Nap sleep benefits in recognition memory and their modulation by reward – evidence from behavioral and electrophysiological data

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To my family

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For your love, care and encouragement

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This dissertation is based on two experiments from which results are in parts published/accepted as ‘original’ articles in international peer-reviewed journals. I am the first author of the articles but other authors contributed to the work and are listed below. The articles are not exactly presented in the dissertation, but paragraphs of the introduction and discussion, as well as some figures and methods as well as parts of the results sections are similar.

Content	
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Abstract

Sleep is assumed to serve different functions, particularly in playing a major role in the consolidation of memories. Shorter daytime sleep intervals ("naps") have as well been shown to benefit memory retention. Certain neurophysiological components such as sleep spindles are thought to be essential for memory consolidation during sleep. Recently it has been shown that selection processes might occur during sleep given that not all learnt information is retrieved equally well after sleep. Motivational relevant memories which are of some value for the future seem to be consolidated most preferentially during sleep. The aim of the present thesis was to investigate the role of naps on recognition memory processes behaviorally and with electrophysiological measures. Further, it was aimed to link this to physiological parameters occurring during sleep. Finally, it was tested whether motivational cues at encoding impact a subsequent nap as well as memory retention post-sleep.

The aim of the first experiment was to test whether and how sleep influences recognition memory. According to the dual-process theory it is assumed that recognition memory is comprised of two distinct processes. Familiarity is assumed to be context-independent; eliciting a feeling of knowing something. Conversely, recollection is assumed to be context-dependent, concrete details and associations can be remembered, and it is described as a hippocampus-dependent process. Both processes have also been associated with distinct event-related potential (ERP) old/new effects. An early mid-frontal old/new effect has been associated with familiarity while a late parietal old/new effect has been shown to be linked to recollection. In the first experiment, participants learnt single words and word-pairs before performing an item memory (IM) and an associative memory (AM) test (baseline). One group was subsequently allowed to nap for 90 minutes while the other watched DVDs (control group). Afterwards, both groups performed a final IM- and AM-test for the learned stimuli (posttest). IM performance decreased for both groups, whereas AM performance decreased for the control group but endured for the nap group. ERP old/new effects were observed in both groups but did not differ between groups. In an additional ERP analysis taking the associative discrimination ability into account, however, group differences were found. Participants of the nap group showed larger ERP effects which are linked to a process of recollection. Positive correlations were observed between

spindle density during SWS and AM posttest performance as well as between spindle density during non-REM (NREM) sleep and AM baseline performance.

It was thus questioned whether a general superior learning before sleep impacts spindle density in a subsequent nap, i.e. that better learners show more spindles. Alternatively, it was assumed that spindle density might be related to selective memory performance for items which are associated with high future values as recent findings show that sleep seems to selectively benefit memories that are relevant for the future. The second experiment therefore investigated whether the processing of different reward cues at encoding is associated with changes in electrophysiological measures and sleep physiology as well as memory retention. Participants' memory was tested after learning a list of non-associated word-pairs both before and after taking a 90-minute nap. During learning, word-pairs were preceded by a cue indicating either a high or a low reward for correct memory performance at test. As expected, memory declined to a greater extent from pre- to post-sleep for low rewarded than for high rewarded word-pairs what was also reflected in differential ERP correlates of recollection. Positive correlations between spindle density during NREM sleep and general memory performance pre- and post-sleep were found. In addition to this, however, a selective positive relationship between memory performance for highly rewarded word-pairs at posttest and spindle density during NREM sleep was also observed. Further, a tendency of a positive relationship between ERPs to high reward cues at encoding and spindle density was found. These results support the view that motivationally salient memories are preferentially consolidated and that sleep spindles may be an important underlying mechanism for selective consolidation.

Taken together, the results of the present thesis show that nap sleep benefits memory retention in an associative memory paradigm what is also reflected in ERP correlates of recollection. Additionally, memory retention is linked to density of sleep spindles both before and after sleep. The present dissertation extends previous research by showing distinct effects of sleep and wake on ERPs related to recollection in the ability of associative memory discrimination. Additionally, by finding a link between sleep spindles and post-sleep memory performance for highly relevant information, recent assumptions of a selective influence of sleep on memory retention can be supported.

Zusammenfassung

Dem Schlaf werden verschiedene Funktionen zugeschrieben, insbesondere soll er eine wichtige Rolle in der Gedächtnisbildung spielen. Auch kürzere Tages-Schläfchen („Nickerchen“) haben sich als vorteilhaft erwiesen, um Erinnerungen zu bewahren. Neurophysiologische Komponenten im Schlaf wie z.B. Spindeln werden als essentiell für die schlaf-abhängige Gedächtniskonsolidierung angesehen. Zusätzlich hat sich in den letzten Jahren gezeigt, dass im Schlaf scheinbar Selektionsprozesse ablaufen, da nicht alle gelernten Informationen gleichermaßen gut nach dem Schlaf abrufbar sind. Dabei scheinen insbesondere relevante Erinnerungen verstärkt abgespeichert zu werden, welche einen zukünftigen Nutzen haben. Das Ziel der Thesis war zunächst die Rolle eines Nickerchens auf Prozesse des Wiedererkennens mit behavioralen und auch elektrophysiologischen Maßen zu untersuchen sowie dies in Verbindung mit neurophysiologischen Prozessen während des Schlafens zu setzen. Ferner wurde der Effekt von Belohnungsreizen während des Lernens auf ein darauffolgendes Nickerchen und die anschließende Gedächtnisleistung untersucht.

Im ersten Experiment wurde der Einfluss eines Nickerchens auf die beiden Prozesse untersucht, die dem Wiedererkennen zugrunde liegen. Im Rahmen des zwei-Prozess Modells wird angenommen, dass das Wiedererkennen anhand zweier verschiedener Prozesse abläuft, die sich allerdings nicht zwangsweise ausschließen müssen. Familiarität ist kontext-unabhängig und ruft ein Gefühl der Vertrautheit hervor während Rekollektion kontext-abhängig ist. Hier können spezifische Details und Assoziationen erinnert werden, daher wird Rekollektion auch als Hippokampus-abhängig beschrieben. Beide Prozesse lassen sich auch an Hand von Ereignis-korrelierten Potentialen (EKPs) unterscheiden, ein früher frontaler alt/neu Effekt wird mit Familiarität, und ein später parietaler alt/neu Effekt mit Rekollektion assoziiert. Im ersten Experiment lernten die Teilnehmer einzelne Worte und nicht-assoziierte Wortpaare bevor je ein Test für die Worte (IM-Test) und die Wortpaare (AM-Test) absolviert wurde (Baseline). Während die eine Hälfte der Teilnehmer danach ein Nickerchen machte (~ 90 Minuten), schaute die andere Hälfte DVDs (Kontrollgruppe). Anschließend absolvierten beide Gruppen die zweiten Tests für die gelernten Stimuli (Posttest). Die Gedächtnisleistung im IM-Test sank für beide Gruppen ab, während die Leistung im AM-Test sich nur für die Kontrollgruppe verschlechterte. EKPs in den alt/neu Vergleichen unterschieden sich nicht zwischen den beiden Gruppen, in einer

zusätzlichen EKP-Analyse der assoziativen Diskriminierungsfähigkeit wurden jedoch Gruppenunterschiede gefunden. Die Nap-Gruppe zeigte hier größere Rekollektion-assoziierte EKPs. Die Spindeldichte während des Tiefschlafs korrelierte positiv mit der Gedächtnisleistung nach dem Schlaf, und die Spindeldichte während des non-REM-Schlafs korrelierte mit der Gedächtnisleistung vor dem Schlaf.

Daher stellte sich die Frage ob besseres Lernen und Erinnern vor einem Nickerchen zu hohen Spindeldichten im darauffolgenden Schlaf führt, d.h., dass bessere Lerner höhere Spindeldichten zeigen. Alternativ wäre es möglich, dass die Spindeldichte ein Maß für die selektive Konsolidierung von relevanten Gedächtnis-inhalten während des Schlafens ist. Letzteres würde neuere Befunde stützen, welche zeigen, dass Schlaf selektiv Erinnerungen bevorzugt, die wichtig für die Zukunft sind. Im zweiten Experiment wurde daher untersucht, inwieweit sich verschiedene Belohnungshinweise während des Lernens auf elektro- und schlafphysiologische Maße sowie die Gedächtnisleistung auswirkten. Die Teilnehmer lernten nicht-assoziierte Wortpaare und wurden dazu dann sowohl vor als auch nach einem 90-minütigen Nickerchen getestet. Während des Lernens wurde ein Hinweis vor jedem Wortpaar eingeblendet, der entweder eine hohe oder eine niedrige (Geld-) Belohnung für das richtige Erinnern im Test anzeigte. Wie erwartet sank die Gedächtnisleistung für niedrig-belohnte Wortpaare stärker ab als für höher-belohnte, was auch in den EKPs von Rekollektion widergespiegelt wurde. Positive Korrelationen ergaben sich zwischen der Spindeldichte und der generellen Gedächtnisleistung vor und nach dem Schlafen. Zudem wurde eine selektive Korrelation zwischen der Leistung am Posttest für hoch-belohnte Wortpaare und der Spindeldichte gezeigt. Weiterhin ergab sich tendenziell ein positiver Zusammenhang zwischen EKPs auf hohe Belohnungsreize beim Lernen und der Spindeldichte.

Zusammengefasst zeigen die Ergebnisse der vorliegenden Thesis, dass ein Nickerchen die Gedächtnisleistung in assoziativen Gedächtnisaufgaben fördert. Außerdem scheint die Gedächtnisleistung sowohl vor als auch nach dem Schlaf mit der Dichte von Schlafspindeln zusammenzuhängen. Die vorliegende Dissertation erweitert bisherige Befunde indem gezeigt wird, dass Schlaf und Wachheit sich unterschiedlich auf Rekollektions-EKPs in einem assoziativen Gedächtnistest auswirken. Indem ein Zusammenhang zwischen Spindeln und hochwertigen Gedächtnisinhalten gefunden wird, werden zusätzlich neuere Befunde gestützt, die einen selektiven Einfluss von Schlaf auf die Gedächtnisleistung annehmen.

Content

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List of Abbreviations

ACC:	Anterior Cingulate
AM:	Associative Memory
ANOVA:	Analyses of Variance
DA:	Dopamine
DC:	Direct Current
EEG:	Electroencephalography
EOG:	Electro-Ocular Activity
ERP:	Event-Related Potential
ESS:	Epworth Sleepiness Scale
fMRI:	Functional Magnetic Resonance Imaging
HC:	Hippocampus
IM:	Item Memory
IQ:	Intelligence Quotient
ISI:	Inter-Stimulus-Interval
LTP:	Long-Term Potentiation
MTL:	Medial Temporal Lobe
NAcc:	Nucleus Accumbens
NREM:	non Rapid Eye Movement
PET:	Positron Emission Tomography
PFC:	Prefrontal Cortex
PHc:	Parahippocampal
PPT:	Penduculopontine Tegmental Nuclei
RAM:	Reward Activation Model
REM:	Rapid Eye Movement
RT:	Reaction Time
S1:	Stage 1 sleep
S2:	Stage 2 sleep
S3:	Stage 3 sleep
S4:	Stage 4 sleep
SD:	Standard Deviation
SL:	Sleep Latency
SME:	Subsequent Memory Effect

SN:	Substantia Nigra
SO:	Slow Oscillation
SpD:	Spindle Density
SSS:	Stanford Sleepiness Scale
SWS:	Slow-wave-sleep
TST:	Total Sleep Time
vPFC:	ventral Prefrontal Cortex
VS:	Ventral Striatum
VTA:	Ventral Tegmental Area

1 General introduction

"If sleep does not serve an absolutely vital function, then it is the biggest mistake the evolutionary process has ever made", Allan Rechtschaffen (1971, p. 88).

Sleep is a highly vulnerable state as it is marked by unconsciousness, reduced physical activity and elevated arousal thresholds (Pace-Schott, 2009). Hence, it is assumed that sleep must serve essential functions which by now have been discussed for a long time. Sleep deprivation studies are demonstrating the need of sleep for surviving and intact cognitive functioning (Allan Rechtschaffen, 1971). Next to endocrine and immunological functions which have been assigned to sleep, it's role in learning and memory became very central in recent years (Rasch & Born, 2013). Sleep has frequently been shown to benefit the consolidation of different kind of memory types in comparison to equivalent time intervals of wakefulness (Diekelmann, Wilhelm, & Born, 2009). During sleep, memory processes take place especially in hippocampal and neocortical sites which are associated with memory consolidation but are as well associated to encoding (Inostroza & Born, 2013).

The ability to gain and apply knowledge, and to flexibly adapt this according to changing needs, is an elementary feature of human beings (Baddeley, 2010). Next to learning information which is to be recalled freely at a specific time point (e. g. an emergency number); the recognition memory system is also an essential component of the memory system (e. g. recognizing the emergency doctor) (Anderson, 2010). As processes of recognition memory are fast-acting, electroencephalography is a sensitive and objective measure of their magnitude and temporal pattern as it provides a temporal resolution in the milliseconds range (Luck, 2005). Next to the importance of being able to recognize harmful or threatening situations or objects, recognition of potentially rewarding stimuli also enables important environmental adaptations for the organism (Ward, 2010). Recently, it has been discussed that sleep plays a role in selectively strengthening these rewarding – or future relevant – information (Stickgold & Walker, 2013). Next to beneficial effects of night sleep on memory formation, shorter sleep periods ("naps") have been also shown to be advantageous for memory retention (Diekelmann & Born, 2010).

The present thesis investigated the effects of nap sleep on recognition memory using electrophysiological and behavioral measures in study one; in study two

additionally the impact of motivational cues during encoding on sleep and selective memory consolidation was examined. To begin with, chapter 2 gives an overview about theoretical and practical foundations which led to the main research questions of the first experiment. Methods and results as well as discussion of the first experiment are described in chapter 3. Recent developments in sleep and memory research, in combination with the results of experiment one, were leading to the aims for the second experiment. Chapter 4 therefore deals with theoretical and practical foundations underlying the expectations for the second experiment. Methods, results and related discussion for the second experiment can be found in chapter 5. The following chapter 6 comprises the general discussion in which results of both experiments are conjointly discussed and put into relation with former research findings. The results of the present thesis will contribute to the understanding what type of memory benefits from nap sleep as well as demonstrate sleep effects on their electrophysiological correlates. Further, it is shown how behavioral and electrophysiological findings are both related to neurophysiological events during sleep and how motivational manipulation at encoding can alter sleep-related physiological components and post-sleep memory retention.

2 Theoretical and empirical review – Part 1

Part 1 of the theoretical background will deal with the human memory system especially the recognition memory system and associated neuronal correlates (chapter 2.1). Following this, the method of electroencephalogram (EEG) will shortly be described (chapter 2.2) as it was used for the estimation of event-related potentials (ERPs) on the one hand (chapter 2.2.2) and the classification of sleep stages and physiological markers during sleep on the other hand (chapter 2.3.1). Chapter 2.3 mainly summarizes literature about the interaction of sleep and memory as well as possible underlying processes. Sleep effects on recognition memory processes and associated ERPs are described in chapter 2.4. The first theoretical part closes with a summary and the description of the objectives for the first study (chapter 2.5).

2.1 Human memory system

Memory can be divided in several sub-systems according to the timeframe in which information is retained. It is subdivided in sensory, short-term and long-term memory (Baddeley, 2010; Squire, 1986). Sensory memory combines perception and memory and lasts for several seconds whereas short-term memory lasts for several minutes. Long-term memory stores information for much longer periods, lasting from days to several years (Baddeley, 2010). In humans, long-term memory is divided into two different types (see Figure 2.1; Squire (1992); Squire & Zola (1996)). One is called non-declarative (or procedural) memory which is comprised by several different memory processes which are all not consciously controlled and is also called implicit memory. Skills, priming, conditioning and non-associative learning are belonging to this system (Squire, 1992). The other is named declarative memory which consists of memories that are accessible to conscious retrieval and is therefore also called explicit memory (Squire, 1998). Declarative memory is further divided in episodic memory and semantic memory (Squire, Knowlton, & Musen, 1993; Tulving, 1972). The latter encompasses general knowledge without explicitly knowing when and where the knowledge has been acquired (e. g. the fact that Madrid is the capital of Spain). Episodic memories comprise events that are associated with spatial, temporal and/or

autobiographical information (Squire et al., 1993). The next paragraphs will deal with the episodic memory system[1] including learning, storage and retrieval of information, in a further section recognition memory which is also belonging to the episodic memory system will be explained in more detail as well as the associated neuronal correlates.

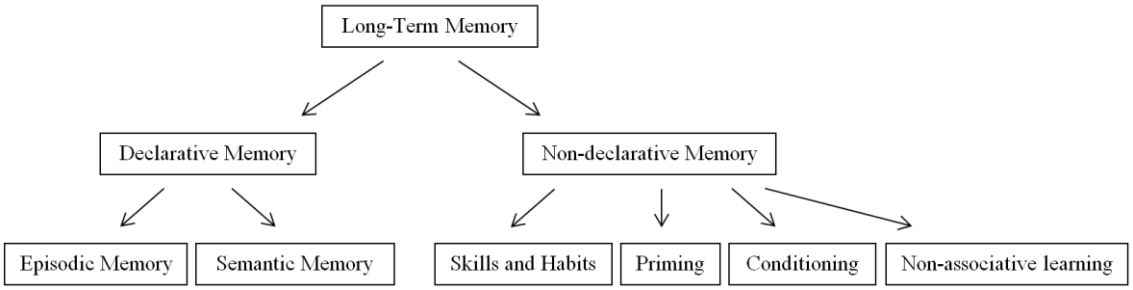

Figure 2.1. A schematic illustration of the division of the human long term memory system (adapted and modified from Squire (1992)).

2.1.1 Episodic memory

If one is thinking about spending the past winter holidays learning skiing in a little town in northern Norway, one is referring to his episodic memory system. Episodic memory is thought to allow a "mental time travel" (Tulving, 1993, p. 67) while recollecting specific experiences and events. In experimental designs, one is usually forced to learn lists of words, faces or objects and often tested with (cued) recall or recognition memory tasks. There are several factors which determine if an item will be remembered later or if it will be forgotten. To remember an event successfully, three steps need to be completed effectively: *encoding* (learning), *consolidation* and *retrieval* of the information. At each of these three points a failure would lead to forgetting.

To have a chance to remember something, firstly, the *encoding* needs to be successful. Next to paying attention to material being learnt, other aspects are also important. There are hints that it is helpful to encode items both visually and verbally (Paivio, 1969) by e.g. imaging visual relationships between words on a list. Another important factor of successful encoding is the depth of encoding (*levels of processing hypothesis*, Craik & Lockhart (1972)) which means that the deeper the processing the better the memory. The intention to learn (see also 4.1) is also very helpful for

[1] Throughout the dissertation the usage of the term "memory" will reflect episodic memory, except otherwise noted.

memorization but only in combination with a good learning strategy (e. g. elaborate processing of information).

After encoding, the newly created memory traces need to undergo a process of *consolidation* to be retrievable later on as they are initially labile and easily disrupted (e. g. by interfering material). During the process of consolidation which can be divided in system and synaptic consolidation (Dudai, Karni, & Born, 2015; Frankland & Bontempi, 2005; Rasch & Born, 2013), the memory traces are strengthened, becoming therefore more robust and stable. Synaptic consolidation refers to changes in synaptic connectivity; growth of new synaptic connections or the alteration of already existing connections and is usually completed within a few hours after learning. System consolidation refers to a longer process which involves a re-organization of memory representation on a (brain) system level. New information is initially encoded in both the hippocampus (HC) and neocortex from where it is gradually transformed so that neocortical memories slowly become independent of the hippocampus (O'Reilly, Bhattacharyya, Howard, & Ketz, 2011; Rasch & Born, 2013). It is assumed that a wealth of memory consolidation takes place during sleep (Born & Wilhelm, 2012; Diekelmann & Born, 2010) which is explained in more detail in chapter 2.3.

After successfully encoding and consolidating a memory, it must as well be able to be *retrieved* to be successful in remembering an event (Anderson, 2010). The long-term memory system is capable of storing a huge amount of information but it is necessary to retrieve the one someone is interested in. Cues are needed, either intrinsic or extrinsic, to activate the memory traces of interest. In laboratory settings a bunch of retrieval tests is used to measure memory performances. Participants can be asked to freely recall learnt items, also implicit tests could be used or they can be asked if they recognize learnt material which then needs to be distinguished from previously not seen (new) one. Recognition memory is, however, thought to involve not one but two retrieval processes (*dual process theory*, Mandler (1980), Yonelinas (1999)) and as it is the main focus of the present thesis it will be explained in more detail in the next section.

2.1.2 Recognition memory and neuronal correlates

Imagine the following situation; you are reading a book a colleague borrowed to you. After a few pages, you feel like you read this book some time ago. This feeling of familiarity *grows stronger while continuing reading, and after strongly thinking about it more and more you eventually start to remember, you* recollect *details: the end of the book; that you borrowed it the first time from a (school) friend and were reading it at the swimming pool during school holidays.*

This example illustrates the two processes which are belonging to the concept of recognition memory (Yonelinas, Aly, Wang, & Koen, 2010). In order to decide whether someone or something is known, a judgement can be made either by familiarity-based recognition or by means of recollection. According to dual-process accounts, familiarity is a fast process without context information whereas recollection is a much slower process; it is supposed to be more effortful while contextual details of a prior episode can be recalled (Yonelinas, 2002). In laboratory settings, usually not a whole book needs to be recognized but e. g. single words, faces or pictures. After learning a set of words, people are presented with learnt and new stimuli and need to decide whether they have been seen them before or not. This can be done based on familiarity or recollection or a combination of both processes. There are different types of tests which try to disentangle the different contribution of familiarity and recollection to recognition memory. Examples would be the remember/know task (Tulving, 1985), the process dissociation procedure (Jacoby, 1991) or associative tests (Bader, Mecklinger, Hoppstadter, & Meyer, 2010). The first procedure asks people whether they recognize an item based on "remembering" it i.e. recollecting specific details of the study event or on "knowing" it that means without remembering any details. Recollection is associated with the "remember"-answers whereas familiarity is assumed to be reflected in the "know"-answers (see also Yonelinas (2002) for further details on this procedure). In the second procedure (process dissociation procedure), the ability of participants to recollect details is tested directly by using different stimuli sets to be learnt (e. g. one list of words is presented visually, the other auditory). For the recognition test, two conditions are compared. In the inclusion condition, participants are instructed to say "old" for each item they remember of either the seen or heard list. For the exclusion condition, they need to say "old" only for the items which were on the second (e. g. heard) list. For the inclusion task, familiarity and recollection could lead to correct

recognition, whereas in the exclusion task, answers based on familiarity could lead to mistakes (e. g. saying "old" to an item which was presented visually). By subtracting these errors from the overall recognition performance of the inclusion condition, an estimate of recollection can be generated (Drosopoulos, Wagner, & Born, 2005; Jacoby, 1991).

The third type of tests is called associative tests; this is a kind of memory task which is thought to make familiarity-based decisions insufficient to support correct responding (Yonelinas et al., 2010). Whereas in item memory tests (single items; e. g. words) stimuli can be either classified as old (learnt) or new (not learnt) on the basis of familiarity as well as recollection, in associative memory tests subjects are required to discriminate between old (learnt) pairs and recombined (learnt but new configurations of items) pairs. By this, associative memory tests provide a sensitive measure for recollection because old and recombined pairs cannot be discriminated on the basis of familiarity (Hockley & Consoli, 1999; Yonelinas, 1997). Even, under some circumstances, familiarity is thought to be useful in associative tests (Mecklinger, 2006), i.e. with certain kinds of semantic associations (Kriukova, Bridger, & Mecklinger, 2013) what can be minimized by using semantically unrelated word-pairs.

According to dual process models, familiarity and recollection are not mutually exclusive but there is nevertheless evidence that recollection- and familiarity-based recognition decisions are supported by distinct neuronal systems (Skinner, Manios, Fugelsang, & Fernandes, 2014; Yonelinas, Otten, Shaw, & Rugg, 2005) as for example studies of patients with lesions in hippocampal sites showed that familiarity-based recognition was intact but the use of recollection failed (Aggleton et al., 2005; Holdstock et al., 2002). In a study by Yonelinas and colleagues (2005) it was shown that the hippocampus is related to recollection as well as an anterior medial region of the prefrontal cortex and the posterior cingulate. Within the lateral parietal cortex, a lateral/temporal region was also related to recollection whereas a more superior region was associated with familiarity. Familiarity was also linked with activation in precuneus as well as anterior and dorsolateral prefrontal cortex. Notably, familiarity- and recollection-based processes have also been associated with distinct event-related potentials (ERPs) (Friedman & Johnson, 2000; Mecklinger, 2000; Rugg & Curran, 2007) which will be described, next to the physiological basis of EEG and ERPs, in the following chapter (2.2).

2.2 Electroencephalogram (EEG)

The method of EEG is very useful for both scientific and clinical purposes due to its high temporal resolution (Luck, 2005). It was already shown by Hans Berger in 1929 that it is possible to measure the electrical activity of the human brain with electrodes on the surface of the scalp (Berger, 1929). In the present thesis, the method of EEG was used for the estimation of event-related potentials (ERPs) as functional markers of familiarity and recollection as well as for the classification of sleep stages and further physiological variables during sleep (section 2.3.1). The next parts will deal with the recording and underlying physiology of EEG (2.2.1) and the technique of ERP primarily in relation to recognition memory (2.2.2).

2.2.1 Recording and physiological basis of EEG

The EEG recording is obtained by placing electrodes on the scalp along with a conductive paste to facilitate a low-resistance recording. As the signal is only recorded, that means typically no stimulation occurs, EEG is a non-invasive and painless method of brain activation estimation. The signal consists of small voltage fluctuations between specified pairs of electrodes (Coles & Rugg, 1995; Luck, 2005). The measured voltage is generated by postsynaptic dendritic currents of pyramid cells in the cerebral cortex; due to the binding of neurotransmitter on receptors in the membrane of postsynaptic cells, ion channels are opened or closed, leading to a subtle change across the cell membrane potential (Luck, 2005; Proverbio & Zani, 2003). As the signal of a single neuron is too small, it is required that thousands of neurons are activated together to generate a measurable electric field. Further, these neurons need to be aligned in parallel so that their activation can be summed to be measurable (Coles & Rugg, 1995). Typically, the electrodes are arranged at specified locations during the recording (Klem, Lüders, Jasper, & Elger, 1999). However, activity recorded at one location must not mean that this is due to the underlying neurons as activity in one location can be measured at distant locations as well (Luck, 2005; Proverbio & Zani, 2003). Further, activation of more than one electrical source can lead the effect that the maximum of one source and the minimum of another source cancel each other out (Proverbio & Zani, 2003). Therefore, the method of EEG has only poor spatial resolution, but importantly it has a good temporal one (Luck, 2005). As both processes of recognition memory

(familiarity even faster than recollection) evolve in the range of hundreds of milliseconds after stimuli onset, the superior temporal resolution of EEG is very advantageous for the investigation of recognition memory processes. Therefore, EEG respectively event-related potentials (ERPs) have been used in a number of studies to investigate these processes; they will be explained in more detail in the following section.

2.2.2 ERPs in recognition memory analysis

An event-related potential (ERP) refers to an averaged EEG signal which is recorded in response to a stimulus presentation (Coles & Rugg, 1995; Luck, 2005; Proverbio & Zani, 2003). The signal needs to be averaged over a certain number of trials in each condition of interest because the occurring voltage changes after one stimulus presentation are relatively small and difficult to identify within the background EEG (low signal-to-noise ratio) (Luck, 2005; Rugg, 2002). The resulting ERP waveform then consists of several peaks and troughs which occur at specific times (ERP components) which are defined by their amplitude (μV), peak latency (ms), polarity and electrode position and seem to be related to different aspects of cognitive processes (Coles & Rugg, 1995; Rugg, 2002).

It could be shown repetitively in recognition memory research (review Rugg & Curran (2007)) that ERPs which are linked to correct answers to old items are more positive going than those of correct answers to new items, therefore called ERP old/new effects (Sanquist, Rohrbaugh, Syndulko, & Lindsley, 1980; Wilding & Sharpe, 2003). Further, the two processes of recognition memory, familiarity and recollection, are associated with distinct ERP old/new effects (Curran, 2000; Friedman & Johnson, 2000; Mecklinger, 2000; Rugg & Curran, 2007; Rugg et al., 1998). An early mid-frontal old/new effect has been shown to operate in a way which is consistent with an index of familiarity while the late parietal old/new effect has been shown to correlate with recollection-based memory judgments (Bridger, Bader, & Mecklinger, 2014; Curran & Cleary, 2003; Johansson, Mecklinger, & Treese, 2004; Paller, Kutas, & McIsaac, 1995; Smith, 1993; Wilding, 2000; Wilding & Rugg, 1996; Woodruff, Hayama, & Rugg, 2006; Yu & Rugg, 2010). The early mid-frontal old/new effect usually occurs between

300-500 ms after stimulus presentation whereas the late parietal old/new effect shows an onset between 400-500 ms and ends between 700-800 ms (Rugg & Curran, 2007).

Despite the aforementioned ERP studies, which show these associations between familiarity and recollection with distinct old/new effects, it is problematic to link these to their electrical sources within the brain as a lot of electrical currents in different regions could be measured together in one position (see also 2.2.1). Simultaneous recording of EEG and functional magnetic resonance imaging (fMRI) is a rather new approach that was used to investigate which brain regions are activated while old/new effects are observed in a recent exploratory study by Hoppstädter and colleagues (2015). With a yes-no recognition memory paradigm using concrete nouns it was shown that fMRI activation in right dorsolateral prefrontal cortex and right intraparietal sulcus was associated with the amplitude of the early frontal old/new effect. The amplitude of the late parietal old/new effect was correlated with activation in the right posterior hippocampus, parahippocampal cortex and retrosplenial cortex (Hoppstädter et al., 2015). These results support other studies which demonstrate that the hippocampus is central for recollection-driven memory decisions (Addante, Ranganath, Olichney, & Yonelinas, 2012; Bowles et al., 2010; Yonelinas et al., 2002).

There are studies which suggests that the late parietal old/new effect varies dependent on the amount of information which is recollected (Vilberg, Moosavi, & Rugg, 2006; Wilding, 2000). Wilding (2000) recorded ERPs while participants had to judge words as old (studied) or new (not studied) plus giving two source judgments for the old items. They showed reliable old/new effects at frontal and parietal sites, but only the magnitude of the parietal effect varied with the number of correct source answers. Vilberg and colleagues (2006) used a modified remember/know paradigm with visually presented object-pairs to investigate the ERP correlate of recollection. In addition to the answer options new, know and remember ("remember 1"), they used a second remember ("remember 2") option. The first one, "remember 1", was to be used when a minor aspect of the study episode could be recollected, and "remember 2" was to be chosen only if the picture which was paired at study with the test picture could be recalled. The left parietal old/new effect was varying according to the either fully or partly recollected information; a greater amplitude of the parietal old/new effect was shown when correct "remember 2" compared to "remember 1" answers were given to the tested objects. Further, an early frontal old/new effect was present for correct old vs. correct new answers which did not vary according to remember or know answers.

Taken together, the two processes of recognition memory, familiarity and recollection, can be differentiated by ERP old/new effect, which are likely to be supported by distinct neuronal systems (Skinner et al., 2014; Yonelinas et al., 2005) with only the amplitude of the late parietal old/new effect - but not the early frontal old/new effect - varying with the amount recollected (Vilberg et al., 2006; Wilding, 2000).

2.3 Sleep and memory formation

Sleep is defined by several criteria, e. g. behavioral quiescence, reduced motor activity, elevated arousal thresholds, rapid spontaneous reversibility (Pace-Schott, 2009) and it is controlled by circadian biorhythms (Rosenwasser, 2009). The following subsections will explain shortly the sleep architecture and summarize possible functions of sleep; thereby the main focus will be the interaction between sleep and memory consolidation as well as the possible underlying neuronal systems.

2.3.1 Sleep architecture

Normal night sleep consists of several sleep cycles (each ~90-120 min) with rapid eye movement (REM) and non-REM (NREM) sleep (Pace-Schott, 2009). NREM is divided in four stages (A. Rechtschaffen & Kales, 1968), stage 1 (S1) and stage 2 (S2) refer to light sleep and stage 3 (S3) and 4 (S4) to deep sleep. Stage 3 and 4 are often combined to slow-wave-sleep (SWS). S1 is characterized by low-voltage and mixed frequency (3-7 Hz) activity and a rather low muscle tonus. The eye channel can depict slow rolling eye movements. S2 consists of mixed theta and delta activity in a rather low frequency range but shows also sleep spindles (12-15 Hz) and K-complexes and low muscle activity. S3 and S4 are characterized by high-amplitude (>75 mV), delta frequency activity (1-4 Hz) and slow oscillations (0.5-1 Hz). These stages correspond to sleep-depth; S1 has the lowest arousal threshold and S4 the highest. During REM sleep EEG-activity shows a low-voltage and high-frequency pattern with sawtooth waves (2-5 Hz, 20-100 µV), basically absent muscle activity with some muscle twitching and

saccades of eye movements/REM occur on the EOG channel (A. Rechtschaffen & Kales, 1968).

Sleep is assumed to serve different functions; it is supposed that sleep serves to reverse and restore biochemical and physiological processes, thus allows body restoration and energy conservation (Rosenzweig, Breedlove, & Leiman, 2002). Sleep deprivation in humans leads to impaired cognitive functioning and labile mood (Banks & Dinges, 2007; Durmer & Dinges, 2005). Furthermore, partial or chronic sleep deprivation leads to impairments in immune function, psychological disturbances and impaired learning and memory function (Minkel, Banks, & Dinges, 2009). In recent years, the importance of sleep for memory consolidation was demonstrated by a wealth of studies (for recent reviews see Ackermann & Rasch (2014); Diekelmann (2014); Feld & Diekelmann (2015); Genzel, Kroes, Dresler, & Battaglia (2014); Inostroza & Born (2013); Rasch & Born (2013); Tononi & Cirelli (2014)). The next sections will highlight some of these studies and discuss possible neuronal processes which trigger the beneficial effects of sleep for memory processes.

2.3.2 Memory consolidation during sleep

One of the first studies showing a positive impact of sleep on memory consolidation was already published by Jenkins and Dallenbach in 1924 (Jenkins & Dallenbach, 1924). They tested the retention of learnt non-sense syllables over time and demonstrated a better memory performance in recall after retention periods filled with sleep compared to wake retention intervals. Until today, an increasing number of studies have shown benefits in different memory tasks after sleep compared to a comparable time awake (Diekelmann, 2014; Rasch & Born, 2013). In declarative memory tasks, sleep benefits have been demonstrated, amongst others, for associated items (Marshall, Molle, Hallschmid, & Born, 2004; Tucker & Fishbein, 2008; Tucker et al., 2006) and in spatial memory tasks (Peigneux et al., 2004; Plihal & Born, 1999). Benefits for procedural memory were for example shown in motoric tasks, e. g. in finger tapping tasks (Fischer & Born, 2009; Walker, Stickgold, Alsop, Gaab, & Schlaug, 2005) or mirror tracing (Plihal & Born, 1997). Sleep has been shown to benefit consolidation in a variety of different memory types compared to wake not only after full nights of sleep but also after daytime napping (Alger, Lau, & Fishbein, 2010; Cox, Hofman, &

Talamini, 2012; Lahl, Wispel, Willigens, & Pietrowsky, 2008; Lau, Tucker, & Fishbein, 2010; Mander, Santhanam, Saletin, & Walker, 2011; Mednick, Cai, Kanady, & Drummond, 2008; Mednick, Nakayama, & Stickgold, 2003; Saletin, Goldstein, & Walker, 2011; Schönauer, Pawlizki, Köck, & Gais, 2014; Tucker & Fishbein, 2008; Tucker et al., 2006; van der Helm, Gujar, Nishida, & Walker, 2011; Wamsley, Tucker, Payne, & Stickgold, 2010). An advantage of using a nap design to investigate sleep effects compared to wake is the circadian equality for both conditions as it has been suggested that circadian influences can modify effects of sleep on memory (Koulack, 1997; Nesca & Koulack, 1994).

