preference per se did not affect prospective memory performance (all $p > .26$ for main effects ‘circadian preference’). Likewise, participants did not perform better at their preferred time of day, when separating participants into ‘morning preference’ and ‘evening preference’ subgroups according to a median split of MEQ data. In this analysis, the difference between evening and morning groups remained marginally significant for overall PM (main effect ‘morning/evening’: $F(1,34) = 2.95$, $p = .095$) and event-based PM (main effect ‘morning/evening: $F(1,34) = 4.12$, $p = .05$), and non-significant for time-based PM (main effect ‘morning/evening’: $F(1,34) = 1.29$, $p =.28$), with no general effect of circadian preference (all $p \geq .40$ for main effects ‘circadian preference’ and interactions ‘morning/evening x circadian preference’).

None of the prospective memory measures correlated significantly with the time participants spent in bed the previous night, nor with the starting time of the experiment, the time participants got up in the morning before the experiment, and the time between getting up in the morning and the start of the experiment (all p > .12).

Ongoing task performance

Participants in the morning and evening groups performed equally well in the ongoing activities of the Dresden Breakfast Task, completing 70.83 ± 3.17% (morning) and 66.67 ± 3.00% (evening) of the six different tasks of breakfast preparation (U = 155.50, z = -0.78, p = .45) (Table 7). Overall performance in the six tasks was also comparable between groups (morning: 76.45 ± 1.26, evening: 72.94 ± 1.82, t(36) = 1.61, p = .11), just like performance in the six tasks analyzed separately (all p > .51, Table 7). Note that on a descriptive level, performance in the ongoing activities was slightly worse in the evening than in the morning. This is also reflected in the finding that participants in the morning group completely solved 58% of all 26 subtasks, while participants in the evening group only solved 27% completely (Chi^2 = 5.04, p = .025, Table 7).

Morning and evening groups were comparable in general activity measures of the ongoing task, i.e. room switching (morning: 25.45 ± 0.98, evening: 27.67 ± 2.09, U = 152.00, z = -0.82, p = .42), task switching (morning: 19.40 ± 1.25, evening: 18.22 ± .91, t(36) = .75, p = .46), time monitoring (morning: 6.65 ± .69, evening: 6.89 ± 1.11, U = 158.00, z = -0.65, p = .53), and the number of overall actions (measured as mouse clicks, morning: 655.15 ± 17.51, evening: 649.00 ± 17.01; t(36) = .22, p = .83).

Table 7. Ongoing task performance in the Dresden Breakfast Task

	Morning group (*M ± SEM*)	**Evening group (*M ± SEM*)**	**p values**
Task completion (% out of 6)	70.83 ± 3.17%	66.67 ± 3.00%	p(U) = .45
Overall performance (out of 86 points)	76.45 ± 1.26	72.94 ± .82	p(t) = .12
Table setting	44.75 ± .65	41.94 ± 1.3	p(U) = .13
Placing food	11.80 ± .12	10.72 ± .62	p(U) = .15
Preparing eggs	8.35 ± .83	9.00 ± .90	p(U) = .59
Preparing bread	8.55 ± .40	8.28 ± .54	p(U) = .74
Preparing tea	constant: 2	constant: 2	-
Placing butter on table	constant: 1	Constant: 1	-
Subtasks with max score (% out of 26 subtasks)	58%	27%	p(Chi^2) = .025

Means and standard error of the means are shown if not indicated otherwise, as well as p values of t-tests (p(t)) in case of normally distributed data, and Mann-Whitney-U tests (p(U)) in case of not normally distributed data, and p value of Chi^2 test (p(Chi^2)) for comparison of frequencies.

Control tasks

Participants in the morning group and in the evening group were overall comparable in their performance on the vigilance task regarding reaction time (morning: 432.21 ± 10.53 ms, evening: 441.57 ± 14.20 ms, U = 166.00, z = -0.41, p = .68) and error rate (morning: 3.63 ± .88%, evening: 3.90 ± .65%, U = 154.50, z = -0.77, p = .44). Subjective sleepiness was generally higher at the end of the experimental session compared to the beginning (main effect ‘start/end’: F(1,37) = 18.21, p <.001, η_p^2 = .33), but this effect was comparable between the evening and morning groups (main effect ‘morning/evening’: F(1,37) = 2.72, p = .11; interaction ‘start/end x morning/evening’: F(1,37) = 2.71, p = .11). Habitual sleep quality measured by the Pittsburgh Sleep Quality Index (PSQI) was comparable in the morning group (4.10 ± .41) and the evening group (4.16 ± .35, U = 178.00, z = -0.34, p = .73). Likewise, circadian preference was comparable in the two groups (Table 5; main effect ‘morning/evening’ for MEQ: F(1,34) = 0.01, p = .92, for MSFsc: F(1,34) = 0.01, p = .94). The morningness-eveningness questionnaire (MEQ) indicated that participants in the morning group (52.13 ± 9.54, min: 33.0, max: 73.0) as well as in the evening group (52.63 ± 9.64, min: 27.5, max: 68.0) were on average neither types. In fact, most participants were neither types (64%), while only one participant was definitely morning type and one participant was definitely evening type. However, as expected following the median split, MEQ and MSFsc scores differed significantly between subgroups with a morning preference and an evening preference (main effect 'circadian preference' for MEQ: F(1,34) = 40.55, p < .001, for MSFsc: F(1,34) = 69.14, p < .001), with this difference being equally pronounced in the morning and evening groups (interaction 'morning/evening x circadian preference' for MEQ: F(1,34) = 0.16, p = .69, for MSFsc: F(1,34) = 0.22, p = .64; Table 5).

Participants in the morning group spent less time in bed in the night prior to the experiment (07:20 ± 0:39 hours) compared to participants in the evening group (08:17 ± 0:44 hours, t(37) = -4.32, p < .001) and they got up significantly earlier (07:04 ± 0:18 min) than the evening group (07:34 ± 0:24 min, U = 66.0, z = -3.52, p < .001). Importantly, time in bed as well as getting up time was not correlated with prospective memory performance (see above).

