

Does Sleep Selectively Strengthen Certain Memories Over Others Based on Emotion and Perceived Future Relevance?

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Abstract: Sleep has been found to have a beneficial effect on memory consolidation. It has furthermore frequently been suggested that sleep does not strengthen all memories equally. The first aim of this review paper was to examine whether sleep selectively strengthens emotional declarative memories more than neutral ones. We examined this first by reviewing the literature focusing on sleep/wake contrasts, and then the literature on whether any specific factors during sleep preferentially benefit emotional memories, with a special focus on the often-suggested claim that rapid eye movement sleep primarily consolidates emotional memories. A second aim was to examine if sleep preferentially benefits memories based on other cues of future relevance such as reward, test-expectancy or different instructions during encoding. Once again, we first focused on studies comparing sleep and wake groups, and then on studies examining the contributions of specific factors during sleep (for each future relevance paradigm, respectively). The review revealed that although some support exists that sleep is more beneficial for certain kinds of memories based on emotion or other cues of future relevance, the majority of studies does not support such an effect. Regarding specific factors during sleep, our review revealed that no sleep variable has reliably been found to be specifically associated with the consolidation of certain kinds of memories over others based on emotion or other cues of future relevance.

Keywords: sleep, memory, emotion, REM sleep, consolidation, forgetting

Introduction

A large body of studies has found sleep, as compared to wake, to be beneficial for memory consolidation (for an extensive review, see Rasch & Born¹). It has further frequently been suggested that sleep does not benefit all memories equally, but that sleep preferentially strengthens memories believed to be of high future relevance. Factors that determine the future relevance of a memory could be intrinsic to the material, such as emotion or personal interest, or manipulated extrinsic factors, such as information about a reward for successful remembering, knowledge that there will be a subsequent memory test, or forgetting instructions during encoding. Looking at peer-reviewed papers published 2018 and forward only, claims that sleep preferentially benefits memories based on their emotional value or their perceived future relevance are often repeated in both review papers and in the introduction sections of empirical studies as undisputed facts, or at least as if it was the typical finding in the field.²⁻²³ In this review paper, we aim to examine how robust these kinds of effects really are, by thoroughly reviewing the literature.

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The review consists of two parts based on what kind of future relevance has been examined. The first part examines the role of sleep in the consolidation of stimuli that are intrinsically emotional (and hence, by definition, relevant). The second part examines studies of sleep effects on intrinsically neutral material that has in some way been manipulated to establish a degree of future relevance (such as reward value, test-expectancy, or different forms of forgetting instructions).

We include studies in which items with different degrees of future relevance have been encoded, and in which there has been a delay interval containing sleep between encoding and the memory test. In each part, we will first discuss the literature that has contrasted sleep and wake groups, and then the literature examining whether there are any factors during sleep that are specifically involved in strengthening certain kinds of memories over others based on their perceived future relevance. Regarding specific factors during sleep, a special focus will be on the frequently made assertion that rapid eye movement (REM) sleep preferentially benefits emotional memories. Looking at literature published from 2018 and forward only, this is often cited as a fact or as the typical finding.^{7,9,16,18,19,21,24–30}

Scope and Methods

The literature search was mainly done by searching the database PsycINFO using the search terms “Sleep” AND “Memory” and combining them with either “Emotion”, “Emotional”, “Reward”, “Test-expectancy”, or “Forgetting”. Only articles published in peer-reviewed journals were considered, and we have only been interested in studies with human subjects. The first author scanned titles and abstracts of eligible studies to determine if they fitted the scope of the review. Beyond this search, we also examined the publication lists of all first and last authors of the papers we found, examined all papers cited in the reference lists of all eligible papers, and used Google Scholar to see which papers had cited the included papers. Finally, some papers were included because we heard about them from colleagues, on social media, or during conferences.

Scope for Studies on Sleep and Emotional Memory

For studies where the material has been intrinsically emotional, studies were included if they contained both emotional (positive and/or negative) and neutral stimuli. As the research question has been whether sleep has a different

effect on emotional memories as compared to neutral ones, we have not included studies that have contained only emotional stimuli, even if the emotions have been different (eg comparing negative vs positive material).

This part of the review only contains results concerning explicit memory performance for declarative memories, and not findings regarding, for example, affective ratings, or the effect of sleep on fear conditioning and extinction learning. Such paradigms only include emotional material (fear and safety stimuli, respectively), and thus do not allow for the examination of whether sleep strengthens emotional memories more than neutral ones.

Scope for Studies on Sleep and Other Factors Determining Future Relevance

Regarding studies using other cues of future relevance, we have considered additional kinds of outcome measurements (such as procedural memory). In this category, we have considered studies that have manipulated future relevance by, for example, informing participants about an upcoming memory test, or by incorporating a reward (eg cash) for successful remembering. Such manipulations allow the use of the same stimuli combined with different instructions, which is not possible when the material is intrinsically emotional.

Limits to the Scope

We have maintained a narrow focus so as to more thoroughly address the question whether sleep preferentially benefits memories based on their emotion or perceived future relevance. Thus, we have not considered changes in response times, or in neural or physiological responses. Additionally, we have focused on healthy participants only. When studies have included patient groups, we have simply focused on the results of the healthy control group. When a study has included different age groups, we have presented the results of these groups separately, and we have not been interested in interactions with age. When the age range of participants has not been reported, we have reported the mean age. When studies have not separated healthy controls from patient groups, or adults from children, we have attempted to contact the authors. We have omitted the one study for which the authors did not respond. We have further not considered groups added to control for circadian effects, correlations between changes in sleep architecture between baseline- and post-learning nights, or studies examining the effect of encoding strength based on the number of encoding trials, or

whether items were successfully learned during encoding. Lastly, we have not discussed results regarding the effects of different kinds of learning on sleep.

Structure of the Review

Results of studies with a strong degree of similarity to each other are presented in tables, whereas more unusual paradigms are described in text. Several studies have combined many different outcome measures for memory performance, and we believe it has been important to report all of these in order to not exaggerate the degree of significant findings.

Although it would have been preferable to perform a meta-analysis, this was not possible due to the large variation in experimental designs, and because statistics are not always reported in a manner that allows for calculation of effect sizes.

We have aimed to present studies so that they are as comparable to each other as possible. Therefore, we have mainly been interested in the interaction between Group (Sleep/Wake, or comparisons between different kinds of sleep groups) and Memory (of different kinds of items based on such factors as emotion or reward value), and in associations between different sleep variables and memory performance. When such information has been missing from studies, we have contacted the authors of the studies. In the cases where we did not receive answers from the study authors, we have settled for simply reporting what can be found in the articles. Some studies have, in the absence of significant interactions, still conducted post hoc *t*-tests and found significant results, but we have not included the results of these in this review (unless they are the only statistics reported). Thus, if no interaction has been found (ie, if the difference between different types of memories did not significantly differ between groups), we have considered it as a null-result, regardless of what post hoc *t*-tests might have shown.

The Effect of Sleep on the Consolidation of Emotional Memories

This section includes studies in which participants have encoded both emotional and neutral material (images, video clips, written stories or words), and have then been tested after a delay interval containing sleep. We will first present studies that have contrasted memory performance between emotional and neutral stimuli between a sleep and

a wake group. We will then describe the literature examining whether any specific factors during sleep preferentially benefit emotional memories. These are primarily correlational studies, but also include studies that have manipulated sleep in some other way without having a wake control group (eg comparing early sleep with late sleep, or studies where participants have been selectively deprived of a specific sleep stage). The majority of studies has looked at both sleep/wake contrasts and at variables during sleep. When this has been the case, we have divided the presentation of the results such that we discuss them in their respective sections.

The emotion of the material has often been varied along two dimensions: valence (ranging from negative to positive) and arousal (ranging from low intensity/activation to high intensity/activation). Almost all studies presented here, for which arousal and valence ratings have been explicitly reported, used stimulus material in which the emotional items differed from the neutral ones in both valence and arousal, such that negative and positive stimuli were more arousing than the neutral. We will therefore only discuss valence and arousal separately in the few studies where the predictive value of each has been explicitly tested.

Some studies have examined whether emotion and other factors associated with future relevance further interact to affect sleep-dependent memory consolidation. If these studies have manipulated the presence of other future relevance-factors between-groups, only the data from the groups that encoded neutral and emotional memories only (without any other information about future relevance), are discussed here, whereas the addition of other factors predicting future relevance are discussed in the section “Studies with Multiple Cues of Future Relevance”. Studies in which all participants were exposed to additional information affecting the future relevance of the stimuli are discussed only in the section “Studies with Multiple Cues of Future Relevance”.

Results from Studies Examining Sleep/Wake Contrasts

Two recent important contributions to the field have been two meta-analyses that examined if sleep, compared to wake, has a larger effect on emotional memories than on neutral ones. Schäfer et al³¹ only included studies using recognition tasks, and found that the aggregated studies on this topic does not support that sleep would have such an

effect. Furthermore, this was independent of what kind of sleep manipulation had been used (ie, naps or full night designs), or if memory encoding was incidental or explicit. In the other meta-analysis, Lipinska et al³² included all kinds of memory tasks, and also found no overall effect of sleep preferentially benefitting emotional memories. An analysis of moderators did, however, reveal that the effect of sleep specifically benefitting emotional memories was stronger in studies using free recall rather than recognition during the memory test, and when memory scores after the delay interval were controlled for by measurements of initial learning. One limitation of the Lipinska et al study,³² as pointed out by Schäfer et al,³¹ is that when comparing the effect on emotional memories with the effect on neutral memories, they treated these two as independent variables, without controlling for the potential within-subject correlations.

By writing a narrative review instead of a meta-analysis, our overview of the literature will include a greater scope of studies, and provide more detail about the differences between experimental paradigms and results, in order to give the reader a more comprehensive presentation of the field.

In this section, we have categorized studies based on which kind of memory task was used. We will first cover studies where emotion has varied between stimuli. We then describe studies that have examined whether sleep affects emotional and neutral components within the same stimuli to a different degree. Then, in the section “Other Tradeoff-Paradigms”, we discuss studies that have examined whether sleep affects memory for if neutral stimuli have previously been seen in neutral or negative contexts.

Recognition Tasks

Studies using recognition memory tests are presented in Table 1. When discussing studies using recognition tests, we have throughout the review only been interested in the difference between hits and false alarms, and not in either of these two outcome measures separately (unless that is the only thing that has been reported).

As shown in Table 1, only a small minority of studies using recognition memory tasks have found support for sleep selectively strengthening the memory of emotional stimuli.

In Bolinger et al study,⁶ the interaction was caused by an effect in the opposite direction, with sleep having a larger benefit for neutral items. In the Prehn-Kristensen

et al study,⁴⁸ sleep increased memory performance for happy and angry faces, but not for fearful or neutral ones.

In Tempesta et al,⁵⁰ the sleep group was additionally divided, post-hoc, into poor and good sleepers depending on their sleep quality. Contrasting these two groups revealed no differences in emotional memory performance. In two of the studies presented here,^{36,40} participants were also tested on memory for which location on the screen the objects had been shown on, using forced choice tasks.

Note that the results from the Wiesner et al study⁵³ refer to the comparison between all sleep participants (the slow-wave sleep (SWS)- and REM-deprived groups combined) and the wake control group (the comparison between the two sleep groups is presented in the section “Early Sleep/Late Sleep and Selective Sleep Deprivation Designs”). A similar distinction has been made for the Morgenthaler study,⁴⁴ where the results reported here are for all sleep participants (the normal sleep condition and the REM deprivation (REMD) condition combined), compared with the wake condition (the comparison of the REMD group with the normal sleep group is presented in the section “Early Sleep/Late Sleep and Selective Sleep Deprivation Designs”).

Forced Choice and Cued Recall Tasks

Studies using forced choice and cued recall are presented in Table 2.

As evident in Table 2, only one study has found sleep to have a larger effect on memory for emotional as compared to neutral stimuli. This was the Wagner et al study,⁵⁹ in which the early and late sleep groups were collapsed together, as were the two different wake control groups, to create a clear sleep/wake contrast (the initial test was an early sleep/late sleep design, reported in another paper,⁶⁰ discussed in the section “Early Sleep/Late Sleep and Selective Sleep Deprivation Designs”). Even though it is remarkable that the effects from the original study were still present four years later, no other studies using forced choice or cued recall tasks have found similar effects, even after much shorter delay intervals.

Moreover, one study⁵⁴ even found the opposite effect in one outcome measurement, with sleep having a larger effect on neutral memories. It should also be mentioned that Wagner et al⁵⁹ additionally tested memory performance for both free and cued recall, but found no differences in either of these measures (according to the authors, this was because these measurements were insensitive

Table 1 Studies Using Recognition Tasks

Study	Genders	Age Range	N	Between-Groups/ Within-Subjects	Sleep Manipulation	Stimulus Material	Emotions	Main Effect of Sleep	Interaction Sleep x Emotion
Ashton et al, 2019 ³³	Mixed	Mean=20	48	Between	DW/INS	Pictures	NN	No	No
Baran et al, 2012 ³⁴	Mixed	18–30	82	Between	DW/INS	Pictures	NN	Yes	No
Bolinger et al, 2018 ⁵	Mixed	8–11	16	Within	DW/INS	Pictures	NN	Yes	Yes, see text
Bolinger et al, 2019 ²⁴	Mixed	19–29	32	Between	DW/INS with a 2nd memory test one week later	Pictures	NN	Test 1 - No Test 2 - No	Test 1 - No Test 2 - No
Cellini et al, 2016 ³⁵	Mixed	20–30	46	Between	Nap design (either a 90-or 120-minute nap)	Pictures	NNP	Yes	No
Cox et al, 2018 ³⁶	Mixed	18–33	71	Between	DW/INS	Pictures PLA	NN	Pictures- No PLA - Yes	Pictures- No PLA - Yes
Cross et al, 2020 ³⁷	Mixed	18–41	21	Within	Nap design	Pictures	NNP	Yes	No
Göder et al, 2015 ³⁸	Mixed	19–39	16	Within	DW/INS	Pictures	NN	Yes	No
Gui et al, 2019 ³⁹									
Dataset 1	Mixed	18–25	57	Between	DW/INS with a 2nd memory test 72 h later	Pictures	NNP	Test 1 – Not reported Test 2 - Not reported	Test 1 - No Test 2 - No
Dataset 2	Mixed	58–78	62	Between	DW/INS with a 2nd memory test 72 h later	Pictures	NNP	Test 1 - Not reported Test 2 - Not reported	Test 1 - Yes Test 2 - No
Huan et al, 2020 ⁴⁰									
Dataset 1	Mixed	19–23	60	Between	DW/INS	Pictures PLA	NNP	Pictures- No PLA - No	Pictures- No PLA - No

(Continued)

Table 1 (Continued).