There are different theoretical accounts regarding the role of sleep for memory consolidation which might be, however, not exclusive on each other (Rasch & Born, 2013). Next to the assumption that sleep helps to protect memories passively (through reduced interference), the *dual process hypothesis* (NREM sleep especially SWS is beneficial for declarative, REM sleep beneficial for non-declarative memory) and *sequential hypothesis* (cyclic succession of NREM and REM sleep is important for memory consolidation) have been supported by some experiments but not others (Rasch & Born, 2013). A more recent account combining aspects of the two hypotheses is the *active system consolidation hypothesis* (Diekelmann & Born, 2010; Rasch & Born, 2013).

The active system consolidation hypothesis postulates that repeated reactivation of newly encoded information, especially during SWS (Walker, 2009), leads to memory consolidation; thus new declarative information which is initially encoded in both the hippocampus and neocortex is gradually transformed so that neocortical memories become independent of the hippocampus (Inostroza & Born, 2013; O'Reilly et al., 2011; Rasch & Born, 2013) (Figure 2.2). Consistent with this view, neuronal reactivations have been reported during sleep, particularly in regions that were active during encoding (Bergmann, Mölle, Diedrichs, Born, & Siebner, 2012; Ji & Wilson, 2007; Peigneux et al., 2004; Rasch, Buechel, Gais, & Born, 2007; Sirota, Csicsvari, Buhl, & Buzsaki, 2003). Next to showing neuronal reactivation during sleep in animal studies (Ji & Wilson, 2007; Sirota et al., 2003), it has also been possible to investigate neural (re)activation during sleep in humans with neuroimaging methods (Bergmann et al., 2012; Peigneux et al., 2004; Rasch et al., 2007). Peigneux and colleagues (2004) used positron emission tomography (PET) in a between-subject design to disentangle brain regions that are active during virtual route learning and during sleep. Activity in similar

hippocampal areas was found during learning and sleeping (SWS); and the amount of hippocampal activity during SWS was positively correlated to memory performance after sleep. In another imaging study by Rasch and colleagues (2007) possible reactivation of memories during sleep was examined with fMRI in a within-subject design. The learning of object-locations was linked to the exposure of an odor, which was then administered in subsequent sleep or wake retention periods. Only re-exposure of the odor during SWS but not during REM or wakefulness led to a better retention of object-locations. A procedural finger-tapping task did not benefit from odor-exposure in any condition, showing that reactivation during sleep seem to rely on hippocampus-dependent memory processing. In agreement with this finding, hippocampal activation during SWS was found after odor re-exposure.

Additionally, there is also empirical evidence that the consolidation of hippocampus-dependent memories includes a transfer to neocortical sites (Gais et al., 2007; Takashima et al., 2009; Takashima et al., 2006) as for example Takashima and colleagues (2009) found a decrease in hippocampal activity over time but an increase in connectivity between cortical regions. Gais and colleagues (2007) investigated neural activity at retrieval of word-pair associations at different time points; directly after learning (immediate recall), two days after learning (first delayed recall) and after six months (second delayed recall). Participants were either allowed to sleep the night after immediate recall or were sleep-deprived but underwent both conditions (within-subject design). The right hippocampus was found to be more active and stronger linked to activation of the ventral prefrontal cortex (vPFC) at the first delayed recall session for participants who were allowed to sleep than for the sleep-deprived ones. The second delayed recall session after six months revealed more activation in the vPFC for stimuli that had been learnt before sleep compared to sleep deprivation. Hence, sleep might be necessary to initiate the system consolidation process and relocating activity at retrieval from hippocampal sites to more cortical ones (Gais et al., 2007; Takashima et al., 2009; Takashima et al., 2006).

During sleep, memory activations in the hippocampus have been linked to sharp wave-ripples (Axmacher, Elger, & Fell, 2008; Eschenko, Ramadan, Mölle, Born, & Sara, 2008; Ramadan, Eschenko, & Sara, 2009). These ripples and thalamo-cortical spindles – which are linked to plastic changes in cortical areas – are grouped temporally by slow oscillations during SWS (Mölle, Eschenko, Gais, Sara, & Born, 2009) according to the active system consolidation hypothesis (see Figure 2.2). Studies using

simultaneous EEG and fMRI measurements could show that the occurrence of sleep spindles is linked with neuronal activation in hippocampus (Andrade et al., 2011; Bergmann et al., 2012; Schabus et al., 2007), frontal cortex, paralimbic areas and thalamus (Schabus et al., 2007). Bergmann and colleagues (2012) could demonstrate that sleep spindles are involved in the reactivation of memory representations and that their occurrence is tight to activity in hippocampal and neocortical sites. Their participants either had to learn face-scene associations or needed to perform a non-learning (visuomotor) control task (within-subject design). During subsequent sleep, learning led to a stronger joint activation of hippocampal and neocortical regions than did the visuomotor control task, and these reactivations were temporally tight to the occurrence of spindle events. Further, reactivations were only found in regions that were active during learning. A positive relationship between learning performance before sleep and following spindle-coupled hippocampal activation further indicate that spindles are involved in the reactivation of declarative memories during sleep.

And indeed, a number of other studies has shown that the density or number of sleep spindles is associated with enhanced declarative memory (Clemens, Fabó, & Halász, 2005; Cox et al., 2012; Gais, Molle, Helms, & Born, 2002; Mednick et al., 2013; Saletin et al., 2011; Schabus et al., 2004; Schmidt et al., 2006; Wilhelm et al., 2011). Gais and colleagues (2002), for example, found positive correlations between spindle density at fronto-central sites and cued recall performance in a declarative paired-associate task both before and after a night of sleep but not in a non-learning task which was matched in all stimulus and task characteristics except the intention to learn. Mednick and colleagues (2013) experimentally increased spindle density with a drug during a daytime nap, which led to better word-pair associate memory performance compared with a placebo. A further study by Cox et al. (2012) indicated that the beneficial effect of sleep spindles on memory is specific to SWS by showing not only that spindle density in SWS is higher than in light sleep (S2) but that only spindle density in SWS and not in S2 sleep was positively correlated with memory performance (Cox et al., 2012). The importance of slow oscillations and associated sleep spindles for memory consolidation could also be demonstrated in a recent stimulation study by Ngo and colleagues (2013) in which slow oscillatory activity was enhanced via auditory stimulation. Stimulation in phase with ongoing rhythmic slow oscillations was enhancing grouping of slow oscillations and phase coupled spindle activity and in turn improving declarative memory (Ngo et al., 2013). These results support the active

system consolidation hypothesis particularly that the beneficial effect of sleep spindles on memory consolidation might be dependent on the co-occurrence of slow oscillations.

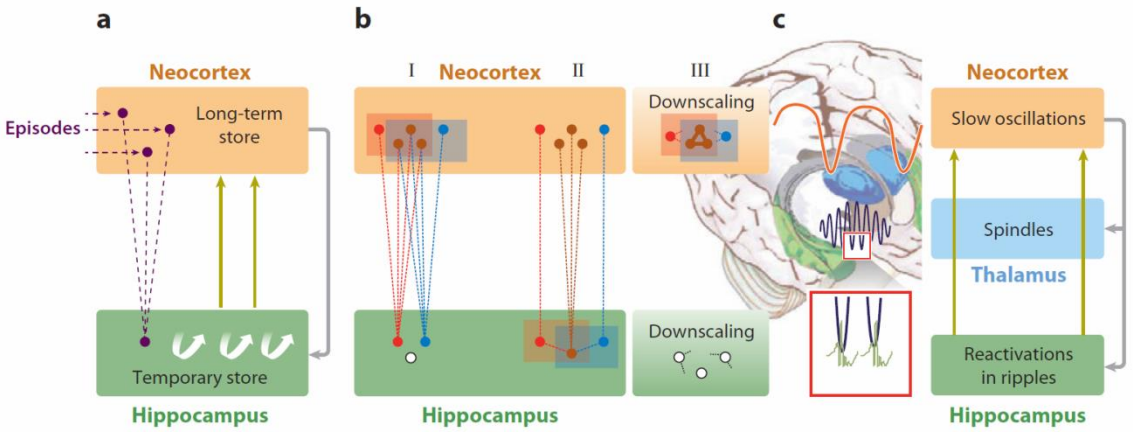

Figure 2.2. Active system consolidation during sleep (adapted from Inostroza & Born (2013)).

(a) Episodes are initially encoded in both hippocampus and neocortex while it is assumed that the hippocampus is only a temporal store. (b) Episodic representations are reactivated, and reactivations that originate in hippocampal sites are fed into neocortical networks. Synaptic downscaling weakens representations which are less reactivated. (c) Spindle-ripple events which are grouped by the depolarizing up-phases of slow oscillations are assumed to mediate the bottom-up transfer from reactivated memory information in the hippocampus into mainly neocortical regions.

Findings of sleep effects on recognition memory are less consistent (Daurat, Terrier, Foret, & Tiberge, 2007; Drosopoulos et al., 2005; C. C. Lin & Yang, 2014; Maurer et al., 2015; Mograss, Godbout, & Guillem, 2006; Mograss, Guillem, & Godbout, 2008; van der Helm et al., 2011; U. Wagner, Kashyap, Diekelmann, & Born, 2007). Some studies find benefits for overall recognition memory performance (C. C. Lin & Yang, 2014; Mograss et al., 2006; Mograss et al., 2008; U. Wagner et al., 2007), others only for emotional but not neutral content (Hu, Stylos-Allan, & Walker, 2006; Nishida, Pearsall, Buckner, & Walker, 2009; Payne, Stickgold, Swanberg, & Kensinger, 2008) (see 4.2.2 for a detailed description on emotional impact on memory formation) and others show benefits for recollection or associative memories (Maurer et al., 2015) but not for familiarity and item memory measures (Daurat et al., 2007; Drosopoulos et al., 2005; Mander et al., 2011; van der Helm et al., 2011). As described in Chapter 2.1.2, recognition memory is composed of two processes, familiarity and recollection. As only recollection is thought to depend on the hippocampus, and in agreement with

the assumption that mainly hippocampus-dependent memory consolidation benefits from NREM sleep, some studies investigating sleep effects on recognition memory demonstrate benefits only for recollection but not for item familiarity estimates (Daurat et al., 2007; Drosopoulos et al., 2005; van der Helm et al., 2011). Using a word list discrimination task together with a process dissociation procedure to estimate familiarity and recollection, Drosopoulos and colleagues (2005) found that early night sleep enhanced explicit recollection, whereas familiarity was not affected by sleep. Daurat et al. (2007) used a remember/know paradigm to examine the effects of SWS and REM sleep on familiarity and recollection. The recollection estimate was enhanced after a 3-hour retention interval filled with SWS as compared to retention intervals filled with REM sleep or no sleep at all. Once again, familiarity was not modulated by any of the retention interval manipulations. In a study by van der Helm and colleagues (2011) item memory was compared with context memory after participants either had either napped or had to stay awake. No group-differences in item-memory were revealed but context memory was benefitted substantially by the nap; and additionally positively correlated with sleep spindles and amount of S2 sleep.

A recent study conducted by Maurer and colleagues (2015) showed more confident and correct answers in an associative memory task (face-name-associations) after sleep compared to wake. This was also demonstrated by Mander and colleagues (2011) who used the same learning task (face-name-associations); and additionally showed no beneficial effect of sleep for item recognition (memory for faces). Only for associative memory performance a positive correlation with amount of S2 sleep was revealed. In a recent study by Schönauer and colleagues (2014) beneficial effects of sleep were found in a number of declarative memory tasks, including recognition memory measures (i.e. word-pairs and drawings). Compared with a wake control group, benefits of a nap were found for associative memory performance but not for recalling single items in the first experiment, however, a direct comparison of item vs. associative memory was not significant. Experiments two and three also showed general benefits of sleep for memory performance, but again no differences in a comparison of item and associative memories. A benefit in recalling single items (objects) was revealed. This is, however, in accordance with other studies which uses (cued) recall as a measure of episodic memory retention at retrieval as this test type is also assumed to rely on hippocampal functioning (Rugg & Vilberg, 2013).

Studies which do present a general improvement in recognition memory after sleep compared to wake either used an associative memory task, i.e. participants had to learn unrelated word-pairs and needed to discriminate word-pairs at test into old, recombined or new categories (C. C. Lin & Yang, 2014) or they needed to learn and remember faces (Mograss et al., 2006; Mograss et al., 2008) with different emotional expressions (U. Wagner et al., 2007) and which are also complex in nature. Superior recognition memory performance for the photographs of unknown faces for sleep compared to a wake group were found, but as solely an item memory test was used (old/new decision) in which choices can be made based on feelings of familiarity or by means of recollection or a combination of both, the possibility that familiarity and recollection have been differentially impacted by sleep could not be disentangled in these studies (Mograss et al., 2006; Mograss et al., 2008; U. Wagner et al., 2007).

Concluding it is to state that findings of sleep on recognition memory are not definite but it seems that context-rich or associative memories benefit more from sleep than item memory. However, it remains to be further investigated how benefits in recognition memory can be related to neurophysiological parameter during sleep as previous literature indicates some contradictory findings; e.g. sometime finding a relationship between memory retention and spindle density in light sleep (S2) (Schabus et al., 2004; Schmidt et al., 2006) and sometimes not (Cox et al., 2012). Moreover, research that directly compares effects of sleep vs. wake on item and associative memory has been scarcely conducted, especially under both the use of electrophysiological and sleep-dependent neurophysiological measures. The next section will deal with some studies which employed a recognition memory task and as well investigated associated ERPs.

2.4 Recognition memory and associated ERPs after sleeping

There are few studies which examined the impact of sleep on recognition memory and associated event-related potentials (Groch, Wilhelm, Diekelmann, & Born, 2013; C. C. Lin & Yang, 2014; Mograss et al., 2006; Mograss et al., 2008). Mograss et al. (2006; 2008) reported enhanced recognition memory performance for the photographs of unknown faces and larger ERP old/new effects at frontal and posterior recording sites

for a sleep as compared to a wake control group. However, polysomnographic data was not recorded during sleep periods in these studies, precluding the possibility to test for correspondences between enhanced memory performance and specific sleep parameters. Groch and colleagues (2013) were interested in determining the effects of sleep on the consolidation of emotional pictures and associated changes in electrophysiological measures. Subjects had to study negative and neutral pictures before retention intervals that were either filled with SWS-rich or REM-rich sleep (split night design, see also 4.2.2). Next to a better retention of emotional than neutral memories after REM-rich compared to after SWS-rich sleep, ERPs at learning showed greater positivity for emotional vs. neutral pictures in two time intervals (early: 300-500 ms; late: 500-800 ms) mostly pronounced at central and parietal sites. ERPs at retrieval were also more positive for emotional compared to neutral pictures across the early and late time window and also most pronounced over centro-parietal sites. Independent of emotionality, highly confident correct remembered old pictures demonstrated a greater positivity than correct rejections; this was most pronounced at frontal sites in the early time window.

In a recent study by Lin and Yang (2014) the effect of sleep vs. wake on an associative memory task was examined. In a self-paced study phase, participants had to learn unrelated word-pairs for which they needed to create own associations before conducting a pretest. Nightly retention intervals were either filled with sleep or wakefulness. After an additional night of (recovery) sleep, the posttest took part in the morning. Stimuli needed to be classified as old, recombined or new while EEG was measured both at pre- and post-sleep test phases. Whereas performance in the pretest was similar for both groups, subjects in the sleep group performed better at posttest. They showed faster reaction times and an increase in correct judgements from pre- to post-sleep while the wake group showed a decrease in memory accuracy for old and new pairs. At pre- and posttest, the N400 component which is supposed to be among others an index of semantic associations (Kutas & Federmeier, 2011) was investigated. It was shown that the peak of N400 was more attenuated after sleep than after wakefulness. As a smaller deflection in the N400 indicates strong semantic associations, Lin and colleagues (2014) concluded a facilitating effect of sleep on the creation of new and strong associations.

In conclusion, the presented studies could show effects of sleep on electrophysiological correlates in recognition memory tests. These were either larger

old/new effects for sleep compared to wake control subjects (Mograss et al., 2006; Mograss et al., 2008) or a reduced N400 component after sleep but not after wakefulness (C. C. Lin & Yang, 2014). Groch and colleagues (2013) also showed ERPs for correctly remembered old items to be more positive than correct rejections, however, as this study did not use a wake control group it is not possible to determine whether sleep vs. wake could have had a differential impact here.

2.5 Interim summary and objective of Experiment I

New declarative information needs to undergo several steps before it can be remembered successfully; next to paying attention to and encoding of the information, it also needs to be consolidated to be retrieved correctly later on (O'Reilly et al., 2011). Sleep is supposed to play an important role in memory consolidation and many studies have shown better performance in distinct memory tasks after sleep compared to a comparable time awake (Fischer, Hallschmid, Elsner, & Born, 2002; Jenkins & Dallenbach, 1924; Lau et al., 2010; Mednick et al., 2008; Plihal & Born, 1997; Rasch et al., 2007; Tucker & Fishbein, 2008; Tucker et al., 2006; van der Helm et al., 2011; U. Wagner et al., 2007; Walker et al., 2005; Wilhelm et al., 2011). Noteworthy, benefits of sleep are not only revealed after a night of sleep but also after shorter periods of sleep (Cox et al., 2012; Lahl et al., 2008; Lau et al., 2010; Mander et al., 2011; Mednick et al., 2008; Saletin et al., 2011; Schönauer et al., 2014; Tucker & Fishbein, 2008; Tucker et al., 2006; van der Helm et al., 2011). Despite the evidence for the beneficial impact of (nap) sleep on memory consolidation, less is known about the impact of nap sleep on the two processes of recognition memory; familiarity and recollection. The aim of the first experiment was to use behavioral and ERP measures of recognition memory together with polysomnographic data to investigate the benefits of nap sleep and the mechanisms by which nap sleep enhances measures of recognition memory.

So far, findings of sleep effects on recognition memory are inconsistent as some studies find benefits for overall recognition memory performance (C. C. Lin & Yang, 2014; Mograss et al., 2006; Mograss et al., 2008; U. Wagner et al., 2007) but others show benefits only for recollection but not familiarity measures (Daurat et al., 2007; Drosopoulos et al., 2005; Mander et al., 2011; van der Helm et al., 2011). Yet, some of

the former studies solely used item memory tasks in which stimuli need to be judged as old (learnt) or new; a decision which can be made based on both familiarity and recollection. Thus it is not possible to disentangle potential distinct contributions of familiarity and recollection to the overall recognition memory performance in that studies. The other studies used amongst others a remember/know paradigm (Daurat et al., 2007) or a process dissociation procedure (Drosopoulos et al., 2005) to estimate the impact of sleep on familiarity- and recollection-driven processes separately. In the present thesis, the first experiment (see next chapter 0) aimed to investigate a possible differential effect of nap sleep on the two processes of recognition memory applying both an item memory task and an associative memory test. The latter test provides a sensitive measure for recollection because old and recombined pairs cannot be certainly discriminated on the basis of familiarity (Hockley & Consoli, 1999; Yonelinas, 1997). It is questioned whether sleep related changes in an associative memory task and no corresponding differences in an item memory task can be revealed by means of behavioral and electrophysiological measures which would be evidence that recollection is principally affected by nap sleep and which would be further support for a main role of NREM sleep in consolidation of hippocampus-dependent memories. Further, it is questioned whether sleep-dependent increases in performance can be induced on the basis of nap sleep alone and whether there are relationships between memory performance and specific sleep parameters such as sleep spindles as a number of studies has been shown that density of sleep spindles is associated with enhanced declarative memory (Gais et al., 2002; Mednick et al., 2013; Saletin et al., 2011; Schabus et al., 2004; Schmidt et al., 2006).

3 Experiment I

3.1 Introduction

Sleep is thought to play an important role in memory consolidation. According to the active system consolidation hypothesis, benefits come about because new declarative information is initially encoded in both the hippocampus and neocortex. Next, memory representations are gradually transformed so that with time neocortical memories become independent of the hippocampus (O'Reilly et al., 2011; Rasch & Born, 2013). It is assumed that much of this transfer takes place during sleep by covert neuronal reactivations (Rasch & Born, 2013) which is supported by studies which show neuronal reactivation during sleep, particularly in regions that were active during encoding (Bergmann et al., 2012; Ji & Wilson, 2007; Peigneux et al., 2004; Rasch et al., 2007; Sirota et al., 2003).

Although some of the neurophysiological mechanisms by which sleep can boost declarative memory have been identified, findings of sleep effects on recognition memory are less consistent and much less is known about how recognition memory can benefit from nap sleep in particular (Daurat et al., 2007; Drosopoulos et al., 2005; Hu et al., 2006; C. C. Lin & Yang, 2014; Maurer et al., 2015; Mograss et al., 2006; Mograss et al., 2008; Schönauer et al., 2014; van der Helm et al., 2011; U. Wagner et al., 2007). According to dual process models, recognition memory is composed of two processes; familiarity (fast and context-free) and recollection (slower and effortful, recovering of contextual details) (Yonelinas, 2002; Yonelinas et al., 2010). These two processes are not mutually exclusive but there is nevertheless evidence that recollection- and familiarity-based recognition decisions are supported by distinct neuronal systems (Skinner et al., 2014; Yonelinas et al., 2005) e. g. studies which demonstrate that the hippocampus is central for recollection-driven but not familiarity-based memory decisions (Addante, Ranganath, Olichney, et al., 2012; Bowles et al., 2010; Yonelinas et al., 2002). Furthermore, familiarity- and recollection-based processes have also been associated with distinct ERP old/new effects (Friedman & Johnson, 2000; Mecklinger, 2000; Rugg & Curran, 2007). An early mid-frontal old/new effect has been shown to correlate with an index of familiarity (Bridger et al., 2014; Yu & Rugg, 2010) while the

late parietal old/new effect has been linked to recollection-based memory judgements (Curran & Cleary, 2003; Paller et al., 1995) with the amplitude of this late parietal old/new effect varying with the amount recollected (Vilberg et al., 2006; Wilding, 2000).

In the first experiment, two independent approaches to assess recollection and familiarity were used. Firstly, two separate recognition tasks - differing in the extent to which recollection is required for task performance - were employed. Secondly, indices of putative neural correlates of recollection and familiarity were recorded. Based on the aforementioned data points indicating that hippocampus-dependent (declarative) memory seems to benefit from sleep, in particular SWS, a beneficial effect of sleep on memory performance only in the associative memory (AM) test was predicted. This should be reflected by less deterioration from pre- to post-sleep in associative as compared to item memory (IM) performance for the nap compared to control group. Furthermore, AM posttest performance within the nap group should be associated with high spindle density (in particular spindle density during SWS; Cox et al. (2012)). Corresponding correlations between IM performance and sleep EEG parameters, as well as group differences in IM performance and the ERP correlate of familiarity at posttest were not expected. In line with the expectation that the benefit of hippocampus-dependent memory from sleep reflects an enhancement of recollection, the late parietal old/new effect, the putative ERP correlate of recollection, was expected to be larger after sleep compared to the control group.

3.2 Materials and Methods

3.2.1 Participants

73 healthy young adults from Saarland University/HTW Saarland participated in this experiment. Data from 17 subjects were excluded due to being at chance level in their baseline memory performance (average performance across conditions at or below 50% in the IM baseline test and/or 33% in the AM baseline test). The remaining 56 participants were randomly divided into two groups, either a nap or a control group. Data from an additional 15 subjects were excluded due to performance below 2 SD of

the mean of the group at IM posttest and/or AM posttest (n = 5), not sleeping (no occurrence of S2 sleep) in the nap group (n = 5), or sleeping (occurrence of S2 sleep) while being in the wake control group (n = 5). From the remaining 41 participants, the nap group (n = 22) consisted of 13 females and 9 males with a mean age of 22.1 (SD 2.4). The mean age of the control group (n = 19, 10 females) was 22.1 (SD 2.2) years. All participants stated that they did not have any sleep disorders, had no known neurological problems and that they were right-handed (Oldfield, 1971). All participants gave written informed consent and were paid at a rate of 8€/h or with course credit.

3.2.2 Stimuli

180 German nouns (Bridger & Mecklinger, 2012) and 180 semantically unrelated German word-pairs were used as stimuli (compare appendix Table B.1). All single words were concrete nouns with a length between 3-9 letters and a frequency between 6 and 869 (Baayen, Piepenbrock, & Gulikers, 1995). 168 of the word-pairs were evaluated in terms of semantic relationship and suitability to build a compound in order to reduce the pre-experimental associations within pairs in another study of the lab (Bader et al., 2010) and 12 were newly created using the same evaluation criteria. For all 180 word-pairs recombined pairs were created using the same evaluation criteria as for the new pairs. To build recombined word-pairs, study pairs were separated into two different lists within each block, each of which corresponded to items to be presented either within the baseline test or posttest. Within blocks, single words were recombined but the position of words (first or second within a pair) remained constant across study and test. An additional 30 subjects rated the semantic relatedness and unitizability of the new and recombined word-pairs and only word-pairs with low semantic relatedness and low unitization values (each ≤ 2 on a scale from 1-4) were included as test stimuli. All word-pairs had a mean length of 4-8 letters and a mean frequency between 6.5 and 454.5. The order of learning and testing single words or word-pairs first was counterbalanced across participants. In total, there were six different stimuli-sets for single words and nine different stimuli-sets for word-pairs which ensured that, across the sample, all items appeared equally often as old or new (IM) or as old/new/recombined (AM).

3.2.3 Design and Procedure

The experiment was divided into two sessions (see Figure 3.1) which were separated by at least 7 days. The first session served to record various covariate measures e. g. IQ (CFT 20-R) and to explain the sleep log (compare appendix Questionnaire A.3) which was to be filled in for one week prior to session 2. The sleep log asked for habitual bed, wake and rise times as well as for the occurrence of day naps and the ingestion of alcohol. Feeling of tiredness was also measured over several time points during the day. Participants were instructed to maintain a normal sleep/wake pattern during the week but were asked to sleep one hour less than their average from day 6 to day 7 (experimental day 2) if possible, to increase their sleep pressure.

Session 2 always started at 13.45 pm with the electrode setup and filling in the Epworth and Stanford Sleepiness Scales. The *Epworth Sleepiness Scale* is a questionnaire measuring daily sleepiness by assessing the likelihood of falling asleep in different situations (compare appendix Questionnaire A.1). The *Stanford Sleepiness Scale (SSS)* measures the current feeling of sleepiness ranging on a 1-7 scale (compare appendix Questionnaire A.2). Both groups were asked about their feeling of sleepiness at four different time points, SSS1: before learning; SSS2: after baseline test; SSS3: after watching the DVD; and SSS4: at the end of the experiment. The nap group was additionally measured at an extra time point (SSS3a) after waking from their nap. Two electrodes were applied to the chin of participants in the nap group to measure muscle activity during sleep, before these participants were asked to lie down at around 15:30 pm (±15 minutes). Participants were given the opportunity to sleep for a maximum of 90 minutes (see Figure 3.1). The control group watched two movies: *Powaqqatsi* and *Relaxing: The most beautiful landscapes on earth*. Both are movies with only instrumental sound, lasting in sum 2 hours. After waking, nap participants also watched 30 minutes of the *Relaxing* movie to prevent any sleepiness effects on the second test (posttest). This also ensured that the interval between baseline and posttest was matched for the two groups.

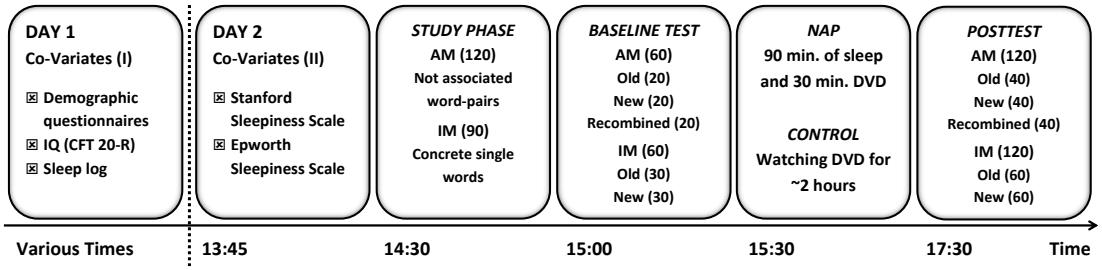

Figure 3.1. Overview and timeline of the experimental procedure on session one and session two.

The study phase consisted of 120 word-pairs and 90 single words to be learnt. For the baseline test 60 word-pairs (20 in each category) and 60 single words (30 in each category) were tested. The posttest was double the size of the baseline test.

Memory tasks

The memory tasks were programmed using E-Prime 2.0 (Psychology Software Tools, E-Studio 2.0.8.90). Participants sat in front of the monitor at a viewing distance of about 65 cm. Stimuli were presented in black on a grey background (maximal horizontal visual angle ≈ 5.7°). Single words were presented in the center of the screen (vertical visual angle ≈ 1.3°), whereas word-pairs were presented slightly below and above central vision in study and test phases (vertical visual angle ≈ 4°). The learning of single words and word-pairs was blocked and whether participants first learnt single words or word-pairs was counterbalanced. The presentation time of all stimuli at study was 5000 ms. Participants were instructed to memorize items for a later memory test but no specific learning strategy was given. The study list of 90 single words was divided into two blocks, while the study list with 120 word-pairs was divided into three blocks. There was a self-paced break in between blocks as well as between the two study-lists. Stimuli were presented in random order with an inter-stimulus-interval (ISI) of 550 ms (fixation cross shown for 500 ms). The duration of the study phase was about 22 minutes.

The first memory test (baseline/pretest)[2] was conducted immediately after the study phase. Here, participants had to decide whether the presented single word was old or new (item memory test, IM) or whether the presented word-pair was old, new or recombined (associative memory test, AM). Participants responded on one of two keys

[2] The first experiment uses mainly the term baseline whereas the second test only uses the term pretest. That is to differentiate experiment one with a comparison of two groups (nap and control) from experiment two with a within-subject design.

for single words (old/new decision) and on one of three keys for word-pairs (old/new/recombined decision). The key assignment to right and left hand was counterbalanced across subjects. Participants were instructed to respond as fast and as accurately as possible. Single words were presented for 500 ms, followed by a 2000 ms long response window and an ISI of 1000 ms. Word-pairs were presented for 750 ms, followed by a 2000 ms long response window with an ISI of 1000 ms. The baseline test included 30 old and 30 new single words for the IM test as well as 20 new, 20 old and 20 recombined word-pairs in the AM test. There was a self-paced break in between blocks as well as between the two test-lists. After the baseline test, participants were informed about which group they belonged to. At around 17:30 (±15 minutes) the second test (posttest) was conducted. The posttest consisted of 60 old single and 60 new single words for the IM test as well as 40 new, 40 old and 40 recombined word-pairs in the AM test. The response procedure and test order was the same as in the baseline test and remained constant for each participant.

3.2.4 Data acquisition and processing

Electroencephalogram (EEG)

EEG was recorded with BrainVision Recorder Version 1.20 (Brain Products) throughout the entire experiment. In total, 32 Ag/AgCl electrodes were used according to the extended 10-20 system, including electrodes which were located above and below the right eye and outside the outer canthi of both eyes in order to assess electro-ocular activity (EOG). Data were recorded with amplifier band pass filter settings from DC to 100 Hz and a Notch-filter at 50 Hz. The sampling rate was 500 Hz for all study and test phases. All electrodes were recorded referenced to the left mastoid electrode and re-referenced to the average of the left and right mastoid (offline). Electrode impedances were kept below 5 kΩ. EEG was also recorded at 32 standard locations for polysomnographic data acquisition during the nap; but with a sampling rate of 1000 Hz and with the inclusion of 2 electrodes at the chin for electromyographic recordings.

Event-Related Potentials

Data processing was conducted offline with EEProbe (ANT Software) for ERP analysis of the posttest. A digital 0.2-30 Hz band-pass filter was first applied. Individual

epochs of 1100 ms were then created, including a 100 ms baseline before stimuli onset. The waveforms were baseline corrected (i.e. the mean value of the baseline was subtracted from each data point in the waveform), before correction of eye-movements and blinks with a linear regression algorithm (Gratton, Coles, & Donchin, 1983). After this and the rejection of other trials showing artifacts (whenever the standard deviation in a 200 ms time interval exceeded 25 microvolt at one of the EOG channels), the remaining trials were averaged and individual averages were only used for analyzing ERPs when they contained a minimum of 13 artifact-free trials (Addante, Ranganath, & Yonelinas, 2012; Gruber & Otten, 2010). A 12-Hz low pass filter was applied for illustration purposes only.

Sleep stage scoring

Preprocessing of the sleep data was conducted using BrainVision Analyzer (2.0, Brain Products). Each 30 sec epoch of sleep was scored visually into rapid-eye-movement (REM)-sleep or non-REM sleep stages 1, 2, 3 or 4 according to standard criteria (A. Rechtschaffen & Kales, 1968). Slow-wave-sleep was calculated as the sum of sleep stages 3 and 4. The time in minutes for each sleep stage, the total sleep time, the sleep onset latency and the percentage of sleep time in each stage with reference to total sleep time (TST) were determined.

Sleep spindle analysis

After preprocessing, sleep spindle detection was conducted with MATLAB 2011b (MathWork) for the Fz, Cz and Pz recording sites based on an established method (Ferrarelli et al., 2007). In brief (see Figure 3.2), a band-pass filter between 12 and 15 Hz was applied. Time intervals containing muscle artifacts or analog/digital saturation were excluded. Following this, the envelope of the individual sleep EEG signal was computed using the Hilbert transform and its resulting absolute values. The computed envelope leads to a smoothing of the signal by outlining the extremes in EEG amplitudes. For each participant unique thresholds for spindle detection were used which were the mean plus two SD (lower threshold) and the mean plus four SD (higher threshold) of the participant's filtered EEG signal. To classify a spindle, two criteria had to be fulfilled:

i) the duration between the points at which the signal falls above and below the lower threshold needed to be at least 500 ms and

ii) the signal also had to cross the upper threshold within this 500 ms time window.

Spindle density was calculated for NREM (stage 2 + SWS) sleep by dividing the number of spindles by minutes of NREM sleep and for SWS by dividing the number of spindles during SWS by minutes of SWS.

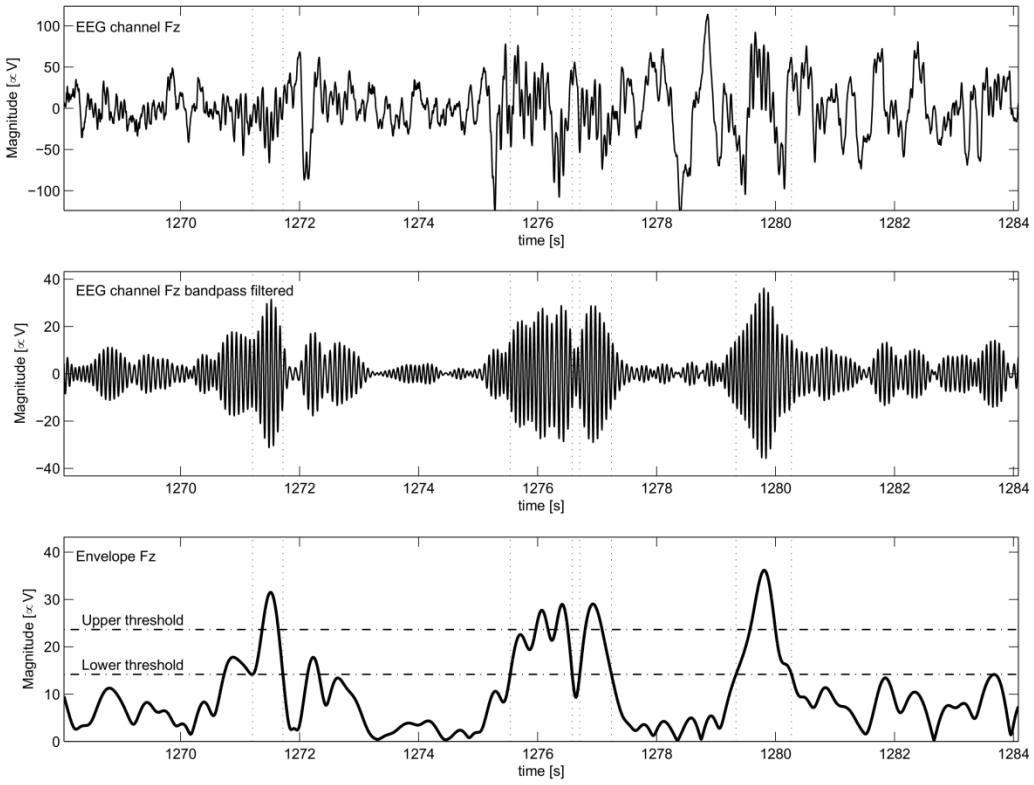

Figure 3.2. Spindle detection.