Discussion

Here we investigated time-of-day and synchrony effects on prospective memory in young and healthy subjects in a pilot study and a main experiment. Overall, we found time-of-day effects in three out of four prospective memory tasks, with participants performing better in the evening than in the morning. We did not find any evidence for a synchrony effect, meaning that participants did not show better prospective memory performance at their preferred circadian times. Rather, participants with a morning preference tended to perform generally better in one of the prospective memory tasks, irrespective of when they were tested. Contrary to our hypothesis, the time-of-day effect was not modulated by attention capacities.

The four prospective memory tasks differed in a number of task characteristics with regard to the complexity of the prospective memory instruction, the complexity of the ongoing task, as well as the type of prospective memory (event-based vs. time-based). The tasks included two rather simple one-item prospective memory tasks (Red Pencil Task and Color Task) and two more complex more-item prospective memory tasks (Syllable Detection Task and Dresden Breakfast Task). We deliberately chose a set of very different types of tasks to cover a wide variety of prospective memory demands, ranging from standard laboratory tasks to more ecologically valid everyday-like prospective memory tasks. This is important because prospective memory relies on elements of various different cognitive functions, including attention, executive functions, response inhibition, working memory, planning and episodic memory (McDaniel & Einstein, 2000; Scullin et al., 2013). Time-of-day and synchrony effects have previously been studied in these cognitive functions separately, suggesting that different cognitive functions show optimal performance at different times of day as well as for different chronotypes (for an overview see (Schmidt et al., 2007)). So far, it has been entirely unclear how these different effects interact to support (or not) optimal prospective remembering, considering that different prospective memory tasks vary drastically with regard to the involvement of different cognitive functions.

The finding of higher evening performance in the Red Pencil Task suggests that even very simple intentions (like saying ‘red pencil’ upon encountering a red pencil) can display time-of-day effects. This finding is in line with a previous study showing time-of-day effects for simple simulated real life-like intentions (like taking medication at a designated time) (Leirer et al., 1994), although that study tested older subjects and found that performance was comparable between morning and evening hours but lower during midday. No difference between morning and evening was observed in the simple Color Task in the present study, which might be explained by a ceiling effect in this task. Nearly all participants (~95%) successfully remembered the intention (i.e. realizing that the wrong color of the vigilance task was presented), indicating that this task may have been too easy. Alternatively, since this was the last prospective memory task to be tested, participants might have been in a retrieval mode at the end of the session (Ballhausen, Schnitzspahn, Horn, & Kliegel, 2017; Guynn, 2003; Tulving, 1985), which might have eased task realization, masking possible time-of-day effects.

Time-of-day effects were also evident in both of the more complex prospective memory tasks, the Syllable Detection Task and the Dresden Breakfast Task. The Syllable Detection Task is a classical laboratory event-based prospective memory task (i.e. detecting cue syllables during an ongoing lexical decision task). Detecting syllables as part of lexical decisions is generally assumed to rely mainly on attention-based monitoring strategies, considering that the syllables are non-focal cues in this context. Non-focal cues are defined as not being in the attentional focus during the ongoing task and being processed independently from the ongoing task cues, which requires additional attentional processes (Einstein et al., 2005; Harrison & Einstein, 2010; Kliegel, Jäger, & Phillips, 2008; McDaniel & Einstein, 2000; McDaniel et al., 2004). Because of the non-focal nature of the Syllable Detection Task, our findings suggest that processes of attention-based monitoring might be more effective in the evening than in the morning. In line with the arousal hypothesis (Colquhoun, 1971; Monk, 1982), better attention-based strategies in the evening might have been the result of higher arousal levels during this time of the day. To test for this hypothesis directly, we experimentally manipulated attentional resources in the Syllable Detection Task by introducing a parallel auditory attention task during the REALIZATION phase. Unexpectedly, divided attention by the parallel auditory attention task did not affect performance of syllable detection when compared to full attention conditions, neither in the morning nor in the evening. Divided attention generally slowed down reaction times in the lexical decision ongoing task, indicating that the manipulation of attentional resources was in fact successful. Despite slower responses in the ongoing task, prospective memory performance was not impaired by reduced attentional resources. This finding contradicts predictions by the multiprocess framework, which postulates that more absorbing ongoing activities (like performing several ongoing tasks in parallel) reduce the available resources for strategic monitoring, thereby impairing prospective memory retrieval (McDaniel & Einstein, 2000; Scullin et al., 2013). The unexpected finding of preserved prospective memory performance under divided attention conditions might be explained by the fact that attentional resources are generally high in healthy young adults, who might be able to allocate sufficient attentional resources to monitoring processes despite engaging in a parallel attention task. This interpretation is also supported by the finding that costs of syllable detection (i.e. slowing down of ongoing task performance in the presence of prospective memory cues) were comparable in the morning and in the evening. Thus, better prospective memory performance in the evening did not seem to have occurred at the expense of higher costs. It could be speculated that subjects recruited additional spontaneous memory-based retrieval strategies in the evening to boost prospective memory performance. Some studies have indeed suggested that memory functions in young adults are more effective in the evening than in the morning (Hidalgo et al., 2004; Koulack, 1997). In line with generally better memory functions in the evening, intentions may be more easily maintained in memory in a heightened activation state during evening hours compared to morning hours. According to the theory of the intention superiority effect, still to-be-executed intentions show a higher level of activation in memory such that they are more readily accessible and retrievable (Goschke & Kuhl, 1993). This intention superiority effect might be stronger in the evening due to higher arousal levels (in line with the arousal hypothesis (Colquhoun, 1971; Monk, 1982)). These potential mechanisms should be tested systematically in future studies.