Study	Genders	Age Range	N	Between-Groups/ Within-Subjects	Sleep Manipulation	Stimulus Material	Emotions	Main Effect of Sleep	Interaction Sleep x Emotion
Dataset 2	Mixed	61–71	60	Between	DW/NS	Pictures PLA	NNP	Pictures- No PLA - No	Pictures- No PLA - No
Jones et al, 2016 ⁴¹									
Dataset 1	Mixed	50–80	42	Between	DW/NS	Pictures	NN	No	No
Dataset 2	Partially the same participants as in Baran et al, 2012 ³⁴								
Dataset 3	Mixed	50–80	48	Between	DW/NS	Pictures	NP	Yes	No
Dataset 4	Mixed	18–30	84	Between	DW/NS	Pictures	NP	No	No
Jones et al, 2018 ¹¹									
Dataset 1	Mixed	18–30	38	Between	DW/NS	Pictures	NN	Yes	No
Dataset 2	Mixed	35–50	41	Between	DW/NS	Pictures	NN	No	No
Jones & Spencer, 2019 ¹²	Mixed	18–28	62	Between	Nap design	Pictures	NN	Yes (trend)	No
Kashyap, 2019 ⁴²	Males	18–22	12	Within	TSD with the memory test ~ 21 h after encoding	Faces Scenes	Faces- NNP Scenes - NNP	Faces – Yes Scenes - Yes	Faces – No Scenes - No
Kurz et al, 2019 ³	Males	9–12	19	Within	DW/NS	Pictures	NN	Yes (trend)	No
Mantua et al, 2017 ³									
Partially the same participants as in Dataset 1 in Jones et al, 2018 ¹¹									
Morgenthaler et al, 2014 ⁴⁴	Mixed	19–25	29	Within	DW/NS	Pictures	NN	Yes	No
Nishida et al, 2009 ⁴⁵	Mixed	18–30	31	Between	Nap design	Pictures	NN	No	Yes
Prehn-Kristensen et al, 2009 ⁴⁶	Males	10–13	20	Within	DW/NS	Pictures	NN	Yes	Yes
Prehn-Kristensen et al, 2013 ⁴⁷									
Dataset 1	Males	9–12	16	Within	DW/NS	Pictures	NN	Yes	Yes

Dataset 2	Males	20–28	20	Within	DW/NS	Pictures	NN	Yes	No
Prehn-Kristensen et al, 2017 ⁴⁸	Males	9–11	16	Within	DW/NS	Faces	Angry, Fearful, Happy, Neutral	Yes	Yes, see text
Sawangjit et al, 2013 ⁴⁹	Males	18–25	10	Between	Nap design	Pictures	NNP	Not reported	No ANOVA reported, but t-tests revealed better performance for neutral items in the sleep group
Tempesta et al, 2015 ⁵⁰	Mixed	Mean=24	75	Between	TSD, with the re-test 24 h after encoding	Pictures	NNP	Yes	No
Tempesta et al, 2017 ⁵¹	Mixed	20–28	48	Between	TSD, with the re-test 48 h after encoding	Film clips	NNP	Yes	No
Wagner et al, 2007 ⁵²	Mixed	19–30	12	Within	TSD, with the re-test 43 h after encoding	Faces	Neutral, Angry, Happy	Yes	No
Wiesner et al, 2015 ⁵³	Mixed	18–30	62	Between	DW/NS, see text	Pictures	NN	No	No

Abbreviations: DW/NS, daytime wake/nighttime sleep; NN, neutral and negative; NNP, neutral, negative, and positive; PLA, picture-location associations; NP, neutral and positive; TSD, total sleep deprivation.

Table 2 Studies Using Forced Choice and Cued Recall

Study	Memory Task	Genders	Age Range	N	Sleep Manipulation	Stimulus Material	Emotions	Main Effect of Sleep	Interaction Sleep x Emotion
Alger & Payne, 2016 ⁵⁴	FC	Mixed	Mean=20	58	Nap design	FOA	NN	AM - Yes RM - Yes	AM - Yes, but in the opposite direction with sleep preferentially benefitting neutral items. RM - No
Gilson et al, 2016 ⁵⁵	CR	Mixed	Mean=22	24	Short nap vs long nap	Audio stories	NN	No	No
Huguet et al, 2019 ⁹	FC	Mixed	Mean=20	55	DW/NS	FOA	NN	AM - Yes RM - Yes	AM - No RM - No
Lehmann et al, 2016 ⁵⁶								Yes	No
Dataset 1	CR	Mixed	Mean=22	36	DW/NS	WPA	NN	Yes	No
Dataset 2	CR	Mixed	Mean=22	36	DW/NS	WPA	NP	Yes	No
Schoch et al, 2019 ⁵⁷	CR	Mixed	19–35	22	A night of normal sleep vs a night with repeated awakenings	WPA	NP	No	No
Vermeulen et al, 2017 ⁵⁸	FC	Mixed	9–11	386	DW/NS with two additional groups (one sleep and one wake) that did the memory test additionally 24 h later	Word-pairs	NNP	No	No
Wagner et al, 2006 ⁵⁹	FC	Males	24–34	23	Early sleep/Late sleep with corresponding wake control groups; Memory test 4 years after encoding, see text	Texts	NN	Yes (trend)	Yes

Abbreviations: FC, forced choice; FOA, face-object associations; NN, neutral and negative; AM, associative memory; RM, relational memory; CR, cued recall; DW/NS, daytime wake/nighttime sleep; WPA, word-picture associations; NP, neutral and positive; NNP, Neutral, Negative, and Positive.

Table 3 Studies Using Remember/Know Tasks

Study	Genders	Age Range	N	Between-Groups/ Within-Subjects	Sleep Manipulation	Stimulus Material	Emotions
Atienza & Cantero, 2008 ⁶¹	Mixed	19–28	28	Between	TSD with the test 7 days later	Pictures	NNP
Harrington et al, 2018 ⁸	Mixed	18–25	28	Between	TSD with a second memory test 7 days later	Pictures	NNP
Hu et al, 2006 ⁶²	Mixed	Mean=23	14	Within	DW/NS	Pictures	Same valence, varying in arousal only
Sterpenich et al, 2007 ⁶³	Mixed	Mean=22	39	Between	TSD with the test after 2 recovery nights	Pictures	NNP
Sterpenich et al, 2009 ⁶⁴	Same participants as in Sterpenich et al, 2007, ⁶³ contains the results of a second memory test 6 months later, see text						

Abbreviations: TSD, total sleep deprivation; NNP, neutral, negative, and positive; DW/NS, daytime wake/nighttime sleep.

after such a long time interval). In the Vermeulen et al study,⁵⁸ the separate predictive values of valence and arousal was tested using a regression model that revealed no effect of either.

Only two studies in this section have manipulated sleep within-subjects.^{55,57} The Gilson et al study⁵⁵ did not have a wake group, but compared 45-minute naps with 90-minute naps, with an equal amount of time passing between learning and the memory test in both conditions. All participants were part of two different sessions, one where they listened to a neutral story, and one in which they listened to a sad story.

Two studies^{9,54} tested both associative memory (the ability to remember which objects were previously presented together) and relational memory (the ability to remember the relation between two stimuli that had both been presented together with the same third stimulus, without ever having been presented together).

Remember/Know Tasks

Studies using Remember/Know tasks are presented in Table 3. The methods of these studies have been so varied that we have only included some brief information in the table and then presented the methods and results in running text. All studies reported here have included participants of mixed genders.

The only study using a Remember/Know task that has found a specific benefit of sleep on emotional memory is Hu et al,⁶² who compared high-arousing images with medium-arousing images (valence scores were equivalent between the high- and the low-arousing images). This study found better recognition accuracy for “Know” responses for the arousing images in the sleep condition

compared to in the wake condition. No such effects of sleep were found for the neutral images, or for “Remember” responses regardless of arousal.

Sterpenich et al⁶³ found a trend toward an interaction in the opposite direction at a re-test taking place 72 hours after encoding. This trend was driven by better memory in the sleep group for positive and neutral images, whereas sleep deprivation did not impair memory performance for negative items. This effect was only present for “Remember”, and not for “Know” responses. An additional re-test taking place six months later revealed no differences in memory performance for either emotion between the groups for either response type.⁶⁴

Another study, with the memory test taking place one week after encoding, revealed no interaction effects between group and emotion for either response type.⁶¹ This study systematically varied both the valence and the arousal of the stimulus material, but found no interactions of sleep with either valence or arousal. The Harrington et al study⁸ had two different re-tests, 12 hours and 7 days after the initial encoding respectively. Results revealed no interaction of sleep and emotion for either “Know” or “Remember” responses at either test.

Free Recall Tasks

Studies using free recall tasks are presented in Table 4. The stimulus material and the ways of presenting the results in these studies have been so varied that we have only included some brief information in the table, and then presented the results in running text. All studies included here have manipulated sleep between groups, and included participants of mixed genders.

Table 4 Studies Using Free Recall Tasks

Study	Age Range	Sample Size	Sleep Manipulation	Stimulus Material	Emotions
Ackermann et al, 2015 ⁶⁵	Partially the same participants as in Schoch et al, 2017 ⁶⁶				
Ackermann et al, 2019 ⁶⁷	18–33	39	Nap design	Pictures	NNP
Chambers & Payne, 2014 ⁶⁸	Mean=20	70	DW/NS	Cartoons with captions	Literal, funny, or “weird” captions
McKeon et al, 2012 ⁶⁹	Mean=20	30	DW/NS	Words	NN
Schoch et al, 2017 ⁶⁶	18–35	228	DW/NS	Pictures	NNP
Van Heugten-van der Kloet et al, 2015 ⁷⁰	18–29	56	TSD	Movie clips	NNP

Abbreviations: NNP, neutral, negative, and positive; DW/NS, daytime wake/nighttime sleep; NN, neutral and negative; TSD, total sleep deprivation.

As evident in Table 4, two free recall studies have found sleep to be more beneficial for emotional memories compared to neutral ones. One study found impaired memory performance for a positive video clip, but not for a neutral or negative one, after a night of total sleep deprivation (TSD) with the memory test the next morning.⁷⁰ This study revealed no signs of TSD affecting memory for temporal order for any of the movie clips. Another study found sleep to have a more beneficial effect on memory for humorous material compared to non-humorous material.⁶⁸

One study found an effect in the opposite direction.⁶⁹ No group difference was found in memory performance for the negative items, but the wake group had a higher memory performance for neutral items. This study also examined the effect of sleep on the formation of false memories, but found no group difference, regardless of emotion.

Two studies have found no support for sleep differentially affecting emotional and neutral memories. Schoch et al⁶⁶ used a design that manipulated not only sleep and wake, but also the presence or absence of an immediate recall test right after encoding, and the presence or absence of an interference task (where a set of novel images were viewed right before the memory test after the delay interval). This made for eight groups in total (Sleep/Wake x Immediate recall/No immediate recall x Interference task/No interference task). The groups without either the immediate recall test or the interference task were also reported in Ackermann et al.⁶⁵ Results revealed no specific effect of sleep on emotional memory, regardless of the presence of the immediate re-test (after controlling for initial group differences in memory performance on the immediate re-test). Nor was there any interaction between sleep, emotion and interference, indicating that the effect of interference on

memory performance after sleep or wake was not differently affected by emotion. In another study,⁶⁷ there was no interaction between sleep and emotion. This study also included a manipulation in which participants were subjected to a psychosocial stressor after encoding, for which the results are discussed in the section “Pre-Sleep Stressors”.

The Emotional Trade-Off Paradigm

Beyond comparing emotional and neutral stimuli between each other, it is of interest to examine how sleep affects memory for different components within the same stimuli, depending on their emotional character. In the emotional trade-off paradigm, participants first view scenes consisting of an object placed on a neutral background image. Half of the objects are emotional (typically negative), and the other half are neutral. The memory test is a recognition task in which the objects and backgrounds are shown separately. The aim of this is to examine if there is a specific strengthening of emotional objects, in the absence of a strengthening of the neutral backgrounds on which they have been presented. By adding sleep to this paradigm between encoding and the memory test, it is possible to examine if sleep strengthens this emotional trade-off effect.

The first study⁷¹ using the emotional trade-off paradigm in combination with sleep found improved memory performance in the sleep group for the negative objects, but not for the neutral objects or for the backgrounds (regardless of whether they had previously been associated with a neutral or a negative object). The finding that memory of the backgrounds that had contained the negative objects were not strengthened by sleep suggests that sleep helps to “unbind” the negative objects from their respective backgrounds. In Table 5, we have listed

Table 5 Studies Using the Emotional Trade-off Paradigm

Study	Age Range	N	Sleep Manipulation	Emotions	Interaction Sleep x Emotion x Component
Alger et al, 2018 ³					
Dataset 1	18–39	45	Nap design	NN	Yes
Dataset 2	40–64	35	Nap design	NN	Yes
Bennion et al, 2015 ⁷²	18–34	42	DW/NS	NN	N/A, see text
Bennion et al, 2017 ⁷³	18–34	47	DW/NS	NN	N/A, see text
Chambers & Payne, 2014 ⁷⁴	18–32	60	DW/NS	NP	Remember - No Know - No
Cunningham et al, 2014 ⁷⁵					
Dataset 1	Not reported (students)	39	DW/NS - expecting the memory test	NN	No
Dataset 2	Not reported (students)	41	DW/NS - not expecting the memory test	NN	No
Cunningham et al, 2014 ⁷⁶	The same participants as in Dataset 2 in ⁷⁵				
Payne et al, 2008 ⁷¹	Not reported (students)	48	DW/NS	NN	Yes
Payne & Kensinger, 2011 ⁷⁷	18–29	39	DW/NS	NN	Yes
Payne et al, 2012 ⁷⁸	18–22	44	DW/NS with the re-test 24 h after encoding	NN	Yes
Payne et al, 2015 ⁷⁹	18–26	57	Nap design	NN	Yes
Vargas et al, 2019 ⁸⁰	Mean=23	39	TSD	NN	No

Abbreviations: NN, neutral and negative; DW/NS, daytime wake/nighttime sleep; NP, neutral and positive; TSD, total sleep deprivation.

the studies that have used this paradigm in combination with sleep. All studies mentioned here have manipulated sleep between-groups, and have included participants of mixed genders. We have focused on the most important outcome measurement, ie, the interaction between sleep, emotion and scene component (object/background). Again, we have not considered results from post hoc *t*-tests if the ANOVA did not reveal a significant interaction.