The raw EEG signal for one exemplary time interval is depicted in the upper panel. The middle panel shows the band-pass-filtered (12-15 Hz) EEG signal in the same time interval. The calculated envelope of this signal is shown in the lower panel (exemplar is shown for one specific time interval for one subject).

3.2.5 Data Analysis

For the behavioral data, analyses of variance (ANOVA) with factors of group (nap/control) and time (baseline/posttest) were used separately for item memory (IM) and associative memory (AM). For IM tests, an old/new discrimination Pr index (Pr-Score) was calculated by subtracting false alarms to new pairs from the hit rate

(Pr = hits-FA_{neu}). In AM tests, the ability of participants to discriminate between old and recombined pairs was of particular interest, so an associative PrA-Score was computed. This was calculated by subtracting the proportion of recombined pairs which were incorrectly classified as old (false alarms to recombined) from the hit rate (PrA = hits-FA_{rec}). By including recombined pairs in the test phases, it was ensured that participants could not make their response based on item memory alone but that they needed to retrieve the associations.

For the reaction time data, ANOVAs with the factors group (nap/control) and the within-subject factors time (baseline/post) and item-type (IM: old/new; AM: old/new/recombined) were conducted for correct answers separately for IM and AM tests.

ERPs were derived from the posttest EEG data. For old/new analyses, ERPs in the IM test were limited to correct responses to old (hit) and new (CR) items. For the AM test, recombined items were created such that both items were re-presented at test, albeit with different old items. Recombined pairs were included in the test phase to ensure participants responded on the basis of associative recognition and could not make their responses solely on the basis of item memory. In line with previous ERP studies on associative memory, recombined pairs were not included in the ERP analyses because of difficulties in interpretation and a lack of artifact-free trials (Bader et al., 2010; Greve, van Rossum, & Donaldson, 2007; Kriukova et al., 2013). For old/new analyses, ERP analyses in the AM test were thus restricted to correctly responded to old and new items. A further ERP analysis was conducted for hits and incorrect answers in the AM test. Hits refer to the combination of old and recombined correct answers. Incorrect answers comprise old pairs endorsed as recombined and recombined pairs endorsed as old. To create a subject average, at least 13 artifact-free trials were needed in each of the categories. For old/new analysis, one participant of the nap group had to be excluded in the IM test, and three participants of the nap and four participants of the control group needed to be excluded for the ERP analysis at AM test. For the hits/incorrect answers comparison in the AM test, sufficient trial numbers were obtained for nine participants of the nap and 13 participants of the control group. For old/new comparisons mean amplitudes in an early (300-500 ms) and a late (500-700 ms) time window were subjected to ANOVAs with factors of group (nap/control), item-type (hit/CR) and laterality (left/midline/right). ANOVAs included amplitudes from three frontal (F3, Fz, F4) electrodes for the early time interval and three parietal (P3, Pz, P4) electrodes for

the late time window. These sites and time points correspond to the standard specifications of the early frontal and late parietal putative correlates of familiarity and recollection (Rugg & Curran, 2007). For the hits/incorrect answers comparison, mean amplitudes were subjected to ANOVAs with factors item-type (hits, incorrect answers), lateralization (left/midline/right) and group (nap, control) separately in an early (350-500 ms, electrodes F3, F4, Fz) and a late time window (500-700 ms, electrodes P3, P4, Pz). Only main effects and interactions that involve the factor item-type are reported because these indicate that an old/new (hits/incorrect answers) difference is present or varies with group or electrode location. Where necessary, analyses included Greenhouse-Geisser corrections for nonsphericity with corrected p-values and uncorrected degrees of freedom (Greenhouse & Geisser, 1959). For all analyses, the significance level was set to $\alpha = 0.05$ and for the correlation analyses a modified Bonferroni test (Keppel, 1991) was used to correct for multiple comparisons.

3.3 Results

3.3.1 Behavioral data

Figure 3.3 shows the mean Pr-/PrA-Scores for the IM (a) and AM (b) baseline and posttest for both groups. The hit rates, false alarm rates and the bias index Br/BrA are shown in Table 3.1. To test the hypothesis that group differences will be present in the AM posttest but not in the IM posttest or IM/AM baseline tests, separate two-way ANOVAs (with factors group and time) were conducted for the Pr (IM Test) and PrA scores (AM test). For IM tests, a main effect of time ($F(1,39) = 22.29$, $p < .01$) but no group with time interaction ($p = .2$) was found. For AM tests, the corresponding ANOVA revealed a main effect of time ($F(1,39) = 15.07$, $p < .001$) and a significant group and time interaction ($F(1,39) = 7.77$, $p < .01$). PrA scores at posttest were lower than at baseline in the control group ($t(18) = 4.41$, $p < .01$), whereas in the nap group, there was no difference between PrA scores at baseline and posttest ($p = .42$). At posttest the difference in memory performance between the nap and control group was marginally significant ($p < .06$).

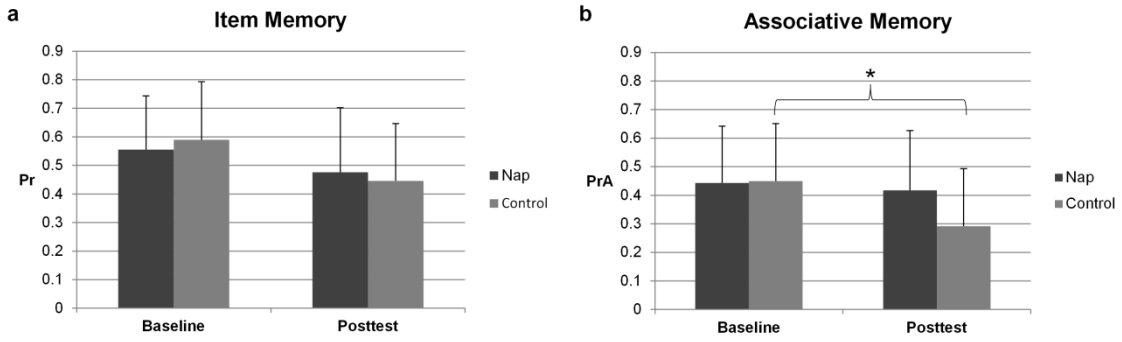

Figure 3.3. Behavioral memory performance.

(a) Item memory test performance depicted by Pr-Scores (hits minus false alarms) and (b) associative memory tests depicted by PrA-Scores (hits to old pairs minus false alarms to recombined pairs). Error bars show one standard deviation. The asterisk denotes the significant difference ($p < .05$) in PrA for the control group from baseline to posttest.

Table 3.1: Hit rates (Hits), false alarm rates (FA) and bias index (Br/BrA) for both groups and tests (standard deviation in parentheses) are depicted.

		Baseline Test			Posttest		
		Br/BrA*	**Hits**	**FA**	**Br/BrA***	**Hits**	**FA**
	Nap	0.34	0.71	0.15	0.37	0.66	0.19
Item		(0.17)	(0.14)	(0.09)	(0.20)	(0.20)	(0.15)
Memory	**Control**	0.38	0.74	0.15	0.35	0.64	0.20
		(0.26)	(0.16)	(0.11)	(0.10)	(0.12)	(0.11)
	Nap	0.06	0.61	0.17	0.10	0.55	0.14
Associative		(0.04)	(0.17)	(0.11)	(0.08)	(0.22)	(0.10)
Memory	**Control**	0.07	0.63	0.18	0.12	0.49	0.20
		(0.05)	(0.21)	(0.13)	(0.05)	(0.19)	(0.09)

*Br refers to IM and BrA to AM calculated response bias.

To explore whether response bias was modulated by the sleep and wake conditions a two-way ANOVA (factors group and time) was conducted for Br/BrA in both tests. No effects were obtained for the bias index in the IM test (p-values > .30). In the AM test, the bias index increased from baseline to posttest ($F(1,39) = 27.28$,

$p < .001$), suggesting that participants responded more liberally at posttest irrespective of nap/control condition.

Table 3.2: Control measures experiment one.

	Nap mean (SD)	**Control** mean (SD)	t_{39}	**p**
IQ (CFT 20-R)	113.01 (12.8)	110.95 (12.4)	0.54	.59
ESS	7.59 (3.53)	7.37 (2.99)	0.22	.83
TST night before experiment	6.9 (1.1)	7.2 (0.9)	-1.07	.29
TST average across 7 nights	7.4 (1.2)	7.4 (1.1)	0.17	.87
Wake-up time morning (hh:mm)	7:49 (1:06)	8:10 (1:12)	-0.97	.34
Sleepiness before learning (SSS1)	2.8 (1.2)	2.7 (1.2)	0.09	.93
Sleepiness after baseline test (SSS2)	3.2 (1.2)	3.3 (1.1)	-0.25	.80
Sleepiness after DVD (SSS3)	2.0 (0.6)	3.1 (1.5)	-3.09	.01*
Sleepiness at end of study (SSS4)	1.6 (0.5)	2.1 (0.9)	-2.42	.03*

* Marks significant contrasts ($p < .05$); TST: total sleep time (in hours); ESS: Epworth Sleepiness Scale; SSS1-4: Stanford Sleepiness Scale time points 1-4; df: 39

Control measures are displayed in Table 3.2. T-tests revealed no group differences for most of these measures except for SSS3 and SSS4. A mixed ANOVA with time of sleepiness (four levels) and group as factors revealed a main effect of time of sleepiness ($F(3,37) = 18.18$, $p < .01$) and a significant interaction between time of sleepiness and group ($F(3,37) = 3.40$, $p < .05$). Paired t-tests revealed that both groups reported being more awake at the end of study compared to after watching DVD (p-values < .01 in both groups). The interaction reflects the fact that the nap group reported being more awake at SSS3 (after DVD) compared to SSS2 (after baseline test) ($p < .01$) whereas reported sleepiness in the control group did not differ between SSS2 and SSS3 ($p = .62$). Sleepiness was also reported to be higher in the control group than in the nap group at SSS3 and SSS4 but not at the other two time points. To rule out the possibility that significant group differences in sleepiness before posttest differentially impacted memory performance for the two groups, an ANCOVA with factors group and time and with sleepiness score at SSS3 as a covariate was conducted on PrA-scores. The interaction between group and time remained significant ($p < .05$) indicating that differences in sleepiness cannot explain group differences in memory performance.

A summary of sleep parameters for the nap group is shown in Table 3.3. The average time spent in sleep was about 64 minutes and about half of this time (51.5%) was spent in S2 sleep. Participants showed about 24.7% (SD 18.8) of SWS and 8.6% (SD 9.6) of REM sleep. Most participants showed SWS (n = 19) and around half of them reached REM sleep (REM: n = 12) which accounts for the large variability of these measures.

Table 3.3: Sleep parameters experiment one.

	Minutes mean (SD)	**% of TST** mean (SD)
SL	14.18 (12.53)	
TST	64.25 (16.3)	
Stage 1 (S1)	9.64 (7.84)	15.14 (10.97)
Stage 2 (S2)	32.77 (10.85)	51.49 (13.13)
Stage 3 (S3)	11.2 (9.94)	17.13 (14.08)
Stage 4 (S4)	4.52 (5.21)	7.61 (9.22)
SWS (S3+S4)	15.73 (12.19)	24.74 (18.78)
REM	6.11 (6.74)	8.63 (9.63)

SL : latency until sleep onset; TST: total sleep time; SWS: slow-wave-sleep; REM: rapid-eye-movement

Mean reaction times (RTs) for each of the conditions are shown for IM and AM for the two groups in Table 3.4. For IM tests, a three-way ANOVA with factors of group, item-type and time only revealed a main effect of item-type ($F(1,39) = 16.41$, $p < .01$) with response times to hits being faster than to correct rejections. For AM, there was also a main effect of item-type ($F(2,38) = 42.81$, $p < .01$), again because response times to old items were faster than to new items ($p < .01$) and recombined word-pairs ($p < .01$) and because reaction times for new pairs were faster compared to recombined pairs ($p < .01$).

Table 3.4: Mean reaction times [ms] and SD (in parentheses) for all conditions of item memory (IM) and associative memory (AM) baseline and posttest for the nap and the control group.

			Nap	Control
Item Memory	***Baseline***	Hits	870.93 (209.77)	838.46 (192.34)
		CR	961.90 (284.71)	896.28 (235.77)
	Posttest	Hits	894.65 (197.90)	822.28 (165.10)
		CR	963.72 (257.88)	869.19 (245.96)
Associative Memory	***Baseline***	$Hits_{OLD}$	1497.71 (301.82)	1385.64 (253.92)
		CR	1622.27 (362.22)	1535.43 (357.20)
		$Hits_{REC}$	1754.15 (329.04)	1684.11 (374.90)
	Posttest	$Hits_{OLD}$	1491.24 (292.01)	1374.21 (259.92)
		CR	1576.12 (362.24)	1407.75 (332.35)
		$Hits_{REC}$	1767.08 (321.47)	1580.68 (369.52)

3.3.2 Sleep spindle data

A correlation between spindle density (SpD) and PrA score at AM posttest but not between spindle density and Pr-score at IM posttest was expected. In line with other reports of spindle density analyses, data from 3 midline electrodes – Fz, Cz and Pz – were examined (Gais et al., 2002) for the total amount of NREM sleep as well as separately for SWS (Cox et al., 2012). There were no significant correlations between spindle density in NREM sleep and Pr at IM posttest (all p-values > .5) or between spindle density in NREM sleep and PrA at AM posttest (all p-values > .1). Notably, an analysis of the subset of participants (n = 19) who did reach SWS revealed a significant correlation between PrA at AM posttest and spindle density in SWS at Fz ($r = 0.59$; $p < .01$, Figure 3.4a) that remained significant when correcting for multiple testing.

To explore whether the correlation between spindle density and AM posttest performance is modulated by performance at baseline, a partial correlation analysis was conducted between posttest memory performance and spindle density with memory performance at baseline as covariate. The correlation is no longer significant when the baseline performance is controlled for, which is not surprising given the high common variance between AM baseline and posttest performance ($r = 0.76$, $p < .001$).

In some reports, spindle density has been shown to correlate with memory performance/learning prior to sleep (Gais et al., 2002; Schmidt et al., 2006). To explore this possibility in the current data set, correlation analyses between baseline performance measures and spindle density at Fz, Cz and Pz were conducted. There was no correlation between the Pr-score of the baseline IM test and spindle density in NREM sleep (all p-values > .271) but the correlation between the PrA score at AM baseline test and spindle density in NREM sleep at Fz was marginally significant ($r = 0.45$; $p = .036$; Figure 3.4b) when corrected for multiple comparisons[3].

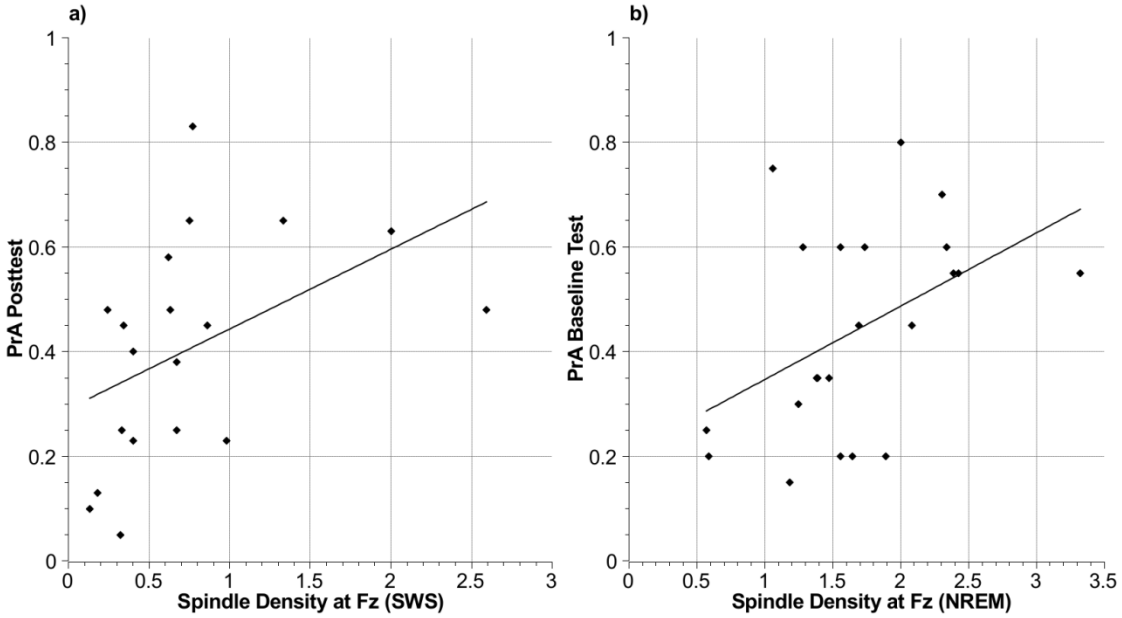

Figure 3.4. Correlation data is shown for spindle density and PrA-scores.

(a) Relationship between PrA (hits to old pairs minus false alarms to recombined pairs) scores in the associative memory test at posttest and spindle density per minute at electrode Fz during slow-wave-sleep (SWS). (b) Relationship between PrA scores in the associative memory test at baseline and spindle density per minute at electrode Fz during non-REM sleep (NREM).

To summarize the results of the correlation analyses, positive relationships between PrA scores at AM posttest and spindle density during SWS as well as between PrA score at baseline test and spindle density during NREM sleep were found in the AM task only.

[3] The adjusted significance level used to evaluate the correlations between spindle density at the three electrodes in the modified Bonferroni test was p=.034 (Keppel, 1991).

3.3.3 Electrophysiological data

Item Memory Test

The grand average ERP data and topographical contrasts for the IM posttest for both groups are presented in Figure 3.5.

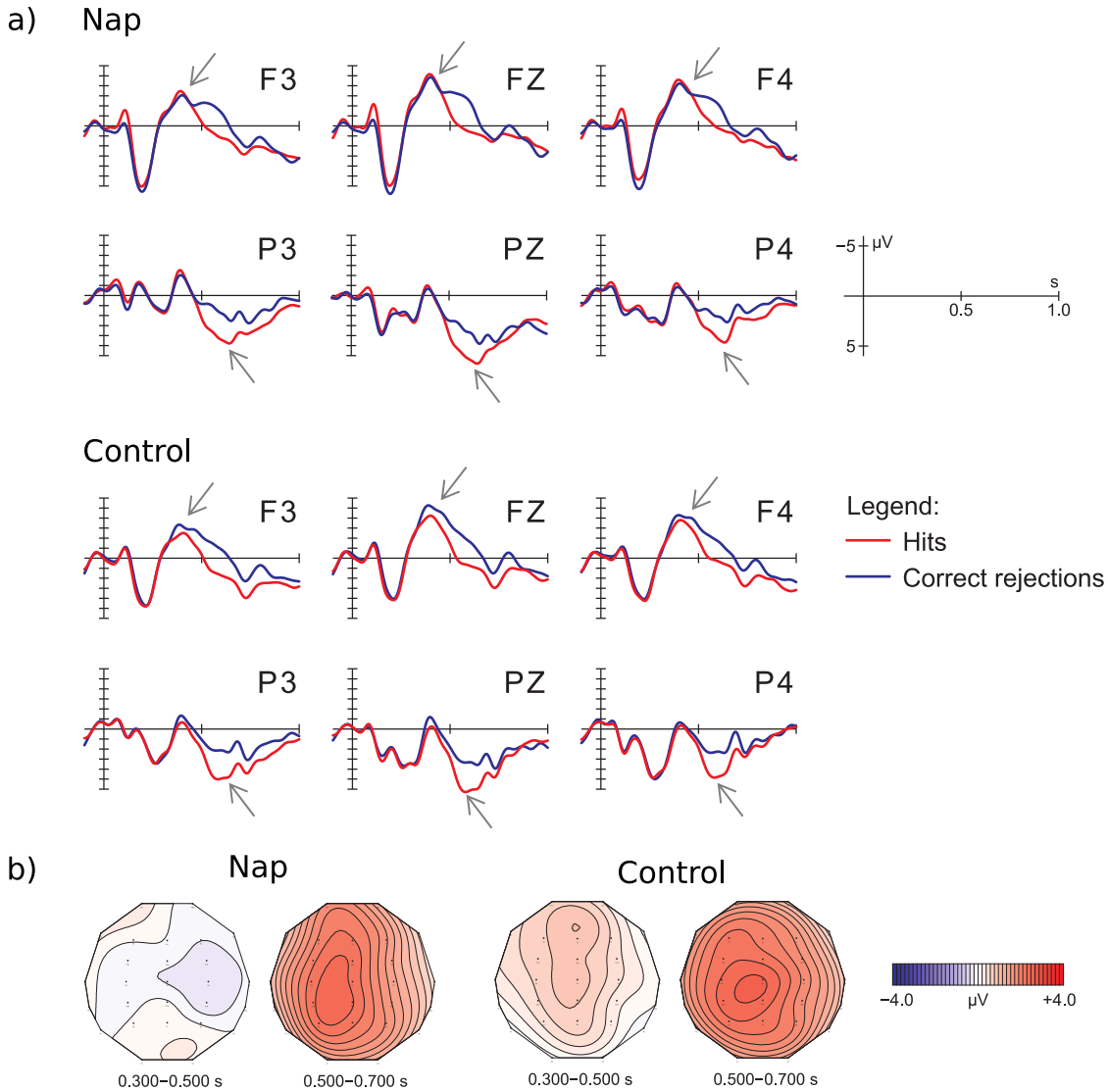

Figure 3.5. Grand average ERPs (a) and topographical maps (b) for the IM old/new comparison.

(a) Grand average ERPs elicited by hits and correct rejections at F3, Fz and F4 and P3, Pz and P4 in the item memory posttest for the nap and control group. The arrows highlight the early midfrontal old/new effect and the late parietal old/new effect. The y-axis denotes the onset of the test word and negative polarity is plotted upwards. (b) Topographical maps show the contrast hits minus correct rejections in two time windows (300-500 ms, 500-700 ms).

Differences between hits and correct rejections emerge at around 300 ms at frontal recording sites in the control group and are slightly delayed in the Nap group. Starting at around 500 ms, there are pronounced and posteriorly distributed old/new effects in both groups (Figure 3.5). Three-way ANOVAs with factors of group, item-type and lateralization (left/midline/right) performed for both the early time window (at frontal sites) and late time window (at posterior sites) revealed main effects of item-type (early: $F(1,39) = 5.23$, $p < .05$ and late: $F(1,39) = 28.56$, $p < .01$). For the late time window, the interaction between item-type and lateralization did not reach significance ($F(2,38) = 2.44$, $p = .11$). There were no interactions including the factors item-type and group.

Associative Memory Test

ERPs elicited by correct old and new responses in the AM posttest (Figure 3.6) at frontal and parietal recording sites were compared between two sub-groups (nap: $n = 19$; control: $n = 15$). The ERPs and topographical contrasts shown in Figure 3.6 indicate that both groups show more positive going waveforms for hits compared to correct rejections at posterior sites from approximately 500 ms onwards. A three-way ANOVA for the early time window (300-500 ms) at frontal sites revealed neither a significant main effect for item-type nor any interaction including the factor item-type (all p-values > .43), thus providing no evidence of an early mid-frontal old/new effect in either group. For the late time window (500-700 ms) at posterior sites, a marginally significant main effect of item-type was present ($F(1,32) = 3.18$, $p = .08$), but again, there was no interaction with the group factor.

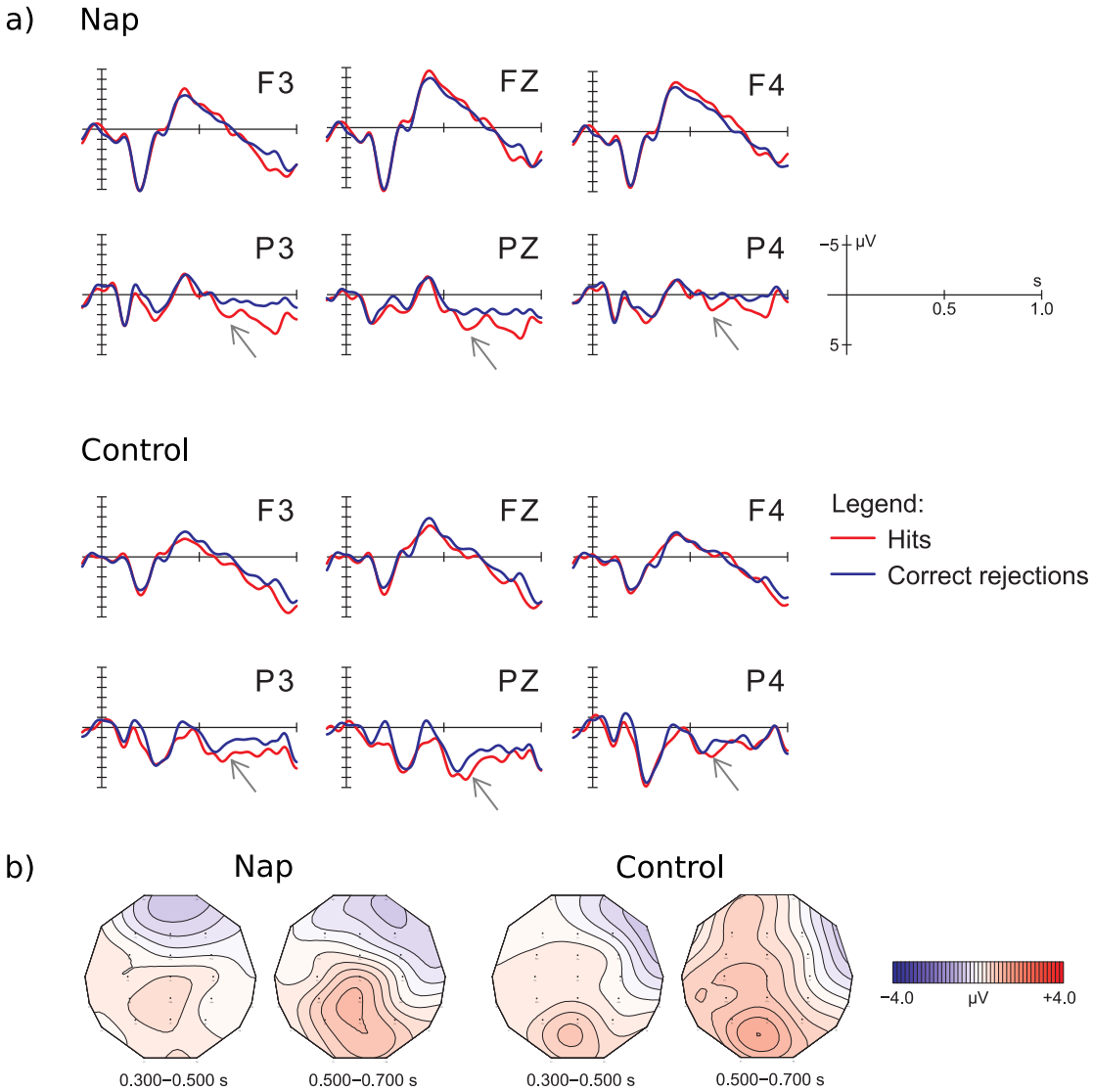

Figure 3.6. Grand average ERPs (a) and topographical maps (b) for the AM old/new comparison.

(a) Grand average ERPs elicited by hits and correct rejections at F3, Fz and F4 and P3, Pz and P4 in the associative memory posttest for the nap and control group. The arrows highlight the late parietal old/new effect. The y-axis denotes the onset of the test word and negative polarity is plotted upwards. (b) Topographical maps show the contrast hits minus correct rejections in two time windows (300-500 ms, 500-700 ms).

3.3.4 Post-hoc: Hits and incorrect answers to old and recombined pairs

It is of special interest to compare the ability to discriminate old and recombined pairs not only behaviorally between the nap and control group but also with electrophysiological measures. The next section describes an approach (also see Kriukova et al. (2013)) in addition to the above-mentioned old/new effects to disentangle processes which support the discrimination of old and recombined word-pairs. The following analysis takes incorrect answers and hits to old and recombined pairs into account. Hits refer to the combination of old and recombined correct answers. Incorrect answers refer to old pairs endorsed as recombined and recombined pairs endorsed as old. Any differences between these two categories should be due to associative discrimination, as the two conditions (old and recombined) are comparable for item familiarity (all words have been seen during the study phase). Due to low trial numbers for many subjects in one of the conditions, for the nap group only nine datasets and for the control group 13 datasets were analyzed. The mean number of trials for hits and incorrect answers in the nap group was 36 (range 18-50) and 20 (range 17-26), respectively, and for the control group 33 (range 19-44) and 18 (range 14-22); therefore highly comparable between groups. The ERPs and topographical maps shown in Figure 3.7 indicate more positive going waveforms for hits compared to incorrect answers at left posterior sites (from 500 ms onwards) for the nap compared to the control group. This observed difference was subjected to an ANOVA with factors item-type (hits, incorrect answers), lateralization (left/midline/right) and group (nap/control) in a 500-700 ms time window (electrodes P3, P4, Pz). Again, only main effects and interactions that involve the factor item-type are reported because these indicate that a hits/incorrect answers difference is present or varies with group or electrode location. A significant two-way interaction of item-type and group ($F(2,19) = 5.64$, $p < .05$) and a three-way interaction of item-type, lateralization and group were revealed ($F(2,19) = 9.33$, $p = .001$). In order to dissolve the interactions, separate two-way ANOVAs with factors group and item-type were conducted for each of the three electrodes. For electrodes Pz and P4 a main effect of item-type was present (Pz: $F(1,20) = 5.16$, $p < .05$; P4: $F(1,20) = 7.71$, $p < .05$) but no interaction (all $p > .33$), however, for electrode P3 an item-type and group interaction was revealed ($F(1,20) = 12.05$, $p < .01$). The amplitude difference between hits and incorrect answers at P3 was larger for the nap than for the control group whereas there were no group differences at Pz and P4.

ERPs at frontal sites in an earlier time window (350-500 ms) also seemed to differ between nap and control subjects, in that the control group showed more negative waveforms for hits than incorrect answers. An ANOVA with factors item-type (hits, incorrect answers), lateralization (left/midline/right) and group in a 350-500 ms time window (electrodes F3, F4, Fz) revealed only a marginal main effect of item-type ($F(1,20) = 3.28$, $p = .085$) but no interaction with group (all $p > .16$).

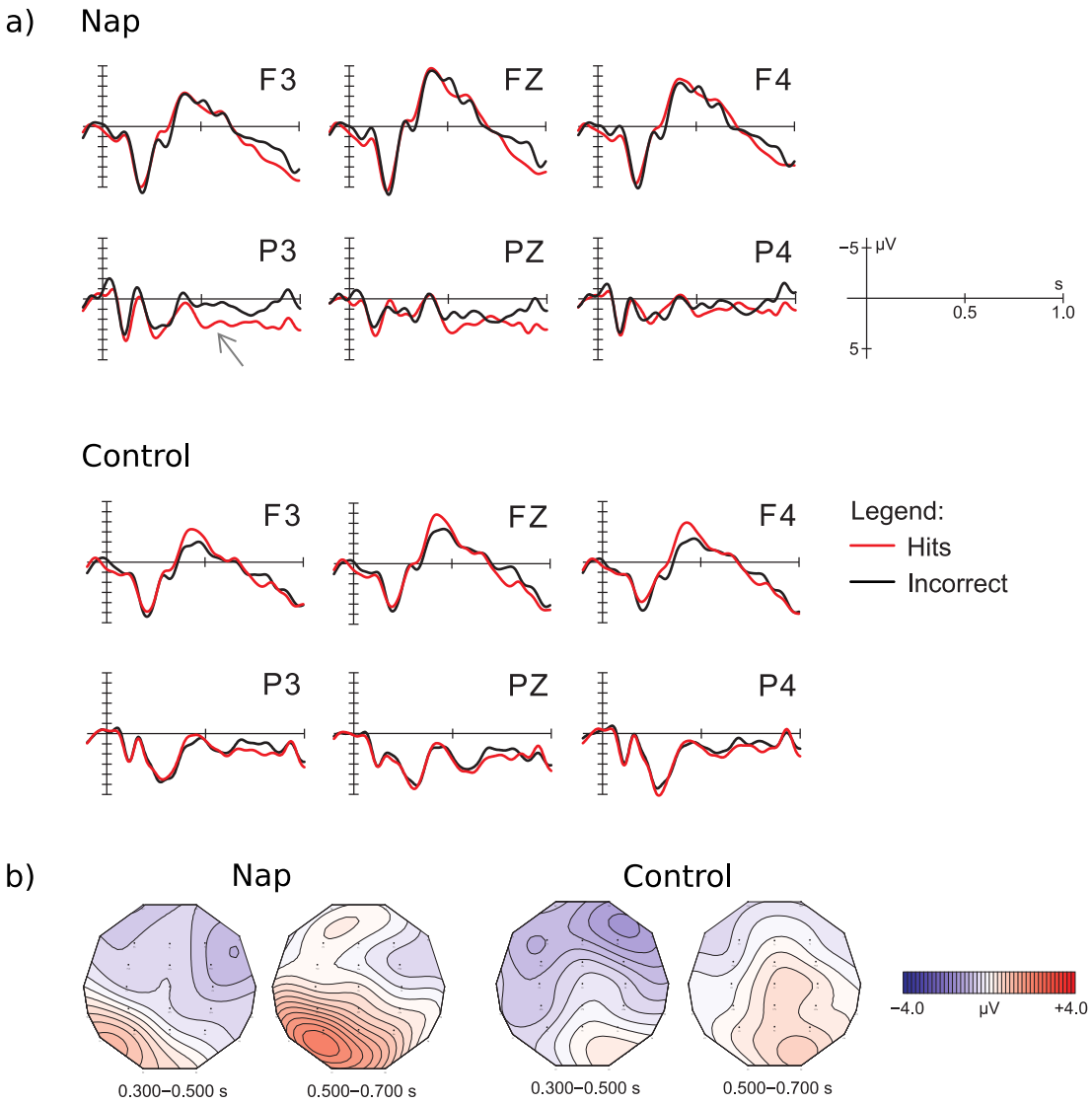

Figure 3.7. Grand average ERPs (a) and topographical maps (b) for the AM hits and incorrect answers comparison.

(a) Grand average ERPs elicited by hits and incorrect answers at F3, Fz and F4 and P3, Pz and P4 in the associative memory posttest for the nap and control group. The arrow highlights the late parietal old/new effect which differs with group. The y-axis denotes the onset of the test word and negative polarity is plotted upwards. (b) Topographical maps show the contrast hits minus incorrect answers in two time windows (300-500 ms, 500-700 ms).

To summarize, the ERP analyses for the item memory test revealed an early mid-frontal and a late parietal old/new effect, the putative ERP correlates of familiarity and recollection, respectively. Conversely, only a marginally significant late parietal old/new effect was obtained for the associative memory test and no differences were obtained between the two groups in either old/new contrast. There were, however, group differences by comparing a purer ERP index of the ability to discriminate between old and recombined pairs which was found at a left parietal site in the typical time interval of recollection.

3.4 Discussion

An associative memory task was compared with an item memory task to explore the effects of nap sleep on different forms of recognition memory. It was predicted that a memory benefit for the nap group relative to the wake control group would be observed only for recollection-dependent measures in the AM test – in this case, PrA scores (differentiation between old and recombined pairs) – after the retention period (AM posttest) whereas no group differences for Pr-scores in the IM task (old/new differentiation) should arise. In line with these predictions for the IM test, no group differences in behavioral measures of recognition memory were observed at baseline or posttest, and both groups showed a decrease in performance from baseline to posttest. As predicted, a different picture emerged for the AM test. While the control group showed a significant deterioration from AM baseline to AM posttest, performance in the nap group remained constant over time. This finding is consistent with studies showing that short periods of sleep are sufficient to induce a measurable benefit in declarative memory (Cox et al., 2012; Lahl et al., 2008; Lau et al., 2010; Mander et al., 2011; Mednick et al., 2008; Saletin et al., 2011; Schmidt et al., 2006; Schönauer et al., 2014; Tucker & Fishbein, 2008; Tucker et al., 2006; van der Helm et al., 2011). It also adds to the few recognition memory studies which show a beneficial impact of sleep for recollection, i.e. context-dependent memory but not for familiarity or item memory (Daurat et al., 2007; Drosopoulos et al., 2005; Mander et al., 2011; van der Helm et al., 2011).