The Dresden Breakfast Task likewise showed better performance in the evening than in the morning. This task requires complex planning steps and entails different real life-like prospective memory instructions, embedded in virtual breakfast preparation. This task allowed us to separate time-of-day effects on time-based and event-based prospective memory. Although the main prospective memory measures (i.e. average performance scores) revealed only descriptive but non-significant time-of-day effects, we found significantly better prospective memory performance in the evening when comparing the number of good performers in overall prospective memory and time-based prospective memory and a trend towards better performance in event-based prospective memory. These findings suggest that both types of prospective memory, event-based and time-based, are sensitive to time-of-day effects in young adults. Interestingly, ongoing task performance of breakfast preparation was slightly impaired in the evening compared to the morning (descriptively in 7 out of 9 measures, significantly in 1 out of 9 measures). It could be speculated that this slight reduction in ongoing task performance reflects costs of better prospective memory in the evening. Yet, this speculation requires further investigation, particularly because no such difference between costs in the evening and morning was observed in the Syllable Detection Task.

Considering the combined evidence from the four different tasks, it seems that time-of-day effects are evident in prospective memory tasks of different complexity and different task characteristics: for one-item and more-item intentions, in different ongoing tasks like simple everyday activities, lexical decisions and complex virtual breakfast preparation, as well as in both event-based and time-based prospective memory. Although not all tasks and not all measures showed strong time-of-day effects, for those measures that did show the effect, performance was consistently better in the evening than in the morning. This finding is partly in line with previous findings from Rothen and Meier (Rothen & Meier, 2017), who observed better prospective memory performance at individually optimal times compared to non-optimal times in young adults; and since in that study most young adults were evening types, they generally performed better in the evening than in the morning.

We can only speculate about possible neurophysiological mechanisms underlying the observed advantage for prospective memory during evening compared to morning hours. Based on the arousal hypothesis (Colquhoun, 1971; Monk, 1982), it could be assumed that participants show higher arousal levels in the evening. In keeping with this assumption, previous evidence suggests that young adults exhibit increased glucose metabolism in brain areas of the arousal system during the evening compared to the morning (Buysse et al., 2004). Higher arousal levels in the evening may in turn ease the activation of cortical areas implicated in prospective memory. Prospective memory essentially relies on the anterior prefrontal cortex (Burgess et al., 2007, 2003) as well as dorsal fronto-parietal and ventral fronto-parietal networks for attention-based strategic monitoring and memory-based spontaneous retrieval, respectively (Cona et al., 2015). Higher arousal levels in the evening may aid the recruitment of some or all of these regions during prospective memory tasks. Increased activation of the dorsal fronto-parietal network may facilitate strategic monitoring, directing attention towards prospective memory cues as well as maintaining the intention active in mind in a top-down controlled process. Higher activation of the ventral fronto-parietal network may support the bottom-up automatic detection of prospective memory cues, reflexively triggering the associated intention in memory. Both processes may separately or collectively improve the successful execution of intentions during the evening. However, since we did not obtain neurophysiological measures in the present study, these speculations should be treated with caution and should be subject to further investigation.

Interestingly, the observed time-of-day effects were not influenced by circadian preference and chronotype (tested only in the Syllable Detection Task and the Dresden Breakfast Task). This finding speaks against a synchrony effect in prospective memory, contradicting the previous evidence from Rothen and Meier (Rothen & Meier, 2017) who observed better performance at individuals' optimal time of day. However, synchrony effects have not been reported consistently in other cognitive domains. While some studies report better performance at optimal times, e.g. for inhibitory control (May & Hasher, 1998), memory (Adan, 1991; Petros et al., 1990), vigilance (Lara et al., 2014) and academic achievement (Itzek-Greulich, Randler, & Vollmer, 2016), others report no synchrony effect for visual search, logic reasoning, spatial reasoning and mathematical search (Natale, Alzani, & Cicogna, 2003), with some studies even reporting an advantage of non-optimal times, e.g. for tasks involving creativity (Wieth & Zacks, 2011). Possible explanations for these divergent findings may relate to specific task characteristics and inter-individual differences (Blatter & Cajochen, 2007; Schmidt et al., 2007). For example, with regard to the classical event-based prospective memory task as applied in the present study (i.e. the Syllable Detection Task), we chose to use non-focal cues (i.e. syllables to be detected within words), which demands mainly attention-based monitoring strategies (Einstein et al., 2005; McDaniel & Einstein, 2000; McDaniel et al., 2004). Rothen and

Meier (Rothen & Meier, 2017), on the other hand, applied a focal task (words to be detected among words), which can be solved by more spontaneous memory-driven retrieval strategies. Both strategies may be differentially affected by circadian fluctuations and chronotype. Moreover, the synchrony effect might only be prevalent in extreme chronotypes or even only in evening types, which constituted the majority of Rothen and Meier´s (Rothen & Meier, 2017) sample, while the majority of participants in the present study were neutral types.

Although we did not observe a synchrony effect, meaning that circadian preference did not influence the time-of-day effect, circadian preference per se had an effect on prospective memory in one of the four tasks, i.e. the Syllable Detection Task. Subjects with a higher morning preference showed generally better prospective memory performance in this task, independent of time of day. Some previous studies likewise observed a benefit of morningness irrespective of testing time, for example in academic achievement (Beşoluk, Önder, & Deveci, 2011; Enright & Refinetti, 2017; Kolomeichuk, Randler, Shabalina, Fradkova, & Borisenkov, 2016; Preckel et al., 2013, 2011; Smarr, 2015; Tonetti et al., 2015), while others found divergent results, e.g. general cognitive ability showing a positive association with eveningness (Kanazawa & Perina, 2009; Killgore & Killgore, 2007; Piffer, Ponzi, Sapienza, Zingales, & Maestripieri, 2014; Preckel et al., 2011) and a negative association with morningness (Preckel et al., 2011). The overall better performance in participants with a morning preference may be explained by the observation that morning/neutral types show higher alertness scores in the second half of the day, possibly to compensate for a decline in subjective alertness in the evening and to maintain reactions to upcoming cues (Matchoock & Mordkoff, 2009). Another explanation may relate to the finding that other psychological measures, which may affect prospective memory performance, co-vary with time of day and chronotype. Morningness, for example, is associated with higher learning and performance goals (Escribano & Díaz-Morales, 2016) and need for cognition (Preckel et al., 2013), which might facilitate cognitive performance in general and prospective memory in particular, independent of time of day.