As seen in Table 5, sleep has been found to result in a larger emotional trade-off effect than wake in the majority of studies. In two of the studies,^{3,78} there were also signs of sleep actively impairing memory for the backgrounds that had previously been associated with negative objects. The two Bennion et al papers^{72,73} were based on the same data collection, with one presenting results from the objects and the other from the backgrounds. Neither study found an interaction between sleep and emotion.

Two studies have showed larger trade-off effects when sleep occurs in closer proximity to encoding,^{3,78} and one study found a larger effect after sleep even when the sleep group had a longer delay interval between encoding and the memory test.⁷⁹ For the results regarding the interaction between test-expectancy, sleep, and emotional trade-off in the Cunningham et al study,⁷⁵ see the section “Studies with Multiple Cues of Future Relevance”.

Other Tradeoff-Paradigms

There are paradigms that are similar to the emotional trade-off paradigm in the sense that they have measured whether sleep affects different components within the same stimuli based on their emotional value. The difference is that in these other paradigms, the objects have been neutral and the contexts have varied in emotion. These studies are listed in Table 6, and are described further below. All studies

Table 6 Other Trade-off Paradigms

Study	Age Range	N	Sleep Manipulation	Stimulus Material	Emotions	Main Effect of Sleep	Interaction Sleep x Emotion
Cairney et al, 2014 ⁸¹	Same participants as in Dataset 2 in Lewis et al, 2011 ⁸²						
Kuriyama et al, 2010 ⁸³	20–33	28	TSD with a 2nd memory test 7 days later	Video clips	NN	Test 1 - No Test 2 - No	Test 1 - No Test 2 - No
Kuriyama et al, 2013 ⁸⁴	20–29	30	TSD with the test 48 h after encoding	Video clips	NN	No	No
Lewis et al, 2011 ⁸²							
Dataset 1	19–32	22	DW/NS	OBA	Objects - Neutral Backgrounds - NN	OM - No CM - Yes	OM - No CM - No
Dataset 2	18–34	38	Nap design	OBA	Objects - Neutral Backgrounds - NN	OM - No CM - Yes	OM - No CM - No
Sopp et al, 2018 ²¹	Mean=23	46	Nap design; second re-test 22 h later	OSA	Objects - Neutral Scenes - NN	IM test 1 - No AM test 1 - Yes IM test 2 - No AM test 2 - Yes, such that there was a larger performance decrease in the nap group between the first and second re-test	IM test 1 - No AM test 1 - No IM test 2 - No AM test 2 - No

Abbreviations: TSD, total sleep deprivation; NN, neutral and negative; DW/NS, daytime wake/nighttime sleep; OBA, object-background associations; OM, object memory; CM, context memory; OSA, object-scene associations; IM, item memory; AM, associative memory.

mentioned here have manipulated sleep between-groups, and all have included participants of mixed genders.

As evident in Table 6, no studies have found support for an interaction between sleep and emotion when it comes to remembering whether neutral objects have previously been presented in neutral or negative contexts.

Lewis et al⁸² had participants first view neutral objects imposed on either negative or neutral backgrounds. During the memory test, participants were re-exposed to only the objects. The outcome measurements were recognition (object memory) and whether participants remembered if the objects had been previously presented on either neutral or negative backgrounds (ie context memory).

Sopp et al²¹ had participants first view combinations of neutral objects and either neutral or negative scenes.

During the memory test, participants viewed object-scene combinations that were either the same as the ones presented during encoding, completely novel objects and scenes, or novel combinations of the objects and scenes seen during encoding. Item memory was assessed by measuring participants' ability to separate old and recombined images from new images. Associative memory (ie, which items were linked to which scenes) was assessed by measuring the ability to distinguish old combinations from recombined ones.

Kuriyama et al^{83,84} tested whether sleep affected memory for if neutral images had previously been seen as part of a video clip containing a motor vehicle accident, or part of a video clip showing normal traffic. The memory test also contained some novel images that had not been seen

before. One of these studies⁸⁴ also included a group that received directed forgetting instructions during encoding, the results of which are discussed in the section “Studies with Multiple Cues of Future Relevance”.

Summary of Sleep/Wake Contrasts

As we have seen in this section, studies finding sleep to be specifically beneficial for emotional memories are the exception rather than the rule. The emotional trade-off paradigm has, however, reliably replicated sleep to have a larger benefit for emotional compared to neutral items in a majority of studies. Other similar paradigms have, however, not revealed an emotion-specific unbinding role of sleep.

Results from Studies Focusing on Specific Sleep Variables

This section will focus on studies examining whether there are any factors during sleep that selectively benefit the consolidation of emotional memories. Most findings regard the contributions of different sleep stages, but various other factors, such as sleep duration, targeted memory re-activation (TMR), and pharmacological manipulations, will be discussed as well.

We will first present studies that have manipulated sleep in some way to compare the effect of different sleep stages (comparing sleep in the early half of the night with sleep in the late half of the night, and selective sleep deprivation designs). We will then discuss results from correlational studies, where we will also present correlational results from groups in which sleep has been manipulated in some way. Finally, we will discuss studies that have manipulated sleep in some other way than those previously mentioned, such as pharmacologically, or with target memory re-activation.

Early Work with a Psychodynamic Approach

Early studies on the contribution of specific sleep stages to memory consolidation had a special focus on the role of REM sleep and had a clear psychodynamic approach, where REM was viewed as synonymous with dreaming.^{85,86} The suggested role of REM sleep/dreaming in these accounts was to integrate novel stressful experiences with similar experiences from the past. Without REM sleep, no such integration would occur, which would make people less able to deal with threatening experiences, prompting the need to repress them. This repression was in turn expected to make these experiences less accessible for retrieval during memory tests. Results from these studies revealed that

REMD decreased memory performance for personality traits participants wished they had more of,⁸⁵ and for anagrams they had failed to solve.⁸⁶

Sleep and memory studies are rarely conducted with this kind of psychodynamic approach anymore, and it is difficult to say that better memory for anagrams that one has failed to solve, or for personality traits one wishes to have more of, is synonymous with a decreased need to repress these items.

Early Sleep/Late Sleep and Selective Sleep Deprivation Designs

Comparing the effect of sleep in the early half of the night with sleep in the late half of the night allows for comparisons between two sleep periods with different sleep architecture (as the early night is dominated by SWS, and the late night by REM). Another way of manipulating the presence of a sleep stage is by simply waking participants up every time they enter the stage one wants to reduce the presence of. The meta-analysis by Schäfer et al³¹ showed that when combining early sleep and REMD groups, and comparing them with late sleep and normal sleep groups, there was a significant effect of REM-rich sleep intervals resulting in increased memory performance specifically for emotional items. Early sleep/Late sleep and selective sleep deprivation designs are presented in Table 7.

In the Groch et al study,⁸⁹ participants were also tested on memory for the color of a frame that preceded each image, as well as the location on the screen where the image had been presented. Results revealed a trend toward better memory for the associated color frames after early sleep compared to after late sleep. This effect was, however, only evident for the frames preceding the neutral pictures, and not for the frames preceding negative ones. Similar results were found by Sopp et al,⁹¹ where source memory (picture-location associations) was better for neutral items compared to negative items after early sleep. The opposite effect was found following late sleep, where source memory performance was better for the negative images. This study also included a wake group that did the encoding in the morning and the re-test three hours later. The data of this group were analyzed separately from the sleep groups and were therefore not directly contrasted, but results revealed that unlike in the sleep groups, source memory for negative and neutral images decreased to a similar extent during the wake delay interval.

Harrington et al²⁵ used a Remember/Know task as their memory test, but only reported results of the “Remember”

Table 7 Early Sleep/Late Sleep and Selective Sleep Deprivation Designs

Study	Genders	Age Range	N	Sleep Paradigm	Between-Groups/Within-Subjects	Stimulus Material	Emotions	Type of Memory Test	Interaction Sleep Type x Emotion
Goldschmied et al, 2015 ⁸⁷	Mixed	18–48	12	Overnight vs SWSD	Within	Words	NNP	R/K, see text	No
Groch et al, 2013 ⁸⁸	Males	20–26	16	Early sleep/Late sleep	Within	Pictures	NN	Recog	Yes, see text
Groch et al, 2015 ⁸⁹	Mixed	18–26	18	Early sleep/Late sleep	Within	Pictures PCA PLA	NN	Pictures - Recog PCA - FC PLA - FC	Pictures - Yes (trend) PCA - Yes PLA - No
Harrington et al, 2018 ²⁵	Mixed	18–29	12	Early sleep/Late sleep	Within	Pictures	NNP	R/K, see text	No
Morgenthaler et al, 2014 ⁴⁴	Mixed	19–25	29	Overnight vs REMD	Between	Pictures	NN	Recog	No
Solomonova et al, 2017 ⁹⁰	Not reported	Not reported	14	Overnight vs REMD, see text	Between	Faces	NN	Recog	No
Sopp et al, 2017 ⁹¹	Mixed	Mean=23	38	Early sleep/Late sleep	Between	Pictures PLA	NN	Pictures - R/K PLA - FC	R responses - No K responses - No R and K combined - No PLA - Yes
Wagner et al, 2001 ⁶⁰	Males	20–30	12	Early sleep/Late sleep	Within	Texts	NN	FR	Yes
Wiesner et al, 2015 ⁵³	Mixed	Mean=24	62	Wake/REMD/SWSD	Between	Pictures	NN	Recog	No

Abbreviations: SWSD, slow-wave sleep deprivation; NNP, neutral, negative, and positive; R/K, remember/know; NN, neutral and negative; Recog, recognition; PCA, picture-color associations; FC, forced choice; PLA, picture-location associations; REMD, REM deprivation; R, remember; K, know; FR, free recall.

responses. Similarly, in the Goldschmied et al study,⁸⁷ the memory test was a Remember/Know task but results were presented for “Remember” answers only, and “Know” responses were considered incorrect. SWS reduction was accomplished using a tone that suppressed slow waves during sleep. In the Solomonova et al study,⁹⁰ participants in the REMD group were repeatedly woken up five minutes after the first sign of REM, whereas the control group were subjected to an equal number of awakenings but 25 minutes after the first sign of REM. It should also be mentioned that the Wagner et al study⁶⁰ additionally contained two wake control groups.

Correlational Studies

Even if it would be established that REM-rich sleep specifically benefits memory for emotional items, early sleep/late sleep and selective REMD designs cannot decisively tell us that REM is the main factor behind this, considering that early and late sleep also differ in other ways. To further examine if REM sleep, or any other sleep variable, preferentially consolidates emotional memories, and if it does so in a dose-dependent manner, we will in this section present correlational studies on sleep and memory performance for emotional and neutral items respectively. We will present all correlational findings here, also for studies in which sleep has in some way been manipulated. When possible, we have presented correlations for each subgroup separately (such as different kinds of manipulations of sleep). Group comparisons between these different subgroups are reported in either the section “Early Sleep/Late Sleep and Selective Sleep Deprivation Designs” or in the section “Other Ways of Manipulating Sleep to Affect Sleep-Dependent Emotional Memory Consolidation”.

When procedures for correcting for multiple comparisons have been included in the papers, we have only included correlations that survived after such corrections. When the procedure for such corrections have not been reported, we have included all correlations that have been presented. We have only included correlations that are significant, and only those that have concerned either emotional or neutral items specifically. Thus, when a sleep variable has been correlated with memory performance regardless of emotion, this has not been reported. Most studies have carried out separate correlations between sleep variables and neutral and emotional memories respectively, whereas some have subtracted the score for neutral items from the score for emotional items to create an emotional memory bias variable. Studies using

actigraphy instead of polysomnography (PSG) have only been included if correlations have been reported.

Some studies have examined the correlation between memory performance and time spent in a sleep stage during only a half or even a quartile of the night. Such correlations will not be mentioned here, as very little is known about how different sleep stages would have different functions depending on when during the night they occur. Until we have more knowledge of this, we find the meaning of those results difficult to interpret, and that including them greatly increase the risk of false positives. Correlations in studies that beyond emotions have also included other manipulations of the perceived future relevance of items are not discussed here, but instead in the section “Factors During Sleep in Studies with Multiple Cues of Future Relevance”.

Studies examining correlations between sleep variables and memory performance specifically for either neutral or emotional items are presented in Table 8. We have written “None” when there were no significant correlations, and “None reported” when information about correlations has not been reported in the article. When correlations have not been reported, we have attempted to contact the authors.

We would like to give special attention to the (by far) largest study conducted on this topic to date. Ackermann et al⁶⁵ tested 929 participants, almost half as many as all the other studies combined. Nothing in the PSG; percentage or duration of time spent in either sleep stage, spindle count, spindle density (number of spindles divided by total time spent in non-rem (NREM) sleep), theta activity during REM, REM density (number of rapid eye movements divided by time spent in REM sleep) or REM latency correlated with memory for either neutral or emotional images. This is the largest study ever carried out on the topic, and considering that it found no significant correlations between any sleep variable and the specific consolidation of emotional memories, the results of the other studies presented in this section, which have considerably less power, should be taken with a large grain of salt.

As evident by the table, among all the studies that have included PSG, only four^{45,53,78,88} have found clear correlations between REM sleep and memory for emotional items specifically. This represents a very small minority of the conducted studies.