In addition to findings of other studies in which benefits of sleep on recognition memory were reported, a selective correlation between AM posttest performance and spindle density during SWS was found. This is in accordance with recent evidence that memory consolidation processes rely on sleep spindles and co-occurring slow oscillations during SWS (Cox et al., 2012). The role of SWS for memory consolidation was also revealed in a recent stimulation study in which slow oscillatory activity was enhanced via auditory stimulation. Stimulation in phase with ongoing rhythmic slow oscillations enhances grouping of slow oscillations and phase coupled spindle activity and in turn improved declarative memory (Ngo et al., 2013). In fact, spindle activity and percentage of SWS showed a strong positive correlation with the overnight retention of word-pairs. The authors concluded that it is the synchronization of spindles with slow oscillations which might be critical for memory consolidation (Ngo et al., 2013). The correlation between AM posttest performance and spindle density in SWS in the present study may thus provide further evidence for the active system consolidation hypothesis (Born & Wilhelm, 2012).

The current data also show that AM baseline performance before the nap correlated with spindle density in the following sleep period such that controlling for baseline performance removed the relationship between posttest memory performance and spindle density. One reason for this is because of the general association between baseline and posttest memory performance. It is also possible that the current correlations reflect the possibility that baseline performance has an impact on both spindle density and posttest memory performance. Indeed a number of studies have also reported relationships between sleep parameters such as spindle density and memory performance prior to the sleep period (Gais et al., 2002; Schmidt et al., 2006). Gais and colleagues (2002), for example, found positive correlations between spindle density at fronto-central sites and cued recall performance in a declarative paired-associate task both before and after a night of sleep but not in a non-learning task which was matched in all stimulus and task characteristics except the intention to learn. This pattern is in line with the possibility that these spindles relate to intentional learning and speaks for the presence of a common mechanism involved in sleep spindle generation and intentional build-up of long-term memory representations (Gais et al., 2002). The present study supports this possibility by demonstrating a positive correlation between spindle density at Fz and memory performance in the AM baseline test. Another study conducted by Schmidt and colleagues (2006) reported a relationship between pre-sleep

encoding difficulty and spindle density. Here, participants learned lists of unrelated word-pairs in two different conditions. One condition comprised concrete words that could easily be encoded on the basis of preexisting semantic knowledge, whereas the abstract words employed in the second condition were (assumed to be) more difficult to encode. Spindle density was significantly increased over left frontal cortex for difficult but not for easy to encode word-pairs and spindle density was positively correlated with nap-related changes in memory performance. This finding is consistent with the view that sleep modulates memory consolidation when completely new memory associations are built up (as is presumed to be the case for the difficult to encode pairs) and less so when encoding relies on pre-existing semantic relations (Schmidt et al., 2006). Consistent with the two aforementioned studies, the correlation between AM baseline memory performance and spindle density in NREM sleep in the data of experiment one can be taken as further evidence that sleep only consolidates associative memories which are efficiently built up in the pre-sleep period as reflected in superior AM performance at baseline testing.

Another prediction derived from the current design was that the late parietal old/new effect – the putative ERP correlate of recollection – should be larger after nap sleep compared to the control group whereas no corresponding differences for the early mid-frontal old/new effect were expected. There was evidence of a late parietal old/new effect as well as an early frontal old/new effect in the IM test in both groups in accordance with the assumption that successful performance in the item memory task is associated with both familiarity and recollection. Neither of these old/new effects was modulated by sleep, however. Comparable early mid-frontal old/new effects in both groups supports the view that item memory for which no contextual information is provided is not modulated by sleep (Drosopoulos et al., 2005). However, as recollection also occurs for item memory a group difference in the amplitude of the late parietal old/new effect could have been expected, but this was not observed.

For the AM posttest data, there was no observable early frontal old/new effect, in line with the assumption that familiarity does not contribute to associative tests with arbitrary associations (Yonelinas et al., 2010). The late parietal old/new effect was marginally significant in line with the notion that recollection is required for this task. The amplitude of the effect in this task also did not differ between nap and wake groups, however, and the behavioral finding (less forgetting in AM after nap sleep) was not paralleled by corresponding changes in the ERP old/new effect. There are several

possible reasons for not finding group differences in the late parietal old/new effect. One possibility could be that the late parietal old/new effect is not sensitive enough to detect subtle changes in recollective processing which is supported by the results of the hits vs. incorrect answers analysis which takes the discrimination ability between old intact learnt stimuli and recombined ones into account and in which sleep effects were found. Here, the amplitude differences between hits and incorrect answers at a left parietal site were larger for the nap than for the control group in the typical time interval associated with recollection. Accordingly, it could be that beneficial effects of sleep in recognition memory studies could come about a better discrimination between old and recombined word pairs and facilitated access to associative memories, what is not necessarily reflected in amplitude differences in the late parietal old/new effect in which solely old and new items need to be discriminated.

To conclude, the first experiment showed a differential influence of nap sleep compared to a wake retention period on associative memory but no corresponding effects for item memory. The selective effect of nap sleep at AM posttest memory performance is consistent with the view that even short periods of nap sleep have a beneficial effect on hippocampus-dependent memory consolidation. The beneficial effects of nap sleep on post-sleep AM performance were not paralleled by differences in the ERP old/new effect but in an additional ERP comparison of hits and incorrect answers concerning the differentiation between old and recombined pairs, suggesting that the former effect might be not sufficiently sensitive to capture differences arising after sleep vs. wake in associative recognition. It might therefore be that sleep boosts associative memory by strongly improving the ability to discriminate between learnt and recombined word-pair associations. Positive correlations between spindle density in SWS and AM post-sleep performance and between spindle density in NREM sleep and AM baseline test performance were found. The former effect adds to the increasing evidence that SWS is of high relevance for the consolidation of declarative memories although the possibility that baseline performance determines both spindle density and posttest memory performance cannot be excluded from the current data. On the basis of the correlation between spindle density in NREM sleep and AM baseline performance it is tempting to speculate that sleep only consolidates memories which are efficiently built up and newly formed prior to the sleep period (Stickgold & Walker, 2013).

These results of the first experiment, in addition to previous literature (Hu et al., 2006; Oudiette, Antony, Creery, & Paller, 2013; Payne et al., 2008; Saletin et al., 2011;

Stickgold & Walker, 2013; van Dongen, Thielen, Takashima, Barth, & Fernández, 2012; Wilhelm et al., 2011), led to the aims of the second study. Here, it was the intention to investigate if expected reward can influence whether information will be retained or forgotten after sleep. Further, it was questioned whether superior learning and memory performance before sleep are influencing physiological parameter during a subsequent nap and memory retention post-sleep, or if sleep plays a selective role in determining which memories will endure by only strengthening that information which is associated with some relevance for the future as has been suggested in recent years (Stickgold & Walker, 2013).

4 Theoretical and empirical review – Part 2

Part 2 of the theoretical background starts with an overview about the effects of motivational cues on memory formation including possible neuronal underlying's (4.1), followed by a review of literature about selective memory consolidation during sleep (4.2). Following this, a model for reward-activation during sleep will be explained which combines findings of both motivational impact on learning and memory consolidation during sleep (4.3). Chapter 4.4 provides a summary and description of the objectives for the second study.

4.1 Motivational impact on memory formation

Not all information which is encountered is retained for the future; and the influence of motivation on determining which memories will be stored into long-term memory has been of interest for many decades (Heyer Jr & O'Kelly, 1949), presenting already early that motivation influences learning (Heinrich, 1968). To date, a wealth of studies present a beneficial effect of different motivational cues presented at learning on later memory performance (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006; Feld, Besedovsky, Kaida, Münte, & Born, 2014; Gruber & Otten, 2010; Heinrich, 1968; Wittmann et al., 2005; Wolosin, Zeithamova, & Preston, 2012). Motivational cues in memory studies have been implemented in different ways; often monetary reward is associated with to-be-learnt material which is then tied to correct remembering (Adcock et al., 2006; Gruber & Otten, 2010; Oudiette et al., 2013; Wolosin et al., 2012), in other cases solely task relevance is enhanced by telling subjects that they will be tested later on the learnt material (Wilhelm et al., 2011), or memories will be made more salient when they are embedded in an emotional context (Payne et al., 2008). It is assumed that two neural systems are acting together to support motivated learning; the medial temporal lobe system which is important for declarative memory formation (see also 2.1) and the (mesocorticolimbic) dopaminergic system which is involved in reward processing (Adcock et al., 2006; Perogamvros & Schwartz, 2012; Wise, 2004). The next section will therefore describe the dopaminergic system and its

role in motivational learning and memory formation before describing an ERP approach to disentangle neural activity at encoding as a function of successful memory formation.

4.1.1 Dopaminergic system and motivational learning

Dopamine (DA) is an important neurotransmitter which is assumed to play a major role in mediating preferential learning of highly rewarding stimuli (Feld et al., 2014; Wise, 2004). There are three main DA-pathways in the brain, which are also interacting (Wise, 2004). The nigrostriatal pathway is thought to be relevant for movements and behavioral habits and involves neurons projecting from the substantia nigra (SN) to the dorsal striatum (Perogamvros & Schwartz, 2012). The mesolimbic and mesocortical dopamine systems originate from dopamine cells in the ventral tegmental area (VTA) and are thought to be important for motivational processes (Wise, 2004). Due to highly overlapping projections, the mesolimbic and mesocortical system are often referred to as mesocorticolimbic system. Combined, it then projects to structures such as the hippocampus, hypothalamus, nucleus accumbens (NAcc), amygdala, olfactory tubercle and to the anterior cingulate (ACC) and prefrontal cortex (PFC) (Perogamvros & Schwartz, 2012; Wise, 2004). Several studies suggest that it is involved in reward, emotional processing and learning (Adcock et al., 2006; Alcaro, Huber, & Panksepp, 2007; Feld et al., 2014).

Adcock and colleagues (2006) used an event-related fMRI design to investigate the neural mechanisms which underlie memory formation associated with monetary reward. Their participants had to study pictures of indoor and outdoor scenes which were either preceded by a high-reward or low-reward promising cue for later correct retrieval. At retrieval testing one day later, participants recognized significantly more high-reward associated pictures than low-rewarded ones. By comparing neural activity at learning in the high-reward promising cue interval, greater activity in the VTA, nucleus accumbens and hippocampus was found for later remembered but not for forgotten highly rewarded stimuli (subsequent memory paradigm (Friedman & Johnson, 2000; Paller & Wagner, 2002), see also 4.1.2). Further, functional connectivity analyses revealed a correlation between activity in the right VTA and posterior hippocampus during cue intervals preceding remembered but not forgotten high-rewarded pictures. Thus combined brain activation in regions of the mesolimbic dopamine system and

structures of the medial temporal lobe before the actual encoding of the stimulus already predicted if a memory will be efficiently build up (Adcock et al., 2006). In another brain imaging study by Wittmann and colleagues (2005) an association between reward-predicting cues and activity in midbrain regions (e. g. substantia nigra) as well as anterior cingulate, nucleus accumbens, caudate nucleus and putamen was also found. Additionally, higher activation in dopaminergic midbrain regions was as well found for recognized compared to forgotten pictures in a delayed (three weeks after initial encoding) surprise memory task. In this delayed memory task, stimuli that initially predicted a high reward were remembered more confidently and associated with a better source memory than neutral stimuli. As these answers were requiring recollection, it was concluded that reward anticipation specifically improved hippocampus-dependent memory (Wittmann et al., 2005). In a further fMRI-study carried out by Wolosin and colleagues (2012), the influence of motivation on associate encoding and cued recall at retrieval - which is also assumed as being hippocampus-dependent - was examined. During encoding, participants needed to create an association between two objects which were either preceded by a high or low reward cue. At cued recall testing, participants showed better memory for high-value compared to low-value associations. Subsequent memory analyses revealed greater activation in VTA/SN and parahippocampal (PHc) areas for high-value associations that were remembered compared to forgotten ones. At retrieval, PHc, VTA/SN as well as hippocampus showed enhanced activation for high-value relative to low-value associations (Wolosin et al., 2012). Taken together, it could be shown that reward anticipation impacts hippocampus-dependent memory and activates structures associated with reward-processing such that reward cues presented at encoding influence latter memory retrieval (Adcock et al., 2006; Wittmann et al., 2005; Wolosin et al., 2012).

4.1.2 Reward-processing reflected in ERPs at encoding

Next to examining ERPs at retrieval which were already explained in chapter 2.2.2, it is also possible to investigate ERPs during encoding. One possibility is the subsequent memory paradigm; the accuracy at a memory test is used to mark stimuli at encoding as either “hits” (items that were remembered) or “misses” (items that were forgotten) (Friedman & Johnson, 2000; Paller, McCarthy, & Wood, 1988; Wilding &

Sharpe, 2003). This paradigm enables the investigation whether neural activity at encoding differs depending on either successful or failure in retrieval. This can be done by using neuroimaging methods such as fMRI (Park & Rugg, 2010; A. D. Wagner, Koutstaal, & Schacter, 1999; A. D. Wagner et al., 1998) but also by using ERPs (Gruber & Otten, 2010; Otten, Quayle, Akram, Ditewig, & Rugg, 2006). An advantage compared to fMRI is the better temporal resolution of ERPs. Studies show that ERP waveforms typically start to differ with higher amplitudes for remembered compared to forgotten stimuli at approximately 400 ms after stimulus onset lasting until 800 ms (Paller, Kutas, & Mayes, 1987) or even longer (Gruber & Otten, 2010).

Gruber and Otten (2010) investigated how the motivation to encode influences prestimulus activity and neural activity related to encoding. Monetary reward cues preceding the presentation of to-be learnt words indicated how much money participants could earn if the word would be remembered correctly in a later recognition memory test. Participants had to judge words as learnt (old) or new; and rate their confidence on a 5-point scale. This was made to be sure to discriminate recollected ("remember") answers (very confident old answers with recalling specific details) from answers which were assumed to be more based on a feeling of familiarity (old answers without recollecting details). Behavioral results showed memory performance to be better for high-rewarded compared to low-rewarded words and highly rewarded words were more confident remembered than low-rewarded words. To analyze how the motivation to encode influences prestimulus activity, ERPs for high vs. low reward cues were contrasted without taking later memory performance into account. High reward cues led to more positive going ERPs from around 200 ms to 1100 ms compared to low reward cues. Successful encoding was examined by using the subsequent memory paradigm. A subsequent memory effect was only present for high-rewarded but not low-rewarded stimuli, and was most pronounced for "remembered" items. It started at around 300 ms after cue onset and maintained until word onset (~2000 ms). Together, these results indicate that prestimulus activity is particularly important for processes at encoding that lead to the subsequent recollection of highly-rewarded memories.

Summed up, the results of neuroimaging and electrophysiological measures indicate that reward anticipation is able to alter encoding (processes) and consequently has an impact whether subsequent memory retrieval will be successful or not. Regions in medial temporal lobe such as the hippocampus and surrounded regions (Adcock et

al., 2006; Wolosin et al., 2012) as well as midbrain areas associated with reward processing seem to be most relevant for the superior memory formation of adaptive and highly rewarded information (Adcock et al., 2006; Wittmann et al., 2005; Wolosin et al., 2012). The preferential processing of memory information that is successful remembered later on is further reflected in ERP correlates at encoding (Otten et al., 2006; Paller et al., 1987), especially pronounced for stimuli that are promised a high reward (Gruber & Otten, 2010)

4.2 Selective memory consolidation during sleep

The former section summarized the beneficial effects of reward anticipation on memory formation. Sleep also has been associated with benefits for memory retention by a number of studies (see also chapter 2.3) linking this as well to physiological variables during sleep (Rasch & Born, 2013). Recently it has been questioned whether sleep could work as a filter by predominantly strengthening memories that are adaptive or of relevance to the future as such a mechanism would be advantageous for long-term memory capacity as both the utility would be maximized and the load would be reduced (Saletin & Walker, 2012; Stickgold & Walker, 2013; van Dongen et al., 2012). Stickgold and Walker (2013) assume a selective mechanism of memory consolidation by sleep in that consolidation of information will only occur if items were tagged as important during or after the encoding phase. These tags could be induced by motivational factors such as expected reward (Fischer & Born, 2009; Oudiette et al., 2013; van Dongen et al., 2012), task relevance (Saletin et al., 2011; Wilhelm et al., 2011) or emotionality (Hu et al., 2006; Nishida et al., 2009; Payne et al., 2008; U. Wagner, Gais, & Born, 2001) (see also chapter 4.2.1 - 4.2.3).

The underlying mechanism of selective memory consolidation during sleep are still not fully understood, but there is evidence that theta activity in hippocampal and prefrontal circuits during encoding might be critical for tagging of motivational relevant memories and subsequent consolidation during sleep as the network which is activated by theta also includes regions such as the ventral tegmental area (VTA) and the amygdala (Rasch & Born, 2013), areas which are involved in motivational processing (Perogamvros & Schwartz, 2012). The next sections describe empirical findings of

selective memory consolidation during sleep induced by task relevance (4.2.1), emotionality (4.2.2) and expected reward (4.2.3) before a model of reward-activation during sleep will be described which combines findings of selective memory consolidation during sleep with findings on motivational impact on learning.

4.2.1 Task relevance and selective memory consolidation during sleep

One of the motivational factors which is discussed as having an impact on the sleep selectivity in memory consolidation is future relevance, i.e. elicited by task relevance. Wilhelm and colleagues (2011) asked participants to learn lists of semantically-related word-pair associates before 9 hour retention intervals filled with either sleep or wakefulness. Critically, participants were randomly allocated to be either informed or uninformed that they would be later tested on their memory for these items after the retention interval. Participants who were informed that they would be later tested performed better on the final memory test than their uninformed counterparts, but only if they slept in the retention interval. These participants also demonstrated a robust increase in slow oscillation activity and sleep spindles during SWS.

Saletin and colleagues (2011) investigated the role of sleep in directed forgetting and remembering. Their participants had to study words which were either cued to be forgotten or to be remembered. Half of them were allowed to nap (nap group) while the other half had to stay awake (control group) before performing a free recall test. Subjects were instructed to recall as many words as possible from the learning phase, however, independent of the associated cue before. Participant's responses were classified in different categories; e. g. "R-words" means recalled words with the associated remember-cue, "F-words" are recalled words which were cued to be forgotten. To estimate the efficiency of the directed forgetting effect an R-F-difference measure was used by subtracting the proportion of "F-words" recalled from the proportion of "R-words" recalled. Both groups knew more "R-words" than "F-words" but in total the nap group recalled significant more "R-words" compared to the control group. In addition, the R-F-score was higher for the nap group compared to control group and there was a strong correlation between the R-F-score and fast sleep spindles at posterior sites (P3). In a study by Rauchs and colleagues (2011) a directed forgetting paradigm was used in combination with functional MRI (fMRI) at both encoding and

delayed recognition testing. Half of the participants had a normal night of sleep whereas the other half was sleep-deprived post-learning. Memory was tested three days after encoding for all learnt words irrespective if they were cued as to-be-remembered or as to-be-forgotten. Recognition accuracy for to-be-remembered words was similar between the sleep and sleep-deprived group but the latter group recognized more to-be-forgotten words than the sleep group and showed a higher false alarm rate. Further, it was shown that higher hippocampal activity for to-be-remembered compared to to-be-forgotten items during encoding was specifically observed in the sleep group but not in the sleep-deprived group. It seems that the two types of memories are processed in a different way for sleep compared to wake and that hippocampal activity at encoding has an exclusive impact on sleep-dependent memory consolidation.

Summed up the mentioned studies add some evidence for the idea of selective memory consolidation during sleep induced by task relevance (Saletin et al., 2011; Wilhelm et al., 2011) and show a possible underlying mechanism namely hippocampal activity which is associated with selective encoding of memories (Rauchs et al., 2011).

4.2.2 Emotional impact on selective memory consolidation during sleep

Next to the selective consolidation of relevant memories induced by task requirements, it has also been shown in some studies that sleep stabilize emotional over neutral contents (Hu et al., 2006; Nishida et al., 2009; Payne et al., 2008; U. Wagner et al., 2001; Wiesner et al., 2015). Hu and colleagues (2006) investigated the consolidating effect of sleep on emotional and neutral memory by using a memory task with arousing (emotional) and non-arousing (neutral) pictures. After a 12-hour retention period filled with either sleep or wakefulness, subjects performed a recognition task showing that recognition of arousing compared to neutral pictures was specifically enhanced. In a study by Payne and colleagues (2008) memory for neutral scenes (a neutral object on a neutral background, e. g. a car on a street) was contrasted to negative scenes (a negative object on a neutral background, e. g. a car accident on a street) across different retention intervals; a short retention period of 30 minutes and a 12-hours retention interval, which was either filled with sleep or wakefulness. They found memory to be better for negative than neutral objects at both the immediate and delayed testing. In addition, after sleep, the memory for negative objects was preserved in contrast to the

background information, a pattern that was not found for the wake group. These results demonstrate that memories are differentially processed depending on sleep or wake and that sleep selectively strengthened information which is of high emotional value. This was also demonstrated in a nap study by Nishida and colleagues (2009) in which memory performance for emotional but not neutral pictures was benefitted by sleep but not by time spent awake. It was further shown that the both the amount of REM sleep as well as prefrontal theta activity during REM correlated with the improvement in emotional memory. There are also further studies which support a role of REM sleep for emotional memory consolidation (Groch et al., 2013; Groch, Zinke, Wilhelm, & Born, 2015; U. Wagner et al., 2001; Wiesner et al., 2015).

The influence of REM sleep on emotional memory retention was investigated by using a split-night design in some studies (Groch et al., 2013; Groch et al., 2015; U. Wagner et al., 2001) and with selective deprivation of REM or SWS in another one (Wiesner et al., 2015). Wiesner and colleagues (2015) selectively deprived REM or SWS in a 9-hour retention period, and compared the memory retention of emotional and neutral pictures of these groups to a wake control group. They showed that memory retention for emotional material was better than for neutral in the SWS-deprived group where REM sleep is present, and was generally worse for the REM-sleep deprived and awake group. The impact of REM sleep on emotional memory was also shown by Wagner and colleagues (2001). They used a split-night design in which memory is tested and compared after periods which contain high amount of NREM sleep especially SWS (first half of the night) and after periods containing high amounts of REM sleep (second half of the night). It was shown that only after the second half of the night, with REM-rich sleep, memory for emotional compared to neutral texts was enhanced (U. Wagner et al., 2001). Similar results in a comparable design were found for emotional pictures in comparison to neutral ones (Groch et al., 2013). In a recent split-night study by Groch and colleagues (2015) the effects of SWS and REM on emotional and neutral item memory as well as source memory were investigated. Better memory retention for emotional compared to neutral pictures was only found after REM-rich sleep whereas SWS-rich sleep led to a benefit in retention of neutral picture-frame color associations compared to after REM-rich sleep (Groch et al., 2015). Summed up, these studies indicate that emotional content can lead to a preferential consolidation during sleep, which might be related to the amount of REM sleep and that

on the other side processes during SWS might be beneficial for associative memory (Groch et al., 2015, see also chapter 2.3.2).

4.2.3 Influence of reward on selective memory consolidation during sleep

Reward-promising cues are discussed as another motivational factor which could influence selective memory consolidation during sleep (Stickgold & Walker, 2013). In one study by Fischer and Born (2009) participants had to learn two sequences of a finger-tapping task. After learning, they were informed that only one sequence would be rewarded at a later test before they were allowed to sleep or had to stay awake. Before the final test, participants were informed about an additional payment that would not depend on the sequence they were informed about, but on the average performance of both sequences. Improvement in speed as well as accuracy was found to depend on whether reward was expected or not. Furthermore, these gains were significantly greater for those participants who were allowed to sleep, showing that sleep-dependent motor memory consolidation is influenced by expected future reward. A similar approach but with a declarative memory task was used by van Dongen and colleagues (2012) to test whether sleep selectively preserves associative memories based on future relevance. Participants had to learn two sets of picture-location associations and were instructed after a baseline test that only one of the sets would be tested and monetary rewarded after a 14-hour delay. The retention period was either filled by sleep or wakefulness and at the delayed test both sets of picture-location associations were tested unexpectedly. Memory retention for relevant picture-location associations remained at a similar high performance level from pre- to delayed test for participants that slept but not for those who stayed awake. These two studies show that it is possible to use hints of future relevance and reward to modulate the retention of procedural and declarative memories tested post-sleep.

A beneficial effect of promised reward was shown in another study using a spatial memory task and a nap design (Oudiette et al., 2013). Here, participants had to learn object-location associations with half of the objects associated with low and the other half with high reward values. These were indicated by numbers (1, 2: low reward; 8, 9: high reward) superimposed on the objects. A representative sound was played while the object was presented (e. g. for a cat a “meow”). Half of the low-value-

associated sounds were played again for a subsample of participants during a retention period filled with either sleep or wakefulness. The position of high-value associated objects was later better remembered than from low-value ones in both the wake and nap group. Interestingly, the performance for all low-value associated object locations was increased after playing some of the sounds during SWS although not all low-value associated sounds were played again. For the wake group, however, the performance was better only for the object-locations for which the associated sounds had been presented. This study demonstrates that spatial memories are possibly reactivated during sleep and wakefulness, but that during sleep additionally categorically connected memories are linked together.

A recent study by Feld and colleagues (2014) could demonstrate the impact of the DA system on memory processing during sleep. Before a night of sleep, their participants needed to learn pictures that were associated with either low or high reward cues, afterwards receiving either a placebo or DA-receptor agonist (pramipexole). At retrieval testing 24 hours later, the placebo group retrieved more high-rewarding pictures than low-rewarding yet this effect was absent for the group which got pramipexole. For the latter group, performance for low and high rewarded pictures was equally high. It was therefore concluded that the DA reward system is activated during sleep and that enhancement of DA activity led to enhanced memory consolidation such that low- and high-rewarded stimuli are equally well retained.

Taken together, these findings generally support the influence of motivational factors on learning and subsequent selective memory consolidation during sleep. Some studies indicate that some sleep stages might contribute especially to the preferential consolidation of some memories during sleep (e. g. REM sleep for emotional material; SWS for associative memories) (Groch et al., 2013; Groch et al., 2015; U. Wagner et al., 2001; Wiesner et al., 2015) or demonstrate relationships between memory consolidation and distinct physiological characteristics of sleep (e. g. SO- or sleep spindle activity) (Saletin et al., 2011; Wilhelm et al., 2011). Others indicate that reward processing brain regions might be active during sleep (Feld et al., 2014). The next section will therefore describe a model (“Reward Activation Model”) which describes the importance of the mesolimbic dopaminergic system and the interplay with regions in the medial temporal lobe (MTL) in being recruited not only during wakefulness but also during sleep (Perogamvros & Schwartz, 2012).

4.3 Reward processing and memory consolidation during sleep

The former sections show that highly rewarding stimuli are preferentially memorized, and that sleep seems to play a role in selectively consolidating these stimuli respectively these ones that have a future value (i.e. expected memory test, monetary reward) or are emotional in nature. The following section aims to combine these aspects by introducing a model for reward-activation during sleep (Reward Activation Model (Perogamvros & Schwartz, 2012)). It has been shown that parts of the mesolimbic DA system are activated during sleep in animal (Dahan et al., 2007; Lansink, Goltstein, Lankelma, McNaughton, & Pennartz, 2009) as well as in human studies (Nofzinger et al., 2002; Nofzinger, Mintun, Wiseman, Kupfer, & Moore, 1997; Schabus et al., 2007). Further, regions that are associated with memory formation are also active during sleep (Ji & Wilson, 2007; Lansink et al., 2009; Nofzinger et al., 2002; Peigneux et al., 2004; Rasch et al., 2007; Schabus et al., 2007; Sirota et al., 2003; Wilson & McNaughton, 1994). The Reward Activation Model (RAM) questions whether these activations contribute to the preferential processing of motivational relevant information (Perogamvros & Schwartz, 2012).[4] It is assumed that regions of the medial temporal lobe and structures of the dopaminergic system are interacting (Lisman & Grace, 2005) to enable the reactivation and resulting consolidation of motivational or emotional relevant memories during sleep (Perogamvros & Schwartz, 2012). Lisman and Grace (2005) propose a functional loop between VTA and hippocampus which determines what will be stored into long-term memory.

Based on this functional loop, the RAM assumes an interaction between reward processing and memory consolidation during sleep (Perogamvros & Schwartz, 2012). The loop consists of a downward arc which is supposed to be active during SWS and an upward arc which might be active during REM sleep (see Figure 4.1). The hippocampus detects novelty signals and in turn stimulates the firing of DA-neurons via ventral striatum (VS)/NAcc in the VTA (downward arc). The combined activation of hippocampal and striatal sites leads to a memory trace including motivational and context information; thereby supporting the consolidation of the memory-reward associations (Lansink et al., 2009; Perogamvros & Schwartz, 2012). The upward arc

[4] The authors also assume in their model that dreaming might play a role in learning and memory. The current thesis does not investigate the impact of dreams, therefore the interested reader is directed to the original article by Perogamvros and Schwartz (2012) "The roles of the reward system in sleep and dreaming" for further information.

comprises DA-projections from the VTA to the hippocampus. The activation of the VTA might therefore lead to the reactivation and subsequent consolidation of reward-memory associations in hippocampal sites by also contributing to long-term potentiation (LTP) which is supposed to be DA-dependent (Feld et al., 2014; Li, Cullen, Anwyl, & Rowan, 2003).

Taken together, it could be shown that areas of the mesocortical DA system are active during sleep, as are regions in the medial temporal lobe (e. g. hippocampus). A functional loop between these structures might be a possible mechanism to describe the selective memory consolidation which occurs during sleep.

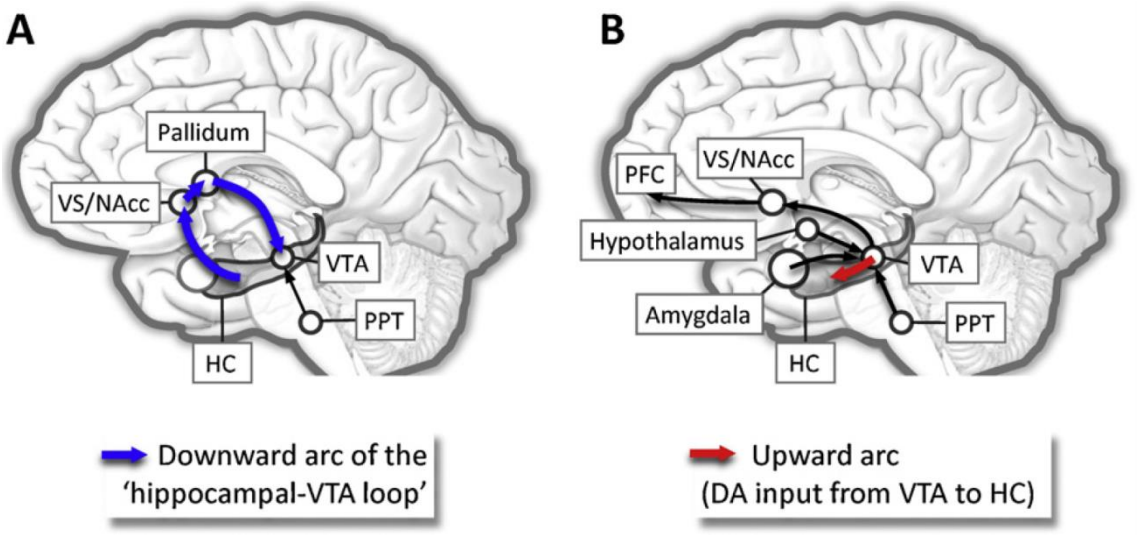

Figure 4.1. Schematic illustration of the hippocampal-VTA-loop (adapted from Perogamvros and Schwartz (2012)).

(a) Downward arc: The hippocampus detects novelty signals and in turn stimulates the firing of DA-neurons via ventral striatum/NAcc and pallidum in the VTA and (b) the upward arc comprises amongst others DA-projections from the VTA to the hippocampus.
Abbreviations: HC: Hippocampus; VS/NAcc: ventral striatum/Nucleus accumbens; VTA: ventral tegmental area; PPT: penduculopontine tegmental nuclei; PFC: prefrontal cortex

4.4 Interim summary and objective of Experiment II

Memory formation is an adaptive process; not all encountered or learnt information is retained for the future and it is assumed that sleep plays a major role in determining which memories will endure (Stickgold & Walker, 2013). Highly motivational cues (e. g. monetary reward) presented at encoding have been shown to benefit memory formation by recruiting both regions in MTL (e. g. hippocampus) and dopaminergic midbrain structures (Adcock et al., 2006; Wittmann et al., 2005; Wolosin et al., 2012). Further, the consolidation of memories is thought to depend in part on physiological processes engaged during sleep, such as slow oscillations (Marshall et al., 2004; Ngo et al., 2013), sharp wave-ripples (Axmacher et al., 2008; Eschenko et al., 2008; Ramadan et al., 2009) and spindles (Cox et al., 2012; Gais et al., 2002; Mednick et al., 2013; Saletin et al., 2011; Schabus et al., 2004). Recently, evidence is accumulating that sleep works as a filter by predominantly strengthening memories that are motivationally or emotionally relevant or of importance in the future (Fischer & Born, 2009; Hu et al., 2006; Nishida et al., 2009; Oudiette et al., 2013; Payne et al., 2008; Saletin et al., 2011; van Dongen et al., 2012; U. Wagner et al., 2001; Wiesner et al., 2015; Wilhelm et al., 2011). In one model of selective memory consolidation during sleep, Stickgold and Walker (2013) assume that consolidation of information will only occur if items are tagged as important during or after encoding. These tags could be induced by expected reward (Fischer & Born, 2009; Oudiette et al., 2013), task relevance (Saletin et al., 2011; Wilhelm et al., 2011) or emotionality (Payne et al., 2008). The neural underlying of the tagging mechanism are not fully understood yet (Stickgold & Walker, 2013). It has been reported that hippocampal activity at encoding is related to the amount of sleep related memory consolidation (Rauchs et al., 2011). This fits well with the assumptions of the Reward Activation Model which postulates that there is a functional link between memory and reward processing during sleep through the interaction of the hippocampus and parts of the midbrain dopaminergic system (e. g. ventral tegmental area) (Perogamvros & Schwartz, 2012). In the first study of the present dissertation benefits of nap sleep were demonstrated for hippocampus-dependent memories. Further, associative recognition memory performance after sleep was found to be associated with sleep spindle density at frontal sites during SWS, and performance before sleep was correlated with sleep spindle density at frontal sites during NREM sleep. It was therefore questioned whether superior learning and baseline

memory performance have an impact on spindle production in a subsequent sleep episode (Gais et al., 2002; Schmidt et al., 2006).

The aim of the second experiment was to investigate the impact of different motivational incentives during encoding on subsequent sleep physiology and memory retention. Reward cues should make high reward items motivationally more relevant and tagged for selective consolidation during sleep compared to low reward items (Stickgold & Walker, 2013) thereby leading to a better memory retention for high-rewarded stimuli. Further, it was examined whether sleep selectively strengthens some information over others by investigating the relationship between spindle density and memory performance for high vs. low rewarded items. If a correlation between spindle density and post-sleep memory performance for high but not low rewarded items could be observed, this would provide evidence for a selective role of sleep in memory consolidation. A final aspect of the experiment was to investigate encoding (Gruber & Otten, 2010) and retrieval processes by using ERPs. As several studies could show that the neural activity before stimuli occurrence is important in determining whether stimuli will be remembered or forgotten (Adcock et al., 2006; Gruber & Otten, 2010; Otten et al., 2006; Park & Rugg, 2010), neural activity elicited by high reward cues was expected to be larger than for low reward cues; and subsequent memory effects were expected to arise only for high-rewarded stimuli (Gruber & Otten, 2010). Concerning ERPs at retrieval it was assumed that nap sleep leads to an enhancement of recollection; as it was demonstrated in a comparison of hits vs. incorrect answers in the AM task in experiment one, for motivationally high salient memories. This should be evident in larger ERP-correlates of recollection for correctly recognized high rewarded as compared to low rewarded stimuli.