There are several limitations of the present study that should be investigated more systematically in future studies. First of all, we only assessed prospective memory performance at two time points, in the morning and in the evening of a normal working day, making it impossible to map potential non-linear fluctuations of time-of-day effects, e.g. performance peaks or dips around noon (Kleitman, 1933; Matchoock & Mordkoff, 2009). Interestingly, and contrary to the prospective memory measures, the control tasks in the present study did not show any differences between testing in the morning and in the evening, neither in subjective sleepiness nor in objective vigilance. In line with this finding, many classical subjective sleepiness measures like the Visual Analogous Scale (VAS) (Johnson et al., 1992) and objective vigilance measures like the PVT (Cajochen et al., 1999; Doran et al., 2001; Graw et al., 2004) remain relatively stable throughout the day and only decline in parallel with core body temperature after prolonged wakefulness during night hours (Blatter & Cajochen, 2007; Cajochen et al., 1999; Doran et al., 2001; Graw et al., 2004; Johnson et al., 1992). However, non-linear circadian fluctuations have been reported for other, possibly more complex tasks, like the number facility test, for which peak performance was observed at noon (Kraemer et al., 2000). Future studies should evaluate prospective memory as well as performance on different control tasks at various time points across the day and potentially also during the night using more controlled and standardized protocols like the constant routine and the forced desynchrony paradigm (Blatter & Cajochen, 2007). To this end, it would be important to develop parallel versions of ecologically valid prospective memory tasks that can be applied in within-subject crossover designs. In the present study, we used a between-subject design with different groups of subjects being tested in the morning and in the evening. Yet, to determine time-of-day effects reliably, the same subjects should be tested at different times of day using prospective memory tasks that can be applied repeatedly or with matched parallel versions. It might also be informative to use tasks with more prospective memory cues in future studies. Here, prospective memory was assessed with relatively small numbers of trials (between one and eight). Although this is consistent with the prospective memory literature (e.g. (Altgassen et al., 2014; Loft, Kearney, & Remington, 2008; Scullin & McDaniel, 2010)), such small numbers of events might lead to a lack of sensitivity for small effects, which should be considered in future research.

Another limitation is that most participants in the present sample were neutral chronotypes, making it difficult to assess possible synchrony effects, because these effects may be more pronounced in extreme chronotypes rather than neutral types.

We also did not select participants according to chronotype but only measured chronotype in our sample of the main experiment. In the pilot study, circadian preference and chronotype were not determined at all. Moreover, we did not directly control for participants' sleep-wake history before the experiment, although we only included subjects with a fairly normal and regular self-reported sleep-wake rhythm. The fact that participants kept their natural sleep-wake rhythm allows for higher ecological validity, yet at the expense of experimental control and power. Future studies should select participants more systematically with regard to circadian preference and chronotype and should test for possible associations with prospective memory in a wider range of chronotypes, specifically targeting extreme morning and evening types and controlling for sleep-wake history before the experiment.

CONCLUSIONS AND GENERAL DISCUSSION

This thesis aimed at enlightening the role of sleep and circadian rhythmicity on future-directed memories. Future-directed memory is of fundamental importance for every-day life, since it enables human beings to behave in a goal-directed way. From preparing breakfast in the morning to setting the alarm for the next day in the evening, it is a ubiquitous phenomenon relevant for every individual. Failures in the memory of planned and intended actions might cause undesired consequences. The lack of sleep and the misalignment of the sleep-wake rhythm from the timing of behavioral tasks have been shown to lead to vehicular accidents, performance errors and to industrial and engineering disasters like the partial melt down of a nuclear power plant in Pennsylvania in the United States of America (Mitler et al., 1988). Both sleep and its correct timing has been shown to be fundamental for efficient mental performance like vigilance, executive functions and memory functions (Rasch & Born, 2013; Schmidt et al., 2007). Here, I assess conditions for a beneficial sleep effect and assessed the role of circadian timing in future-directed memory. Results show that the activation state of an intention is crucial for whether prospective memory is consolidated during sleep. Specifically, intention realization was better if it was expected to take place after the sleep phase, and if intentions were instructed in temporal proximity to the learning session, in order to undergo consolidation during sleep (study 1). Complex planning seems to benefit from sleep too. Plan realization was better after a night of sleep than after an equal time of wakefulness in some measures (study 2). I further assessed the role of circadian rhythmicity in future-directed memory and showed that the memory for intentions is better in the evening compared to the morning hours, independent of the chronotype and independent of how much attention is available (study 3). Overall, these findings highlight the contribution of different phases of the circadian cycle, like the sleep phase during the night and phases of wakefulness at different times of a day, for efficient future-directed memories. These findings also reveal conditions and modulators that contribute to a sleep and a time-of-day effect.

Conditions for sleep-dependent consolidation of intentions

In study 1, I investigated the conditions under which intentions are consolidated during sleep. Results showed that the activation state of an intention determines whether the intention benefits from sleep. While it has been known that to-be realized intentions, i.e. active intentions, are realized better after a night of sleep compared to a night of wakefulness (Diekelmann et al., 2013a; Scullin & McDaniel, 2010), this thesis adds the novel finding that once intentions are completed, i.e. deactivated, they are no longer consolidated during sleep and thus cannot be realized efficiently (experiment 1 of study 1). This is in line with a growing body of studies demonstrating that consolidation is modulated by whether memory is relevant for future behavior. As mentioned above, memories are preferentially consolidated during sleep, e.g. when retrieval is announced (Van Dongen et al., 2012; Wilhelm et al., 2011), when emotionality of a stimulus is present (Groch et al., 2013; Hu et al., 2006; Payne et al., 2012, 2015; Payne & Kensinger, 2010), when reward is promised (Fischer & Born, 2009) or when intentions are instructed for later realization (Diekelmann et al., 2013b). In accordance with the active systems consolidation theory, relevance acts as a selection criterion for consolidation (Diekelmann & Born, 2010; Rasch & Born, 2013). Study 1 adds the crucial finding that the activation state of an intention is another modulator assigning relevance to memory. By manipulating this activation state (active vs. inactive), it shows that the sleep effect for intentions is abolished as soon as intentions are completed. This result lends evidence to the notion that the selection of memories for consolidation seems to be a dynamic process insofar that newly encoded memory traces are prone to modifications for a certain time before sleep begins.