Regarding correlations with factors related to NREM-sleep, there has been some significant findings related to spindles and SWS, but these have not been reliably

Table 8 Factors During Sleep Specifically Associated with Consolidation of Emotional Memories

Study	Genders	Age Range	N	Type of Sleep	Stimulus Material	Emotions	Memory Task	Correlations with Memory Performance
Ackermann et al, 2015 ⁶⁵	Mixed	18–35	929	Overnight	Pictures	NNP	FR	None
Ackermann et al, 2019 ^{67 a}								
Dataset 1	Mixed	18–33	20	Nap + preceding stressor	Pictures	NNP	FR	None
Dataset 2	Mixed	18–33	20	Nap + no stressor	Pictures	NNP	FR	None
Alger & Payne, 2016 ⁶⁴	Mixed	Mean=20	28	Nap	FOA	NN	AM - FC RM - FC	Neg. corr: betw. %REM and AM for neutral items; Pos. corr: betw. %REM and RM for neutral items
Alger et al, 2018 ³								
Dataset 1	Mixed	18–39	29	Nap	ETO	NN	Recog	Pos. corr: betw. %SWS and negative objects; Pos. corr: betw. SO power and negative objects; Pos. corr: betw. delta power and negative objects; Pos. corr: betw. total number of spindles during SWS and negative objects; Pos. corr: betw. spindle density during SWS and negative objects (trend); Pos. corr: betw. average duration of spindles during SWS and negative objects; Pos. corr: betw. spindle amplitude during SWS and negative objects; Pos. corr: betw. spindle power during SWS and negative objects
Dataset 2	Mixed	40–64	24	Nap	ETO	NN	Recog	None
Datasets 1 and 2 combined	Mixed	18–64	53	Nap	ETO	NN	Recog	Pos. corr: betw. %SWS and negative objects; Pos. corr: betw. the total number of spindles during SWS and negative objects; Pos. corr: betw. spindle density during SWS and negative objects (trend); Pos. corr: betw. average duration of spindles during SWS and negative objects; Pos. corr: betw. spindle amplitude during SWS and negative objects; Pos. corr: betw. spindle power during SWS and negative objects
Ashton et al, 2018 ⁵	Mixed	18–29	19	Nap + TMR	Pictures PLA	NN	Pictures -R/K Locations -FC	None

Baran et al, 2012 ³⁴	Mixed	Mean=20	25	Overnight	Pictures	NN	Recog	None
Benedict et al. 2009 ⁹² a								
Dataset 1	Males	20-36	14	Overnight + IL-6	Texts	NN	FR	None
Dataset 2	Males	20-36	14	Overnight + Placebo	Texts	NN	FR	None
Bennion et al, 2015 ⁷²	Mixed	18-34	25	Overnight	Pictures	NN	Recog (objects only, backgrounds reported in Bennion et al ⁷³)	None reported
Bennion et al, 2017 ⁷³	Mixed	18-34	26	Overnight	Pictures	NN	Recog (backgrounds only, objects reported in Bennion et al ⁷²)	None reported
Bolinger et al, 2018 ⁶	Mixed	8-11	16	Overnight	Pictures	NN	Recog	None
Bolinger et al, 2019 ²⁴	Mixed	19-29	16	Overnight with a 2nd memory test 7 days later	Pictures	NN	Recog	None
Bueno-Lopez et al. 2020 ⁹³ a								
Dataset 1	Males	20-30	30	Overnight + RF-EMF	Faces	Neutral Happy Angry	Recog	None
Dataset 2	Males	20-30	30	Overnight + Sham	Faces	Neutral Happy Angry	Recog	None
Cairney et al, 2014 ²⁴	Mixed	18-28	15	Overnight + TMR	PLA	NN	FC	None
Cairney et al, 2014 ⁸¹	Mixed	Mean=21	19	Nap	Objects OBA	Objects - Neutral; Backgrounds -NN	Recog/FC	Neg. corr. betw. spindle count and neutral contexts; Pos. corr. betw. S2 duration and negative contexts
Cairney et al, 2015 ⁹⁵	Mixed	19-28	16	Overnight	Pictures	NNP	R/K	Pos. corr. betw. %SWS and negative items; Neg. cor betw. %REM and positive items
Cellini et al, 2016 ³⁵	Mixed	20-30	30	60 or 90 minute naps (both nap groups combined for the analysis)	Pictures	NNP	Recog	Pos. corr. betw. S2 duration and negative items; Pos. corr. betw. spindle count during S2 and negative items; Pos. corr. betw. TST and negative items
Cellini et al, 2019 ⁹⁶	Mixed	Mean=23	30	Sleep averaged over 7 nights	Pictures	NN	Recog	None (actigraphy)

(Continued)

Table 8 (Continued).

Study	Genders	Age Range	N	Type of Sleep	Stimulus Material	Emotions	Memory Task	Correlations with Memory Performance
Chambers & Payne, 2014 ⁷⁴	Mixed	18-32	31	Overnight	ETO	NP	R/K	Neg. corr: betw. REM latency and positive objects (for Know responses only)
Cox et al, 2018 ³⁶	Mixed	18-33	46	Overnight	Pictures PLA	NN	Pictures - Recog PLA - FC	None
Cross et al, 2020 ³⁷	Mixed	18-41	21	Nap	Pictures	NNP	Recog	Pos. corr: betw. theta power during REM and positive items; Pos. corr: betw. theta power during REM and neutral items ^b
Denis et al, 2021 ²³								Same participants as in Kim et al, 2020 ²⁷
Gilson et al, 2016 ^{55 c}								
Dataset 1	Mixed	Mean = 22 for the whole sample	12	45-minute nap	Audio story	Sad	CR	None
Dataset 2	Mixed	Mean = 22 for the whole sample	12	90-minute nap	Audio story	Sad	CR	Pos. corr: betw. REM density and memory performance
Dataset 3	Mixed	Mean = 22 for the whole sample	12	45-minute nap	Audio story	Neutral	CR	None
Dataset 4	Mixed	Mean = 22 for the whole sample	12	90-minute nap	Audio story	Neutral	CR	None
Göder et al, 2015 ³⁸	Mixed	19-39	18	Overnight	Pictures	NN	Recog	Pos. corr: betw. spindle density during S2 and neutral items
Goldschmied et al, 2015 ⁸⁷	Mixed	18-48	12	Overnight + SWSD	Words	NNP	R/K	None
Groch et al, 2011 ^{97 a}								
Dataset 1	Males	19-28	14	Early sleep + Norepinephrine decrease	Texts Pictures	NN	Texts - FR; Text temporal order - FR/CR Pictures - FR & Recog;	None
Dataset 2	Males	19-28	14	Early sleep + Placebo	Texts Pictures	NN	Texts - FR Text temporal order - FR/CR; Pictures - FR & Recog	None
Groch et al, 2013 ^{88 a}								
Dataset 1	Males	20-26	15	Early sleep	Pictures	NN	Recog	None

Dataset 2	Males	20–26	15	Late sleep	Pictures	NN	Recog	Pos. corr. betw. %REM and negative items
Groch et al, 2015 ⁸⁹ a								
Dataset 1	Mixed	18–26	18	Early sleep	Pictures PCA PLA	NN	Pictures - Recog PCA - FC PLA - FC	None
Dataset 2	Mixed	18–26	18	Late sleep	Pictures PCA PLA	NN	Pictures - Recog PCA - FC PLA - FC	None
Gui et al, 2019 ³⁹								
Dataset 1	Mixed	18–25	28	Overnight, second memory test 72 h later	Pictures	NNP	R/K (collapsed for the analysis)	Re-test 1 - Negative corr. betw. % deep sleep and negative items; Re-test 2 - None reported (Actigraphy)
Dataset 2	Mixed	58–78	29	Overnight, second memory test 72 h later	Pictures	NNP	R/K (collapsed for the analysis)	Re-test 1 - None; Re-test 2 - None reported (Actigraphy)
Harrington et al, 2018 ²⁵								
Dataset 1	Mixed	18–29	12	Early Sleep	Pictures	NNP	R/K	None
Dataset 2	Mixed	18–29	12	Late Sleep	Pictures	NNP	R/K	None
Harrington et al, 2018 ⁸	Mixed	18–25	14	Overnight, second memory test 7 days later	Pictures	NNP	R/K	Re-test 1 - Neg. corr. betw. REM duration and R responses for positive items; Re-test 2 - None
Harrington et al, 2019 ⁷ d	Females	Mean=19	36	Overnight	Pictures	NNP	R/K	None
Huan et al, 2020 ⁴⁰								
Dataset 1	Not reported	19–23	30	Overnight	Pictures PLA	NNP	Pictures - Recog PLA - FC	None
Dataset 2	Not reported	61–71	30	Overnight	Pictures PLA	NNP	Pictures - Recog PLA - FC	Neg. corr. betw. TST and negative items (trend; actigraphy)
Huguet et al, 2019 ⁹	Mixed	18–26	24	Overnight	FOA	NN	AM - FC RM - FC	None
Hutchison et al, 2021 ⁹⁸								
Dataset 1	Females	18–27	18	Overnight + TMR during SWS	SPA	NN	FC	None

(Continued)

Table 8 (Continued).

Study	Genders	Age Range	N	Type of Sleep	Stimulus Material	Emotions	Memory Task	Correlations with Memory Performance
Dataset 2	Females	18–27	15	Overnight + TMR during REM	SPA	NN	FC	None
Johnson & Durrant, 2018 ^{26 a}								
Dataset 1	Mixed	18–22	15	Overnight + Sham	Words	NNP	R/K	Pos. corr. betw. theta power and negative items (trend)
Dataset 2	Mixed	18–22	15	Overnight +tDCS at SO frequency	Words	NNP	R/K	Pos. corr. betw. SWS duration and positive items (trend)
Dataset 3	Mixed	18–22	15	Overnight +tDCS at Theta frequency	Words	NNP	R/K	Pos. corr. betw. theta power and positive items; Pos. corr. betw. theta power and negative items
Jones et al, 2016 ⁴¹								
Dataset 1	Mixed	50–80	23	Overnight	Pictures	NN	Recog	None
The same participants as in Baran et al, 2012 ³⁴								
Dataset 2								
Dataset 3	Mixed	50–80	23	Overnight	Pictures	NP	Recog	None
Dataset 4	Mixed	18–30	19	Overnight	Pictures	NP	Recog	None
Jones et al, 2018 ¹¹								
Dataset 1	Mixed	18–30	14	Overnight	Pictures	NN	Recog	None reported
Dataset 2	Mixed	35–50	16	Overnight	Pictures	NN	Recog	None reported
The same participants as in Jones & Spencer, 2019 ¹²								
Jones et al, 2019 ¹⁰								
Jones & Spencer, 2019 ¹²	Mixed	18–28	27	Nap	Pictures	NN	Recog	Pos. corr. betw. Sigma activity and negative items
Jones et al, 2021 ⁴⁹	Mixed	10–18	10	Overnight	Pictures	NN	Recog	None
Kaestner et al, 2013 ^{100 a}								
Dataset 1	Mixed	18–39	28	Nap + Zolpidem	Pictures	NNP	Recog	None

Dataset 2	Mixed	18–39	28	Nap + Sodium oxybate	Pictures	NNP	Recog	Pos. corr. betw. sleep spindle density and negative items; Pos. corr. betw. sleep spindle density and high-arousal items (negative and positive combined); Pos. corr. betw. S2 duration and negative items; Neg. corr. betw. REM duration and low-arousal items (negative and positive combined); Pos. corr. betw. S2 duration and low-arousal items (negative and positive combined)
Dataset 3	Mixed	18–39	28	Nap + Placebo	Pictures	NNP	Recog	None
Kashyap, 2019 ⁴²	Males	18–22	12	Overnight	Faces Scenes	Faces – NNP Scenes - NNP	Recog	None reported
Kim et al, 2020 ²⁷								
Dataset 1	Mixed	18–31	28	Overnight + preceding social stressor	LDPA	NNP	Recog	Pos. corr. betw. theta during REM and positive items; Neg. corr. betw. SO-spindle couplings and positive and negative items ^e
Dataset 2	Mixed	18–31	29	Overnight +no preceding social stressor	LDPA	NNP	Recog	None
Kurz et al, 2019 ¹³	Males	9–12	20	Overnight	Pictures	NIN	Recog	None
Lehmann et al, 2016 ¹⁰¹								
Dataset 1	Mixed	Mean=22	21	Early Sleep + TMR during NREM	WPA	NN	CR	None reported, but see the section “Targeted memory re-activation”
Dataset 2	Mixed	Mean=22	20	Overnight + TMR during REM	WPA	NN	CR	None reported, but see the section “Targeted memory re-activation”
Lewis et al, 2011 ⁸²	The PSG participants the same as in Cairney et al, 2014 ⁸¹							
Mantua et al, 2017 ⁴³	Partially the same participants as in Dataset 1 Jones et al, 2018 ¹¹							
Morgenthaler et al, 2014 ⁴⁴								
Dataset 1	Mixed	19–25	14	Overnight	Pictures	NN	Recog	None
Dataset 2	Mixed	19–25	15	Overnight + REMD	Pictures	NN	Recog	None

(Continued)

Table 8 (Continued).

Study	Genders	Age Range	N	Type of Sleep	Stimulus Material	Emotions	Memory Task	Correlations with Memory Performance
Nishida et al, 2009 ⁴⁵	Mixed	18–30	15	Nap	Pictures	NN	Recog	Pos. corr. betw. REM duration and negative items; Pos. corr. betw. %REM and negative items; Neg. corr. betw. REM latency and negative items; Pos. corr. betw. right-lateralized prefrontal theta activity during REM and negative items
Payne et al, 2012 ⁴⁸	Mixed	18–25	27	Overnight	ETO	NN	Recog	Pos. corr. betw. REM duration and negative objects; Pos. corr. betw. %REM and negative objects
Payne et al, 2015 ⁴⁹	Mixed	18–26	22	Nap	ETO	NN	Recog	Pos. corr. betw. delta power and negative objects; Pos. corr. betw. SWS duration and negative objects
Prehn-Kristensen et al, 2013 ⁴⁷								
Dataset 1	Males	9–12	16	Overnight	Pictures	NN	Recog	None
Dataset 2	Males	20–28	20	Overnight	Pictures	NN	Recog	None
Datasets 1 and 2 combined	Males	9–12, 20–28	36	Overnight	Pictures	NN	Recog	Pos. corr. betw. SO power during SWS and emotional memory bias; Pos. corr. betw. delta power during SWS and emotional memory bias; Pos. corr. betw. theta oscillations during REM and emotional memory bias
Prehn-Kristensen et al, 2017 ⁴⁸	Males	9–11	16	Overnight	Faces	Angry Fearful Happy Neutral	Recog	None
Sawangjit et al, 2013 ⁴⁹	Males	18–25	5	Nap	Pictures	NN	Recog	Neg. corr. betw. S2 duration and neutral items
Schoch et al, 2019 ^{57 a}								
Dataset 1	Mixed	19–35	22	Overnight + Repeated awakenings	WPA	NP	CR	None
Dataset 2	Mixed	19–35	22	Overnight + No awakenings	WPA	NP	CR	None
Solomonova et al, 2017 ⁶⁰								
Dataset 1	Not reported	Not reported	7	Overnight + REMD	Faces	NN	Recog	None reported
Dataset 2	Not reported	Not reported	7	Overnight + awakenings from other sleep stages	Faces	NN	Recog	None reported

Sopp et al, 2017 ⁹¹								
Dataset 1	Mixed	Mean=23	19	Early sleep	Pictures PLA	NN	Pictures - R/K PLA - FC	Pos. corr: betw. slow spindle power and neutral pictures
Dataset 2	Mixed	Mean=23	19	Late sleep	Pictures PLA	NN	Pictures - R/K PLA - FC	Pos. corr: betw. right-frontal theta lateralization and PLA for negative items
Sopp et al, 2018 ²¹	Mixed	18-30	23	Nap with a 2nd memory test ~22 h later	Scenes OSA	Objects - Neutral; Scenes - NN	Objects - Recog OSA - Recog	Re-test 1 - Pos. corr: betw. spindle density and OSA for neutral items; Re-test 1 - Pos. corr: betw. right-frontal and fast spindle power and OSA for neutral items; Re-test 2 - Pos. corr: betw. spindle density and OSA for neutral items; Re-test 2 - Pos. corr: betw. spindle density and negative scenes
Tessier et al, 2015 ¹⁰²	Males	7–12	13	Overnight	Faces	NNP	Recog	Pos. corr: betw. beta spectral activity over left and right occipital sites and neutral items; Pos. corr: betw. theta spectral activity over left and right occipital sites and neutral items
Vargas et al, 2019 ⁸⁰	Mixed	Mean=23	19	Overnight	ETO	NN	Recog	None reported
Van Marle et al, 2013 ¹⁰³								
Dataset 1	Males	19–31	20	Overnight + Cortisol	Pictures	NN	Recog	None
Dataset 2	Males	19–26	18	Overnight + Placebo	Pictures	NN	Recog	None
Wagner et al, 2001 ⁶⁰								None reported
Dataset 1	Males	20–30	12	Early sleep	Texts	NN	FC	None reported
Dataset 2	Males	20–30	12	Late sleep	Texts	NN	FC	None reported
Wagner et al, 2005 ^{104 a}								
Dataset 1	Males	Mean=25	14	Overnight+ Cortisol inhibitor	Texts	NN	FR	None reported
Dataset 2	Males	Mean=25	14	Overnight + Placebo	Texts	NN	FR	None reported
Wagner et al, 2006 ⁵⁹	The same participants as in Wagner et al, 2001 ⁶⁰ - four years later							
	None reported							

(Continued)

Table 8 (Continued).