5 Experiment II

5.1 Introduction

The preceding considerations of the existent literature strongly indicate that sleep should preserve memory for word-pair associations that are relevant for the future. Moreover, data repeatedly demonstrating the engagement of SWS mechanisms predicts that the mnemonic benefits for information that undergoes a specific learning experience should be evident even after a 90-minute nap, so long as this is sufficient for individuals to engage in a prolonged phase of SWS. In the second experiment, all participants learnt a list of word-pairs and were tested on their memory both before and after taking a nap. Critically, half of the word-pairs were preceded by a cue which indicated that later correct performance would be rewarded at a high level; whereas for the remainder, the cue indicated that the reward was relatively low (see Oudiette et al. (2013) for a similar approach to induce motivational salience). The logic behind this manipulation was that these reward cues should make high reward items motivationally more relevant and tagged for selective consolidation during sleep compared to low reward items (Oudiette et al., 2013; Stickgold & Walker, 2013). This should lead to better memory performance for high- than low-reward items after sleep, manifest as a significantly smaller decline in memory performance for high-rewarded associations over time. In line with the notion that the physiological variables during NREM sleep are associated with selective consolidation, however, specific predictions about the relationship between spindle density and memory performance were explicitly considered. If a correlation between spindle density and memory performance for high but not low rewarded items can be observed, this would provide evidence for a selective role of sleep in memory consolidation, in particular a role for sleep spindles in the selective tagging of memories from a specific learning experience, in the present case memories for events with a high motivational value.

In the second experiment therefore, behavioral and ERP measures were used together with polysomnographic data to investigate how reward cues during encoding might interact with the benefits of nap sleep on associative recognition and how this would relate to physiological variables during sleep. A final aspect of the current design was the employment of an associative recognition memory test as was the case in the

first experiment, in which word-pairs were to be classified as old, recombined or new. Responses to these categories were used to create two discrimination measures. An old/new discrimination Pr index (PrI- score), calculated by subtracting false alarms to new pairs from the hit rate for old pairs was taken to represent item memory performance whilst an associative PrA-score, calculated by subtracting the proportion of recombined pairs incorrectly classified as old (false alarms to recombined) from the hit rate for old pairs, was employed as a measure of recollection/associative memory (Bader et al., 2010; Kriukova et al., 2013). Sleep was expected to show greater benefits for the recollection-dependent measure (Daurat et al., 2007; Drosopoulos et al., 2005). The preferential processing of high rewarded vs. low rewarded stimuli was assumed to be reflected in ERPs at encoding; neural activity elicited by high reward cues was expected to be larger than for low reward cues; and subsequent memory effects were expected to arise only for high-rewarded stimuli (Gruber & Otten, 2010). A final assumption was that a preferential processing of high-rewarded associations was expected to be reflected in a larger ERP correlates of recollection at retrieval for high-rewarded compared to low-rewarded correct answers.

5.2 Methods

5.2.1 Participants

30 healthy young adults from Saarland University participated in this experiment. Data from 9 subjects were excluded due to (a) not sleeping (no occurrence of stage 2 sleep; n = 3), (b) technical problems[5] (n = 3) and (c) incorrect use of response buttons at pretest (n = 3). The latter refers to two subjects who pressed two out of three possible buttons on at least 80 % of all trials and one subject who consistently confused "old" and "recombined". All three of these excluded participants had a discrimination score at least 2 SDs lower than the mean in at least one of the two reward categories. The final sample (n = 21) consisted of 14 females and 7 males with a mean age of 21.7 ± 2.6. All participants stated that they did not have any sleep disorders, no known

[5] This refers to two instances in which the sleep EEG recording did not work and a further instance in which E-prime failed to record responses so the session had to be stopped after the pretest.

neurological problems and that they were right-handed (Oldfield, 1971). All gave written informed consent and were paid 20 € or equivalent course credit plus an additional reward which was dependent on their test performance (average: 9 € ± 3 €). The maximum additional reward was set to 20 €.

5.2.2 Stimuli

270 semantically unrelated German word-pairs were used as stimuli (compare appendix Table B.1). All words were nouns with a length between 3-10 letters and a frequency between 6 and 869 (Baayen et al., 1995). 180 of the word-pairs were used in the previous experiment. The remaining 90 word-pairs were newly created and evaluated in terms of semantic relationship and suitability to build a compound in order to reduce the pre-experimental associations within pairs (Bader et al., 2010). 30 additional subjects who did not participate in the main experiment rated the relatedness and unitization ability of the new and recombined word-pairs and only word-pairs with low relation and low unitization values (each ≤ 2 on a scale from 1-4) were included as test stimuli. There were six different stimuli-sets for word-pairs which were counterbalanced across the initial sample so that all items appeared equally often in each category (high/low reward; old/new/recombined). Recombined pairs were always rearranged within either the low or high reward category.

5.2.3 Design and Procedure

The experiment always began at 13:30 pm (see Figure 5.1), at which time the sleep log (see appendix Questionnaire A.3) – filled over the preceding three days – was checked by the experimenter. The sleep log asked for habitual bed, waking and rising times as well as for the occurrence of day naps and the ingestion of alcohol. Feelings of tiredness were also measured over several time points across the three days. Participants were instructed to maintain a normal sleep/wake pattern during the days before the experiment. At 13.45 pm the electrode setup began and the Handedness questionnaire as well as the Epworth and Stanford Sleepiness Scales were filled out (see 3.2.3 and appendix Questionnaire A.1 and Questionnaire A.2) There were six different time points for the Stanford Sleepiness Scale (SSS) questionnaire, SSS1: before learning;

SSS2: after learning SSS3: after pretest; SSS4: after napping; SSS5: before posttest and SSS6: at the end of the experiment.

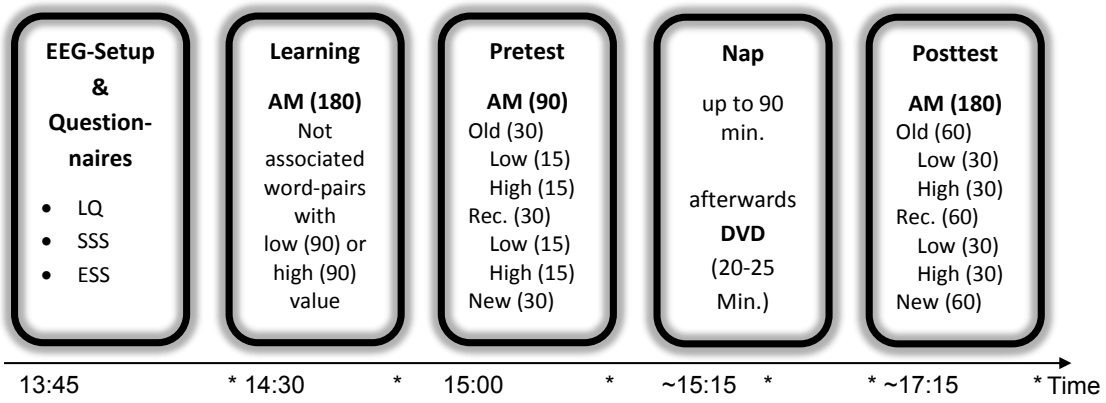

Figure 5.1. Study design of experiment two.

Overview and timeline of the experimental procedure: The study phase consisted of 180 word-pairs to be learnt; half of which were associated with high and the other half with low reward cues. For the pretest 90 word-pairs (30 in each category) were tested. The posttest was double the size of the pretest. The asterisks mark all measured time points of the Stanford Sleepiness Scale.

The memory task was programmed using E-Prime 2.0 (Psychology Software Tools, E-Studio 2.0.8.90). Participants sat in front of the monitor at a viewing distance of about 65 cm. Stimuli were presented in black on a grey background (maximal horizontal visual angle ≈ 5.7°). After a fixation cross (500 ms), reward symbols were shown for 1000 ms. Reward symbols were either € or €€€, the latter depicting the high- and the former the low-reward upcoming stimuli (see Figure 5.2). Participants did not know the exact value of either reward type (which was 0.20 € for high- and 0.02 € for low-reward correct answers) but were informed that the maximum additional reward they could earn was 20 €, if they recognized all high-reward stimuli correctly at pre- and posttest.[6] Word-pairs were presented slightly below and above central vision at both study and test (vertical visual angle ≈ 4°). The presentation time of all word-pairs at study was 5000 ms. Participants were instructed to memorize items for a later memory test by imagining both items together in one picture. The study list with 180 word-pairs was divided into six blocks. There were self-paced breaks in-between blocks. Stimuli

[6] It was made clear to the participants that low-reward stimuli contributed very little towards the additional 20 €.

were presented in random order with an interval of 550 ms (of which 500 ms was a fixation cross). The duration of the study phase was approximately 26 minutes.

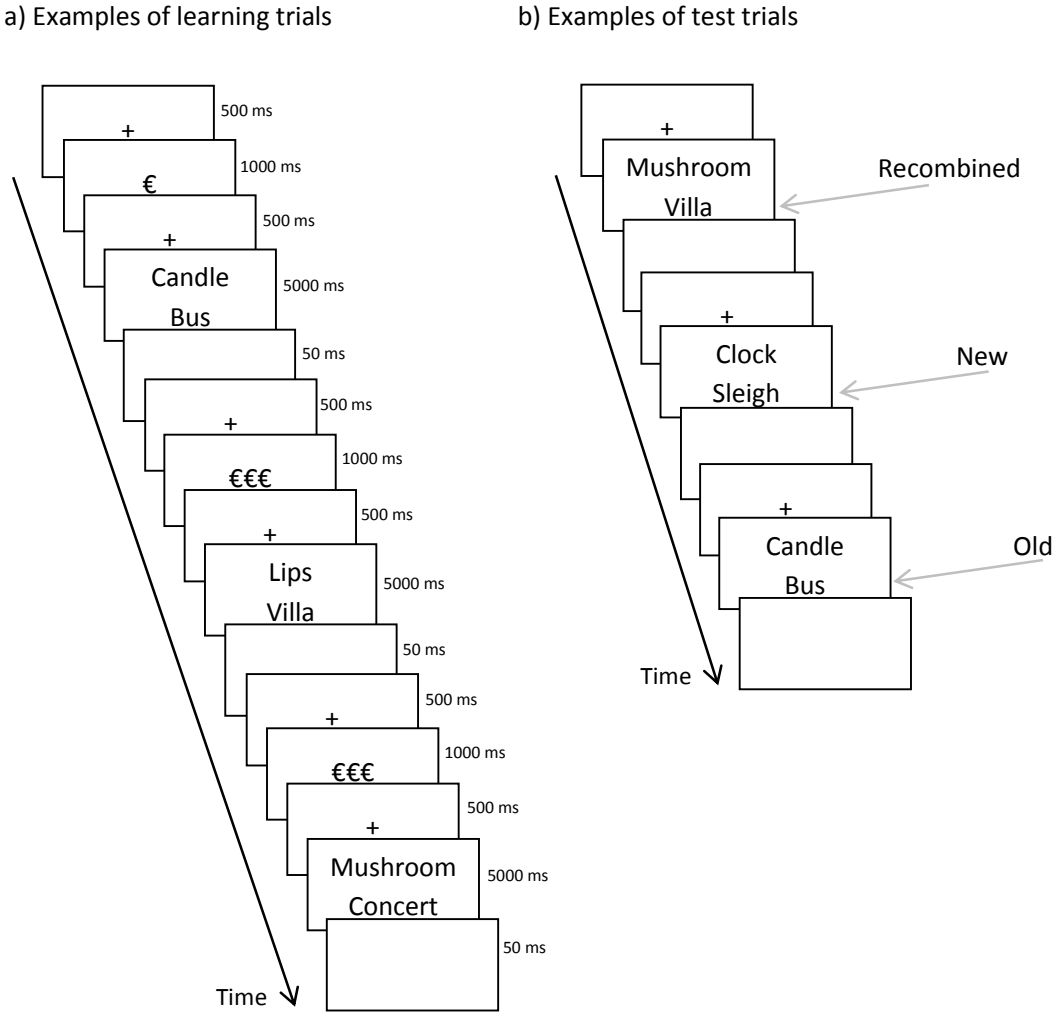

Figure 5.2. Examples of learning (a) and test trials (b) are presented.

(a) The left side of the figure presents firstly a low-reward trial ("€" shown before onset of word-pair). For a high-reward trial "€€€" was shown before the onset of a word-pair (presentation of either € or €€€ as well as old and recombined categories was at random). Presentation times for fixation cross (500 ms), cue (1000 ms), stimuli (5000 ms) and blank slide (50 ms) are shown. (b) The right side presents test trials for each answer category (old, new, and recombined) and presentation times for fixation cross (500 ms), stimuli (1000 ms) and response window (2000 ms). As participants were allowed to answer already at stimulus presentation, the total response time comprised 3000 ms.

5.2.4 Data acquisition and processing

Electroencephalogram (EEG)

EEG was recorded with BrainVision Recorder Version 1.20 (Brain Products) throughout the entire experiment. In total, 32 Ag/AgCl electrodes were used according

to the extended 10-20 system, including electrodes which were located above and below the right eye and outside the outer canthi of both eyes in order to assess electro-ocular activity. Data were recorded with amplifier band pass filter settings from DC to 100 Hz and a Notch-filter at 50 Hz. The sampling rate was 500 Hz for all study and test phases. All electrodes were recorded referenced to the left mastoid electrode and re-referenced to the average of the left and right mastoid (offline). Electrode impedances were kept below 5 kΩ. EEG was also recorded at 32 standard locations for polysomnographic data acquisition during the nap; but with a sampling rate of 1000 Hz and with the inclusion of 2 electrodes at the chin for electromyographic recordings.

Event-Related Potentials

Data processing was conducted offline with EEProbe (ANT Software) for ERP analysis of the study phase and posttest. A digital 0.2-30 Hz band-pass filter was first applied. Individual epochs of 1100 ms were then created, including a 100 ms baseline before stimuli onset (encoding: reward cue/word-pair; retrieval: word-pair). Eye-movements and blinks were corrected with a linear regression algorithm (Gratton et al., 1983). After this and the rejection of other trials showing artifacts (whenever the standard deviation in a 200 ms time interval exceeded 25 microvolt at one of the EOG channels), the remaining trials were averaged and individual averages were only used for analyzing ERPs when they contained a minimum of 13 artifact-free trials (Addante, Ranganath, & Yonelinas, 2012; Gruber & Otten, 2010). A 12-Hz low pass filter was applied for illustration purposes only.

Sleep stage scoring

Preprocessing of the sleep data was conducted using BrainVision Analyzer (2.0, Brain Products). Each 30 second epoch of sleep was scored visually into rapid-eye-movement (REM)-sleep or non-REM (NREM) sleep stages 1, 2, 3 or 4 according to standard criteria (A. Rechtschaffen & Kales, 1968). Slow-wave-sleep was calculated as the sum of sleep stages 3 and 4. The time in minutes for each sleep stage, the total sleep time, the sleep onset latency and the percentage of sleep time in each stage with reference to total sleep time (TST) were determined.

Sleep spindle analysis

Sleep spindles were detected using an adaption of the algorithm originally provided by Ferrarelli et al., (2007) (see also Cox et al., 2012). In short, the envelope of the individual sleep EEG signal was computed using the Hilbert transform and its resulting absolute values. Unique thresholds for spindle detection were used for each participant. These were derived by calculating the mean plus two SD (lower threshold) and the mean plus four SD (higher threshold) of the participant's filtered EEG signal. The average envelope amplitude was examined for spindle-comprising sleep stages (2, 3, and 4).[7] To classify a spindle, two criteria had to be fulfilled:

i) the duration between the points at which the signal fell above and below the lower threshold needed to be at least 500 ms and

ii) the signal also had to cross the upper threshold within this 500 ms time window (Ferrarelli et al., 2007).

Spindle density (SpD) at electrode Fz was calculated for NREM (S2+SWS) sleep by dividing the number of spindles by minutes of NREM (S2+SWS) sleep.

5.2.5 Data Analysis

For the behavioral data, analyses of variance (ANOVA) with factors of reward (high/low), time (pretest/posttest) and item-type (item/associative) were used. An old/new discrimination Pr index (PrI-score) was calculated by subtracting false alarms to new pairs from the hit rate for old pairs ($PrI = hits_{old} - FA_{new}$) and aimed to provide a measure of item memory. Of principal interest was the ability of participants to distinguish between old and recombined pairs, so an associative PrA-score was computed (Bader et al., 2010; Kriukova et al., 2013) to reflect associative memory. This was calculated by subtracting the proportion of recombined pairs incorrectly classified as old (false alarms to recombined) from the hit rate for old pairs ($PrA = hits_{old} - FA_{rec}$). For the reaction time data, ANOVAs with the factors time (pretest/posttest) and item condition ($old_{high}/old_{low}/new/rec_{high}/rec_{low}$) were conducted for correct answers.

ERPs were derived from the study phase and posttest EEG data. ERPs at study were investigated for the cue and for the stimulus interval. For the cue interval, ERPs

[7] Note: Compared to experiment one the spindle algorithm was slightly adapted in experiment two, in that the average was only computed for these NREM sleep stages that compromise spindles (i.e. without stage 1) (Cox et al., 2012).

elicited by high and low reward signs were contrasted with an ANOVA with the factors reward type (high, low), laterality (left, midline, right), location (frontal, central, parietal) and time window (early, middle, late) comparable to Gruber and Otten (2010). For the stimulus interval, subsequent memory effects (contrast: hits vs. misses) were examined for each reward condition. Due to low trial numbers in both misses-conditions, only a subset of $n = 8$ could enter the SME- analysis. An ANOVA with factors item-type (hits, misses), laterality (left, midline, right), location (frontal, central, parietal) and time window (300-500 ms, 500-700 ms, 700-900 ms) was conducted for each reward condition separately. Only main effects and interactions that involve the factor item-type are reported because these indicate that a hits/misses difference is present or varies with electrode location.

ERPs in the posttest were limited to correct responses to new (CR), old high-rewarded (hit-high) and old low-rewarded (hit-low) items. Recombined pairs were not included in the ERP analyses (see also chapter 3.2.5). To create a subject average, at least 13 artifact-free trials were needed in each of the categories. On third of the participants needed to be excluded for the ERP analysis due to too few trials in the old low-rewarded condition (range 6-10) but were retained for all other analyses. This led to $n = 14$ for the posttest-ERP-analysis.[8] Mean amplitudes in an early (300-500 ms) and a late (500-700 ms) time window were subjected to ANOVAs with factors of item condition (hit-high/hit-low/CR) and laterality (left/midline/right). ANOVAs included amplitudes from three frontal (F3, Fz, F4) electrodes for the early time interval and three parietal (P3, Pz, P4) electrodes for the late time window. These sites and time points correspond to the standard specifications of the early frontal and late parietal putative correlates of familiarity and recollection (Rugg & Curran, 2007). Only main effects and interactions that involve the factor item condition are reported because these indicate that an old/new difference is present or varies with reward type or electrode location. Subsidiary analyses were performed using t-tests which were corrected for multiple comparisons applying Holm's sequential Bonferroni correction (Holm, 1979). Only contrasts are reported that survived correction, except where noted. For all analyses, the significance level was set to $\alpha = 0.05$. Where necessary, analyses included

[8] Note: Behaviorally, the only differences in correct answers at posttest between the subgroup of $n = 14$ and the whole sample was found in the old low-rewarded condition. The subgroup of $n = 14$ had a better hit rate for old low-rewarded items than the whole sample (subgroup: 0.68 ± 0.11; whole sample: 0.55 ± 0.22; $p < .05$) which explains that the subgroup could render sufficient trials for the ERP-analysis for the old low-rewarded category.

Greenhouse-Geisser corrections for nonsphericity with corrected p-values and uncorrected degrees of freedom (Greenhouse & Geisser, 1959).

5.3 Results

5.3.1 Behavioral data

Figure 5.3 shows the mean PrI- (a) and PrA-scores (b) for pre- and posttest separated by reward. To test the hypothesis that there will be a smaller decrease in memory performance from pre- to posttest for the high-rewarded compared to the low-rewarded word-pairs, a three-way ANOVA (with factors reward, item-type and time) was conducted. Main effects of time ($F(1,20) = 18.86$, $p < .001$), item-type ($F(1,20) = 86.05$, $p < .001$) and reward ($F(1,20) = 5.29$, $p < .05$) and a marginally significant reward with time interaction ($F(1,20) = 4.26$, $p = .052$) were revealed. To deconstruct the interaction, Bonferroni-corrected ($p = .0125$) follow-up tests were conducted, collapsed across item-type. At pretest, there was no significant reward effect ($p = .447$) whereas this was significant at posttest ($t(20) = 3.413$, $p = .003$). The effect of time on performance was significant for low ($t(20) = 6.099$, $p < .001$) but not high-reward discrimination ($p = .188$).

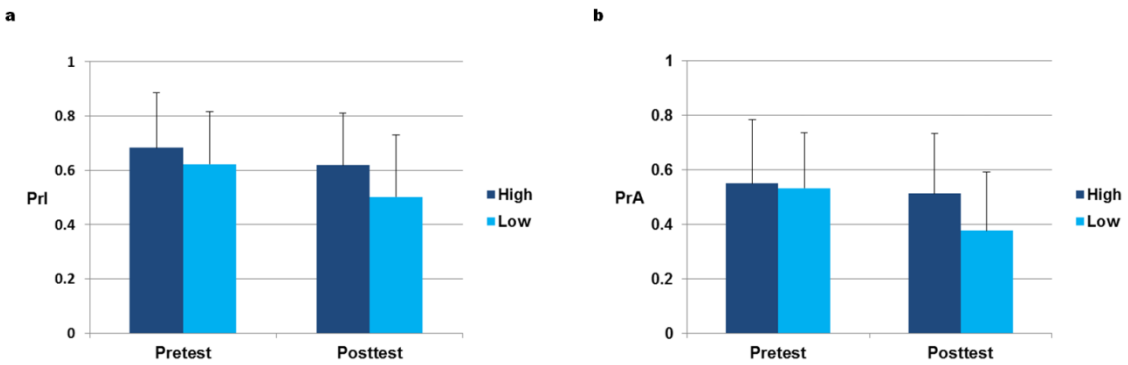

Figure 5.3. Behavioral memory performance.

(a) PrI-scores (hits-FA_{new}) and (b) PrA-scores (hits-FA_{rec}) are shown for pre- and posttest. Error bars show one standard deviation.

For an overview, Table 5.1 shows the hit and FA rates as well as reaction times for pre- and posttest for each item- and reward condition. As the discrimination indices associated with item and associative memory (PrI and PrA) are derived from the same test phase and are therefore not independent from each other (both scores are based on correct judgments to old items and differ only in their estimation of false alarms), a post-hoc analysis using percentage of correct answers in each old/recombined condition were conducted. As the interest was now to disentangle whether there might be a differentiation between old items, which can be judged based on familiarity and recollection, and recombined items, which rely stronger on recollection, ANOVAs were separately conducted in each reward condition for factors hit rate (old vs. recombined) and time (baseline/posttest).

The ANOVA within the high reward condition, solely revealed a significant main effect of hit rate ($F(1,20) = 7.66$, $p < .05$). Hit rates to old pairs were higher than to recombined pairs ($p = .05$). An ANOVA within the low reward condition revealed a significant main effect of time ($F(1,20) = 25.61$, $p < .001$). Hit rates to both old and recombined pairs were lower at posttest compared to pre-sleep ($p < .05$). High reward thus led to a preservation of both types of memory over sleep (no main effect of time) whereas low reward led to a similar decrease for both types of memory.

Table 5.1: Hit rates (%), FA rates (%) and reaction times (ms) for pre- and posttest.

		Pretest			Posttest		
		Hit rate (SD)	**FA rate* (SD)**	**RT (SD)**	**Hit rate (SD)**	**FA rate* (SD)**	**RT (SD)**
Old	**High**	.71 (.19)	-	1486 (204)	.66 (.17)	-	1558 (181)
	Low	.65 (.19)	-	1509 (202)	.55 (.22)	-	1588 (171)
Rec.	**High**	.61 (.19)	.16 (.11)	1832 (268)	.58 (.19)	.15 (.12)	1873 (253)
	Low	.60 (.20)	.12 (.12)	1865 (273)	.51 (.16)	.17 (.14)	1852 (254)
New		.75 (.20)	.03 (.04)	1681 (202)	.65 (.17)	.05 (.07)	1720 (230)

*FA rate: old answers to new or recombined word-pairs; Rec.: recombined pairs

For reaction times (RTs), an ANOVA with factors time (2) and item condition (5) on correctly responded to items, revealed only a main effect of item condition

($F(4,80) = 49.19$, $p < .001$). Follow-up analyses revealed no difference in response times for high vs. low rewarded pairs within either the old or recombined categories (all $p > .23$). Participants responded faster to correct old responses than correct rejections and recombined pairs (all $p < .01$) as well as faster to correct rejections than recombined pairs (all $p < .01$) irrespective of reward category.

Table 5.2: Control measures experiment two.

Parameter	**Mean (SD)**
Epworth Sleepiness Scale (ESS)	7.19 (2.91)
TST night before experiment	7.26 (0.97)
TST average across 3 nights	7.48 (1.17)
Wake-up time experimental morning (hh:mm)	7:57 (1:26)
SSS1: before learning	1.90 (0.44)
SSS2: after learning	2.90 (0.89)
SSS3: after pretest	2.57 (0.93)
SSS4: after napping	2.90 (0.77)
SSS5: before posttest	2.14 (0.85)
SSS6: end of the experiment	1.38 (0.50)

TST: total sleep time (in hours); SSS1-6: Stanford Sleepiness Scale time points 1-6

For an overview of control measures see Table 5.2. To explore whether there was an influence of sleepiness on memory performance at pre- and posttest, the subjective feeling of sleepiness (as measured with the Stanford Sleepiness Scale; SSS) was subjected to an ANOVA for the six measured time points. A main effect of sleepiness over time was revealed ($F(5,100) = 15.31$, $p < .001$). Participants felt most awake before (SSS1: 1.90 ± 0.44) and after the experiment (SSS6: 1.38 ± 0.5) as well as before the second test (SSS5: 2.14 ± 0.85) and remained relaxed wakeful in-between (SSS2: 2.90 ± 0.89; SSS3: 2.57 ± 0.93; SSS4: 2.90 ± 0.77). Participants felt more awake before the post (SSS5) than the pretest (SSS2) ($p = .012$, uncorrected). This latter effect argues against the possibility that sleepiness accounts for the decrement in memory performance from pre- to post-sleep.

5.3.2 Sleep data

Polysomnographic data

A summary of sleep parameters is shown in Table 5.3. The average time spent in sleep was about 71 minutes, spent mostly in stage 2 (S2) sleep (43.56 %). Participants showed on average about 15.6 minutes of SWS (22.52 %) and about 3 minutes of REM sleep (3.79 %). Most participants showed SWS (n = 18) but only one third reached REM sleep (n = 7) which accounts for the large variability of these measures.

Table 5.3: Sleep parameters experiment two.

	Minutes	(SD)	% of TST	(SD)
SL	14.83	(12.22)		
TST	70.64	(15.83)		
Stage 1 (S1)	8.14	(4.4)	11.56	(5.93)
Stage 2 (S2)	31.52	(13.51)	43.56	(12.68)
Stage 3 (S3)	10.36	(7.83)	15.04	(11.61)
Stage 4 (S4)	5.24	(6.58)	7.48	(9.45)
SWS (S3+S4)	15.6	(12.14)	22.52	(17.99)
REM	3.02	(4.92)	3.79	(6.39)

SL: latency until sleep onset; TST: total sleep time; SWS: slow-wave-sleep; REM: rapid-eye-movement

Sleep spindle data

Table 5.4: Sleep spindle correlations (Fz) with PrI/PrA scores at posttest.

Low reward		High reward	
PrI	**PrA**	**PrI**	**PrA**
r=0.36 (p=.11)	r=0.3 (p=.19)	r=0.54 (p<.05)	r=0.52 (p<.05)
-	-	r=0.43 (p=.06)*	r=0.43 (p=.06)*

* Outcomes of partial correlation analyses with pretest performance as control variable

To test the prediction outlined in the introduction, correlations were calculated between SpD at Fz during NREM sleep (mean spindle density at Fz was 1.01, SD: 0.18) and Pr-scores for high-reward and low-reward pairs. As presented in Table 5.4

significant correlations were obtained between PrA_{high}-score at posttest and SpD in NREM sleep as well as between PrI_{high}-score at posttest and SpD in NREM sleep (Figure 5.4). The corresponding correlations between SpD and PrA_{high}-score/PrI_{high}-score at pretest were not significant (p-values > .10), neither were there any significant correlations between SpD and PrA or PrI measures for low reward trials at pre- or posttest (p-values > .10). A partial correlation analysis revealed that the correlations between SpD and PrA_{high}-/PrI_{high}-scores at posttest were still marginally significant when pretest performance was controlled.

In previous studies of this kind (Gais et al., 2002) as well as in experiment one of the present thesis, correlations between spindle density and overall memory performance at both pre- and posttest have been reported, and this was also tested in the current data. SpD at Fz during NREM correlated significantly with overall memory performance (% correct responses for all word-pairs (old and recombined pairs in the low and high reward condition plus new pairs)) both before and after sleep (pretest: $r = 0.44$, $p < .05$; posttest: $r = 0.53$, $p < .05$, Figure 5.5). A partial correlation analysis (with pretest overall memory performance as covariate) revealed that the correlation between posttest overall memory performance and SpD during NREM is no longer significant ($r = 0.34$, $p = .14$) when pretest performance is controlled for.

Taken together, the current data replicate previous findings that have shown that overall learning is related to NREM spindle density, but in addition reveal a specific correlation between NREM spindle density during a nap and memory performance thereafter, which is unique to items tagged as motivationally salient during learning.

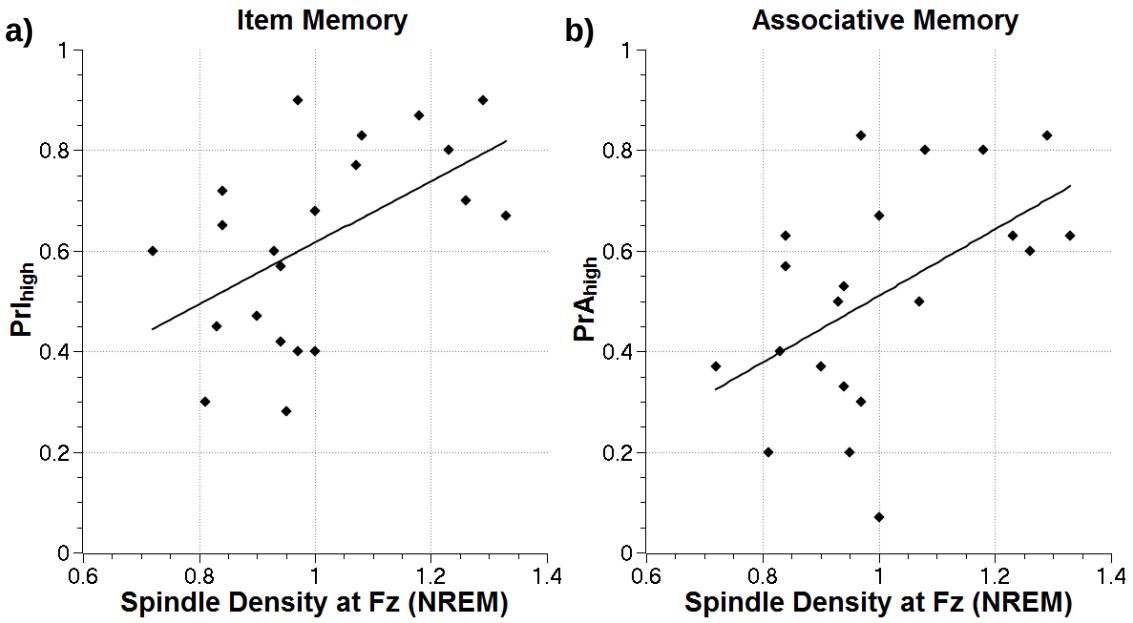

Figure 5.4. Correlation data is shown for spindle density and memory performance for high rewarded word-pairs.

(a) Relationship between PrI_{high} scores (hits to old high rewarded pairs minus false alarms to new pairs) at posttest and spindle density per minute at electrode Fz during NREM sleep. (b) Relationship between PrA_{high} scores (hits to old high rewarded pairs minus false alarms to recombined pairs) at posttest and spindle density per minute at electrode Fz during NREM sleep.

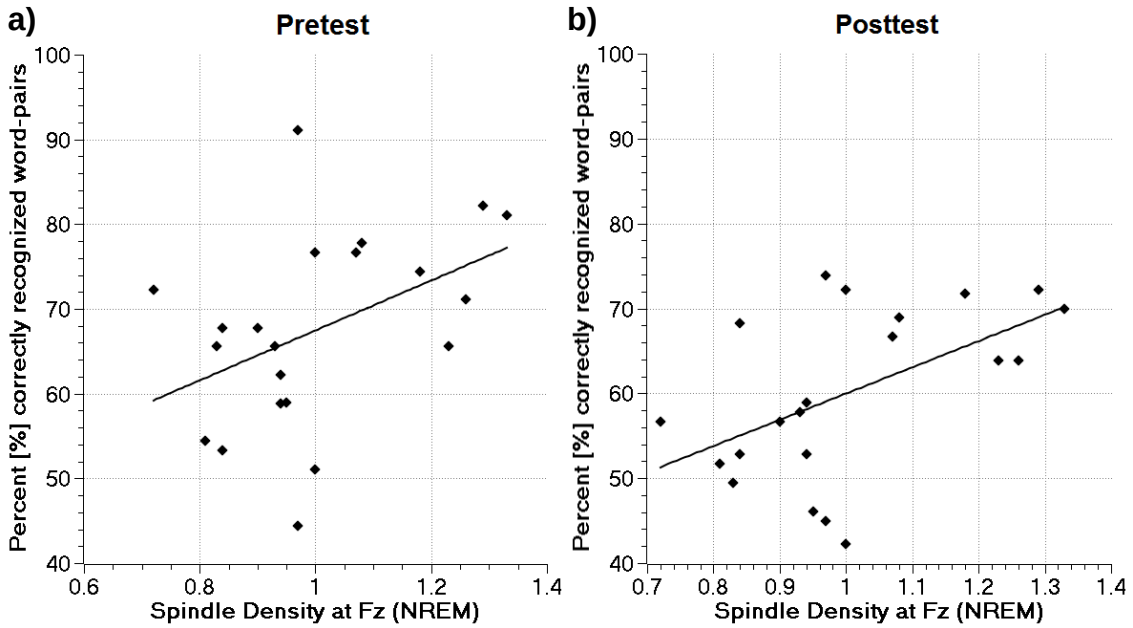

Figure 5.5. Correlation data is shown for spindle density and general pre- and post-sleep memory performance.

(a) Relationship between general memory performance at pretest and spindle density per minute at electrode Fz during NREM sleep. (b) Relationship between general memory performance at posttest and spindle density per minute at electrode Fz during NREM sleep.

5.3.3 Electrophysiological data

ERPs at encoding

Several studies could show that the neural activity before the occurrence of the to-be-learnt stimuli is important in determining whether the stimuli will be remembered or forgotten (Adcock et al., 2006; Gruber & Otten, 2010; Otten et al., 2006; Otten, Quayle, & Puvaneswaran, 2010; Park & Rugg, 2010). Neural activity elicited by high and low reward inducing cues was therefore examined at encoding; in a first step independent of later memory performance (Gruber & Otten, 2010) and in a second step, subsequent memory effects were analyzed.

High vs. low reward cues

Figure 5.6 shows the neural activity during the cue interval elicited by high and low reward-promising signs, irrespective of memory performance at the subsequent recognition tests. High-reward promising cues gave rise to more positive going ERPs from around 200 ms until approximately 800 ms (Figure 5.6a) which seems to be most pronounced for central and parietal sites (Figure 5.6b). According to time intervals used by Gruber and Otten (2010), mean amplitudes were measured in an early (200-300 ms), middle (300-600 ms) and late (600-1000 ms) time interval. The overall ANOVA with the factors reward type (high, low), laterality (left, midline, right), location (frontal, central, parietal) and time window (early, middle, late) revealed significant main effects of reward type ($F(1,20) = 9.75$, $p < .01$), location ($F(1,20) = 7.88$, $p < .01$) and time window ($F(1,20) = 31.77$, $p < .001$), significant two-way interactions between reward and laterality ($F(2,40) = 3.68$, $p < .05$) and reward type and time window ($F(2,40) = 9.87$, $p < .001$), a significant three-way interaction between reward, laterality and time window ($F(4,80) = 6.29$, $p < .01$) and as well as a four-way interaction between reward, laterality, location and time window ($F(8,160) = 2.62$, $p < .05$). To dissolve the interactions, further ANOVAs were conducted within each time window.