Another expected condition has not been confirmed for which intentions are consolidated during sleep. Reinstating an already completed intention for consolidation during sleep was not possible (experiment 2 of study 1). This finding is surprising, since it seems very adaptive to modify (completed) intentions according to changes in the environment in order to ensure flexible behavior. Likewise, if the activation state of an intention signals relevance of a memory, then re-instating an intention should re-activate an intention and thereby allow its consolidation. One possible explanation for this unexpected finding can be derived from prospective memory research. Intention completion might be followed by a refractory period in which recently encoded memories cannot be updated by further incoming information. Intention completion has been shown to inhibit the intention (Scullin et al., 2009) below baseline activation (Marsh et al., 1998), possibly inducing such a strong deactivation impulse, that it cannot be reinstated through verbal instruction. Another possible explanation comes from a neuroscientific viewpoint. The synaptic tagging and capture hypothesis and the account of behavioral tagging state: a multi-stage process is required in order to induce persistent synaptic changes for memories to endure (Martin & Kosik, 2002; Redondo & Morris, 2011). The development of an intentional memory network which is prone to further (systems) consolidation during sleep, might depend on such a multi-stage process. The encoding of an intention might set a tag. However, tags are time-limited and decay after approximately two hours, if they cannot capture plasticity-related proteins within the 30 minutes after the tag was set. These plasticity-related proteins are delivered following strong stimulation (Martin & Kosik, 2002; Redondo & Morris, 2011). The information that the intention should be realized already after two hours (experiment 2), might not allow a stimulation impulse which is strong enough to induce the synthesis of plasticity-related proteins. With no such proteins to be captured by the tag, the tag might have ceased and with it the possibility to create an intentional memory network that is consolidated during sleep. Thus, from this point of view, intention completion and a following refractory period may not play the major role in preventing successful reinstatement of an intention. Rather, the conditions at encoding and shortly afterwards produce an intentional memory network, which is not functional in terms of triggering further consolidation during sleep.

Study 1 reveals a second condition under which intentions benefit from sleep. We showed that intentions benefit from sleep only when the intention is instructed in temporal proximity to the learning session and if it is cued after a sleep period (experiment 3 of study 1). Taking the idea of the synaptic tagging and capture hypothesis and of behavioral tagging (Martin & Kosik, 2002; Moncada et al., 2015; Redondo & Morris, 2011) one step further, it can be speculated that such an instruction might enable the development of an intentional memory network, which holds plastic changes that trigger further consolidation during sleep**.** If the intentional memory network contains the instruction to be realized after a longer time e.g. after a night´s sleep like in experiment 3 and in the basic experiment from Diekelmann et al. (2013a), this long-lasting instruction might induce a stimulation impulse which is strong enough to enable the synthesis of new plasticity-related proteins. These proteins can be captured by the tagged synapses enabling persistent changes and allow for later consolidation during sleep.

Overall, this study adds to the literature findings on sleep and memory. Specifically, about the behavioral level on conditions which allow newly encoded future-directed memories to undergo consolidation during sleep. A combination of the factors (i) activation status of an intention, (ii) expected realization after sleep and (iii) instruction in temporal proximity to the learning session, is required to form an intentional memory network which is functional in terms of being prone to subsequent consolidation during sleep. This process seems to last several hours from encoding to sleep onset and is a dynamic one, fragile to interruptions. Within this process, it remains an open question, which mechanisms effectuate the failing re-activation of a completed intention. A future study could test, whether the account of a refractory period after deactivation or the synaptic tagging account of a decaying tag holds the better explanation. An experiment, challenging the synaptic tagging and capture hypothesis, might apply the study design of experiment 2 (intention completion and reinstatement), with the difference that the intention is completed not after 2 hours, but already after 15 minutes within the critical time window of ~ 30 minutes. This is followed by intention reinstatement. With this, a tag should not have decayed, yet, and plasticity-related proteins should be produced at reinstruction of the intention. These proteins should then be captured by the tag for building an intentional memory network which is prone to consolidation during sleep. Another experiment could challenge the idea of a refractory period, by applying the same protocol, again. Intention completion occurs after 15 minutes. To test whether a refractory period ends after a certain time, the intention would be re-instated after 2 hours (after the critical time window of ~ 30 minutes). A sleep effect (prospective memory performance is comparable under reduced and full attention) in the first experiment would support the synaptic tagging and capture account, a sleep effect in the second experiment would support the refractory account. Such a study would enlighten a potential multi-step process which is necessary in order to establish an intentional memory network before sleep occurs. Such a functional memory network would be prone to consolidation during subsequent sleep.

Mechanisms underlying the consolidation of intentions during sleep are probably similar to those underlying declarative memory, as described by the active systems consolidation theory. During encoding of an intention, prefrontal-hippocampal theta coherence might code for the future relevance of the intention and for the expectancy of a later retrieval. During SWS, memory traces which were active during encoding, would be reactivated and thereby strengthened and redistributed between hippocampal and neocortical areas and within cortical areas for permanent storage (Rasch & Born, 2013). Indeed, two recent studies support the notion that intentions are probably consolidated during SWS. Diekelmann et al. (2013b) show that after the SWS-rich earlier half of the night, intentions are realized more successfully than after the REM sleep-rich second half of the night. Another study further revealed a correlation between intention realization and the amount of SWS (Leong, Koh, et al., 2019).