Study	Genders	Age Range	N	Type of Sleep	Stimulus Material	Emotions	Memory Task	Correlations with Memory Performance
Wagner et al, 2007 ⁵²	Mixed	19–30	10	Overnight	Faces	Neutral Happy Angry	Recog	Pos. corr: betw. NREM duration and happy faces; Pos. corr: betw. NREM duration and angry faces; Pos. corr: betw. TST and happy faces Pos. corr: betw. TST and angry faces (trend)
Whitehurst & Mednick, 2021 ^{105 a}								
Dataset 1	Mixed	18–30	29	Overnight + Psychostimulant	Pictures	NN	Recog	Neg. corr: betw. sleep latency and neutral images; Neg. corr: betw. Stage 2 latency and neutral images; Neg. corr: betw. REM latency and neutral images
Dataset 2	Mixed	18–30	29	Overnight + Placebo	Pictures	NN	Recog	None
Wiesner et al, 2015 ⁵³								
Dataset 1	Mixed	18–30	20	Overnight + SWSD	Pictures	NN	Recog	Pos. corr: betw. REM duration and emotional memory bias
Dataset 2	Mixed	18–30	21	Overnight + REMD	Pictures	NN	Recog	Pos. corr: betw. REM duration and emotional memory bias (trend)
Wilhelm et al, 2011 ^{106 a}								
Dataset 1	Males	Mean=24	14	Nap + Infusion of cortisol	Texts	NN	Content - FR; Temporal order -FC/CR	None reported
Dataset 2	Males	Mean=24	14	Nap + Placebo	Texts	NN	Content - FR Temporal order -FC/CR	None reported

Notes: ^aWithin-subjects design so that all datasets within the study refer to the same participants in different conditions. ^bThis effect was present for negative items as well, but it was significantly stronger for positive and neutral items. This study further revealed some significant interactions between sleep variables, emotion and baseline alpha activity, but that is beyond the scope of this review. ^cMixed within-subjects/between groups design so that both datasets within the 45 minute-nap and the 90-minute nap conditions respectively refer to the same participants in different conditions. ^dThis study did reveal some interactions between sleep, emotion and genetics, but that is beyond the scope of this review. ^eThis result is presented in Denis et al, 2021.²³ This effect was present for neutral items as well, but was significantly stronger for the emotional items.

Abbreviations: NNP, Neutral, negative, and positive; FR, Free recall; FOA, Face-object associations; NN, Neutral and negative; AM, Associative memory; FC, Forced choice; %REM, Percentage of time spent in rapid eye movement sleep; RM, Relational memory; ETO, the Emotional trade-off paradigm, Recog, Recognition; %SWS, Percentage of time spent in slow-wave sleep; SQ, Slow oscillation; SWS, Slow-wave sleep; TMR, Targeted memory re-activation; R/K, Remember/Know; PLA, Picture-location associations; IL-6, Interleukin 6; RF-EMF, Radio frequency electromagnetic fields; OBA, Object-background associations; S2, Stage 2 sleep; TST, Total sleep time; NP, Neutral and positive; REM, Rapid eye movement sleep; CR, Cued recall; SWSD, Slow-wave sleep deprivation; PCA, Picture-color associations; R, Remember; SPA, Sound-picture associations; tDCS, Transcranial direct-current stimulation; LDPA, Line drawing-picture associations; NREM, Non-rapid eye movement sleep; WPA, Word-picture associations; REMD, Rapid eye movement sleep deprivation; OSA, Object-scene associations.

Table 9 Other Manipulations of Sleep

Study	Genders	Age Range	N	Between-Groups/Within-Subjects	Sleep Manipulation	Stimulus Material	Emotions	Memory Task
Pharmacological manipulations								
Benedict et al, 2009 ⁹²	Males	20–36	17	IL-6 - within	Overnight x IL-6	Texts	NN	FR
Groch et al, 2011 ⁹⁷	Males	19–28	15	Norepinephrine - within	Early sleep x Norepinephrine	Texts Pictures	NN	Text content - FR & FC Text temporal order - CR Pictures - FR & Recog
Kaestner et al, 2013 ¹⁰⁰	Mixed	18–39	28	Sleep medication - within	Nap x Sleep medication	Pictures	NNP	Recog
Van Marle et al, 2013 ¹⁰³	Males	19–31	39	Cortisol - between	Overnight x Cortisol	Pictures	NN	Recog
Wagner et al, 2005 ¹⁰⁴	Males	Mean=25	14	Cortisol - within	Overnight x Cortisol	Texts	NN	FR
Whitehurst & Mednick, 2021 ¹⁰⁵	Mixed	18–30	29	Psychostimulant - within	Overnight x Psychostimulant	Pictures	NN	Recog
Wilhelm et al, 2011 ¹⁰⁶	Males	Mean=24	30	Sleep - between Cortisol - within	Nap x Cortisol	Texts	NN	Text content - FR & FC Temporal order - CR
TMR								
Ashton et al, 2018 ⁵	Mixed	18–29	19	TMR - between items	Nap x TMR	Pictures	NN	Pictures - R/K Locations - FC
Cairney et al, 2014 ⁹⁴	Mixed	18–28	15	TMR - between items	Nap x TMR	PLA	NN	FC
Hutchison et al, 2021 ⁹⁸	Females	18–27	33	TMR - between items; TMR during different sleeps tags - between groups	Overnight x TMR	SPA	NN	FC
Lehmann et al, 2016 ¹⁰¹	Mixed	Mean=23	62	TMR during different sleep/wake conditions - between groups; TMR - between items	Early sleep, overnight, & nighttime wake	WPA	NN	CR
Pre-sleep stressors								
Ackermann et al, 2019 ⁶⁷	Mixed	18–33	39	Sleep - between Stress - within	Nap x Stress	Pictures	NNP	FR
Kim et al, 2020 ²⁷	Mixed	18–31	64	Stress - between	Overnight x Stress	LDPA	NNP	Recog
Other forms of stimulation								
Bueno-Lopez et al, 2020 ⁹³	Males	20–30	30	RF-EMF exposure - within	Overnight x RF-EMF exposure	Faces	Neutral Happy Angry	Recog
Johnson & Durrant, 2018 ²⁶	Mixed	18–22	15	tCDS - within	Overnight x tCDS	Words	NNP	R/K

Abbreviations: IL-6, interleukin 6; NN, neutral and negative; FR, free recall; FC, forced choice; CR, cued recall; Recog, recognition; NNP, neutral, negative and positive; TMR, targeted memory re-activation; R/K, remember/know; PLA, picture-location associations; SPA, sound-picture associations; WPA, word-picture associations; LDPA, word-drawing-picture associations; RF-EMF, radio frequency electromagnetic fields; tCDS, transcranial direct-current stimulation.

replicated either. No sleep variable is even close to having been reported to be specifically correlated with emotional memory more often than it has not. Thus, we believe that it at this point is impossible to, with any certainty, say that any sleep variable is specifically associated with the consolidation of emotional memories.

Other Ways of Manipulating Sleep to Affect Sleep-Dependent Emotional Memory Consolidation

In this section, we will present studies that have employed other ways of manipulating sleep to examine if this has selectively affected the consolidation of emotional memories. This section only deals with group comparisons, as correlations are listed in the previous section. This section includes studies that have manipulated sleep pharmacologically, with TMR, by exposing participants to stressors before sleep, or with other forms of stimulations. As there are so few studies in each category, we have presented them all in Table 9. Given the large differences in study designs, as well as variation in the different kinds of sleep manipulations, we have only provided background information in the table, and then described the studies in text.

Pharmacological Manipulations of Sleep

Given that late sleep in some studies has been found to preferentially benefit emotional memories, and that cortisol rises during the latter half of the night, it is of interest to see if cortisol might be a factor behind the effect of late sleep on emotional memory. Three studies have manipulated cortisol levels to examine if this is the case.

Two studies found cortisol to result in increased memory performance for emotional as compared to neutral items. Van Marle et al¹⁰³ found an interaction between emotion and cortisol, such that enhancing cortisol during sleep resulted in better memory for emotional images relative to neutral ones, whereas no such difference was found in the placebo group. Wagner et al¹⁰⁴ instead decreased cortisol and found an interaction between cortisol and emotion, such that cortisol suppression during sleep resulted in impaired memory performance for neutral, but not for negative, texts, thus increasing the memory bias, even if the effect seemed to be driven mainly by the decrease for the neutral items. A third study, which also included wake groups, did not find cortisol to improve memory for emotional stimuli.¹⁰⁶ In this study, cortisol was pharmacologically increased, but there were no interactions between sleep, cortisol, and emotion for either free recall, recognition of content words, or memory for

temporal order. Post hoc *t*-tests did, however, reveal that cortisol during wake, compared to the placebo, increased memory performance for temporal order of the neutral text. Contrary to the two other studies mentioned here, the opposite result was found for cortisol during sleep, with higher memory performance for the neutral text in the cortisol condition. No such effect of cortisol was present for temporal order memory of the negative text.

Benedict et al⁹² examined the role of the pro-inflammatory cytokine interleukin 6 (IL-6). They found a significant interaction of IL-6 and emotion, such that intranasally administered IL-6 increased memory performance for negative, but not for neutral texts, compared to placebo.

One study has examined the effect of norepinephrine on emotional memory consolidation during sleep.⁹⁷ It found no differences in free recall or recognition of context words from neutral and negative texts, or in free recall and recognition of neutral and negative pictures, between a placebo and a pharmacological norepinephrine reduction condition. Memory for temporal order was, however, better for negative texts compared to neutral texts after placebo, but not after norepinephrine reduction.

Kaestner et al¹⁰⁰ compared two different sleep medications, Zolpidem (Ambien) and sodium oxybate (Xyrem), with a placebo. The stimulus material consisted of images that systematically varied in both valence and arousal. Results revealed that Zolpidem increased memory for negative images, and for images with high arousal (regardless of valence) relative to the placebo. No such memory differences were apparent between sodium oxybate and the placebo. This suggests that Zolpidem leads to a specific improvement in memory performance for negative and high-arousing items.

Whitehurst and Mednick¹⁰⁵ examined whether the supposed sleep-impairing effects of psychostimulants would impair sleep-dependent memory consolidation. Participants came to the lab in the morning and were given the psychostimulant dextro-amphetamine or a placebo, and then did the encoding. Participants performed an initial memory test in the evening, then had a full night of sleep, and then performed a second memory test the next morning. Results revealed an interaction between drug and emotion such that there was impaired memory performance for the neutral items in the psychostimulant condition as compared to the placebo condition, but no difference for the negative items.

Targeted Memory Re-Activation

Lehmann et al¹⁰¹ had participants encode associations between words and images. Participants were then divided into three different groups; a NREM group, a REM group and a Wake group. The NREM group had three hours of early sleep between encoding and re-test, during which the words were repeated through speakers. The REM group first had undisturbed early sleep, and then late sleep during which the words were played. The wake group had the words replayed to them while completing a working memory task. Results revealed that cueing only had an effect in the NREM group, which was driven by increased memory performance for the cued negative items. No such effects were evident in the REM- or in the wake group. This study further revealed that, in the NREM group, increases in spindle power, theta power, and slow waves immediately after the cues had been presented were larger for successfully remembered negative items compared to for successfully remembered neutral items. The improvement in memory performance for negative items was positively correlated with cueing-induced spindle power. These effects were not present in the REM group, which instead showed higher theta power for neutral items that would later be successfully remembered compared to negative ones.

Two other studies, with sleep groups only, did not find any effects of TMR during sleep on emotional memory consolidation.^{5,94} These studies found no main effects of TMR, and no interactions between TMR and emotion. One study compared TMR during REM with TMR during SWS and found no main effects or interactions with either emotion or during which kind of sleep TMR was applied.⁹⁸

Pre-Sleep Stressors

Two studies have examined the effects of inducing stress. In the Kim et al study,²⁷ the stressor was introduced before the encoding, and consisted of having to prepare a speech and giving it in front of an audience. In the Ackermann et al study,⁶⁷ the stressor was induced after the encoding, and consisted of repeatedly receiving negative feedback while solving math problems. Both studies had a non-stressful control condition, and neither found an interaction between stress and emotion on memory performance. The Ackermann et al⁶⁷ study also had wake controls, but found no three-way interaction between sleep, stress and emotion.

Other Forms of Stimulation

Only one study has so far attempted to manipulate sleep-dependent memory consolidation through transcranial Direct-Current Stimulation (tDCS). Johnson and Durrant²⁶ had participants in three different conditions. In the two experimental conditions, stimulation was applied during sleep at either a frequency intended to boost slow oscillations (0.75 Hz), or at a frequency intended to boost theta oscillations (5 Hz). A third condition was sham stimulation. Results revealed a trend toward a significant interaction between emotion and stimulation condition, such that stimulation at 0.75 Hz improved memory performance for neutral, but not for negative or positive, items. Stimulation at 5 Hz did not increase memory performance for either neutral, negative or positive items as compared to sham stimulation.