200-300 ms

The ANOVA with factors reward type (high, low), laterality (left, midline, right), location (frontal, central, parietal) in the early time window revealed a main

effect of reward ($F(1,20) = 20.88$, $p < .001$). Cues promising high rewards elicited more positive amplitudes compared to low-reward associated cues, however, no interactions between reward type and laterality or location were found (all $p > .28$).

300-600 ms

The ANOVA with factors reward type (high, low), laterality (left, midline, right), location (frontal, central, parietal) in the middle time window revealed significant main effects of reward ($F(1,20) = 11.97$, $p < .01$) and laterality ($F(1,20) = 5.14$, $p = .01$), as well as a significant two-way interaction between reward and laterality ($F(2,40) = 8.01$, $p = .001$), a marginal significant reward and location interaction ($F(2,40) = 3.63$, $p = .064$) and a three-way interaction of reward, laterality and location ($F(4,80) = 4.37$, $p < .05$). In order to dissolve the interactions involving the factors laterality and location, follow-up t-tests for reward type were performed for each electrode site. After correction ($p < .0055$), significant effects of reward type were obtained for electrodes Cz ($p = .002$), C4 ($p = .005$), Pz ($p = .001$), P3 ($p = .002$) and P4 ($p < .001$). Reward effects were thus most pronounced over central and parietal sites in the middle time window.

600-1000 ms

The ANOVA with factors reward type (high, low), laterality (left, midline, right), location (frontal, central, parietal) in the late time window revealed significant main effects of laterality ($F(1,20) = 4.5$, $p < .05$) and location ($F(1,20) = 64.6$, $p < .001$) and a significant two-way interaction of reward and laterality ($F(2,40) = 5.08$, $p < .05$). The interaction seems to imply a right-lateralized reward effect, however, follow-up tests did not show any significant reward differences (all $p > .2$).

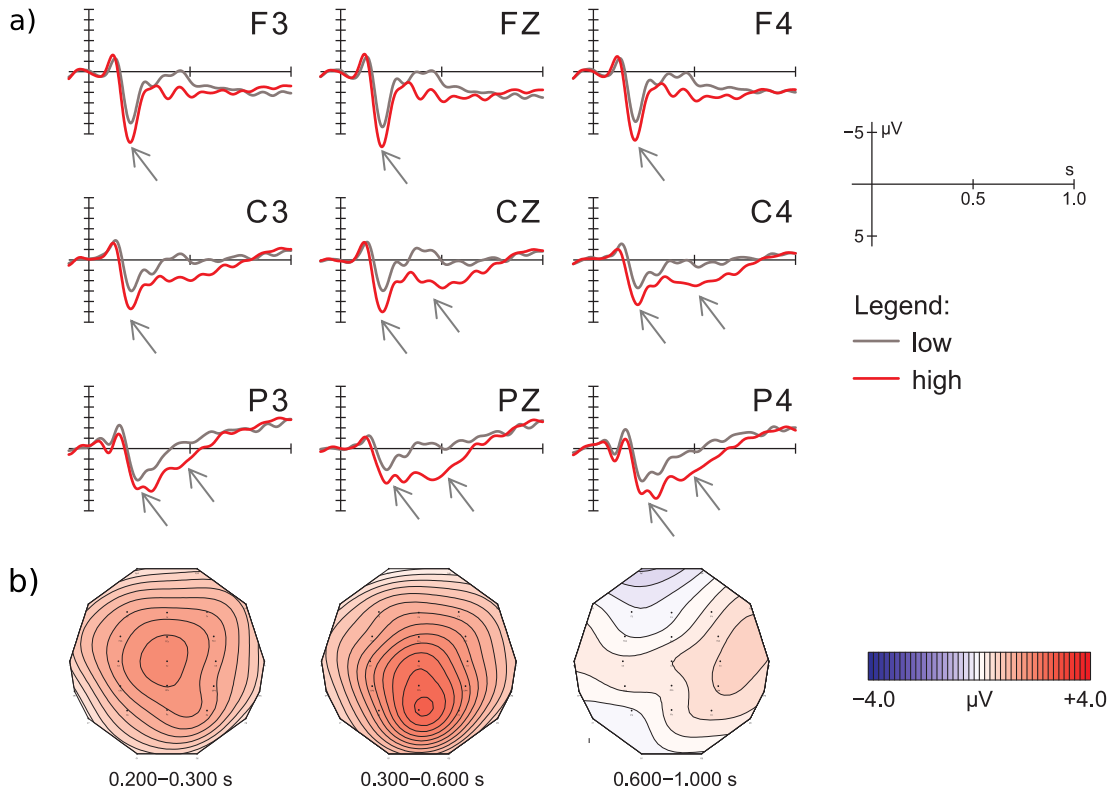

Figure 5.6. Grand average ERPs (a) and topographical maps (b) for the high/low reward comparison at encoding.

(a) Grand average ERPs elicited by high and low reward cues at F3, Fz and F4, C3, Cz and C4, and P3, Pz and P4. The arrows highlight significant differences between ERPs to high and low reward cues. The y-axis denotes the onset of the cue (€ vs. €€€) and negative polarity is plotted upwards. (b) Topographical maps show the contrast high minus low in three time windows (200-300 ms, 300-600 ms, 600-1000 ms).

Subsequent memory effects

Previously, it was shown that subsequent memory effects (SMEs) are only evident in high-reward but not low-reward conditions (Gruber & Otten, 2010). It was, therefore, predicted that only high-reward associated items will show a SME. However, due to low trial numbers in both misses-conditions, only a subset of $n = 8$ could enter the SME-analysis. Figure 5.7a shows ERPs elicited by hits and misses for the high reward condition and topographical contrasts for hits minus misses in three time windows (300-500 ms, 500-700 ms, 700-900 ms). Figure 5.7b shows ERPs elicited by hits and misses for the low reward condition and topographical contrasts for hits minus misses in the same time windows. In the high reward condition, it seems that hits are more positive going than misses from approximately 400 ms until 800 ms at frontal sites, from around 500-700 ms at central sites and do not differ at parietal sites. The pattern for the low reward condition looks considerably different. First, differences between hits and misses i.e. that hits are more positive going than misses are very dominant at the central to right hemisphere, and seem to be greatest at central and parietal electrodes. ANOVAs with factors item-type (hits, misses), laterality (left, midline, right), location (frontal, central, parietal) and time window (300-500 ms, 500-700 ms, 700-900 ms) were conducted separately for each reward condition.

In the high reward condition, no subsequent memory effect was present (main effect of item-type; $p = .56$), but significant item-type and location ($F(2,14) = 7.1$, $p < .05$) and item-type and time window interactions ($F(2,14) = 4.05$, $p = .05$) were revealed. These interactions indicate greater differences between hits and misses (although only marginally significant) at frontal sites in the middle time interval (500-700 ms; $F(1,7) = 4.06$, $p = .08$).

The low reward condition also showed a non-significant main effect of item-type ($p = .1$) but a significant two-way interaction between item-type and laterality ($F(2,14) = 8.8$, $p < .01$). Follow-up analyses (with factors item-type, location and time window) revealed no SME on left and central electrodes (left: $F(1,7) = 0.55$, $p = .48$; central: $F(1,7) = 3.41$, $p = .11$) but a significant main effect of item-type at right electrode sites ($F(1,7) = 8.21$, $p < .05$). Thus in the low reward condition, a subsequent memory effect was present at right electrode sites which did not vary with time or location.

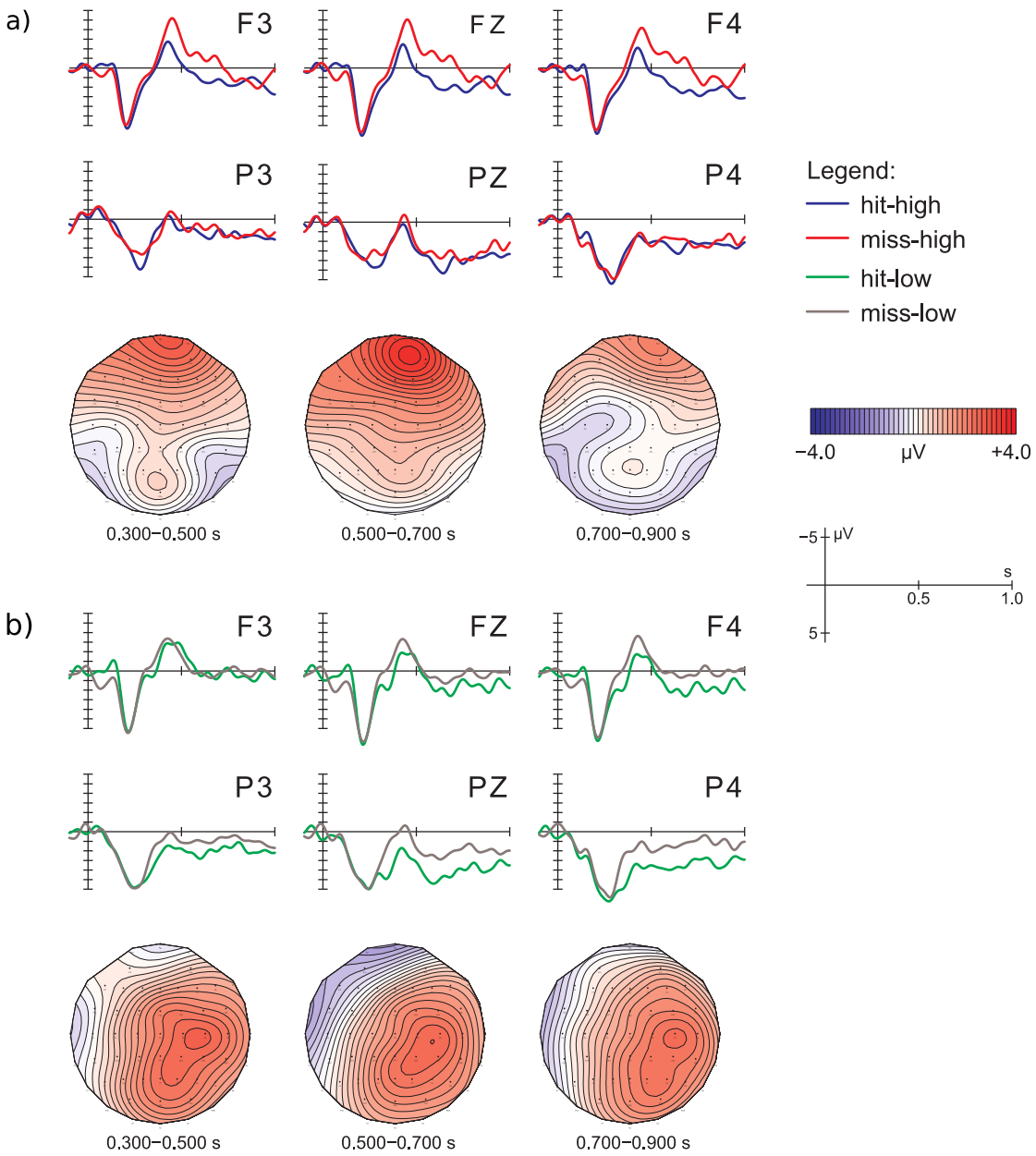

Figure 5.7. Grand average ERPs (a) and topographical maps (b) for the SMEs in the high and low reward conditions.

(a) Grand average ERPs elicited by high and low reward cues at F3, Fz and F4, C3, and P3, Pz and P4. The y-axis denotes the onset of the stimuli (word-pair) and negative polarity is plotted upwards. (b) Topographical maps show the contrast hits minus misses in three time windows (300-500 ms, 500-700 ms, 700-900 ms).

ERPs at posttest

It was questioned whether a presumably differential reward-dependent processing of information during sleep would also be reflected in ERP correlates of familiarity and recollection post-sleep. A preferential processing of high-rewarded associations was expected to be reflected in a larger ERP correlate of recollection for high-rewarded compared to low-rewarded hits.

Old/new effects

Figure 5.8 shows the ERPs elicited by high-hits, low-hits and correct rejections of new pairs (Figure 5.8a) as well as topographical maps contrasting high-hits with correct rejections, low-hits with correct rejections and high-hits with low-hits (Figure 5.8b).

Descriptively, it seems that high-hits differ from low-hits and correct rejections such that high-hits are more positive-going in an early time interval at frontal sites. However, an ANOVA with the factor of item condition (hit-high/hit-low/CR) and laterality (F3, Fz, F4) for the early time window revealed no main effect ($p > .27$) or interaction with item condition ($p > .42$). Across all three parietal recording sites, the ERP waveforms elicited by correct responses to word-pairs associated with high-reward cues at study (high-hits) exhibit more positive going waveforms than both hits in the low reward condition (low-hits) and correct rejections. This pattern was tested with a two-way repeated-measure ANOVA with factors item condition (3 levels) and electrode (P3, Pz, P4) for the mean amplitude measures in the 500 to 700 ms time interval. A main effect of item condition ($F(2,26) = 4.78$, $p < .05$) was revealed. Follow-up t-tests (uncorrected) revealed significant differences between hit-high and both correct rejections ($p < .05$) and hit-low ($p < .05$) but no differences between hit-low and correct rejections ($p = .24$). ERPs elicited by hits to high-rewarded items were more positive going than ERPs to correct rejected new items and to hits which were associated with low reward.

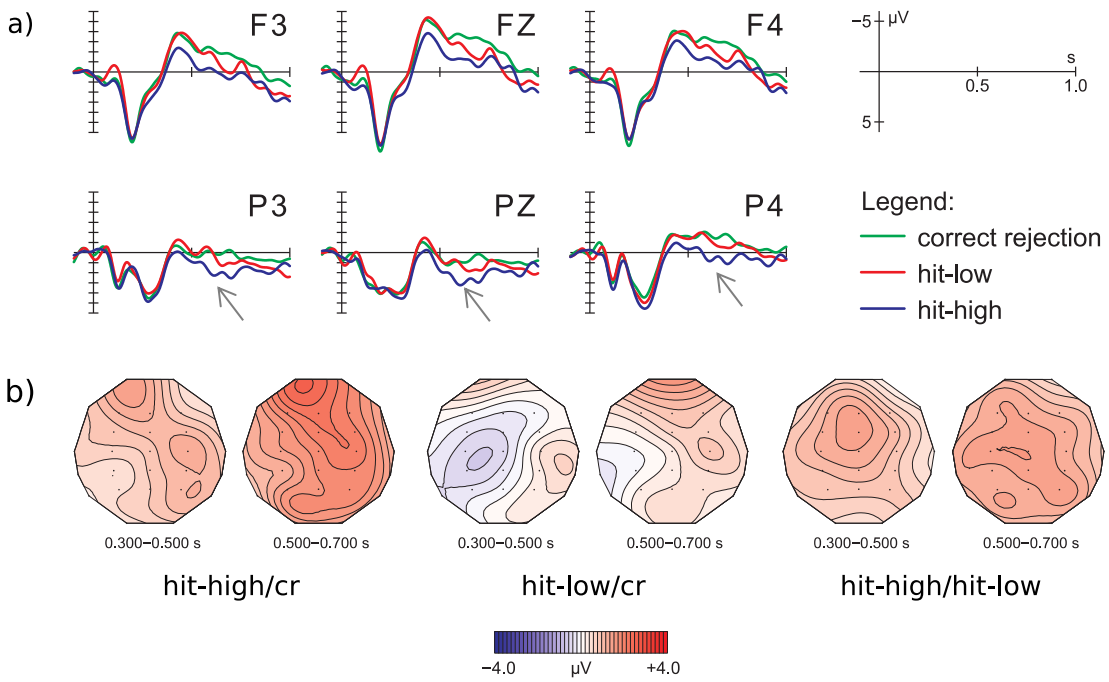

Figure 5.8. Grand average ERPs (a) and topographical maps (b) for the old (high/low)/new comparison.

(a) Grand average ERPs elicited by hits associated with high and low reward as well as correct rejections at F3, Fz and F4, C3, Cz and C4, and P3, Pz and P4. The arrows highlight different recollection effects for hit-high compared to both hit-low and correct rejections. The y-axis denotes the onset of the stimuli and negative polarity is plotted upwards. (b) Topographical maps show the contrast hit-high minus correct rejection (left), hit-low minus correct rejection (middle) and hit-high minus hit-low (right) in two time windows (300-500 ms, 500-700 ms).

Summed up, the ERP analyses on the one hand showed expected differential processing of reward cues at study which were most pronounced at central-parietal sites in the early and middle time interval. Unexpectedly, no subsequent memory effects could be revealed in the high reward condition which might be due to the rather low sample size. On the other hand, in the low reward condition a subsequent memory effect was present at right electrode sites. As assumed, post-sleep ERP old/new effects were shown to reflect larger ERP correlates of recollection for high-rewarded stimuli compared to new and low-rewarded.

5.3.4 Post-hoc: ERPs in the cue interval and spindle density

It was of interest to determine whether correlations between ERPs as a neural marker of cognitive processes at encoding and spindle density as a marker of sleep-dependent memory consolidation could be revealed. Spindle density was shown to be related to overall learning pre- and post-sleep; and additionally selectively to item and associative memory performance in the high-reward condition post-sleep. Hence, it was tested whether higher neural activity at encoding (after presentation of either high or low reward cues) could be related to spindle density. It was shown before that neuronal activity after cue-presentation could predict memory performance for high rewarded stimuli, i.e. higher neural activity at encoding is associated with higher memory performance at retrieval (Gruber & Otten, 2010). In the current dataset no subsequent memory effect was revealed which is probably due to a rather small sub sample size; the ERP data elicited by low and high reward cues irrespective of memory performance was therefore used for the correlational spindle analysis. If stronger neural activity at encoding is related to tagging of information and their subsequent consolidation in sleep, a relationship between ERPs at encoding and spindle density in a following sleep episode should be evident. Correlations were calculated between ERPs in the early (200-300 ms) and middle (300-600 ms) time window were the reward effect was most pronounced for central electrodes (Fz, Cz, Pz) and SpD (NREM) at frontal sites (Fz). A marginal significant correlation was found between SpD and an ERP at Pz associated with a high-reward cue in the early time interval ($r = 0.424$, $p = .055$, Figure 5.9). This means the greater the mean amplitude at parietal sites for the high reward cue at encoding was, the more spindles were evident in NREM sleep of a following nap period.

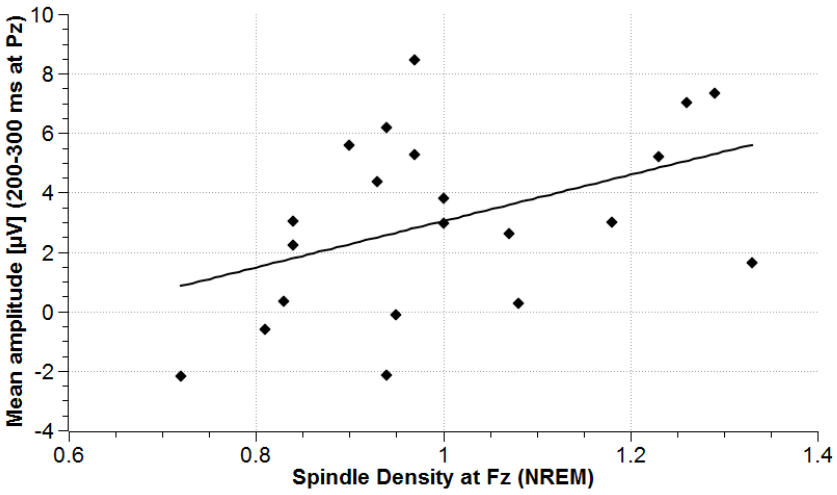

Figure 5.9. Correlation data is shown for spindle density and an ERP linked to high reward cues at encoding.

Relationship between spindle density at electrode Fz during NREM sleep and an ERP in the early time window (200-300 ms) at Pz for high reward cues.

5.4 Discussion

The second experiment investigated whether different reward cues at encoding influence associative memory performance after nap sleep. Participants' memory for associations was tested after learning a list of word-pairs both before and after taking a nap. During learning, word-pairs were either preceded by a cue indicating a high reward for correct performance at test or by a low-reward cue. There is increasing evidence that sleep should preserve memories that are tagged as relevant for the future (Fischer & Born, 2009; Oudiette et al., 2013; Saletin et al., 2011; Stickgold & Walker, 2013; Wilhelm et al., 2011). Since high reward items should be of higher motivational value and therefore be tagged at encoding for selective consolidation during sleep (Stickgold & Walker, 2013), the memory benefit was expected to be larger for high-rewarded pairs than for low-rewarded word-pairs after sleeping. This pattern was obtained: Memory performance declined to a greater extent for low rewarded than for high rewarded word-pairs after the nap.

It was also assumed sleep-related improvements in associative memory to be not only reflected in behavioral but also in ERP measures of recognition memory (C. C. Lin & Yang, 2014; Mograss et al., 2006; Mograss et al., 2008). In accordance with other studies (Vilberg et al., 2006; Wilding, 2000), the late parietal old/new effect, the

putative ERP correlate of recollection, which has been shown to co-vary with the amount of recollected information, was modulated by reward value in the present experiment. For the first time, as far as is known, ERP old/new effects were shown to reflect larger recollection effects for high-rewarded stimuli compared to low-rewarded ones post-sleep which indicates that stronger associations were created for high rewarded compared to low rewarded stimuli.

ERP data from encoding suggests that study information was differentially processed as high-reward cues led to more positive ERPs than low-reward cues. Importantly, an ERP related to the processing of high-reward cues was marginally positively correlated to spindle density at Fz in a following nap episode as it was found in a post-hoc analysis. The more positive the ERP amplitude at a parietal site in an early time interval after cue-onset was, the more spindles were found during the nap. As a correlation does not imply causal relationships, and was only marginal in the present dataset, conclusions must be drawn carefully. However, the correlation between neural (electrophysiological) activity at encoding and a sleep-specific parameter in a subsequent sleep period supports assumptions regarding the tagging (Stickgold & Walker, 2013) of important material before selective consolidation during sleep occurs. Especially, because spindle density at the same frontal electrode was also related to pre- and post-sleep overall memory performance comparable to results of the first experiment and of a study by Gais and colleagues (2002). They compared the influence of a learning experience (paired associate task) with a non-learning task - which was equivalent regarding all stimulus and task characteristics apart from the intention to learn - on sleep spindles in the following sleep episode. Sleep spindle density was found to be higher after the learning task compared to after the non-learning task, and spindle density was found to correlate with performance both before and after sleep. In the second experiment, overall memory performance both before and after napping was also related to spindle density. The findings may therefore imply that consolidation during sleep is equally likely for all memories intentionally learned before sleep. Alternatively, the observation that memory performance before and after sleep correlates with spindle density could also suggest that individual differences in memory performance predict both sleep spindle density and post-sleep memory performance (Fogel & Smith, 2011). Regardless of which account is most appropriate, the link between sleep spindles and overall memory performance reported here supports the

general claims of system consolidation theory concerning the role of spindles for memory retention (Rasch & Born, 2013).

Notably, however, a selective correlation between spindle density and high-reward memory scores at posttest was found in the current dataset as well. This relationship was not obtained for word-pairs in the low reward condition nor could the correlation between spindle density and high rewarded memories be accounted for by memory performance before sleep. This pattern supports the high relevance of sleep spindles for memory consolidation (Diekelmann & Born, 2010) and together with the behavioral data showing smaller decline for high than low reward from pre to posttest, these findings support the view that sleep enables the selective consolidation of memories from a specific learning experience. Other studies also report correlations between sleep spindles and specific memory measures post-sleep (Saletin et al., 2011; Schmidt et al., 2006). Saletin and colleagues (2011), for example, used a directed forgetting paradigm to investigate the role of explicit instructions during encoding on memory retention after sleep. It was shown that memory was selectively preserved after sleep for to-be-remembered items, and that the memory performance difference between to-be-remembered and to-be-forgotten items was correlated with sleep spindle density. The present findings thus add to the converging evidence that learning instructions, intentions or other pre-sleep learning experiences can actively modulate memory consolidation.

Reward-related differences in memory performance were observable at post- but not pretest, which does not reflect patterns reported in some studies (Oudiette et al., 2013; Saletin et al., 2011). One reason for this outcome could be because the short interval between initial study and pretest was sufficiently short that working memory processes were available during pretest and may have obviated any reward effects on episodic memory. An alternative and not necessarily mutually exclusive possibility is that dopamine-mediated reward effects generally require a delay in order to be observed (Adcock et al., 2006; Feld et al., 2014; Wittmann et al., 2005). In line with these possibilities is the observation that in sleep studies (Oudiette et al., 2013; Saletin et al., 2011) as well as in ERP studies (Gruber & Otten, 2010) which have reported reward effects at a test soon after encoding, the interval between learning and test has been longer (i.e. 15-45 minutes) than in the current study. Gruber and Otten (2010) showed memory performance to be better for high-rewarded compared to low-rewarded stimuli which was mainly based on more remember answers for high rewarded items whereas

there was no difference between low- and high rewarded words in the amount of confident old judgements.[9] The current experiment did not estimate confidence level and one could only speculate whether there might be reward-driven memory performance differences at pretest according to feelings of confidence; a next study could possibly apply ratings of confidence to be able to control for this.

Gruber and Otten (2010) further demonstrated in their study that subsequent memory effects were only evident in the high but not low reward condition. This is not replicated in the current dataset; here (i) no overall SME was present but (ii) a marginal significant SME was found at frontal sites for the high reward condition and (iii) right-lateralized SMEs were found for the low reward condition. However, several points need to be kept in mind which might explain the first outcome; (i) in the current experiment, the sample for the SME-analysis was rather small (n = 8) whereas Gruber and Otten (2010) could analyze at least 14-24 participants in their different ERP comparisons;[10] (ii) SMEs were analyzed by taking post-sleep memory performance into account in the current dataset whereas Gruber and Otten (2010) used the task performance ~15 minutes after encoding to estimate the SMEs. Hence, it could be that SMEs differ according to different tested time points (Uncapher & Rugg, 2005). Uncapher and Rugg (2005) used event-related fMRI to determine whether neural activity at encoding, i.e. SMEs, vary according to different retention intervals (30 min. vs. 48 h after encoding). Some brain regions were found to be activated for recollected vs. forgotten items independent of retention time (e. g. hippocampus) but other regions were delay-sensitive (e. g. 48 h: ventral inferior frontal gyrus; 30 min.: fusiform gyrus). The relationship between neural activity at encoding and the retention of the created memory representation could theoretically also be investigated by using ERPs; unfortunately, the current dataset does not contribute sufficient trials for such a pre-/post-sleep SME-comparison. And finally, (iii) it has been shown before, that SMEs in a recognition memory paradigm can be evident only at small time intervals or specific electrodes (Paller et al., 1988).[11] Generally, Paller and colleagues (1988) demonstrated that SMEs were greater for recall than recognition measures; this ties with the finding in the study of Gruber and Otten (2010) in which SMEs were only found for recollected

[9] Reminder: Participants had to judge words as learnt (old) or new; and they had to rate their confidence level. This was resulting in five answer-categories: 1. Remember, 2. Confident old, 3. Nonconfident old, 4. Nonconfident new, 5. Confident new.
[10] But see Sanquist and colleagues (1980) for a study showing SMEs for an even smaller sample size.
[11] This was found for a sample of n=10.

but not confident familiar answers. The current experiment used an associative memory task which should rely strongly on recollection, however, confidence level were not estimated and recollection ability was not further verified thus it is not possible to determine whether there are differences related to these factors within the hit-conditions.

While Gruber and Otten (2010) found subsequent memory effects only for high but not low rewarded stimuli, the current experiment showed a marginal significant SME at frontal sites for the high reward condition, and right-lateralized SMEs for the low reward condition. The finding of SMEs at frontal sites ties with other studies which do also show SMEs to be evident at this location in recognition memory tasks (Otten et al., 2010; Paller et al., 1987; Paller et al., 1988; Sanquist et al., 1980). However, the question arises why SMEs occur in the low reward condition with such a pronounced right-lateralization. A possible answer for the first part is that the analyzed sample only included participants who had sufficient trials in each of the conditions (high-hit; high-miss; low-hit and low-miss). As this means that post-sleep memory performance was reasonably high for low rewarded stimuli, it is tempting to speculate that these participants did both successfully process high rewarded and low rewarded items at encoding which led to SMEs in both conditions. However, this does not explain the right-lateralized vs. frontal distribution of SMEs for low respective high rewarded items. Even though ERPs only have limited spatial resolution, it could nevertheless be, that brain regions were differently activated for the encoding of stimuli in dependence of reward value (McClure, York, & Montague, 2004) which was probably also reflected in the electrophysiological measures in the present experiment.

In contrast to the first experiment (published as Studte et al. (2015)), sleep effects were not selectively related to associative memory retention. One possibility is that this is because the discrimination indices associated with item and associative memory (PrI and PrA) in the current study were derived from the same test phase. This step was taken in order to reduce overall memory load while maintaining sufficient trials to test reward effects. In the first experiment, however, two different memory tasks (single words vs. word-pairs) were employed in different test blocks to examine item and associative memory. Estimates of item and associative memory in the present dataset, therefore, are derived from the same response set which may have reduced the ability to detect dissociable effects of sleep on item and associative memory. Nonetheless, by finding larger effects of sleep on memory performance for high rewarded word-pairs the

data tally with prior reports of the beneficial effects of motivational cues on memory consolidation during sleep (Feld et al., 2014; Fischer & Born, 2009; Oudiette et al., 2013; van Dongen et al., 2012) and extend these effects to another form of reward-related learning.

In sum, the second experiment showed a differential influence of high- and low-reward associated cues on ERPs at encoding and on memory retention in that high-reward information was better retained after 90 minutes of nap sleep. Positive correlations between spindle density during NREM sleep and general memory performance pre- and post-sleep were found. Furthermore there were selective positive relationships between memory performance for highly rewarded word-pairs at posttest and spindle density during NREM sleep. Furthermore, a marginal significant correlation was found for an ERP associated with high reward at encoding and spindle density. Together with the finding of more pronounced ERP correlates of recollection for high rewarded stimuli, these findings support the notion that processes during NREM sleep may be important for preferential consolidation of motivationally salient memories (Stickgold & Walker, 2013). This may indicate that reward cues induce tags (in a top down manner) for information that ensures these items are preferentially consolidated during sleep, leading subsequently to more durable memories.

6 General Discussion

The aim of the present thesis was to investigate the effect of nap sleep on recognition memory processes as well as exploring the relationship between memory and physiological parameters occurring during sleep (e. g. sleep spindles). A second goal was to determine how memory consolidation during nap sleep could be manipulated by motivational cues during encoding prior to sleep as there is increasing evidence that sleep selectively strengthens memories that are of relevance to the future (Stickgold & Walker, 2013). Current data related to the effect of sleep on recognition memory is rather inconsistent showing sometimes benefits for overall recognition memory performance (C. C. Lin & Yang, 2014; Mograss et al., 2006; Mograss et al., 2008; U. Wagner et al., 2007) and sometimes not (Daurat et al., 2007; Drosopoulos et al., 2005; Mander et al., 2011; van der Helm et al., 2011). In the first experiment, therefore, the impact of nap sleep on recollection and familiarity was investigated and compared to a wake control group. It was assumed that only hippocampus-dependent associative memory where recollection is needed, but not hippocampus-independent item memory which can be solved by means of familiarity, will benefit from nap sleep whereas no such effect would be expected after the wake retention period. Additionally, it was examined whether sleep effects could be reflected in corresponding ERP old/new effects associated with either recollection or familiarity. It was assumed that spindle density will be related to memory performance post-sleep according to the active system consolidation hypothesis (Rasch & Born, 2013). As not only this pattern was found in the first experiment but also a relationship between baseline associative memory performance and spindle density, it was questioned whether superior learning and memory performance in an associative memory task before sleep can influence spindle density in a subsequent sleep episode.

The second experiment aimed to investigate this by using different motivational incentives at encoding in a within-subject design by using in parallel electrophysiological measures. Motivationally more relevant items which were associated with extra monetary reward, were expected to be tagged for selective consolidation during sleep compared to less relevant items (Stickgold & Walker, 2013) thereby leading to a better memory retention for high-rewarded stimuli post-sleep. The relationship between spindle density and memory performance for high vs. low

rewarded items was taken as a marker for possible selective consolidation during sleep. If a correlation between spindle density and memory performance for high but not low rewarded items could be observed, this would provide evidence for a selective role of sleep in memory consolidation.

The general discussion is organized into seven sections, firstly a short summary of the results of both experiments will be provided. The following section (6.2) aims to describe the effects of nap sleep on familiarity and recollection by discussing behavioral and electrophysiological findings. Afterwards it is discussed how motivation can modulate memory retention after sleep and associated physiological parameter occurring during sleep (6.3). The fourth section will deal with possible neurophysiological processes which might underlie sleep effects on recognition memory (6.4). Limitations of the current experiments and directions for future research will be provided in the subsequent section (6.5). Possible implications which can be derived from the experimental findings are described afterwards (6.6) before the thesis ends with an overall conclusion (6.7).

6.1 Summary

In the first experiment, participants learnt single words and word-pairs before performing two tests; an item memory test which could be solved based on familiarity and recollection and an associative memory test for which recollection was a necessity. After testing, participants were divided into two groups with one group sleeping while the other watched DVDs. After the retention period a second test on the initial learned stimuli was conducted. Memory performance for single words (item memory test) decreased for both groups whereas memory performance for the word-pairs (associative memory test) decreased for the control group but remained constant for the nap group. ERP correlates of familiarity and recollection were observed in the item memory posttest but only the later recollection-related effect was present in the associative memory test. Notably, none of the ERP old/new effects varied with group. An additional ERP analysis of hits (correct answers to old and recombined items) and incorrect answers (old items classified as recombined and recombined items classified as old) in the associative memory test for subgroups of nap and wake participants,

however, revealed group differences. ERP differences between hits and incorrect answers in the AM test which should reflect participant's ability of associative discrimination, were larger for the nap than the control group at a left parietal site in a time window corresponding to typical recollection (old/new) effects (Rugg & Curran, 2007). The behavioral interaction for the AM test (less forgetting in AM after nap sleep) was thus paralleled by corresponding changes in an ERP analysis of associative discrimination, showing group differences in recollection-associated but not familiarity-modulated ERPs. The findings therefore support earlier findings which show sleep benefits for recollection but not familiarity (Daurat et al., 2007; Drosopoulos et al., 2005; Mander et al., 2011; van der Helm et al., 2011) and extend former findings by demonstrating differential impact of sleep vs. wake on specific electrophysiological correlates linked to associative memory discrimination (Groch et al., 2013; C. C. Lin & Yang, 2014; Mograss et al., 2006; Mograss et al., 2008). Positive correlations were observed between spindle density during slow-wave-sleep and associative posttest memory performance as well as between spindle density during nREM sleep and baseline performance in the AM task. Hence, successful learning and retrieval both before and after sleep are related to spindle density during nap sleep; a finding which led to the development of the second experiment.

The second experiment investigated whether different reward cues at encoding are associated with changes in sleep physiology and memory retention. It was expected that only items for which a high reward was promised would benefit from nap sleep, and further that a selective role of sleep in memory consolidation would be evident in a correlation between spindle density and memory performance for high but not low rewarded items. Participants' associative memory was tested after learning a list of arbitrarily paired words both before and after taking a 90-minute nap. During learning, word-pairs were preceded by a cue indicating either a high or a low reward for correct memory performance at test. The motivation manipulation successfully impacted retention such that memory declined to a greater extent from pre- to post-sleep for low rewarded than for high rewarded word-pairs. In line with previous studies, positive correlations between spindle density during NREM sleep and general memory performance pre- and post-sleep were found. In addition to this, however, a selective positive relationship between memory performance for highly rewarded word-pairs at posttest and spindle density during NREM sleep was also observed. ERP analyses at retrieval showed for the first time post-sleep ERP old/new effects to depict larger

recollection effects for high-rewarded stimuli compared to new and low-rewarded ones. Further, differential processing of reward cues i.e. more positive ERP amplitudes for high reward promising cues was marginally related to spindle density in a subsequent sleep episode. These results strongly support the view that motivationally salient memories are preferentially consolidated and that sleep spindles may be an important underlying mechanism for selective memory consolidation during sleep.