Some methodological remarks should be stated at this point. Instead of sleep facilitating the consolidation of intention, one could argue that sleep deprivation might have prevented optimal reprocessing of the intention and lead to the impaired intention completion under reduced attention. However, the effect after wakefulness is the same in all three experiments, i.e. a drop in reduced attention, irrespective of the manipulation of the intentional state. On the other hand, this drop is abolished in co-variation with intention manipulation only in the sleep group. Thus, it is very likely that sleep deprivation does not explain our results, but sleep does. Moreover, a split-half night design even specifies the sleep effect showing that it is probably SWS and not REM sleep, which consolidates intentions (Diekelmann et al., 2013b; Leong, Koh, et al., 2019). Another remark relates to circadian effects, which have been canceled out by parallel testing times for sleep and wake groups. The learning, consolidation and testing phase took place at the same times of the day. Nonetheless, the circadian timing of the sleep phase might be essential in so far that sleep should occur during the night, embedded in the unique neurochemical environment of neurotransmitters and hormones in order to consolidate intentions, for example, with very low levels of cholinergic activity during SWS. Since the beneficial effect of sleep on intention realization have only been shown in night sleep experiments (Diekelmann et al., 2013a, 2013b; Leong, Koh, et al., 2019; Scullin & McDaniel, 2010), generalization on whether sleep consolidates memory at another time of the day cannot be made. On the other hand, some studies show that naps yield similar consolidation effects, for example in a visual discrimination (Mednick, Nakayama, & Stickgold, 2003), in emotional and neutral memory (Alger, Chen, & Payne, 2019) or emotional and neutral associative memory (Sopp, Michael, & Mecklinger, 2018), hinting that sleep, no matter when it occurs, consolidates memories.

Sleep-dependent consolidation of memory for plans

Study 2 aimed at testing whether complex future-directed memory, like memory for plans, is consolidated during sleep just as it has been shown for more simple future-directed memory tasks, like the memory for intentions. Realizing a complex plan requires the re-organization of a larger amount of information, including the prioritization of some pieces of information over others and the re-combination of information. It has been shown that during sleep, reorganization of new information takes place, for example, problem solving (Beijamini et al., 2014), detecting a hidden rule (Wagner et al., 2004), remembering false memories (Diekelmann, Born, & Wagner, 2010) or remembering the gist of encoded information (Lutz et al., 2017). Study 2 of this thesis showed that the memory for plans do not benefit from sleep as clearly as it has been shown for simple intentions. It might be a valid finding that complex planning tasks do not undergo sleep-dependent consolidation. According to the active systems consolidation theory (Diekelmann & Born, 2010; Rasch & Born, 2013), information is selected for consolidation, especially if it is of future relevance. Selection might not occur for a huge amount of relevant information - like the complex plan we induced to our participants - due to limited capacities (Feld et al., 2016; Ngo et al., 2015). Another possible explanation for this finding might lay in the effect of the planning phase after plan encoding. Participants were allowed to sketch a strategy of how to realize the plan. By finding a kind of solution for their planning problem, they might have mentally completed the task already before the sleep manipulation. As demonstrated in study 1, completed intentions no longer benefit from sleep (intention completion, experiment 1), even if intentions are known to be realized after sleep, once more (intention reinstated, experiment 2). The fact that the plans themselves did not differ in quality between sleep and wake participants and that plan realization showed a ceiling effect further supports the idea that plans were no longer in need of further consolidation.

Conversely, complex plans seem to benefit from consolidation during sleep, which we found in a subscale of the task and in explorative measures. Two major constraints might have masked this effect. Firstly, the strong ceiling effect in the performance of the Dresden Breakfast Task might have concealed a possible sleep effect. Deeply encoded information seems to benefit less from sleep-dependent consolidation than information encoded less intensely (Drosopoulos et al., 2007). Nonetheless, single measures benefit from sleep, hinting at the notion that specific functions are sleep dependent while others are not. In the sub-task which required participants to remember the correct positions of the tableware, such a sleep effect is evident. This result is in line with other findings: object-locations are consolidated during sleep (Rasch et al., 2007; Rudoy, Voss, Westerberg, & Paller, 2009; Van Dongen et al., 2012). Furthermore, explorative analysis showed that after sleep participants realized more subtasks completely compared to after wakefulness. Since participants achieved this result with the same performance speed, it seems that efficiency of plan realization is facilitated during sleep. Instead of single pieces of information, sleep might benefit complex plans by increasing efficiency in realization. Future studies applying more difficult tasks, could reveal, whether a ceiling effect indeed masked the effects that are speculated here.

The second constraint possibly masking a sleep effect on memories for plans is that measures after sleep and wakefulness were not controlled for circadian effects. Testing in the sleep group took place in the evening, testing in the wake group took place in the morning. The better performance in the sleep/morning group could either reflect sleep consolidation, or it could be due to a circadian effect with better performance in the morning hours. However, in study 3 of this thesis, the planning part was used as an ongoing task in a prospective memory task. Planning was comparable in the morning and evening, speaking against a circadian effect in planning and in favor of a consolidation effect.

Time-of-day effects in prospective memory

Study 3 examined time-of-day effects on future-directed memory. In the past, time-of-day fluctuations have been investigated in many cognitive functions with a pronounced focus on vigilance. But executive functions and memory functions have also been shown to fluctuate during the course of a day (Blatter & Cajochen, 2007; Schmidt et al., 2007; Valdez et al., 2012). Both of these functions contribute to future-directed memories, for example prospective memory (Kliegel et al., 2002; Mahy, Moses, & Kliegel, 2014; Szpunar, Mcdermott, & Roediger III, 2007). The reliable completion of a prospective memory task at the designated time is an important task required in many jobs. Dentists, for example, should probe the dental crown before permanent fixation. Forgetting such actions at specific times of the day, for example early in the morning or after a full day of work in the evening, might have undesired consequences. These consequences might sometimes just be unpleasant (removal of a dental crown), but sometimes might have severe impact and lead to accidents or other incidents (Mitler et al., 1988). Here, we provide data to support the notion that prospective memory tasks are completed more successfully in the evening than in the morning. In three out of four tasks, we replicate the finding that young participants perform better during evening hours (Rothen & Meier, 2017).