Bueno-Lopez et al⁹³ examined whether the supposed sleep-altering effects of exposure to the radio frequency electromagnetic fields associated with Wi-Fi networks would affect sleep-dependent memory consolidation. Results revealed no main effect of exposure to Wi-Fi as compared to sham during sleep, and no interaction with emotion.

Interim Summary

The take-away message of this section is that while several different sleep variables have been found to be specifically correlated with emotional memories, no correlation has been reliably replicated between studies.

As previously mentioned, it is often claimed in the literature that REM sleep preferentially benefits emotional memories. Several studies that have contrasted REM-rich sleep with sleep containing less REM have found such an effect, a finding that has been further supported by a meta-analysis.³¹ However, a specific correlation between REM and emotional items has only been found in a small minority of studies, and correlations with variables related to non-REM sleep are just as frequently reported, calling into question whether REM really is what is driving the effect seen in some of the early sleep/late sleep and REMD paradigms. The effects found in these studies could be caused by some other factor during the latter half of the night. This could be a circadian factor, such as the rise of cortisol, even though the literature on the effect of cortisol has been quite mixed as well.

It is also possible that REM sleep has an effect, but that it is not dose-dependent. Perhaps after a certain amount of time spent in REM sleep, a ceiling effect is reached, after

which any additional REM sleep does not further benefit emotional memory consolidation. Similarly, it is possible that there is a REM duration threshold that must be crossed in order to cause an emotional memory bias. This could explain why preferential consolidation of emotional memories is sometimes present in early sleep/late sleep designs, even in the absence of a direct correlation with REM duration. It should, however, also be mentioned that the number of early sleep/late sleep and selective REMD designs are much fewer than the purely correlational studies. Lastly, considering the weak support for sleep having a larger effect on the emotional memory bias effect than wake, it is unclear if any sleep-related variable has a larger effect on this than does time spent awake.

Other Factors That Determine Which Memories are Consolidated During Sleep

The previous section discussed studies examining memory for material that is intrinsically emotional. This section will focus on material that is intrinsically neutral, but has been somehow manipulated to vary in perceived future relevance. The focus here will be on two different kinds of studies. We will first discuss studies that have manipulated the importance of remembering the encoded material. This has been done by manipulating participants' expectations of an upcoming memory test, or by assigning different reward values for successfully remembering different items. Here we will also discuss studies that have measured participants' subjective opinions on the relevance of the material. A second line of studies has examined how sleep affects memory for items that for various reasons can be expected to be forgotten (for instance because of inhibition, or directed forgetting instructions during encoding). Here we will also discuss studies where participants have been asked to attempt to suppress either the encoding or the retrieval of certain items.

Given that the paradigms presented here differ extensively from each other, and are putatively based on different neural mechanisms, we will present results regarding factors during sleep for each section right away. Again, we have only considered studies to support a selective benefit of sleep if there was a significant interaction between sleep and item type. We have not reported post hoc *t*-tests that were not warranted by a significant ANOVA (unless the *t*-tests are the only thing reported).

Future Relevance

Test-Expectancy – Sleep/Wake Contrasts

Test-expectancy has either been manipulated between-groups or within-subjects. When it has been manipulated between-groups, one group has been informed of an upcoming memory test, whereas the other one has not. When done within-subjects, all participants have been informed that there will be a memory test for only a certain part of the encoded material. All the studies mentioned here have included participants of mixed genders. Studies on the interaction between sleep and test-expectancy are presented in Table 10.

In the study by Wilhelm et al,¹⁰⁹ the sleep group that was expecting a memory test performed better than the sleep group that did not. The wake groups did not differ from each other, and the non-expecting sleep group did not outperform either wake group. In the same paper, a second study that did not have a wake control group found that the sleep group that was expecting a memory test outperformed the non-expecting sleep group in both of the two memory tasks that were used. Van Dongen et al¹⁰⁷ found that sleep improved memory performance for items belonging to a category for which a memory test was expected, but not for items from the category for which a test was not expected. The opposite effect was found in the wake group, which surprisingly showed better memory for the category for which a test was not expected. These results were not replicated in another study using a very similar design with a sleep group only, which found no difference in memory performance between the relevant and the irrelevant items.¹⁷

Another study found sleep to have equivalent effects on memory performance regardless of test-expectancy for both memory tasks used (a spatial navigation task and a motor sequence typing task).¹⁰⁸ When reclassifying participants based on whether they afterwards reported that they had expected a memory test or not, there was actually an effect in the opposite direction, with a larger benefit of sleep in the non-expecting group on one of the three outcome measurements of the spatial navigation task.

The Factors During Sleep Associated with Memory Performance Based on Test-Expectancy

A summary of studies examining which sleep variables that interact with test-expectancy to benefit memory is presented in Table 11. All of these studies have looked at overnight sleep.

Table 10 Test-Expectancy

Study	Age Range	N	Test-Expectancy Between/Within	Sleep Manipulation	Stimulus Material	Memory Task	Interaction Sleep x Test-Expectancy
Reverberi et al, 2020 ¹⁷	18–35	38	Within	Overnight (a sleep group only)	OLA	FC	N/A No main effect of expectancy, see text
Van Dongen et al, 2012 ¹⁰⁷	18–33	50	Within	DW/NS	OLA	FC	Yes
Wamsley et al, 2016 ¹⁰⁸	18–30	VMT=75 MST=94	Between	DW/NS	VMT MST	Same VMT & MST as during encoding	No (for either task)
Wilhelm et al, 2011 ¹⁰⁹							
Dataset 1	18–35	104	Between	DW/NS with an additional TSD group	Word-pairs	CR	Yes
Dataset 2	Mean=23	38	Between	Two nightly sleep groups only	OLA FTT	OLA - FC; FTT - same as during encoding	N/A Main effect of expectancy, see text

Abbreviations: OLA, object-location associations; FC, forced choice; DW/NS, daytime wake/nighttime sleep; VMT, virtual maze navigation task; MST, motor sequence typing task; TSD, total sleep deprivation; CR, cued recall; FTT, finger tapping task.

Reward – Sleep/Wake Contrasts

The studies presented here have typically used paradigms where participants have encoded several different items while receiving information about a reward amount that they will receive for successfully remembering each item during the subsequent memory test. This allows for examination of whether sleep selectively benefits memories of items associated with a high reward. Studies on sleep and reward are listed in Table 12. All studies have included participants of mixed genders.

Some of the studies mentioned in the table require some further explanation. In one dataset (experiments 2 and 4) of the Oudiette et al study,¹¹⁴ TMR was used. Half of the sounds that had been associated with the low-reward items during encoding were replayed during the subsequent delay interval in both the sleep and the wake group. Results showed that for the groups for which no sounds were replayed during the delay intervals (experiments 1 and 3), there was no interaction between sleep and reward value, and high-reward items were better remembered than low-reward items regardless of sleep or wake. With TMR during the delay interval, memory for the items associated with the sounds was strengthened in the wake group, whereas in the sleep group, memory was

enhanced also for the low-reward items that had not been cued during sleep. For the contrast between the two different sleep groups, see the following section.

In the Stamm et al study,¹¹⁵ participants navigated through a virtual maze with the goal to reach the exit as quickly as possible. While navigating the maze, one group had a meter ticking down on the screen that indicated the monetary reward they would receive when finding the exit, such that quicker navigation through the maze would result in a higher reward. Another group received no such information. Participants were informed that there would be a similar reward structure during the re-test after sleep. Contrary to expectations, reward information had a negative effect on overnight improvement in navigating in the maze. The authors suggested that the ticking meter might not have been viewed as reward information, but rather as negative reinforcement. This study only included sleep groups, so it is not possible to say whether this effect differs between sleep and wake. It should also be mentioned that the effect of reward on consolidation during sleep was only evident in two of the four outcome measures.

The reward method used in the Tamaki et al¹¹⁶ study is quite different from what has been used in the other

Table 1 | Factors During Sleep – Test-Expectancy

Study	Age Range	N	Sleep x Expectancy	Stimulus Material	Memory Task	Correlations with Memory Performance
Reverberi et al, 2020 ¹⁷	18–35	38	Overnight; All participants expecting a test for half of the items	OLA	FC	None (Actigraphy)
Van Dongen et al, 2012 ¹⁰⁷	18–33	25	Overnight; All participants expecting a test for half of the items	OLA	FC	Pos. corr. betw. high-relevance items and TST (Actigraphy)
Wamsley et al, 2016 ¹⁰⁸						
Dataset 1	18–30	Unclear	Overnight - Expecting a memory test	VMT MST	Same VMT & MST as during encoding	None
Dataset 2	18–30	Unclear	Overnight - Not expecting a memory test	VMT MST	Same VMT & MST as during encoding	None
Wilhelm et al, 2011 ¹⁰⁹						
Dataset 1	18–35	18	Overnight - Expecting a memory test	Word-pairs	CR	Pos. corr. betw. %S4 sleep and memory performance
Dataset 2	18–35	18	Overnight - Not expecting a memory test	Word-pairs	CR	None
Dataset 3	Mean=23	21	Overnight - Expecting a memory test	OLA FTT	OLA - FC; FTT - same as during encoding	Pos. corr. betw. %S4 and OLA performance; Pos. corr. betw. %S4 sleep and OLA performance
Dataset 4	Mean=23	17	Overnight - Not expecting a memory test	OLA FTT	OLA - FC; FTT - same as during encoding	None

Abbreviations: OLA, object-location associations; FC, forced choice; TST, total sleep time; VMT, virtual maze navigation task; MST, motor sequence typing task; CR, cued recall; %S4, percentage of time spent in Stage 4 sleep; FTT, finger tapping task.

Table 12 Studies on Sleep and Reward

Study	Age Range	N	Sleep Between-Groups/Within-Subjects	Reward Manipulation	Sleep Manipulation	Stimulus Material	Memory Task	Main Effect of Sleep	Interaction Sleep x Reward
Baran et al, 2013 ¹¹⁰	18–30	38	Between	Between-items	DW/NS	Words	FR & Recog	FR - Yes Recog - Yes	FR - No Recog - No
Fischer & Born, 2009 ¹¹¹	20–33	76	Between	Between-items + Between groups, see text	DW/NS	FTT	Same FTTs as during encoding	Yes	Yes
Igloi et al, 2015 ¹¹²	18–30	1st test = 30 2nd test = 25	Between	Between-items	Nap design with a 2nd memory test 3 months later	Picture-pairs	FC	1st test - Yes 2nd test - No	1st test - No 2nd test - Yes
Lo et al, 2016 ¹¹³	15–19	1st test = 56 2nd test = 45	Between	Between-items	7 days of PSR versus normal sleep, with a 2nd memory test 5 weeks later, see text	PP	FR	No	No
Oudiette et al, 2013 ¹¹⁴									
Dataset 1 (Experiments 1 and 3)	Mean=21	30	Between	Between-items	Nap design	OLA	FC	Not reported	No
Dataset 2 (Experiments 2 and 4)	Mean=21	30	Between	Between-items	Nap design + TMR	OLA	FC	Not reported	Not reported
Prehn-Kristensen et al, 2018 ¹⁶									
Dataset 1	7–11	16	Within	Between-items	DW/NS	OLA	FC	Yes (trend)	Yes
Dataset 2	21–29	20	Within	Between-items	DW/NS	OLA	FC	No	No
Sopp et al, 2021 ²⁰	18–35	75	Between	Between-items	DW/NS	Pictures	Recog & R/ K	Recog - No R - No K - No	Recog - Yes R - No K - No

(Continued)

Table 12 (Continued).

Study	Age Range	N	Sleep Between-Groups/Within-Subjects	Reward Manipulation	Sleep Manipulation	Stimulus Material	Memory Task	Main Effect of Sleep	Interaction Sleep x Reward
Stamm et al, 2014 ¹¹⁵	18–30	65	N/A	Between-groups	Nightly sleep groups only	VMT	Same VMT as during encoding	N/A	N/A - main effect of reward, but in the opposite direction, see text
Tamaki et al, 2020 ¹¹⁶									
Dataset 1	18–25	47	Between	Between-groups	DW/NS	VPT	Same VPT as during learning	Yes	Yes
Dataset 2	18–25	40	Between	Between-groups	DW/NS	VPT	Same VPT as during learning	Yes	Yes
Dataset 3	18–25	22	N/A	Between-groups	Nap design	VPT	Same VPT as during learning	N/A	N/A - main effect of reward, see text
Tucker et al, 2011 ¹¹⁷									
Dataset 1	Mean=20	75	Between	Between-groups	DW/NS	FOA	CR	Yes	No
Dataset 2	Mean=20	77	Between	Between-groups	DW/NS with the memory test 24 h after encoding	FOA	CR	No	No

Abbreviations: DW/NS, daytime wake/nighttime sleep; FR, free recall; Recog, recognition; FTI, finger tapping task; FC, forced choice; PSR, partial sleep restriction; PP, prose passages; OLA, object-location associations; TMR, targeted memory re-activation; R/K, remember/know; R, remember; K, know; VMT, virtual maze navigation task; VPT, visual perception task; FOA, face-object associations; CR, cued recall.

Table 13 Sleep and Reward – Factors During Sleep

Study	Genders	Age Range	N	Type of Sleep/Manipulation	Stimulus Material	Study Type	Correlations with Memory Performance/Group Differences
Asfestani et al, 2020 ^{4 a}							
Dataset 1	Males	18–30	17	Overnight + Dopamine antagonist	Pictures	Correlational	None
Dataset 2	Males	18–30	17	Overnight + Placebo	Pictures	Correlational	Pos. corr: betw. S4 duration and high-reward items; Neg. corr: betw. S4 duration and low-reward items
Dataset 1 and 2 combined	Males	18–30	17	Dopamine antagonist vs Placebo	Pictures	Group comparison	No Reward x Dopamine interaction
Feld et al, 2014 ^{118 a}							
Dataset 1	Males	19–30	13	Overnight + Dopamine agonist	Pictures	Correlational	None
Dataset 2	Males	19–30	13	Overnight + Placebo	Pictures	Correlational	Neg. corr: betw. REM duration and low-reward items
Datasets 1 and 2 combined	Males	19–30	13	Dopamine agonist vs Placebo	Pictures	Group comparison	Reward x Dopamine interaction, see text
Igloi et al, 2015 ¹²	Mixed	18–30	15	Nap	Pictures	Correlational	Test 1 - Pos. corr: betw. slow spindles and high-reward items; Test 2 - none reported
Lo et al, 2016 ¹³							
Dataset 1	Mixed	15–19	Test 1 = 26; Test 2 = Unclear	7 nights with normal sleep	PP	Correlational	None
Dataset 2	Mixed	15–19	Test 1 = 30; Test 2 = Unclear	7 nights with PSR	PP	Correlational	Test 1 - Pos. corr: betw. S2 duration and low-reward items
Oudiette et al, 2013 ¹⁴							
Dataset 1	Mixed	Mean=21	15	Nap + No TMR	OLA	Correlational	Neg. corr: betw. REM duration and low-reward items
Dataset 2	Mixed	Mean=21	15	Nap + TMR	OLA	Correlational	Pos. corr: betw. SWS duration and low-reward items; Pos. corr: betw. frontopolar delta power during SWS and low-reward items
Datasets 1 and 2 combined	Mixed	Mean=21	30	Reward x TMR	OLA	Group comparison	Reward x TMR interaction, see text

(Continued)

Table 13 (Continued).