6.2 Effects of sleep on familiarity and recollection

This section aims to describe the effects of nap sleep on familiarity and recollection by discussing first behavioral and second electrophysiological findings of the two experiments as well as putting these in relation to former research.

6.2.1 Behavioral estimates of sleep's impact on familiarity and recollection

After a retention period filled with either sleep or wakefulness in the afternoon, a memory benefit for the nap group relative to a wake control group was observed for an associative memory task but not an item memory task in experiment one which is in accordance with initial predictions. Whereas no group differences could be observed at baseline testing, recollection-dependent measures estimated by PrA scores (differentiation between old and recombined pairs) were different between groups at the second test phase whereas no group differences for Pr-scores (old/new differentiation) in the item memory task arose. Similar memory performance at baseline as well as comparable subjective feelings of sleepiness and matched IQs for both groups before randomly splitting them up in either nap or wake groups, reduced the possibility that benefits of sleep on associative memory compared to wake are due to baseline group differences.

These results support former findings which demonstrated a beneficial impact of sleep only for recollection but not familiarity measures (Daurat et al., 2007; Drosopoulos et al., 2005; Mander et al., 2011; van der Helm et al., 2011). In the first experiment, both groups showed a decrease in performance from baseline to posttest in the item memory test. For the associative memory test a different picture emerged;

while the control group showed a significant deterioration from AM baseline to AM posttest, performance in the nap group remained constant over time. Results of experiment one are thus both consistent with studies showing that short periods of sleep are sufficient to induce a measurable benefit in declarative memory (Cox et al., 2012; Mander et al., 2011; Saletin et al., 2011; Schmidt et al., 2006; Tucker et al., 2006; van der Helm et al., 2011) and that SWS-rich sleep is more beneficial for hippocampus-dependent associative as compared to non-hippocampus dependent memory retention (Daurat et al., 2007; Inostroza & Born, 2013; Marshall & Born, 2007).

In the second experiment the discrimination indices associated with item and associative memory (PrI and PrA) were derived from the same test phase; in the first place to reduce overall memory load as a number of participants had to be excluded in the first experiment due to low memory performance. Yet, estimating item and associative memory from the same memory task may have reduced the ability to detect dissociable effects of sleep on item and associative memory which were accordingly not found in the second experiment. However, there are studies presenting benefits for one but not the other memory type, respectively familiarity and recollection, within the same task (Daurat et al., 2007; Drosopoulos et al., 2005).

Drosopoulos and colleagues (2005) used a word list discrimination task together with a process dissociation procedure to estimate familiarity and recollection. Participants had to answer on four buttons to classify old words belonging either to the first (list 1 button) or second (list 2 button) list, old words for which they did not know the list membership (old button), and with the last button they needed to discriminate new words from old ones (new button). To estimate familiarity and recollection, different scores were created, namely inclusion and exclusion scores. Inclusion includes all correct remembered old items (list 1 and list 2 button + old button), whereas the exclusion score was created by the amount of old words that were incorrectly remembered to belong to a certain list plus correct remembered old words for which the list association was unknown. Recollection is then defined as inclusion minus exclusion, thus resulting in a score reflecting only correct memory associations. Familiarity is defined as exclusion/(1-recollection), thus reflecting the knowledge of old items without retrieving of associations. They found sleep effects only for recollection but not for familiarity measures. In contrast to the present experiments, false alarms to new items were not included in the calculations which might account for the different findings. As the current thesis used three answer options (old, new, recombined) and in experiment

two only one stimulus set needed to be learnt it is not possible to apply the process dissociation procedure. However, an analysis of hit rates to old vs. recombined pairs (sparing false alarms) separately for each reward condition was conducted post-hoc to compare sleep effects on memory for which both recollection and familiarity can be used (old intact stimuli) to memory which relies stronger on recollection (recombined stimuli). Two different effects emerged; for the high reward condition only a main effect of hit rate could be found. Hit rates to old items were higher than hit rates to recombined pairs and that was independent of time of retrieval. For the low condition, only time was a significant main effect. Hit rates decreased for both old and recombined pairs from baseline to post-sleep. The earlier effect reflects the fact that old pairs might be easier to recognize as both familiarity and recollection can jointly contribute to recognition. Further, it seems that the association of the learnt pairs with high rewarded cues generally enhanced sleep-dependent processing as performance stayed constant from pre- to post-sleep within both old and recombined hit rate categories.

For low rewarded items, hit rates to old and recombined pairs decreased similarly over time. Generally, no performance differences could be found between both types neither at baseline nor at posttest. Taken together it seems, that a promise of high reward could rule out differential effects of sleep on more item-based (intact old pairs) vs. associative memory (recombined pairs) leading to a preservation of both types of memory over sleep whereas low reward led to a similar decrease for both types of memory. In a recent study by Groch and colleagues (2015) a similar pattern of results was found in an emotional vs. neutral memory paradigm. In the first place, they found better memory retention for neutral picture-frame color associations after SWS-rich sleep, and because there was no effect for emotional pictures, they aimed to enhance task relevance by inducing reward cues in a second study. Now it was found, that rewarded picture-frame color associations were equally well retained after SWS sleep independent on whether the frames were associated with emotional or neutral pictures. Thus, a promise of (monetary) reward ruled out differences between emotional and neutral memory processing during sleep. Transferred to the current data, this might infer that a promise of reward ruled out differences between item and associative memory retention.

Another possibility could be that recognition memory tasks that are difficult or complex benefit more generally from sleep (C. C. Lin & Yang, 2014; Mograss et al., 2006; Mograss et al., 2008; U. Wagner et al., 2007). It was shown, for example, that

general memory performance in an associative word-pair task is enhanced after sleep compared to wakefulness (C. C. Lin & Yang, 2014). Here, participants also had to learn unrelated word-pairs before either spending a night asleep (sleep group) or staying awake (control group). After an additional night of recovery sleep, the posttest in which pairs needed to be classified as old, new or recombined revealed better memory performance measured in percent correct judgements for subjects in the sleep group than for the control group. Next to benefits after sleep in associative tasks (C. C. Lin & Yang, 2014; Maurer et al., 2015), general recognition memory benefits after sleep have been shown in studies using facial stimuli (Mograss et al., 2006; Mograss et al., 2008; U. Wagner et al., 2007) or face-name associations (Maurer et al., 2015). As it is assumed that successful encoding of face-name pairs relies on joint hippocampal and prefrontal functioning (Miller et al., 2008), beneficial effects of sleep on correct responses in a face-name-association task fit well with the systems consolidation hypothesis (Inostroza & Born, 2013). And even though the successful recognizing of faces is assumed to rely on regions in the extrastriate visual cortex (Allison et al., 1994), the processing of semantic categories such as age, gender or facial expression of unfamiliar faces during encoding might led to the building of new episodic memory traces by binding core features of a unknown face together (Mograss et al., 2006). As episodic memories especially the binding of information are assumed to rely on hippocampal functioning (Cohen et al., 1999), benefits of sleep on recognition of unfamiliar faces – for which single features are needed to be bind together – also fits with the active system consolidation theory. Further, it is important to note that behaviorally both familiarity and recollection can contribute to decisions in item memory tasks (old vs. new differentiation) and it might be that both processes contributed differentially to memory performance but it is not possible to disentangle this without separate measures of these processes.

This could be done, next to applying associative memory tests or the process dissociation procedure, by using the remember/know paradigm (see also 2.1.2) which is another common approach to measure different contributions of familiarity and recollection in a memory test (Daurat et al., 2007; Tulving, 1985). Daurat et al. (2007) found the recollection estimate to be enhanced after a 3-hour retention interval filled with SWS compared to retention intervals filled with no sleep at all or REM sleep whereas familiarity was not modulated by any of the retention interval manipulations.

Summarizing behavioral findings concerning the effect of sleep on recognition memory processes thus (i) indicate more pronounced benefits for estimates of recollection measured by the ability to create and retrieve associations between unrelated word-pairs correctly compared to familiarity which was measured with the ability to learn and recognize single words in experiment one in the present thesis and what fits with previous findings (Daurat et al., 2007; Drosopoulos et al., 2005; Mander et al., 2011; van der Helm et al., 2011) but (ii) also demonstrate significant sleep benefits for tasks that are associative or complex in nature (C. C. Lin & Yang, 2014; Maurer et al., 2015; Mograss et al., 2006; Mograss et al., 2008; U. Wagner et al., 2007) as was the associative memory task used in experiment two. Sleep benefits concerning associative memory respective recollection-estimates were not only revealed behaviorally but also with means of electrophysiological (ERP) effects. The next section will therefore describe posttest ERP findings of both experiments and embed them with previous literature.

6.2.2 Electrophysiological reflections in recognition memory after sleep

Due to an assumed facilitative effect of sleep on associative memory, it was initially expected that the late parietal old/new effect – the putative ERP correlate of recollection – should be larger after nap sleep compared to that of the control group (Mograss et al., 2006; Mograss et al., 2008). For the ERP old/new effects in the associative memory posttest in the first experiment, there was no observable early frontal old/new effect, in line with the assumption that familiarity does not contribute to associative tests with arbitrary associations (Yonelinas et al., 2010). The late parietal old/new effect was marginally significant in line with the notion that recollection is required for this task. The amplitude of the effect in this task did not differ between nap and wake groups, however, an additional analysis of hits and incorrect answers in the AM task with subgroups revealed significant group differences. ERP differences between hits and incorrect answers in the AM test which reflect the ability of associative discrimination, were larger for the nap than the control group at a left parietal site in a time window corresponding to the typical recollection (old/new) effect (Rugg & Curran, 2007). The behavioral result of the AM test was thus paralleled by

corresponding changes in an ERP analysis of associative discrimination, showing group differences in recollection-associated but not familiarity-modulated ERPs.

Contrary to previous literature (Mograss et al., 2006; Mograss et al., 2008) sleep neither modulated early or late ERP old/new effects in the first experiment. There was evidence of a late parietal old/new effect as well as an early frontal old/new effect in the item memory test in both groups in accordance with the assumption that successful performance in the item memory task is associated with both familiarity and recollection. Neither of these old/new effects was modulated by sleep, however. Comparable early mid-frontal old/new effects in both groups supports the view that item memory for which no contextual information is provided is not modulated by sleep (Drosopoulos et al., 2005). Concerning the late parietal old/new effect especially in the AM test, there are several possible reasons for not finding group differences. One possibility could be that the late parietal old/new effect is not sensitive enough to detect subtle changes in recollective processing which is actually supported by the results of the hits vs. incorrect answers comparison which takes the discrimination ability between old intact learnt stimuli and recombined ones into account and in which sleep effects were found in experiment one. Accordingly, it could be that beneficial effects of sleep in recognition memory studies could come about facilitated access to associative memories and the discrimination between old and rearranged word-pairs what is not necessarily reflected in amplitude differences in the late parietal old/new effect for whose estimation solely old and new items need to be contrasted. However, the late parietal old/new effect has been shown to be sensitive to the amount of information recollected, when manipulated experimentally within subjects (Vilberg et al., 2006; Wilding, 2000), and it has been shown to vary dependent on sleep vs. wake retention intervals before (Mograss et al., 2006; Mograss et al., 2008). Mograss and colleagues (2006; 2008) reported group differences in ERP old/new effects, next to general benefits in correctly classifying old stimuli after sleep compared to wake. For example, in their study from 2008, Mograss and colleagues showed frontal and parietal old/new effects to be more pronounced in a late time interval (555-765 ms) after sleep compared to wake.

Importantly, the studies differed in at least two main points from the experiments in the present dissertation. Firstly, facial stimuli were used whereas the current experiments used non-associated word-pairs (both experiments) plus single words (experiment one). Secondly, for ERP analyses the current experiments compared mean amplitude values whereas the description of the ERP analysis section in Mograss

et al. (2006; 2008) led one to assume that they compared peak amplitudes of ERPs. Whether or not this understanding is appropriate, the current thesis did not aimed to compare peak amplitudes although differences might arise here between groups. However, according to Luck (2005), the measurement and comparison of peak amplitudes bears several shortcomings; amongst others that the peak amplitude describes one single point though components usually last for several hundreds of milliseconds and that the peak amplitude might be falsely increased by high noise level (which can arise through a small number of trials for example). As the aim of the present experiments was to compare ERP components of recognition memory, and as trial numbers were rather low for posttest ERP comparisons, the use of mean amplitude measures was assumed to be more adequate and less affected by surrounding noise.

Concerning the first point about stimuli categories, it is presumably the case that faces and words are processed differently (Farah, 1994; MacKenzie & Donaldson, 2009), and additionally it might be that recognizing faces relies on other neural structures than the used words in the present experiments which usually describe quite distinct objects (MacKenzie & Donaldson, 2009). Further, it has been proposed that although post-learning sleep both improves verbal and facial memory retention, the underlying mechanism might be different (Clemens et al., 2005). Clemens and colleagues (2005) found verbal overnight memory retention to be correlated with spindle numbers whereas correct recognition of faces was related to duration of NREM sleep but not spindle numbers. This raises the possibility that benefits for these stimuli categories after sleep are based on distinct mechanism what consequently might have contribute to the finding of larger ERP old/new effects post-sleep compared to after wake in the studies conducted by Mograss and colleagues (2006; 2008) compared to the old/new effects of the AM task in the first experiment.

Moreover, ERP posttest data from the second experiment seems to support the assumption that more elaborate processing can modulate the late parietal old/new effect, i.e. the putative correlate of recollection, as ERPs elicited by hits to highly rewarded items were more positive going than ERPs to correct rejected new items and to hits which were associated with low reward. As participants were more motivated to remember highly rewarded stimuli because the correct recognition of these ones would lead to higher monetary reward, they might have created stronger associations at encoding for high-rewarded word-pairs. Though not investigating impact of reward, a recent study (C. C. Lin & Yang, 2014) could also demonstrate that sleep leads to

stronger associations. By using a word-pair task and investigating the N400 component pre- and post-sleep it was shown that the peak of N400 was sensitive to sleep-related consolidation effects. The N400 was more attenuated after sleep than after wakefulness, and because a smaller deflection in the N400 indicates strong semantic associations, the authors concluded a facilitating effect of sleep on the creation of new and strong associations. The posttest ERP old/new data of the second experiment is further support of this notion.

Interestingly, it seems to make a difference whether participants are more explicit vs. implicit pointed to encode one stimuli-set more deeply than another and whether the classifying of these stimuli at retrieval can be based on familiarity or need recollection. Using a memory paradigm with emotional (negative) vs. neutral pictures in a split-night study design, Groch and colleagues (2013) also revealed different ERP effects before and after sleep in both conditions. Emotional pictures elicited more positive ERPs at encoding than neutral ones even without instructing participants to concentrate more on one or the other category (as it was done in experiment two with high vs. low reward trials). More positive ERPs elicited by emotional vs. neutral pictures were also most pronounced at central and parietal sites similar to ERPs elicited by high compared to low reward cues in experiment two, however, the ERP pattern at retrieval looked fairly different between these two studies. Descriptively, ERPs elicited by hits to emotional pictures seems largest at frontal and parietal sites in two time windows (300-500 ms; 500-800 ms), however, this was only significant in an early time interval at frontal sites for the late (REM-rich sleep) but not the early (SWS-rich sleep) sleep condition (Groch et al., 2013). As this frontal ERP old/new effect has been related to item memory respective familiarity (Rugg & Curran, 2007), which was sufficient to correctly recognize single (picture) items in that study, it seems that emotionality can enhance REM-sleep-dependent item recognition, particularly compared to SWS-rich sleep. Contrary to this, an explicit promise of additional (monetary) reward at encoding seems to enhance associative memory's reflection in ERPs at retrieval in a task for whose correct processing recollection is necessary as it was found in experiment two.

Summed up shortly, effects of nap sleep on recollection and familiarity were found to be fairly diverse. While recollection, estimated behaviorally and with electrophysiological measures, was shown to benefit from a nap, familiarity seemed to be unaffected by sleep. This pattern was also reflected in the results of the second

experiment in which reward cues at encoding additionally impacted sleep physiology and post-sleep memory retention. A main finding of the second experiment was the maintenance for high rewarded compared to low rewarded memories in an associative task over a retention period filled with sleep. The next chapter of the general discussion therefore deals with the ability of motivational cues to modulate memory retention related to sleep.

6.3 Motivational impact on memory consolidation during sleep

After sleeping, the second experiment found the memory retention for high-rewarded pairs to be better than for low-rewarded word-pairs. This finding agrees well with a wealth of other studies investigating the impact of reward cues on memory formation (Adcock et al., 2006; Feld et al., 2014; Fischer & Born, 2009; Oudiette et al., 2013; van Dongen et al., 2012; Wittmann et al., 2005; Wolosin et al., 2012), and other studies which demonstrated sleep benefits for motivational and emotional relevant material (Nishida et al., 2009; Payne et al., 2008; Saletin et al., 2011; Wilhelm et al., 2011). Before sleeping i.e. at pretest reward-related differences in memory performance were not observable (for a detailed discussion of this outcome see chapter 5.4). This finding supports the notion that during sleep memory information is differentially processed according to associated relevance before sleep (Stickgold & Walker, 2013). It has been discussed before that more relevant information might be tagged at encoding, and that during sleep these recently encoded and tagged memory representations are reactivated and hence consolidated (Rasch & Born, 2013; Stickgold & Walker, 2013).

The neural mechanisms underlying tagging are still under investigation but it might be that the level of hippocampal activity during encoding of episodic information might be critical; e.g. it was reported in a fMRI study that hippocampal activity at encoding is related to the amount of sleep related memory consolidation (Rauchs et al., 2011). More specifically, enhanced theta-activity at encoding might be related to successful memory consolidation as it was found in some electrophysiological studies (Addante, Watrous, Yonelinas, Ekstrom, & Ranganath, 2011; Gruber, Watrous, Ekstrom, Ranganath, & Otten, 2013). Animal studies further showed that increased theta coherence between hippocampus and prefrontal cortex is associated with

preferential replay during sleep of cells which were active at the same time (Benchenane et al., 2010), also suggesting that theta activity might be critical for tagging memories for sleep-dependent consolidation (Rasch & Born, 2013). In humans, in addition to hippocampus and prefrontal cortex, brain regions associated with the processing of emotional and motivational information are also activated by theta oscillations what supports the notion that their preferential consolidation during sleep might be induced by theta-related tagging (Rasch & Born, 2013). The second experiment supports and extends the idea of a tagging mechanism by using ERPs as markers of neural activity during encoding; on the one hand, high reward promising cues elicited more positive ERPs which were broadly distributed across the scalp compared to low reward cues and one the other hand, there was a tendency of a relationship between an ERP related to high reward cues and spindle density. This might imply that neuronal activity already before the actual stimuli to be learnt determines whether a memory will be retained or forgotten (Gruber & Otten, 2010), that the tagging of information can be reflected in more pronounced ERPs, and further, that this distinct activation at encoding also relates to sleep physiology in a subsequent nap.

Recently, however, it has been questioned whether selective memory consolidation during sleep takes place because memories that have been tagged are just more often reactivated and therefore better consolidated during following sleep than non-tagged ones or whether a targeted reactivation of the midbrain reward circuitry in addition to neuronal activation in medial temporal lobe structures during sleep happens (Feld et al., 2014; Perogamvros & Schwartz, 2012). The latter possibility is reflected in the assumptions of the RAM (Perogamvros & Schwartz, 2012) which proposes that regions of the medial temporal lobe (e. g. hippocampus) and structures of the DA system are interacting (Lisman & Grace, 2005) during sleep to foster the reactivation and resulting consolidation of motivational relevant memories (Perogamvros & Schwartz, 2012). In a recent study by Feld and colleagues (2014) it could be shown that a preferential consolidation of high rewarded memories is indeed associated with the activation of the DA system. Their participants needed to learn pictures that were associated with either low or high reward cues, afterwards receiving either a placebo or DA-receptor agonist (pramipexole). A retrieval test one day later revealed that the placebo group retrieved more high-rewarding pictures than low-rewarding. However, this was not found for the group which got pramipexole. For the latter group, performance for low and high rewarded pictures was equally high. This is evidence not

only for the notion that the DA reward system is activated during sleep, but also that an enhancement of DA activity leads to a general memory enhancement of prior learnt information so that low- and high-rewarded information is equally well memorized (Feld et al., 2014). These results support the assumptions of the RAM i.e. that reward-processing structures are activated during sleep and linked to memory retention post-sleep. Another recent study (Oudiette et al., 2013) demonstrated that a possible tagging mechanism might be flexible in that tags are alterable respectively alterably processed during sleep. Their participants had to learn object-location associations with half of the objects associated with low and the other half with high reward values, and a representative sound was played while the object was presented during learning. The study showed that memory retention of all low-value spatial-object associations – which accordingly should not have been tagged at encoding – could be recovered by playing some of the associated sounds during SWS. Hence, even though not all low-value sounds were presented during SWS, all low-value information was recovered leading to the notion that further research is needed to determine the interplay between the selection (tagging) of memory representations before sleep and consolidation processes that then occur during sleep.

The next chapter aims to combine results of the present experiments with previous literature to discuss possible neurophysiological processes which might underlie these distinct effects of sleep on familiarity and recollection and their modulation by expected reward.

6.4 Neurophysiological processes during sleep and recognition memory

According to the active system consolidation theory (Diekelmann & Born, 2010; Rasch & Born, 2013), spindles play a major role in declarative memory consolidation during sleep (Cox et al., 2012; Gais et al., 2002; Mednick et al., 2013; Saletin et al., 2011; Schabus et al., 2004; Schmidt et al., 2006). The active system consolidation theory assumes that episodes are initially encoded in both hippocampus and neocortex but with the hippocampus being only a temporal store. During sleep, especially SWS, episodic representations are reactivated, and reactivations that originate in hippocampal sites are fed into neocortical networks. Spindle-ripple events which are grouped by the

depolarizing up-phases of slow oscillations are assumed to mediate the bottom-up transfer from reactivated memory information in the hippocampus into mainly neocortical regions (Inostroza & Born, 2013). As ripples can be measured only intracranial (Axmacher et al., 2008; Eschenko et al., 2008; Ramadan et al., 2009), sleep studies in humans usually investigate the relationship between spindles and memory performance to test whether memory consolidation might be tied to sleep processes; and usually they found spindle density/activity to be correlated with memory retention (Cox et al., 2012; Gais et al., 2002; Mednick et al., 2013; Saletin et al., 2011; Schabus et al., 2004; Schmidt et al., 2006). Consistent with this; in experiment one a selective correlation between AM posttest performance and spindle density during SWS was revealed. This is particularly support for other research findings which point to the importance of combined spindles and slow-wave-sleep or slow oscillatory activity (Cox et al., 2012; Ngo et al., 2013; Wilhelm et al., 2011). Further, as other studies could show – by using simultaneous EEG and fMRI measurements – that the occurrence of sleep spindles is linked with activation in hippocampus (Andrade et al., 2011; Bergmann et al., 2012; Schabus et al., 2007), the unique correlation between AM but not IM posttest performance and spindle density in experiment one is also support for the assumption that sleep benefits especially hippocampus-dependent associative memories.

There is also evidence that successful learning measured through pre-sleep memory performance might impact processes occurring in subsequent sleep (Bergmann et al., 2012; Gais et al., 2002; C. C. Lin & Yang, 2014). Next to joint occurrence of spindles and hippocampal activation, Bergmann and colleagues (2012) demonstrated the importance of memory acquisition prior to sleep by showing a positive relationship between learning performance before sleep and following spindle-coupled hippocampal activation. This is also supported by results of the first experiment as AM baseline performance before the nap correlated with spindle density in the following sleep period. Interestingly, in a recent study by Lin and colleagues (2014) correlational analyses revealed a positive correlation between pretest memory performance for unrelated word-pairs and percent of time spent in SWS but a negative correlation between pre- to post-sleep performance improvement and percentage of SWS. In light of this astonishing finding, the authors concluded that a ceiling effect in learning might have prevented any further gains for participants that had performed very well at initial testing. And indeed, it has already been suggested before that sleep benefits might be

absent if initial memory performance (pre-sleep) is too high (Drosopoulos, Schulze, Fischer, & Born, 2007; Verleger, Ludwig, Kolev, Yordanova, & Wagner, 2011).

In the second experiment, overall memory performance both before and after napping was also related to spindle density. In both cases follow-up analyses revealed that when pretest performance was controlled for, the correlations between spindle density and posttest performance were removed. The findings of both experiments may therefore imply that consolidation during sleep is either equally likely for all memories intentionally learned before sleep, or alternatively, that individual differences in memory performance (before sleep) predict both sleep spindle density and post-sleep memory performance (Fogel & Smith, 2011). However, generally both accounts fit with the assumptions of an active system consolidation which solely states that spindles are associated with memory reactivations (Bergmann et al., 2012; Rasch & Born, 2013).

Importantly, the second experiment also demonstrated a selective correlation between spindle density and high- but not low-reward memory scores at posttest. As it has been questioned whether sleep could work as a filter by predominantly strengthening memories that are adaptive or of relevance to the future (Stickgold & Walker, 2013; van Dongen et al., 2012), and it is assumed that consolidation of information during sleep will only occur if items were tagged as important during or after the encoding phase, the selective correlation between spindle density and memory performance for high but not low rewarded items provides further evidence for a selective role of sleep in memory consolidation, in particular a role for sleep spindles in the selective consolidation of memories from a specific learning experience. Particularly important is that the correlation between spindle density and high rewarded memories could not be accounted for by memory performance before sleep. This pattern supports the high relevance of sleep spindles for memory consolidation (Diekelmann & Born, 2010) and together with the behavioral data showing smaller decline for high than low reward from pre- to posttest, these findings support the view that sleep enables the selective consolidation of memories from a specific learning experience as it has been also demonstrated in other studies (Fischer & Born, 2009; Saletin et al., 2011; van Dongen et al., 2012; Wilhelm et al., 2011).

The underlying neuronal mechanism of selective memory consolidation during sleep, e.g. for motivational or emotional relevant information, are still not fully understood (see also section 6.3), but the second experiment provides further insights in how encoding might differ for memory representations that are consolidated and

successfully retrieved compared to forgotten ones by using electrophysiological measures. Firstly, it was found that cues promising high rewards elicited more positive ERP amplitudes than low reward promising cues, and importantly the ERP amplitudes elicited by high reward cues were positively related to spindle density in a subsequent nap. Even though this was only a marginal finding, probably due to a rather small sample size which reduces the power of such analyses, it was shown for the first time that neural activity measured with means of electrophysiology is related to a sleep specific parameter which itself is related to behavioral outcome (posttest memory performance). Generally, this strongly supports assumptions that information is differentially processed at encoding before some of the information is selectively consolidated during following sleep (Stickgold & Walker, 2013).

Taken together, both experiments demonstrate the importance of sleep spindles for memory consolidation processes. However, all of the reported relationships between spindle density and behavioral or electrophysiological data were estimated by correlating data points. However, as correlations do not prove causal relationships the present results need to be interpreted with caution. Interestingly, though, there is a recent study which did experimentally manipulate spindle density with a drug during a daytime nap, with a resulting increase in spindle density leading to better word-pair associate memory performance post-sleep compared with a placebo (Mednick et al., 2013). Nonetheless, some open questions remain:

(i) In experiment one, the posttest correlation was found for sleep spindle density specific for SWS but all other correlations were found for spindle density during NREM sleep i.e. including stage 2 and SWS. This distinct findings of the present thesis are also reflected in results of other studies which found memory retention to be associated with spindles solely in stage 2 (Schabus et al., 2004; Schmidt et al., 2006), NREM sleep (Saletin et al., 2011) or SWS (Cox et al., 2012; Wilhelm et al., 2011). Further research is required to disentangle whether different memory tasks might require different spindle types (see also below) for consolidation.

(ii) Related to this is that all significant correlations in the current experiments were found for a frontal electrode which is also supported by some findings of other studies (Clemens et al., 2005; Gais et al., 2002; Schmidt et al., 2006). Correlations with spindles were also found at central (Clemens et al., 2005; Cox et al., 2012; Schabus et al., 2004; Wilhelm et al., 2011) and parietal sites (Saletin et al., 2011) but with the latter study only finding a correlation for fast spindles (13.5-15 Hz).

(iii) This rises the final point whether slow (11-13 Hz) and fast (13-15 Hz) spindles reflect different processes (Schabus et al., 2007). Unfortunately, definitions of slow and fast spindles are not identical in different studies (Mölle, Bergmann, Marshall, & Born, 2011; Saletin et al., 2011; Schabus et al., 2007; Schmidt et al., 2006) what makes comparison so far rather difficult. Furthermore, one has to keep in mind that all studies used different memory paradigms, e.g. while Schmidt and colleagues (2006) and Gais and et al. (2002) varied either encoding difficulty or learning more generally, Saletin and colleagues (2011) applied a directed-forgetting paradigm whereas Wilhelm et al. (2011) did not vary encoding but retrieval expectancy. Further experiments are therefore required to disentangle possible different neurophysiological processes associated with different spindle types and electrode positions in connection with different memory paradigms.

Summed up, research does point to a critical role of spindles for memory consolidation during sleep but there are still open questions to address in future studies as some example are mentioned above. The next chapter will deal with further limitations of the present thesis, and moreover aims to provide worthwile ideas for future research.

6.5 Limitations and future directions for research

Both conducted experiments provide substantial achievements in the questions whether, how and to which extent nap sleep benefits recognition memory processes. Nevertheless, there are certainly some limitations present in these experiments which should be addressed in future research.

As one interest of the present thesis was to investigate potential different effects of nap sleep on familiarity and recollection, the first experiment employed two different memory tasks. One was assumed to be solvable relying on familiarity and recollection (item memory test), and for the other recollection was assumed to be necessary (associative memory test; Yonelinas et al. (2010)). In the follow-up experiment (experiment two), the main interest was the investigation about how reward modulates associative memory retention respectively the process of recollection which had been shown to be sensitive to the beneficial effect of nap sleep in experiment one. Therefore,

experiment two investigated the impact of reward cues during encoding on subsequent sleep physiology and associative memory retention by way of a within-subject design. As a design of this kind do not licenses causal claims about the association between sleep's impact on reward processing and later memory performance, it might be useful to include a wake control group in a future study. Then, by finding group differences depending on sleep vs. wake in a design as presented in experiment two, it would be more secure to infer claims about the impact of sleep (compared to wake) on reward processing and memory retention.

Next, and also related to the first point, is that the second experiment did not employ a control task (i.e. an item memory task) which was skipped because of a very high study load leading to a high drop-out rate in the first experiment. Due to some advantages by applying an item memory comparison, e.g. testing whether a combination of reward processing and sleep specifically promotes associative but not item memory, one possibility could be to use another measure of recollection and familiarity e.g. the process dissociation procedure or remember/know paradigm which both have been successfully used in previous sleep studies (Daurat et al., 2007; Drosopoulos et al., 2005), and which can be applied within the same memory task. If two memory tasks are to be used, another possibility could be to include a learning criterion. Participants need to reach a certain level in memory performance before they can continue with the study protocol leading to a reduction in drop-out rates based on initial memory performance. However, it has also been suggested that sleep benefits might be absent if initial memory performance (pre-sleep) is very high (Drosopoulos et al., 2007; Verleger et al., 2011). Drosopoulos and colleagues (2007) found a greater memory benefit after sleep for word-pairs that were learned to a criterion of 60 % correct responses compared to a learning criterion of 90 % correct responses. There are however other studies which do present greater benefits of sleep for well learnt memories (Hauptmann, Reinhart, Brandt, & Karni, 2005; Tucker & Fishbein, 2008). It might therefore be the case that both too weak and too strong memories do not benefit from sleep, pointing eventually to an optimal learning criterion laying in-between these extremes for experimental sleep studies (e. g. 60%, Drosopoulos et al. (2007)).

To create grand average of ERPs sufficient trials needed to be obtained. Both experiments showed some limitations in providing enough trials for all participants. As many analyses were thus performed for a rather low subsample in the present thesis, future studies should take into account that memory load is not too high but that

sufficient trial numbers can be reached in the memory task. Related to this is the question whether it might be advantageous to investigate ERPs elicited at a memory test before a retention period filled with either sleep or wake to be able to compare this to posttest ERPs for determining any time- and sleep-dependent changes that might occur or might differ depending on sleep vs. wake retention intervals.

Related to the high drop-out rate in the first experiment is the question about the amount of forced sleep deprivation the night before the experiment. Experiment one and two differed in this point, as participants in experiment one were requested to sleep one hour less than their weekly average sleep duration the night before the actual experiment, and participants in experiment two were just told to not sleep more than 8 and less than 6 hours. In experiment one, this might also have contributed to lower memory performance at pre-sleep testing due to higher feelings of sleepiness before starting the study phase (as measured with the Stanford Sleepiness Scale, time point one in both experiments; experiment one: 2.8 ± 1.2; experiment two: 1.9 ± 0.4; $p < .01$, see also appendix Table C.1 for further comparisons). As participants of experiment one and two did not differ in any nap parameter (compare Table C.2) amongst others in their ability to fall asleep (sleep latency (in minutes); experiment 1: 14.2 ± 12.5; experiment 2: 14.8 ± 12.2; $p = .82$), nor in the average nap duration (experiment 1: 64.3 ± 16.3; experiment 2: 70.6 ± 15.8; $p = .73$) or amount of calculated SWS (experiment 1: 15.7 ± 12.2; experiment 2: 15.6 ± 12.1; $p = .98$), future studies might therefore apply the approach used in experiment two to avoid sleepiness effects on initial learning ability.

Moreover, it might be helpful to include the possibility for an adaptation nap before conducting the actual experiment as it is usually done for sleep studies which cover sleep at night (Bergmann et al., 2012; Drosopoulos et al., 2005; Gais et al., 2002; Groch et al., 2013; Groch et al., 2015; Plihal & Born, 1999; Schabus et al., 2004; U. Wagner et al., 2007; Wilhelm et al., 2011) to minimize drop-out rates related to not sleeping in the nap condition. Furthermore, an adaptation nap would have several advantages; firstly, participants which are not able to sleep during the given time interval or which show very low sleep efficiency could be filtered out before the actual experiment is conducted, and secondly, participants are already used to the procedure, therefore they eventually are less frightened by the actual experiment what might result in better sleeping behavior.

A further limitation is concerned with the methodology of ERPs. Although hippocampal activations were assumed to take place while associative memories are

encoded, consolidated and recollected (Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000; O'Reilly et al., 2011; A. D. Wagner et al., 1999; Yonelinas et al., 2010), no direct measure of hippocampal activation was included in the present experiments. Even though ERP correlates of recollection have been associated with hippocampal activation in previous literature (Hoppstädter et al., 2015), a future study might substantially profit from a combination of ERP and fMRI to examine sleep effects on memory processes which are assumed to be hippocampus-dependent. A combination of both techniques would lead to excellent temporal resolution (ERPs) combined with precise spatial localization (fMRI) (Huster, Debener, Eichele, & Herrmann, 2012) therefore enabling to gain more exact knowledge about sleep benefits in (associative) recognition memory and associated neurophysiological parameter.

Both experiments demonstrate that short periods of sleep during the day are sufficient to induce a measurable benefit in episodic memory, and therefore support previous literature (Cox et al., 2012; Mander et al., 2011; Saletin et al., 2011; Schmidt et al., 2006; Tucker et al., 2006; van der Helm et al., 2011). Actually, memory benefits have been shown for even shorter sleep periods of about six minutes, although benefits were greater for a longer sleep period (Lahl et al., 2008). Despite the advantages of a daytime nap study to compare influences of sleep and wake on memory retention because of e.g. similar circadian level, it might nevertheless be interesting to investigate whether enhancement of memory performance might be equally well for a nap during the day compared to a full or half night of sleep.

Results of such a comparison could be especially interesting for older people as they often show disturbed night sleep; i.e. spending more time awake during night after initial sleep onset and showing less SWS (Scullin, 2013) as well as needing a longer time to fall asleep than younger adults (Carskadon & Dement, 2011; Ohayon, Carskadon, Guilleminault, & Vitiello, 2004). A decrease in spindle density has also been reported (Mander et al., 2014; Martin et al., 2013). Interestingly, declarative memory also declines with aging (Prull, Gabrieli, & Bunge, 2000) with studies showing a link with decrease of SWS and memory decline (Backhaus et al., 2007; Scullin, 2013). As it might be that these changes in sleep physiology are related to the development of memory deterioration in the process of aging, future studies should first of all investigate whether there are age differences between younger and older adults concerning the beneficial effect of nap sleep on recognition memory processes and next, within the older age-range, whether a nap compared with a wake retention period can

induce measurable benefits in recognition memory, and whether this might be related to other physiological parameter during sleep (e. g. spindles).