Time-of-day effects were evident in tasks of different complexity of the intention, (1, 4 and 8 PM cues), in different types of prospective memory (3 event-based and 1 time-based task) and of different complexity in the ongoing task (a classical lexical decision task, a breakfast preparation task and a plan encoding task). With the broad range of tasks we applied, it seems that the time-of-day effects apply to PM tasks in general.

Attention and circadian preference did not modulate the time-of-day effect, which was an unexpected result. Reducing attention in a task which critically relies on it (non-focal task) did not impair performance specifically in the evening. Rather, performance in the evening was even better than in the morning, suggesting that either a compensatory attention-based mechanism was at work, or that additional memory-based retrieval strategies were applied. The account of memory-based retrieval strategies is supported by results testing for a time-of-day effect in memory retrieval. Semantic memory retrieval is better during evening hours for positive words (Millar, Styles, & Wastell, 1980; Tilley & Warren, 1983). Better retrieval might have driven the better performance in the evening. Furthermore, circadian preference is a typical modulator of time-of-day effects. Morning preference often is associated with better performance in the morning and evening preference is often associated with better performance in the evening, the so-called synchrony effect (Adan et al., 2012; Schmidt et al., 2007). However, we did not find such a synchrony effect in the memory for intentions. Rather, we found in an exploratory analysis that morningness was associated with better memory for intentions in the two tasks where it was tested, irrespective of whether testing took place in the morning or evening. This benefit for morning preference is quite a robust finding in academic achievement. Both pupils and students show better academic performance the more they tend to prefer morning hours (Preckel et al., 2011; Tonetti et al., 2015). This is in contrast to the fact that young subjects from the start of puberty to the young adult age (~12-25) tend to prefer evening hours (Adan et al., 2012) and only after the end of adolescence return to prefer morning hours (Roenneberg et al., 2004). On the other hand, evening preference has been associated with better academic achievement among high-achieving students (Piffer et al., 2014) and with higher general cognitive abilities (Preckel et al., 2011). Taken together, it can be assumed that synchrony effects are less pronounced than time-of-day effects.

In order to peg the area of validity of the time-of-day effect in prospective memory, some methodological remarks should be stated. Firstly, future-directed memories - like prospective memory - depend on the stages of encoding, retention, retrieval and realization. Like most research in the prospective memory field, study 3 assessed all of these stages in a short time window and did not manipulate testing time independently for different stages. Thus, it cannot disentangle which stages specifically contribute to the better performance during evening hours. By manipulating attentional resources during task realization, the focus was set on retrieval strategies like attention-based and memory-based strategies. The finding that reduced attention does not impair prospective memory specifically during evening hours, but rather prospective memory performance is even higher in the evening, might be due to additional memory-based processes during retrieval. Whether evening times benefitted the encoding, the retention or the retrieval of prospective memory, cannot be clarified in this study.

A second remark is related to the shape of a time-of-day effect. Time-of-day effects might not only exist between morning and evening hours. Prospective memory might peak around midday, in parallel with the circadian system. Such a parallelism has been shown for many cognitive functions like attention, vigilance, working memory, declarative memory and procedural memory (Cajochen et al., 1999; Cleeremans & McClelland, 1991; Colquhoun, 1971; Johnson et al., 1992; Kleitman, 1933; Kleitman et al., 1938; Wright et al., 2002; Wyatt et al., 1999). Additionally, sleep inertia in the early morning and an afternoon dip has been shown for different cognitive functions (Wright et al., 2012). Since only two measurements were taken in the approach of the present study, neither non-linear time-of-day effects can be mapped, nor complex interactions between time-of-day effects and the circadian preference can be revealed. Prospective memory in the elderly, for example, is best in the morning and declines towards midday, with no further decline towards the evening (Leirer et al., 1994). Future studies could assess time series spanning the whole day for mapping possible non-linear effects.

A third remark relates to the contribution of the circadian factor and the homeostatic factor. The time-of-day effects in prospective memory probably emerge due to the interplay between these two factors, as demonstrated for many other cognitive functions (Schmidt et al., 2007; Wright et al., 2012). Future studies might apply a classical forced desynchrony protocol (exposure to artificial day lengths of more or less than 24 hours encapsulated from external Zeitgeber) or constant routine protocols during prolonged wakefulness (wakefulness in a semi-recumbent position under constant light, temperature and food supply), in order to assess the contribution of these two factors.

Critical appraisal and future directions

Sleep effects and time-of-day effects in future-directed memory

The studies of this thesis show that for future-directed memories, consolidation effects during sleep and time-of-day effects are entangled in a manifold way. Study 1 and 3 complement each other in answering the question, whether consolidation effects, time-of-day effects or both effects occur in prospective memory. It can be stated that intentions are consolidated during sleep, when controlling for circadian timing by keeping the testing times constant (study 1). Prospective memory tasks also underlie a circadian effect, when neglecting consolidation, with intentions being realized better during the evening hours (study 3). Thus, there is evidence for both effects in prospective memory. Prospective memory tasks in study 1 strongly resemble one task of study 3. The same ongoing task was applied, which was a lexical decision task. However, note that they differed in focality (study 1: focal cues, study 3: non-focal cues), and in the number of cues (study 1: 20 cue-associates, vs. study 3: 8 syllables).

Study 1 and 2 complement each other in answering the question whether sleep consolidates future-directed memories of different modes of prospection. Both memories of the intention mode (study 1) and memories of the planning mode (study 2) benefit from sleep. Study 1 suggests that intentions can only be consolidated, if an intentional memory network is established in the time window between instruction and sleep. This implies that intentions are instructed such that retrieval is expected to take place after sleep and that the intention and the information when retrieval should take place are encoded in temporal proximity to each other. Study 2 suggests that the consolidation effect for plans seems to be most pronounced in the domain of spatial memory. The memory for correct positions of tableware was probably consolidated during sleep, while other domains did not seem to benefit from sleep-dependent consolidation. Study designs from study 1 and 2 differ with regard to circadian control. Circadian timing in the sleep and wake group has been well controlled for in study 1 by synchronous testing times for encoding, consolidation and retrieval.