Study	Genders	Age Range	N	Type of Sleep/Manipulation	Stimulus Material	Study Type	Correlations with Memory Performance/Group Differences
Prehn-Kristensen et al, 2020 ^{19 a}							
Dataset 1	Males	8–12	15	Overnight + closed-loop stimulation	Word-pairs	Correlational	None reported
Dataset 2	Males	8–12	15	Overnight + sham stimulation	Word-pairs	Correlational	None reported
Datasets 1 and 2 combined	Males	8–12	15	Closed-loop stimulation vs sham stimulation	Word-pairs	Group comparison	Reward x closed-loop stimulation interaction, see text
Sopp et al, 2021 ²⁰	Mixed	18–35	38	Overnight	Pictures	Correlational	Pos. corr. betw. %NREM and the difference between high-reward items and low-reward items.
Stamm et al, 2014 ¹⁵							
Dataset 1	Mixed	18–30	15	Overnight + Neither reward nor feedback during encoding	VMT	Correlational	None
Dataset 2	Mixed	18–30	15	Overnight + Feedback during encoding	VMT	Correlational	Neg. corr. betw. SWS duration and backtracking improvement
Dataset 3	Mixed	18–30	14	Overnight + Reward during encoding	VMT	Correlational	None
Dataset 4	Mixed	18–30	15	Overnight + Both reward and feedback during encoding	VMT	Correlational	Pos. corr. betw. SWS duration and time improvement; Pos. corr. betw. SWS duration and distance improvement; Pos. corr. betw. SWS duration and backtracking improvement
Studte et al, 2017 ²⁰	Mixed	Mean=22	21	Nap	Word-pairs	Correlational	Pos. corr. betw. spindle density and high-reward items
Tamaki et al, 2020 ¹⁶							
Dataset 1	Mixed	18–25	11	Nap + Reward during encoding	VPT	Correlational	Pos. corr. betw. performance gain and averaged power density at the prefrontal region during REM
Dataset 2	Mixed	18–25	9	Nap + No reward during encoding	VPT	Correlational	None reported

Note: ^aWithin-subjects design so that both datasets within the study refer to the same participants in different conditions.

Abbreviations: S4, stage 4 sleep; REM, rapid eye movement sleep; PP, prose passages; PSR, partial sleep restriction; S2, stage 2 sleep; TMR, targeted memory re-activation; OLA, object-location associations; SWS, slow-wave sleep; NREM, percentage of time spent in non-rapid eye movement sleep; VMT, virtual maze navigation task; VPT, visual perception task.

Table 14 Sleep and Subjective Relevance

Study	Age Range	N	Sleep Manipulation	Memory Task	Main Effect of Sleep
Abel & Bäuml, 2013 ¹²¹					
Dataset 1	18–32	96	DW/NS plus an additional short delay group	FR	Yes
Dataset 2	19–35	96	DW/NS plus an additional short delay group	Recog	Yes
Stare et al, 2018 ²²	18–47	56	DW/NS	CR	No
Van Rijn et al, 2017 ¹²²	18–26	79	DW/NS	CR	Yes

Abbreviations: DW/NS, daytime wake/nighttime sleep; FR, free recall; Recog, recognition; CR, cued recall.

studies. Rewards were given during encoding, but participants were not informed about a future reward for successful remembering during a re-test. Participants were instructed to not eat or drink for four hours prior to the learning session. Participants in the reward-groups received a droplet of water for each trial they answered correctly during the learning session. In the third dataset of this paper (dataset 3 in Table 12), there were only two nap groups: one that received reward during learning, and one that did not. Results showed increased performance in the reward group.

In the Lo et al study,¹¹³ participants either slept normally for one week (a nine-hour sleep opportunity per night), or were subjected to sleep restrictions (only a five-hour sleep opportunity per night). It should, lastly, also be mentioned that the Fischer and Born study¹¹¹ also included two additional sleep groups that received no reward information.

Factors During Sleep Associated with Memory Performance Based on Reward Value

Studies examining which variables during sleep that are associated with differential memory consolidation based on the reward value of the items are presented in Table 13.

As evident in Table 13, several different correlations have been found, but no variable has repeatedly been shown to be specifically correlated with memory for either high- or low-reward items, or the difference between them. In the Oudiette et al study,¹¹⁴ comparing the sleep group that received TMR of the low-reward items with the sleep group that did not, revealed an interaction effect where TMR specifically increased memory performance for low-reward items. In the Prehn-Kristensen et al study,¹¹⁹ slow oscillations were increased through acoustic closed-loop stimulation. In the control condition, participants received sham stimulations. There was an interaction between stimulation and reward, so that in the stimulation condition, memory was better for

rewarded items than for non-rewarded items, whereas there was no such effect in the sham condition.

In the Feld et al study,¹¹⁸ participants received either a placebo or a dopamine agonist after encoding. Results revealed better memory for the high-reward items than for the low-reward items in the placebo condition. In the dopamine condition, however, participants showed equal performance for both reward categories. This effect was driven by dopamine enhancing memory for the low-reward items. Such an interaction between dopamine and reward was however not replicated in a study using a dopamine antagonist, with the re-test 22 hours after encoding.⁴ Another study that included reward information, but additionally also emotional stimuli,⁸⁹ is discussed in the section “Studies with Multiple Cues of Future Relevance”.

Subjective Relevance

This section covers studies examining the role of sleep in the consolidation of memories based on their subjective relevance to the participants. The designs of these studies have been highly varied, so we have just provided some brief background information in Table 14, and then described them in running text. All studies presented here have manipulated sleep between groups and have included participants of mixed genders.

Van Rijn et al¹²² had native English speakers who had recently moved to Wales rate how much they valued the Welsh and the Breton language, respectively. Participants then learned the English translation of Welsh and Breton words. Results from the cued recall memory test showed that after sleep, there was a correlation between valuing the Welsh language and memory performance for the Welsh words. This was not the case in the wake group, indicating that the subjective value of the encoded material was a stronger predictor of increased memory consolidation during sleep than during wake. There was no correlation between memory performance and valuing the Breton language for either group.

Table 15 Directed Forgetting – Sleep/Wake Contrasts

Study	Age Range	N	Sleep Manipulation	Stimulus Material	Memory Task	Main Effect of Sleep	Interaction Sleep x Forgetting Instructions
List-method directed forgetting							
Abel & Bäuml, 2013 ¹²⁴							
Dataset 1	18-30	128	DW/NS	Words	CR	Yes (only list 1 analyzed)	Yes, forget instructions had less of an effect after sleep (only List 1 analyzed)
Dataset 2	18-35	112	DW/NS	Words	CR	Yes (only list 1 analyzed)	Yes, forget instructions had less of an effect after sleep (only List 1 analyzed)
Blaskovich et al, 2017 ¹²⁵	18-35	112	Nap design	Words	FR	No	No
Hubbach, 2018 ¹²⁶	Not reported	92	DW/NS	Line drawings	FR	List 1 - Yes List 2 - No (lists analyzed separately)	List 1 - No List 2 - No (lists analyzed separately)
Item-method directed forgetting							
Rauchs et al, 2011 ¹²⁷	Mean=23	25	TSD with the memory test 48 h later	Words	Recog	Not reported	No
Saletin et al, 2011 ¹²⁸	18-30	46	Nap Design	Words	FR	Yes	Yes
Scullin et al, 2017 ¹²⁹							
Dataset 1	18-29	50	Nap Design	Words	FR Recog	FR - Yes Recog - Yes	FR - Yes (trend) Recog - No
Dataset 2	58-83	45	Nap Design	Words	FR Recog	FR - No Recog - No	FR - No Recog - No

Abbreviations: DW/NS, daytime wake/nighttime sleep; CR, cued recall; FR, free recall; TSD, total sleep deprivation; Recog, recognition.

In the Abel and Bäuml studies¹²¹ participants rated words for either their pleasantness or their survival value. This is known as survival processing, and it has previously been shown that rating something's survival value leads to improved memory performance compared to other kinds of ratings that contain the same depth of processing during encoding.¹⁴⁸ Results revealed no interaction between sleep and type of processing.

In the Stare et al study,²² participants were first presented with trivia questions and were asked to rate how curious they were to find out the correct answers to them. Participants then got the answers to these questions and were tested on them after either sleep or wake. Results revealed no interaction effect between sleep and previous curiosity about the answers. There were no correlations between any sleep variables and any memory measures ($n = 23$). As this is the only study on subjective relevance that has included PSG, we have not included a table here.

Studies Inducing Forgetting

In this section, we will present studies that have used paradigms where participants are either explicitly told to forget something during or after encoding, or that have attempted to

induce forgetting through different forms of inhibition during retrieval. The difference from the studies presented in the previous sections is that the forgetting induced by these paradigms is believed to be caused not just by a mere lack of strengthening, but by active inhibition.

Directed Forgetting Tasks

In directed forgetting (DF) paradigm, participants are asked during the encoding to remember half of the items and to forget the other half. The DF paradigm is further divided into list-method (LMDF), and item-method directed forgetting (IMDF). We will briefly describe these paradigms here, but for a more detailed account, see Anderson and Hanslmayr.¹²³

List-Method Directed Forgetting

In the LMDF paradigm, all participants first encode a list of words (List 1). Half of the participants (the “Forget” group) are then told that they for some reason have been given that list erroneously, and are then asked to encode the “real” list (List 2). The other half of participants (the “Remember” group) just go on to encode List 2 without receiving any information that List 1 should be forgotten. During a subsequent memory test, memory for both lists is

Table 16 Sleep and Directed Forgetting – Specific Sleep Variables

Study	Age Range	N	Type of DF	Correlations with Memory Performance
Blaskovich et al, 2017 ¹²⁵				
Dataset 1	18–35	27	LM, R instructions	None
Dataset 1a (the subset of Dataset 1 that entered REM sleep)	18–35	14	LM, R instructions	Pos. corr. betw. REM duration and memory for list 1
Dataset 2	18–35	27	LM, F instructions	Pos. corr. betw. central and parietal sigma power and list 2
Dataset 2a (the subset of Dataset 2 that entered REM sleep)	18–35	13	LM, F instructions	Pos. corr. betw. REM duration and memory for list 2
Datasets 1 and 2 combined	18–35	56	LM - R/F instructions x REM, see text	N/A - see text
Saletin et al, 2011 ¹²⁸	18–30	23	IM	Pos. corr. betw. fast spindle density over the P3 electrode and DF
Scullin et al, 2017 ¹²⁹				
Dataset 1	18–29	30	IM	None
Dataset 2	58–83	29	IM	None

Abbreviations: DF, directed forgetting; LM, list-method; R, remember; REM, rapid eye movement sleep; F, forget; IM, item-method.

assessed. Typically, the “Forget” group remembers more from List 2 than from List 1, whereas the opposite effect is typically evident in the “Remember” group, with better memory performance for List 1. This is hypothesized to occur because “Forgetting” instructions free up “memory space” to encode more information, whereas encoding new information becomes more difficult when one has already memorized List 1, as is the case after “Remember” instructions.

Studies manipulating the presence of sleep and wake during the delay interval between encoding and the memory test are presented in Table 15. Inherent to the paradigm, all these studies have been between-groups, both for the sleep/wake manipulation and for the remember/forget instructions. All studies have included participants of mixed genders.

As evident by the table, one study has (in two different experiments) found sleep, compared to wake, to increase memory performance for List 1, whereas two studies have not found any interactions between sleep and forgetting instructions.

Item-Method Directed Forgetting

Item-method DF is similar to list-method DF, but instead of receiving instructions to remember or forget a whole list of items, each individual item is presented together with a “Remember” or “Forget” instruction. This makes it possible to compare “Remember” and “Forget” items within subjects. The degree of DF is defined as the difference between “Remember” and “Forget” items. Studies on the effect of sleep on IMDF are presented in Table 15.

The Saletin et al study¹²⁸ found sleep to benefit “Remember” items only. A similar effect was found (in young adults only, and not in older adults) by Scullin et al¹²⁹ for free recall, but not for recognition. This effect was not replicated in the Rauchs et al study,¹²⁷ which found similar recognition accuracy in both groups for both “Remember” and “Forget” items. A fourth study examining the role of sleep in IMDF² also included emotional items, and is discussed in the section “Studies with Multiple Cues of Future Relevance”.

Factors During Sleep Involved in Directed Forgetting

Studies examining correlations between sleep variables and directed forgetting are presented in Table 16. All studies have been nap designs.

In the only study using PSG in a LMDF design, beyond the correlations reported in the table, Blaskovich et al¹²⁵ further divided the participants based on whether they had entered REM sleep or not. Results from this revealed a larger DF effect in the REM group compared to the non-REM group.

Retrieval-Induced Forgetting

In the retrieval-practice paradigm, forgetting is induced in a more implicit manner.¹³⁰ Participants first encode items (typically words) belonging to certain categories. After encoding, participants get additional retrieval practice on some of the items belonging to this category (Rp+ items), whereas other items from this category do not receive additional practice (Rp- items). During the memory test, participants are tested on the Rp+ and Rp- items, as well as items belonging to another category that were encoded but not present during the practice phase (Nrp items). This memory test typically reveals improved memory performance for the Rp+ items, and impaired memory for Rp-items, compared to the Nrp items. The suggested explanation for this is that in order to retrieve the Rp+ items during the practice phase, one must also inhibit the interfering Rp- items from the same category, causing the impaired performance for these (compared to the baseline Nrp items that have not been additionally practiced, but not subjected to any inhibition during the retrieval-practice phase either). This forgetting effect is referred to as retrieval-induced forgetting (RIF), and is defined as the difference between Rp- and Nrp items. Studies on sleep and RIF are presented in Table 17. The memory task in all studies mentioned here has been cued recall, and all studies have included mixed genders.