Next to the correlational analyses of spindles and performance in memory tests, future studies could also directly manipulate spindle production as it was done in a study by Mednick and colleagues (2013). In their study spindle density was experimentally increased by giving a certain drug before a daytime nap. This was leading to better word-pair associate memory performance compared with a placebo; a result that might also be interesting in context of age-related spindle and memory decline. Future studies of this kind might also have substantial practical implications by raising the possibility to artificially enhance spindle production in elderly what as a result should diminish decline in post-sleep memory retention under the assumption that pre-sleep memory performance reach a certain level (Drosopoulos et al., 2007).

In spite of the correlational nature of the data present in the current thesis, the results of experiment one and two yield significant insights in the role of nap sleep on recognition memory processes which might also have several (practical) implications for daily life which will be described in the following section (6.6).

6.6 Practical implications

The present thesis revealed a preferential effect of nap sleep on recognition memory processes in tests of initially non-related stimuli. By showing the importance of sleep for maintaining self-created associations between arbitrarily paired words such as is often the case for items to be learnt for a vocabulary test, this has important practical implications for educational settings. Further, the ability to learn arbitrary associations is critical across a wider variety of educational contexts (second language learning, face-name association), and an intervention like nap sleep that promotes learning of previously unassociated information is thus of high relevance for the improvement and acceleration of learning for a range of contexts. The individual learner engaging in self-direct study may perhaps be best placed to apply the lessons learnt from the current data, given that they indicate that students do not need to work late in the evening before sleep to benefit from the consolidation processes in sleep. A nap after learning or

perhaps after a morning's revision for an afternoon test, may be as valuable as a night of sleep for consolidating newly learnt memories.[12]

The finding of the current thesis are further of special value as it is still common to work hard and long during day and night at the expense of getting enough sleep. Not only reveals the current thesis that sleep has a beneficial impact on memory retention but also that participants who were allowed to nap felt more awake, active and vital than participants who were not allowed to nap in the first experiment (control group) as estimated with the Stanford Sleepiness Scale (see Table 3.2 and Table C.1) at the end of the experiment. This positive impact of sleep on energy and concentration ability was also demonstrated by other studies (Smith-Coggins et al., 2006; Taub, 1979). To date, there are already few companies which are practically implementing these research findings by offering nap possibilities to their employees (Baxter & Kroll-Smith, 2005). As this is revealing a positive impact on motivation to work as well as productivity, it might also be worth for other academic/educational and work places to offer quite rooms with the possibility to nap.

Elderly might be another target group to benefit from nap sleep as they show both a decline in memory performance (Prull et al., 2000) and reduced sleep quality during night (Carskadon & Dement, 2011; Ohayon et al., 2004; Scullin, 2013). It might be worth considering for them to nap during the day to diminish these side effects of aging. As it was already stated in the previous chapter, however, future research needs to be conducted to examine beneficial effects of nap sleep in older age groups concerning associative memory retention and possible influence of sleep parameter.

Next to sleep, motivational cues also had a positive impact on associative memory retention of non-related word-pairs post-sleep in the second experiment of the present thesis. Here, motivational manipulation was induced by offering distinct amounts of additional money dependent on pre- and post-sleep test performance. As it might be as well possible to enhance motivation by promising monetary rewards in companies and factories, it is not suitable in e. g. educational settings. However, a study by Lin and colleagues (2012) suggests that monetary and social reward processing is at least partly dependent on the same neural structures, therefore pointing to the possibility that amongst others in educational settings positive feedback might lead to higher

[12] This paragraph is published in a modified version in Studte, S., Bridger E., & Mecklinger, A. (in press). "Sleep spindles during a nap correlate with post sleep memory performance for highly rewarded word-pairs".

motivation at learning and – especially in combination with a subsequent nap – result in higher performance outcomes.

6.7 Conclusion

To finally conclude, the present thesis adds substantial knowledge in determining whether and how recognition memory processes can benefit from nap sleep by applying both item (single words) and associative (word-pairs) memory tasks in combination with electrophysiological and polysomnographic measures. Both experiments show remarkable benefits in the retention of associative memories following nap sleep; additionally the first experiment did not demonstrate such an effect for an item memory contrast. The first experiment showed further that such an advantage in associative memory retention was not observable for a group which needed to stay awake during the retention period. These results are further evidence for a sleep- dependent episodic memory consolidation.

A sleep-dependent memory consolidation is additionally supported by the results of the correlational analyses. The first experiment found both pre- and post-sleep memory performance to be correlated to spindle density at frontal sites (Gais et al., 2002); though the post-sleep correlation was only evident for spindles occurring during SWS (Cox et al., 2012). The post-sleep correlation was further driven by pretest memory performance what demonstrates the influence of pre-sleep experiences on subsequent sleep and associated parameter. The second experiment also showed a correlation between general memory performance pre- and post-sleep with spindle density, with pretest memory performance again driving the post-sleep correlation. Of special interest is, however, that a further correlation was revealed between spindle density and memory performance post-sleep for high rewarded word-pairs only. Showing this for the first time, this is also strong support for the theory of a selective role of sleep in memory consolidation.

A tendency of a correlation between spindle density and an ERP related to high reward promising cues at encoding gives preliminary insights how memories might be tagged as important for a selective consolidation in subsequent sleep; only memories which elicit a strong neural activity might be considered for consolidation during sleep.

However, further research is required here to determine whether a tagging of information at encoding drives their selective consolidation during sleep (Stickgold & Walker, 2013) or whether a conjoint activation of memory and reward processing neural systems during sleep is leading to the selective consolidation of some memories over others (Feld et al., 2014).

The thesis is the first one which demonstrates that ERP correlates of familiarity and recollection are distinctly impacted by nap sleep; while the midfrontal old/new effect - reflecting familiarity - was neither modulated by sleep (vs. wake) nor reward, the late parietal old/new effect – associated with recollective processing – was significantly affected by reward in that mean amplitude were largest for correctly recognized old items linked to high reward compared to both correct rejections and low reward correct answers. Additionally, the first experiment demonstrated an ERP difference in an associative discrimination contrast between nap and wake participants present in larger recollection effects for participants that slept compared to those who stayed awake.

Summarized, the present thesis supports the role of sleep especially sleep spindles as underlying mechanism for the consolidation of associative memories, and further demonstrates the ERP correlates of recollection to be sensitive to both associative discrimination and reward processing. Motivational incentives enhanced memory retention for high rewarded stimuli only, and a relationship between memory performance for high rewarded items and spindle density was revealed; therefore taken together being further support for the assumption of a selective memory consolidation during sleep.

7 References

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Appendix

Appendix A – Questionnaires

Questionnaire A.1: Questionnaire to measure sleepiness during daytime.

Fragebogen zur Tagesschläfrigkeit

(Epworth-Schläfrigkeitsskala)

Datum: .....

Die folgende Frage bezieht sich auf Ihr normales Alltagsleben in der letzten Zeit:

Für wie wahrscheinlich halten Sie es, daß Sie in einer der folgenden Situationen einnicken oder einschlafen würden, - sich also nicht nur müde fühlen?

Auch wenn Sie in der letzten Zeit einige dieser Situationen nicht erlebt haben, versuchen Sie sich trotzdem vorzustellen, wie sich diese Situationen auf Sie ausgewirkt hätten.

Benutzen Sie bitte die folgende Skala, um für jede Situation eine möglichst genaue Einschätzung vorzunehmen und kreuzen Sie die entsprechende Zahl an:

0 = würde *niemals* einnicken
1 = *geringe* Wahrscheinlichkeit einzunicken
2 = *mittlere* Wahrscheinlichkeit einzunicken
3 = *hohe* Wahrscheinlichkeit einzunicken

Situation	Wahrscheinlichkeit einzunicken
Im Sitzen lesend	⓪ ① ② ③
Beim Fernsehen	⓪ ① ② ③
Wenn Sie passiv (als Zuhörer) in der Öffentlichkeit sitzen (z.B. im Theater oder bei einem Vortrag)	⓪ ① ② ③
Als Beifahrer im Auto während einer einstündigen Fahrt ohne Pause	⓪ ① ② ③
Wenn Sie sich am Nachmittag hingelegt haben, um auszuruhen	⓪ ① ② ③
Wenn Sie sitzen und sich mit jemand unterhalten	⓪ ① ② ③
Wenn Sie nach dem Mittagessen (ohne Alkohol) ruhig dasitzen	⓪ ① ② ③
Wenn Sie als Fahrer eines Autos verkehrsbedingt einige Minuten halten müssen	⓪ ① ② ③
Bitte nicht ausfüllen Summe	

II:

Questionnaire A.2: Questionnaire to measure feelings of sleepiness across the experiment.

FRAGEBOGEN ZUR SCHLÄFRIGKEIT

Datum: _____ VP-Nr.:_____

Grad der Schläfrigkeit	Skala	Vor dem Lernen	Nach dem Lernen	Nach dem Pretest	Direkt nach dem Schlafen	Vor dem Posttest	Am Ende des Experimentes
Fühle mich aktiv, vital, hellwach	1						
Wach, aber nicht in Top-Form; kann mich konzentrieren	2						
Wach, entspannt; reagiere, bin aber nicht so ganz da	3						
Etwas benommen, schlaff	4						
Benommen, verliere das Interesse am Wachbleiben, tranig	5						
Schläfrig, benommen, kämpfe mit dem Schlaf, würde mich gerne hinlegen	6						
Kämpfe nicht mehr gegen den Schlaf, schlafe gleich ein; traumartige Gedanken	7						

Gemessene Zeitpunkte = measured time points:

Vor dem Lernen = before learning (SSS1);
nach dem Lernen = after learning (SSS2; only measured in experiment two);
nach dem Pretest = after pretest (SSS3);
direkt nach dem Schlafen = directly after napping (SSS4; only measured for the nap groups);
vor dem Posttest = before posttest (SSS5);
am Ende des Experimentes = at the end of the experiment (SSS6).

Questionnaire A.3: Instructions and example for the sleep log

Anleitung zum Ausfüllen des Schlafprotokolls

Unbedingt vor der Erstbearbeitung lesen

Wir möchten Sie bitten, diesen Protokollbogen vollständig und sorgfältig zu bearbeiten. Dafür brauchen Sie nur wenige Minuten am Abend und am darauffolgenden Morgen.

Das Protokoll ist so aufgebaut, dass Sie alle Tage im Überblick haben. Beginnen Sie am abgesprochenen Abend, indem Sie die erste Spalte des Abendprotokolles (Frage 1-6) für das zutreffende Datum beantworten. Am nächsten Morgen beginnen Sie mit dem Morgenprotokoll in der gleichen Spalte (Morgenprotokoll) und beantworten die Fragen 7-15. Bitte bearbeiten Sie das Abendprotokoll unmittelbar vor dem Lichtlöschen und das Morgenprotokoll unmittelbar nach dem Aufstehen.

Mit Ausnahme der Zubettgehzeit (Frage 6) und der morgendlichen Aufstehzeit (Frage 14), für die Sie Ihre Uhr benötigen, sind wir an Ihrer subjektiven Einschätzung von Zeiträumen interessiert. So sollen Sie die Zeit, die Sie zum Einschlafen brauchen ebenso wie die nächtlichen Wachliegezeiten und die Gesamtschlafdauer lediglich schätzen.
Zur Bearbeitung des Schlafprotokolles brauchen Sie nachts also keine Uhr! Machen Sie sich keine Gedanken darüber, ob Ihre Einschätzung absolut korrekt ist. Gerade nachts fällt es erfahrungsgemäß sehr schwer zu beurteilen, ob man z.B. eine oder zwei Stunden wachgelegen hat.

Wichtig ist ganz alleine Ihr subjektiver Eindruck und nicht die genaue Dauer!

Bei mehreren Fragen (Frage 1,2,5,7 und 8) werden Sie um eine Einschätzung z.B. Ihrer Müdigkeit gebeten. Richten Sie sich hierbei nach der Schulnotensystem (z.B. sehr wach/frisch = 1; sehr müde = 6).
Sollten bestimmte Fragen an einem Tag auf Sie nicht zutreffen, machen Sie einfach keinen Vermerk und gehen zur nächsten Frage über.

Wir danken Ihnen für Ihre gewissenhafte Mitarbeit!

Weitere wichtige Ereignisse/Vorkommnisse in dieser Woche können Sie hier notieren:

_____

_____

_____

_____

_____

_____

_____

_____

_____

_____

VP-Nr.:_____ **Datum:_____**

ABENDPROTOKOLL (vor dem Lichtlöschen)	**Beispiel**	**Abend 1:**	**Abend 2:**	**Abend 3:**
1. Wie ist Ihre Stimmung jetzt? (1: sehr gut …. 6: sehr schlecht)	3			
2. Wie leicht/schwer fiel es Ihnen heute, Leistungen (Beruf, Freizeit, Haushalt) zu erbringen? (1: sehr leicht .... 6: sehr schwer)	3			
3. Haben Sie heute tagsüber geschlafen? Falls ja, geben Sie an, wann und wie lange insgesamt	14:00 30 Min			
4. Haben Sie in den letzten 4 Stunden Alkohol zu sich genommen? Falls ja, was und wieviel?	3 Glas Wein			
5. Wie frisch/müde fühlen Sie sich jetzt? (1: sehr frisch ..... 6: sehr müde)	3			
6. Wann sind Sie zu Bett gegangen?	22:30			
MORGENPROTOKOLL (nach dem Aufstehen)	**Beispiel**	**Morgen 1:**	**Morgen 2:**	**Morgen 3:**
7. Wie frisch/müde fühlen Sie sich jetzt? (1: sehr frisch ..... 6: sehr müde)	3			
8. Wie ist Ihre Stimmung jetzt? (1: sehr gut .... 6: sehr schlecht)	3			
9. Wann haben Sie gestern das Licht ausgemacht?	23:00			
10. Wie lange hat es nach dem Licht löschen gedauert, bis Sie einschliefen? (Min)	40			
11. Waren Sie nachts wach? Wie oft? Wie lange insgesamt? (Min)	2x 30			
12. Wann sind Sie endgültig aufgewacht?	6:30			
13. Wie lange haben Sie insgesamt geschlafen? (Angabe in Stunden:Minuten)	6:40			
14. Wann sind Sie endgültig aufgestanden?	7:00			

Note: In experiment one the sleep log (= Schlafprotokoll) was filled in for one week whereas in experiment two it was filled in for three days.

Appendix B – List of stimuli for IM and AM tasks (in German)

Table B.1: List of stimulus material for both IM (180 words) and AM (270 word-pairs) tasks.

Word-pairs for Associative Memory Tasks						**Words for Item Memory Task**	
Old			**Recombined**				
No.	**Word1**	**Word2**	**No.**	**Word1**	**Word2**	**No.**	**Word**
1*	Akzent	Kandidat	1	Akzent	Zirkel	1	Adler
2*	Wolle	Lehrling	2	Wolle	Turm	2	Figur
3*	Blut	Himmel	3	Blut	Lehrling	3	Boxer
4*	Gemüse	Bibel	4	Gemüse	Klage	4	Geschenk
5*	Kuss	Klage	5	Kuss	Garage	5	Fahne
6*	Stuhl	Faden	6	Stuhl	Himmel	6	Kasse
7*	Kamera	Hund	7	Kamera	Faden	7	Tag
8*	Dorf	Stiefel	8	Dorf	Zunge	8	Halle
9*	Mantel	Schwein	9	Mantel	Engel	9	Hering
10*	Stoff	Garage	10	Stoff	Kloster	10	Husten
11*	Pudding	Wüste	11	Pudding	Elefant	11	Karton
12*	Atom	Wohnung	12	Atom	Hund	12	Kehle
13*	Radio	Zirkel	13	Radio	Wohnung	13	Klub
14*	Frage	Elefant	14	Frage	Stiefel	14	Lager
15*	Rahmen	Turm	15	Rahmen	Bauch	15	Leiter
16*	Eisen	Zunge	16	Eisen	Wüste	16	Magen
17*	Stadion	Bauch	17	Stadion	Bibel	17	Mühle
18*	Nebel	Engel	18	Nebel	Kandidat	18	Natur
19*	Trainer	Kloster	19	Trainer	Blume	19	Paket
20*	Koffer	Blume	20	Koffer	Schwein	20	Podium
21	Gehirn	Käse	21	Gehirn	Fabrik	21	Rettich
22	Magen	Fabrik	22	Magen	Ritter	22	Sahne
23	Parfum	Weg	23	Parfum	Spiel	23	Scherbe
24	Kehle	Spiel	24	Kehle	Aufzug	24	Ski
25	Esel	Podium	25	Esel	Nadel	25	Spritze
26	Kanal	Stirn	26	Kanal	Käse	26	Fabrik

27	Knie	Nadel	27	Knie	Ufer	27	Tempel
28	Rettich	Ritter	28	Rettich	Maurer	28	Trompete
29	Kakao	Aufzug	29	Kakao	Podium	29	Villa
30	Museum	Leber	30	Museum	Rübe	30	Weste
31	Kissen	Ufer	31	Kissen	Weg	31	Löffel
32	Halle	Blatt	32	Halle	Seife	32	Bandit
33	Note	Teppich	33	Note	Stirn	33	Bunker
34	Mai	Zahn	34	Mai	Leber	34	Erde
35	Weste	Treppe	35	Weste	Teppich	35	Fahrrad
36	Adler	Kasse	36	Adler	Diele	36	Gehirn
37	Tempel	Rübe	37	Tempel	Zahn	37	Gipfel
38	Waffel	Seife	38	Waffel	Treppe	38	Hase
39	Tiger	Diele	39	Tiger	Blatt	39	Herz
40	Honig	Maurer	40	Honig	Kasse	40	Januar
41	Dirigent	Aal	41	Dirigent	Falke	41	Käse
42	Flasche	Huf	42	Flasche	Aal	42	Kellner
43	Etage	Bucht	43	Etage	Huf	43	Knie
44	Antrag	Falke	44	Antrag	Burg	44	Lampe
45	Gesicht	Burg	45	Gesicht	Bucht	45	Licht
46*	Traum	Ruine	46	Traum	Turnier	46	Getreide
47*	Wald	Bier	47	Wald	Beichte	47	Mund
48*	Flut	Traktor	48	Flut	Verbot	48	Note
49*	Wagen	Beichte	49	Wagen	Stich	49	Freund
50*	Kugel	Katze	50	Kugel	Dusche	50	Pullover
51*	Wurst	Zigarette	51	Wurst	Bombe	51	Ritter
52*	Ärmel	Verbot	52	Ärmel	Kollege	52	Maske
53*	Fenster	Kollege	53	Fenster	Verein	53	Wunder
54*	Glas	Rakete	54	Glas	Miete	54	Sofa
55*	Stahl	Blüte	55	Stahl	Foto	55	Sprung
56*	Fell	Stein	56	Fell	Rakete	56	Tabak
57*	Trommel	Bild	57	Trommel	Zigarette	57	Teppich
58*	Bank	Dusche	58	Bank	Bild	58	Tür
59*	Gürtel	Verein	59	Gürtel	Ruine	59	Vorhang

60*	Dach	Foto	60	Dach	Bier	60	Whisky
61*	Schwert	Miete	61	Schwert	Traktor	61	Aufgabe
62*	Wein	Bombe	62	Wein	Katze	62	Baron
63*	Staub	Turnier	63	Staub	Verbot	63	Bus
64*	Zwiebel	Stich	64	Zwiebel	Stein	64	Esel
65*	Auto	Hirte	65	Auto	Blüte	65	Band
66*	Hafen	Balkon	66	Hafen	Ohr	66	Schlager
67*	Kapital	Ohr	67	Kapital	Sessel	67	Gräber
68*	Leder	Brief	68	Leder	Balkon	68	Seife
69*	Musik	Fliege	69	Musik	Herd	69	Höhle
70*	Akademie	Volk	70	Akademie	Fliege	70	Kamin
71*	Alkohol	Zeitung	71	Alkohol	Palast	71	Kaserne
72*	Organ	Spitze	72	Organ	Pokal	72	Kerze
73*	Zebra	Finale	73	Zebra	Sportler	73	Kohle
74*	Bahn	Herd	74	Bahn	Rock	74	Leber
75*	Wasser	Daumen	75	Wasser	Zeitung	75	Linde
76*	Hafer	Tante	76	Hafer	Finale	76	Marke
77*	Milch	Taxi	77	Milch	Spitze	77	Museum
78*	Kartoffel	Hammer	78	Kartoffel	Stufe	78	Ofen
79*	Dokument	Stufe	79	Dokument	Volk	79	Partei
80*	Teller	Rock	80	Teller	Taxi	80	Puppe
81*	Garten	Pokal	81	Garten	Brief	81	Säule
82*	Schatten	Sportler	82	Schatten	Pille	82	Salat
83*	Stern	Sessel	83	Stern	Tante	83	Schlitten
84*	Provinz	Pille	84	Provinz	Daumen	84	Heim
85*	Buch	Palast	85	Buch	Hammer	85	Staat
86	Ofen	Feier	86	Ofen	Erde	86	Tablett
87	Bandit	Heide	87	Bandit	Brunnen	87	Theke
88	Tür	Brunnen	88	Tür	Feier	88	Tüte
89	Maus	Säule	89	Maus	Heide	89	Waffel
90	Baby	Erde	90	Baby	Säule	90	Wunde
91*	Graben	Herde	91	Graben	Kinn	91	Aufzug
92*	Vulkan	Gesetz	92	Vulkan	Kind	92	Biene

93*	Kuh	Agent	93	Kuh	Mauer	93	Butter
94*	Benzin	Schule	94	Benzin	Medaille	94	Allee
95*	Strumpf	Team	95	Strumpf	Agent	95	Flamme
96*	Obst	Stunde	96	Obst	Sänger	96	Gemälde
97*	Bett	Mauer	97	Bett	Pfeil	97	Grabung
98*	Tisch	Pferd	98	Tisch	Studium	98	Heide
99*	Armee	Wiese	99	Armee	Ablage	99	Honig
100*	Fett	Jäger	100	Fett	Stunde	100	Kakao
101*	Zirkus	Kinn	101	Zirkus	Jäger	101	Gasse
102*	Mond	Pfeil	102	Mond	Manager	102	Kirche
103*	Futter	Architekt	103	Futter	Schule	103	Kraft
104*	Gitter	Studium	104	Gitter	Team	104	Lehrer
105*	Feder	Sänger	105	Feder	Schild	105	Lippe
106*	Titel	Kind	106	Titel	Wiese	106	Mai
107*	Hügel	Schild	107	Hügel	Gesetz	107	Nacht
108*	Münster	Manager	108	Münster	Herde	108	Orden
109*	Busch	Ablage	109	Busch	Architekt	109	Perle
110*	Kaffee	Medaille	110	Kaffee	Pferd	110	Rasen
111*	Gewitter	Motor	111	Gewitter	Rose	111	Rübe
112*	Amt	Matte	112	Amt	Fisch	112	Sarg
113*	Vogel	Onkel	113	Vogel	Motor	113	Schlüssel
114*	Bogen	Rose	114	Bogen	Auge	114	Roggen
115*	Spur	Auge	115	Spur	Bühne	115	Stange
116*	Klavier	Hemd	116	Klavier	Brötchen	116	Tasche
117*	Paradies	Ente	117	Paradies	Konto	117	Tiger
118*	Schaf	Melodie	118	Schaf	Urlaub	118	Ufer
119*	Feuer	Wurzel	119	Feuer	Tabelle	119	Anzug
120*	Haar	Kiste	120	Haar	Ente	120	Zahn
121*	Papier	Brötchen	121	Papier	Melodie	121	Baby
122*	Feld	Dieb	122	Feld	Schiff	122	Blatt
123*	Ring	Stall	123	Ring	Matte	123	Diele
124*	Pilot	Bühne	124	Pilot	Stall	124	Etage
125*	Geld	Schiff	125	Geld	Pflanze	125	Fleisch

126*	Rohr	Tabelle	126	Rohr	Hemd	126	Gerste
127*	Sattel	Fisch	127	Sattel	Wurzel	127	Grube
128*	Formel	Urlaub	128	Formel	Onkel	128	Soldat
129*	Kopf	Pflanze	129	Kopf	Kiste	129	Hülle
130*	Satz	Konto	130	Satz	Dieb	130	Junge
131	Hase	Kirche	131	Hase	Baron	131	Scheune
132	Hülle	Strand	132	Hülle	Kirche	132	Kissen
133	Zimmer	Gipfel	133	Zimmer	Grube	133	Kübel
134	Walzer	Grube	134	Walzer	Strand	134	Altar
135	Plakat	Baron	135	Plakat	Gipfel	135	Luft
136	Anzug	Kübel	136	Anzug	Hering	136	Maurer
137	Roggen	Flamme	137	Roggen	Licht	137	Nadel
138	Reifen	Butter	138	Reifen	Träne	138	Ort
139	Perle	Beton	139	Perle	Husten	139	Pflaster
140	Herz	Hering	140	Herz	Kübel	140	Räuber
141	Freund	Tüte	141	Freund	Beton	141	Roman
142	Biene	Sprung	142	Biene	Butter	142	Schale
143	Leiter	Fleisch	143	Leiter	Gerste	143	Haus
144	Paket	Husten	144	Paket	Staat	144	Sperre
145	Kamin	Getreide	145	Kamin	Allee	145	Stirn
146	Rasen	Mühle	146	Rasen	Mund	146	Tasse
147	Salat	Staat	147	Salat	Sprung	147	Träne
148	Tasse	Lunge	148	Tasse	Sirene	148	Uniform
149	Lehrer	Allee	149	Lehrer	Mühle	149	Weg
150	Löffel	Licht	150	Löffel	Januar	150	Ziege
151	Lager	Mund	151	Lager	Lunge	151	Banane
152	Nacht	Gerste	152	Nacht	Tüte	152	Boden
153	Eimer	Sirene	153	Eimer	Flamme	153	Eimer
154	Kasten	Träne	154	Kasten	Fleisch	154	Affe
155	Puppe	Januar	155	Puppe	Getreide	155	Parfum
156*	Gewehr	Mönch	156	Gewehr	Spiegel	156	Gespenst
157*	Berg	Graf	157	Berg	Komponist	157	Haken
158*	Sand	Spiegel	158	Sand	Ingenieur	158	Heizöl

159*	Feind	Wolke	159	Feind	Münze	159	Humus
160*	Telefon	Klinik	160	Telefon	Brille	160	Kanal
161*	Korb	Prüfung	161	Korb	Flagge	161	Kasten
162*	Rand	Oper	162	Rand	Rechnung	162	Klammer
163*	Film	Rezept	163	Film	Pfeife	163	Laden
164*	Lohn	Maschine	164	Lohn	Wolke	164	Beton
165*	Messer	Papst	165	Messer	Mönch	165	Lunge
166*	Sauna	Brille	166	Sauna	Oper	166	Monat
167*	Sieger	Rechnung	167	Sieger	Klinik	167	Nagel
168*	Chor	Sendung	168	Chor	Maschine	168	Ozean
169*	Faust	Münze	169	Faust	Zelt	169	Piste
170*	Bein	Zelt	170	Bein	Prüfung	170	Reifen
171*	Kino	Ingenieur	171	Kino	Sonne	171	Sack
172*	Schuh	Flagge	172	Schuh	Graf	172	Köchin
173*	Kuchen	Sonne	173	Kuchen	Papst	173	Sirene
174*	Kreis	Pfeife	174	Kreis	Sendung	174	Spiel
175*	Protest	Komponist	175	Protest	Rezept	175	Strand
176	Ball	Sarg	176	Ball	Ort	176	Taube
177	Bach	Altar	177	Bach	Sarg	177	Treppe
178	Kurve	Dom	178	Kurve	Altar	178	Vater
179	Dose	Ort	179	Dose	Ski	179	Ende
180	Ziege	Ski	180	Ziege	Dom	180	Zigarre
181*	Ernte	Wanderer	181	Ernte	Held		
182*	Abwehr	Kamm	182	Abwehr	Gewerbe		
183*	Fessel	Rat	183	Fessel	Zahl		
184*	Flügel	Waage	184	Flügel	Regel		
185*	Bikini	Familie	185	Bikini	Tafel		
186*	Insel	Keller	186	Insel	Waage		
187*	Hebel	Tafel	187	Hebel	Referat		
188*	Schrank	Siedlung	188	Schrank	Wanderer		
189*	Muskel	Zettel	189	Muskel	Boot		
190*	Pulver	Regel	190	Pulver	Baum		
191*	Brot	Hotel	191	Brot	Siedlung		

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192*	Teil	Held	192	Teil	Nonne		
193*	Mode	Nonne	193	Mode	Löwe		
194*	Transport	Baum	194	Transport	Rat		
195*	Knoten	Löwe	195	Knoten	Familie		
196*	Park	Referat	196	Park	Kamm		
197*	Finger	Boot	197	Finger	Hotel		
198*	Prinz	Zahl	198	Prinz	Zettel		
199*	Fluss	Gebäude	199	Fluss	Keller		
200*	Juli	Gewerbe	200	Juli	Gebäude		
201*	Hals	Woche	201	Hals	Gedicht		
202*	Horn	Welle	202	Horn	Woche		
203*	Heft	Schmuck	203	Heft	Sturm		
204*	Rauch	Apfel	204	Rauch	König		
205*	Sommer	Wange	205	Sommer	Reis		
206*	Platz	Gedicht	206	Platz	Suppe		
207*	Täter	Element	207	Täter	Topf		
208*	Text	Dame	208	Text	Wange		
209*	Sturz	Liga	209	Sturz	Karte		
210*	Blitz	Gras	210	Blitz	Apfel		
211*	Triumph	Nahrung	211	Triumph	Gegend		
212*	Pfad	Taufe	212	Pfad	Element		
213*	Meer	Topf	213	Meer	Liga		
214*	Panzer	Suppe	214	Panzer	Dame		
215*	Markt	König	215	Markt	Gras		
216*	Schnee	Karte	216	Schnee	General		
217*	Absatz	Gegend	217	Absatz	Taufe		
218*	Mutter	Reis	218	Mutter	Welle		
219*	Theater	General	219	Theater	Nahrung		
220*	Schweiß	Sturm	220	Schweiß	Schmuck		
221	Eiche	Abend	221	Eiche	Golf		
222	Theke	Kaiser	222	Theke	Arzt		
223	Kranz	Golf	223	Kranz	Arena		
224	Brett	Arzt	224	Brett	Abend		

225	Verlag	Arena	225	Verlag	Kaiser		
226*	Gold	Hose	226	Gold	Wolf		
227*	Stadt	Mütze	227	Stadt	Nase		
228*	Post	Instrument	228	Post	Krone		
229*	Damm	Heizung	229	Damm	Bremse		
230*	Knochen	Wand	230	Knochen	Mütze		
231*	Zweig	Tonne	231	Zweig	Heizung		
232*	Dichter	Nummer	232	Dichter	Tropfen		
233*	Schach	Hütte	233	Schach	Hose		
234*	Witz	Nase	234	Witz	Instrument		
235*	Sekt	Flotte	235	Sekt	Kapitel		
236*	Heer	Bremse	236	Heer	Tonne		
237*	Fels	Anstalt	237	Fels	Plan		
238*	Weizen	Wolf	238	Weizen	Nummer		
239*	Tal	Gewicht	239	Tal	Flotte		
240*	Regen	Kapitel	240	Regen	Sitz		
241*	Hand	Krone	241	Hand	Hütte		
242*	Ferien	Tropfen	242	Ferien	Wand		
243*	Herbst	Kette	243	Herbst	Anstalt		
244*	Gruß	Plan	244	Gruß	Gewicht		
245*	Atlantik	Sitz	245	Atlantik	Kette		
246	Pilz	Konzert	246	Pilz	Villa		
247	Zink	Winter	247	Zink	Konzert		
248	Schirm	Kohle	248	Schirm	Reh		
249	Metall	Sahne	249	Metall	Monat		
250	Lippe	Villa	250	Lippe	Ozean		
251	Kern	Kellner	251	Kern	Winter		
252	Maske	Taube	252	Maske	Tablett		
253	Huhn	Techniker	253	Huhn	Sahne		
254	Knopf	Monat	254	Knopf	Linde		
255	Tasche	Linde	255	Tasche	Taube		
256	Uniform	Reh	256	Uniform	Salz		
257	Sack	Ozean	257	Sack	Natur		

258	Zoll	Natur	258	Zoll	Wunde		
259	Bunker	Tablett	259	Bunker	Kellner		
260	Fleck	Vater	260	Fleck	Klub		
261	Kerze	Bus	261	Kerze	Fahne		
262	Karton	Klub	262	Karton	Kohle		
263	Schale	Fahne	263	Schale	Vater		
264	Roman	Salz	264	Roman	Techniker		
265	Sofa	Wunde	265	Sofa	Bus		
266	Braut	Fuchs	266	Braut	Fass		
267	Presse	Fass	267	Presse	Blei		
268	Uhr	Schlitten	268	Uhr	Pullover		
269	Kraft	Pullover	269	Kraft	Fuchs		
270	Gespenst	Blei	270	Gespenst	Schlitten		

Note: The grey marked words within the word-pairs were used in experiment one as single words for the IM task. As there was no IM task in the second experiment, they were used to create new non-related word-pairs.

The asterisk marks word-pairs which were used in experiment one and two.

Appendix C – Comparison of experiment one and two

Table C.1: Comparison of IQ, ESS and SSS between experiment one and two (standard deviation in parentheses).

	Experiment one		Experiment two
	Nap; n=22	**Control; n=19**	**Nap; n=21**
IQ	113.01 (12.8)	110.95 (12.4)	-
ESS	7.59 (3.53)	7.37 (2.99)	7.19 (2.91)
SSS1	2.8 (1.2)	2.7 (1.2)	1.9 (0.4)*
SSS2	-	-	2.9 (0.9)
SSS3	3.2 (1.2)	3.3 (1.1)	2.6 (0.9)
SSS4	3.1 (0.8)	-	2.9 (0.8)*
SSS5	2.0 (0.6)	3.1 (1.5)	2.1 (0.9)*
SSS6	1.6 (0.5)	2.1 (0.9)**	1.4 (0.5)*

* Marks significant comparison (after correction) between the **nap groups** of experiment one and two

** Marks significant comparison (after correction) between **nap groups** and **control group** of experiment one.[13]

Intelligence Quotient (IQ) was only estimated in the first experiment with the CFT 20-R; ESS: Epworth Sleepiness Scale; SSS: Stanford Sleepiness Scale; SSS1: before learning; SSS2: after learning (only measured in experiment two) SSS3: after pretest; SSS4: after napping (only measured for the nap groups); SSS5: before posttest, and SSS6: at the end of the experiment.

Participants in experiment two were feeling more awake than the nap participants at experiment one before learning, directly after sleeping and before the posttest as well as at the end of the experiment.

Both nap groups felt more awake at the end of the experiment than did the participants who were not allowed to sleep (control group).

[13] Comparison between nap and control group in experiment one are described elsewhere (Table 3.2).

Table C.2. Comparisons of nap mean characteristics (standard deviations in parentheses) for experiment one and two.

	Experiment one				Experiment two			
	Minutes		% of TST		Minutes		% of TST	
SL	14.18	(12.53)			14.83	(12.22)		
TST	64.25	(16.3)			70.64	(15.83)		
S1	9.64	(7.84)	15.14	(10.97)	8.14	(4.4)	11.56	(5.93)
S2	32.77	(10.85)	51.49	(13.13)	31.52	(13.51)	43.56	(12.68)
S3	11.2	(9.94)	17.13	(14.08)	10.36	(7.83)	15.04	(11.61)
S4	4.52	(5.21)	7.61	(9.22)	5.24	(6.58)	7.48	(9.45)
SWS	15.73	(12.19)	24.74	(18.78)	15.6	(12.14)	22.52	(17.99)
REM	6.11	(6.74)	8.63	(9.63)	3.02	(4.92)	3.79	(6.39)

SL: latency until sleep onset; TST: total sleep time; SWS: slow-wave-sleep; REM: rapid-eye-movement; S1-S4: Stage 1-Stage 2 sleep

Time spent in each sleep stage, sleep latency and TST were compared between the two experiments by using t-tests. No significant differences were obtained (all $p > .33$).

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Publikationsliste

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