However, in study 2, encoding of the plan occurred in the evening for the sleep group and in the morning for the wake group, while retrieval (plan realization) took place in the morning for the sleep group and in the evening for the wake group. Together with previous studies (Diekelmann et al., 2013a, 2013b; Scullin & McDaniel, 2010), data from study 1 suggests that intentions are consolidated during sleep. However, study 2 provides only weak evidence that plans are consolidated during sleep, since this effect was not found in all measures and also due to the lack of a circadian control. Future studies should systematically test whether plans and future-directed memory of other modes like simulation and prediction are consolidated during sleep, controlling for circadian effects. Furthermore, the mechanisms before sleep and during sleep accounting for a sleep effect, are still not very well understood and should be tackled in future studies.

The role of attention in consolidation and time-of-day effects

Attentional strategies during the retrieval of future-directed memories seem to differ depending on whether memories underwent a longer or a shorter retention period. With a relatively short retention interval of ~30 minutes in study 3, the reduction of attention impaired successful realization of the intention. This is in line with the multiprocess framework stating that non-focal tasks depend on attentional retrieval strategies (McDaniel & Einstein, 2000). Conversely, when a relatively long retention interval of ~2 days was induced, experimental reduction of attention only impaired prospective memory when the first night of the retention interval did not contain sleep (study 1). This impairment in PM occurred although a focal task was applied, which according to the multiprocess framework (McDaniel & Einstein, 2000) should not rely very much on attention-based strategies. However, if the retention interval contained sleep during the first night on the retention interval, reduced attentional capacities no longer impair prospective memory. Thus, sleep seems to promote memory-based retrieval of the intention. This finding extends the multiprocess framework (McDaniel & Einstein, 2000), such that - in addition to, for example, the focality of a PM task - the length of the retention interval and sleep during the retention interval seem to be another factor determining the strategy for prospective memory retrieval. Longer retention intervals seem to induce the need for attention-based retrieval strategies in a focal task which usually relies more on memory-based strategies. This effect is revoked by sleep, which seems to consolidate intentions and thus fosters memory-based strategies.

On the other hand, time of day does not seem to be such a modulating factor of retrieval strategies. Since circadian alertness is higher in the evening than in the morning especially in young subjects who tend to prefer evening times (Adan et al., 2012), one would expect that reduction in attention impairs PM performance, especially when a non-focal task is applied, which relies on attention-based monitoring strategies. Although, in study 3, PM performance is impaired when attention is reduced, this impairment is not specifically pronounced during evening hours, which dissents the notion that time of day modulates the attention-based retrieval strategies.

A recent review reveals that prospective memory benefits from sleep specifically when spontaneous retrieval processes are necessary for intention realization while attention-based strategies are less affected by disturbed sleep (Leong, Cheng, Chee, & Lo, 2019), further adding to the picture that sleep and time-of-day effects are less dependent on attention-based retrieval strategies (and fluctuations in attention), but more on memory-based strategies and potential fluctuations in these memory-based strategies. .

It is important to note that the tasks in study 1 and 3 were similar, e.g. in their ongoing task (lexical decision task) and their duration, but differed in focality (focal and non-focal in study 1 and 2, respectively), in the number of PM cues (20 different cues, each presented once vs. 2 different cues, each presented four times, in study 1 and 3 respectively), and in the retrospective load (high vs. low load, in study 1 and 3, respectively) which is why this interpretation has to be drawn with caution. It remains an open question, whether non-focal PM tasks (like in study 3) likewise benefit from sleep, such that they rely less on attentional resources after sleep. Further, it remains an open question, whether focal PM tasks (like in study 1) likewise show a time-of-day effect independent of attentional resources.

An integrative view on consolidation, its conditions and time-of-day effects beyond future-directed memory

Reconsidering Szpunar’s (2014) taxonomy of prospection, research on time-of-day effects is restricted to the mode of intention, since all so far investigated studies were carried out in prospective memory. Time-of-day effects in the remaining modes of simulation, prediction and planning still remain elusive. Research on sleep-dependent consolidation is restricted to the mode of intention and planning, which should be supplemented by studies on the simulation and prediction mode. The memory for simulations, for example, is an interesting field, since deficits in prospective memory can be attenuated by the simulations of future scenarios (Altgassen et al., 2015). Whether memory for such simulations is consolidated during sleep or underlies a time-of-day effect is still an open question. Filling this gap might be essential in understanding how deficits in cognitive functions might be attenuated.

One central aspect of this thesis is related to the conditions under which memories are consolidated during sleep. While the active systems consolidation hypothesis and the synaptic downscaling hypothesis elaborate on how memories are consolidated during sleep (Diekelmann & Born, 2010; Rasch & Born, 2013; Tononi & Cirelli, 2014), the synaptic tagging and capture hypothesis elaborates on how memories are consolidated on a synaptic level immediately after encoding onwards (Redondo & Morris, 2011). It seems that there is a theoretical gap between theories addressing the role of sleep and the synaptic tagging and capture hypothesis. Although it has been stated that tagged synapses probably undergo further consolidation during sleep (Rasch & Born, 2013), it has not been established which part of the synaptic tagging and capture process invites sleep to further consolidate memory. This study shows that conditions before sleep already determine whether memories are consolidated during sleep. Exploring in which way synaptic tagging and capture processes are involved, might allow filling the theoretical gap between these theories. Future-directed memories and specifically the concept of prospective memory seems a quite fruitful one for this purpose, since it allows the dynamic instruction, completion, the delay and suspension of intentions. This provides a wealth of timely precise opportunities for experimental manipulations which might clarify the role of tagging in sleep-dependent memory consolidation. For such an enterprise, the role of time-of-day effects should be investigated further, since the processes of synaptic tagging and capture and sleep-dependent memory consolidation span long intervals in which encoding, consolidation and retrieval of memory potentially occur at different times of day. This work highlighted the importance of both consolidation effects and time-of-day effects for the emergence of successful future-directed memory. Both factors should be systematically taken into account in future enterprises that aim at uncovering those elements in the tagging process that are inevitable for further consolidation during sleep.

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