As evident by the table, studies on sleep and RIF have revealed highly contrasting results, with sleep having been found to both decrease,¹³² and increase,^{131,133} the RIF effect.

The Think/No-Think Paradigm

Unlike in the retrieval practice paradigm, the retrieval inhibition involved in the Think/No-Think (T/NT) paradigm¹³⁶ is more explicit. Participants first learn associations between a cue and an associate (typically, both the cue and the associate are words, but there are also studies that have used, for example, word-image

Table 17 Respectively

Study	Age Range	N	Sleep Manipulation	Sleep Between-Groups/ Within-Subjects	Interaction Sleep x Item Type
RIF					
Abel & Bäuml, 2012 ¹³¹	19–33	96	DW/NS with two additional groups to control for circadian rhythms	Between-groups	Three-way interaction of Sleep x Delay x Item type A significant RIF effect in the sleep group only
Baran et al, 2010 ¹³²					
Dataset 1	Mean=21	46	DW/NS	Between-groups	A larger RIF effect in the wake group Sleep increased memory performance for RP- items Sleep increased memory performance for RP+ items
Dataset 2	Mean=20	20	Nap design	Within-subjects	A larger RIF effect in the wake group Sleep increased memory performance for RP- items (trend) Sleep increased memory performance for RP+ items (trend)
Racsmány et al, 2010 ¹³³					
Dataset 1	19–26	64	DW/NS	Between-groups	A significant RIF effect in the sleep group only
Dataset 2	20–28	96	DW/NS with an additional group that did the encoding in the morning and the test just 1 h later	Between-groups	A significant RIF effect in the sleep group only
T/NT					
Dehanvi et al, 2019 ¹³⁴	19–30	25	Nap design	Between-groups	No
Fischer et al, 2011 ¹³⁵	18–31	25	DW/NS	Between-groups	No

Abbreviations: RIF, retrieval-induced forgetting; DW/NS, daytime wake/nighttime sleep; T/NT, think/no-think.

Table 18 RIF & T/NT – Factors During Sleep

Study	Age Range	N	Paradigm	Type of Sleep	Findings
Baran et al, 2010 ¹³²	Not reported	15	RIF	Overnight	Neg. corr. betw. %REM and RIF; Pos. corr. betw. %SWS and RP+ items
Dehnavi et al, 2019 ¹³⁴	19–30	10	T/NT with Think and No-Think items only	Nap	None
Fischer et al, 2011 ¹³⁵					
Dataset 1	18–31	12	T/NT	Overnight	Pos. corr. betw. %SWS and Think items (trend); Pos. corr. betw. SWS duration and Think items (trend); Pos. corr. betw. S2 duration and No-Think items (trend)
Dataset 2	22–35	8	T/NT	Early sleep	None
Dataset 3	22–35	8	T/NT	Late sleep	None
Datasets 2 and 3 combined	22–35	16	T/NT	Early sleep vs Late sleep	Interaction Sleep time x Item type, see text

Abbreviations: RIF, retrieval-induced forgetting; T/NT, think/no-think; %REM, percentage of time spent in rapid eye movement sleep; %SWS, percentage of time spent in slow-wave sleep; SWS, slow-wave sleep; S2, stage 2 sleep.

Table 19 Targeted Memory Re-Activation to Boost Forgetting During Sleep

Study	Age Range	N	Forgetting Paradigm	Correlations Between Memory Performance and Sleep Variables
Schechtman et al, 2020 ¹⁴⁰	18–34	30	IMDF	None
Schechtman et al, 2021 ¹³⁸	18–29	31	T/NT	None
Simon et al, 2018 ¹³⁹	18–26	18	See text	None

Abbreviations: IMDF, item-method directed forgetting; T/NT, think/no-think.

and face-image pairs). Then, during the T/NT phase, participants are presented with only the cue, written in either green or red font color. If the word is presented in green, participants are instructed to think about the associate that it was previously presented together with (Think items). If the word is presented in red, the participants are asked to attempt to avoid all thoughts about the associate that it was previously presented together with (No-Think items). This is repeated several times for each cue. In a subsequent unexpected memory test, all the cues are presented again, and participants are asked to say which items they were previously associated with. There are also Baseline items that are only present during the initial encoding, but not during the T/NT phase. In the memory test, it is typically found

that Think items are better remembered than Baseline items, and that No-Think items are more poorly remembered than the Baseline items. This indicates that the repeated suppressed retrieval of the No-Think items during the T/NT phase has actually resulted in worse memory performance for them than if they would not have been seen after encoding at all. The difference between Baseline and No-Think items is referred to as Suppression-Induced Forgetting (SIF).

Table 17 presents two studies that have compared the effect of sleep and wake on SIF using the T/NT task. Both studies listed here have included participants of mixed genders. A third study also included emotional items,¹³⁷ and is discussed in the section “Studies with Multiple Cues of Future Relevance”.

In the Dehnavi et al study,¹³⁴ there were no Baseline items but instead only Think and No-Think items.

Specific Sleep Variables in Studies Using RIF and SIF

Although T/NT and RIF paradigms differ in several aspects, as there has only been one RIF study that has used PSG, we have presented both paradigms in the same table. Studies examining which variables during sleep that contribute to SIF and RIF respectively are presented in Table 18.

A second experiment in the T/NT study by Fischer et al¹³⁵ used an early sleep/late sleep design. They found that, for the No-Think items, there was an interaction effect between sleep timing and the number of times they had been subjected to suppression during the T/NT phase. In the late sleep group, items subjected to 8 or 16 No-Think trials during the T/NT phase were actually better remembered than Baseline items. No such effect was evident after early sleep, after which there was no difference between Baseline and No-Think items regardless of the number times a No-Think item had appeared during the T/NT phase. This indicates that late sleep had a “repairing” effect, and actually strengthened memory for items that had been subjected to retrieval-suppression. A fourth study, which also included TMR,¹³⁸ is discussed in the following section.

Targeted Memory Reactivation to Boost Forgetting During Sleep

An exciting new avenue of research is examining whether TMR, beyond strengthening memories during sleep, can also be used to boost forgetting. The three studies conducted on this topic so far are listed in Table 19. None of the studies have included wake control groups, and have all included participants of mixed genders.

In the Simon et al study,¹³⁹ participants first learned associations between objects and locations. Each object was presented together with a sound. During sleep on the post-learning night, a subset of these sounds were replayed together with a sound that had functioned as the “Forget” cue in a DF task performed before the encoding of the object-location associations. At a memory test taking place seven days later, free recall of the objects that were paired with the “Forget” cues during sleep was impaired compared to memory for objects that had not been cued during post-learning sleep. There was no effect of the “Forget”

cues on memory for which locations the objects had been associated with.

In the first Schechtman et al study¹⁴⁰ listed in Table 19, participants first learned to associate objects with three different sounds (ten objects per sound). Two of these sounds were later associated with “Forget” instructions, whereas one of them was associated with “Remember” instructions. Participants then completed an IMDF task, where they were asked to either remember or forget images, as well as their size, frame color and location on a circular grid, depending on what sound that was played when they viewed them. Then, during a subsequent nap, one of the sounds that had been associated with “Forget”-instructions was replayed. Results revealed a larger decrease in memory performance for the “Forget” items that had been cued during sleep, as compared to the items that had not. This result was only evident for memory for locations, and not for image recognition, size or frame color. It should also be mentioned that there was no main effect of item type when also including the “Remember” items in the analysis.

The second Schechtman et al study¹³⁸ listed in Table 19 used a T/NT paradigm and did not find TMR during sleep to affect memory performance for No-Think items, as evident by there being no difference in memory performance between cued and non-cued items. Further, they also attempted to see if they could induce de-novo forgetting of baseline items by combining them with sounds previously associated with No-Think items during sleep. Results showed no support for this, as evident by there being no differences between the three different item types; Baseline words cued during sleep combined with the No-Think sound, Baseline words cued during sleep combined with a novel sound, and Baseline words not cued during sleep.

Studies with Multiple Cues of Future Relevance

The studies discussed so far have only manipulated one variable that predicts subsequent remembering, such as emotion, test-expectancy, reward value, or forgetting instructions during encoding. So far, six studies have examined how sleep affects and interacts with multiple variables that individually predict subsequent remembering in the same study. Given the considerable variations in designs between these studies, we have only provided some basic descriptive details in Table 20, and then described the

Table 20 Studies Manipulating Multiple Variables That Differently Predict Memory Performance – Sleep/Wake Contrasts

Study	Age Range	N	Stimulus Material	Sleep Manipulation	Salience Cues	Emotions	Memory Test
Alger et al, 2019 ²	18–39	46	Pictures	Nap design with two different nap groups, see text	IMDF x Emotion	NN	Recog
Bennion et al, 2016 ¹⁴¹	18–27	74	ETO	Nap design with two different nap groups, see text	Text-expectancy x Reward x Emotion	NNP, see text	Recog
Cunningham et al, 2014 ⁷⁵	Not reported (students)	80	ETO	DW/NS	Test-expectancy x Emotion	NN	Recog
Davidson et al, 2020 ¹³⁷	18–35	33	WPA	Nap design	T/NT x Emotion	Words - neutral; Pictures - NN	CR
Kuriyama et al, 2013 ⁸⁴	20–29	62	Video clips	TSD with the memory test 48 h after encoding	DF x Emotion	NN	Recog

Abbreviations: IMDF, Item-method directed forgetting; NN, Neutral and negative; Recog, Recognition; ETO, The emotional trade-off paradigm; NNP, Neutral, negative, and positive; DW/NS, Daytime wake/nighttime sleep; WPA, Word-picture associations; T/NT, Think/No-Think; CR, Cued recall; TSD, Total sleep deprivation; DF, Directed forgetting.

studies more thoroughly in text. All studies discussed here have included participants with mixed genders.

Studies Combining Emotion with Additional Salience Cues

Two studies have combined emotion with other variables expected to predict an additional memory benefit. In a study that varied both emotion and test-expectancy, Cunningham et al⁷⁵ used the emotional trade-off paradigm in a daytime wake/nighttime sleep design where, after encoding, half of the participants were instructed that there would be a memory test after the delay interval. Results showed that in the wake groups, there was a stronger trade-off effect (increased memory for the objects compared to their backgrounds) for the negative items when a memory test was expected, compared to when it was not. There was no such trade-off effect for neutral objects and their backgrounds. In the sleep groups, the trade-off effect was similar regardless of whether a test was expected or not. Test-expectancy did thus not increase the emotional trade-off effect after sleep, but did so after wake.

The Bennion et al¹⁴¹ study combined images that varied in emotion, test-expectancy, and reward for subsequent remembering. The stimulus material came from the emotional trade-off paradigm, but the results reported contained only memory performance for the objects, and not for their backgrounds. The task included neutral, negative and positive items, with the negative and positive items combined in the analysis. This was a nap design that had a wake group

and two different sleep groups. One sleep group had their nap immediately after encoding and then performed the memory test right away. The other sleep group also had their nap immediately after encoding, but then spent an additional two hours awake before the memory test. Results revealed no two-way interactions between sleep and reward or sleep and emotion, but did reveal a trend toward an interaction between sleep and test-expectancy, so that test-expectancy resulted in a larger benefit for memory performance in the nap groups. There was also a trend toward a three-way interaction between sleep, test-expectancy and emotion, indicating that the benefit of sleep when a memory test was expected was evident for neutral items only, and not for the emotional ones.

Studies Combining Emotion with Forgetting Instructions

Three sleep studies have combined forgetting paradigms with emotion. Alger et al² used an IMDF task with images that were either neutral or negative. This was a nap design that had two different sleep groups in addition to the wake group. One sleep group had their nap immediately after encoding and then spent a few hours awake before the memory test. The second sleep group first spent a few hours awake after encoding, and then had their nap right before the memory test. Results revealed that the nap groups showed a larger DF effect

Table 21 Multiple Salience Cues – Factors During Sleep

Study	Age Range	N	Relevance Cues	Type of Sleep	Correlations with Memory Performance
Alger et al, 2019 ²	18–39	31	Emotion x IMDF	Nap	Pos. corr. betw. %SWS and negative items (both R and F); Pos. corr. betw. spindle density and the DF effect for negative items; Pos. corr. betw. spindle duration and the DF effect for negative items
Davidson et al, 2020 ¹³⁷	18–35	15	Emotion x T/NT	Nap	None
Groch et al, 2015 ⁸⁹					
Dataset 1	18–26	18	Emotion + No reward information	Early sleep	None
Dataset 2	19–25	18	Emotion + Reward information	Early sleep	None
Datasets 1 and 2 combined	18–26	36	Emotion x Reward	Early sleep	N/A - see text for the group comparison

Abbreviations: IMDF, item-method directed forgetting; %SWS, percentage of time spent in slow-wave sleep; R, remember; F, forget; DF, directed forgetting; T/NT, think/no-think.

than the wake group, but only for negative items, and not for neutral ones.

In the Kuriyama et al study⁸⁴ (previously mentioned in the section “Other Tradeoff-Paradigms”), participants viewed film clips depicting either motor vehicle accidents or normal traffic. Participants were told to either try to remember, or try to quickly forget, what they were watching. In the subsequent memory test, participants were asked to indicate if the images presented were taken from either the accident clip, the normal traffic clip, or if they were new. Results revealed no interaction effects of sleep and either emotion or remember/forget instructions during encoding on subsequent memory performance.

Davidson et al¹³⁷ used a T/NT design and combined neutral words with either neutral or negative images (which only varied in valence, and not in arousal). Results revealed no interactions between sleep and either item type (Think, No-Think and Baseline) or emotion, and no three-way interaction.

Factors During Sleep in Studies with Multiple Cues of Future Relevance

Studies examining which factors during sleep that are involved in memory consolidation in paradigms with

multiple variables that predict memory performance are presented in Table 21. All studies presented here have included mixed genders, and in all studies, the emotions of the stimulus material have been neutral and negative.

The Groch et al study⁸⁹ (previously mentioned in the section “Early Sleep/Late Sleep and Selective Sleep Deprivation Designs”) also included a second experiment with an early sleep group that encoded negative and neutral images that were all preceded by a frame with a certain color. For half of the trials, participants were informed that there would be a reward if they successfully remembered the color-image association during the subsequent memory test. Memory performance was then tested for both the images and the image-color associations. Results revealed no interaction between reward and emotion for either the images or the image-color associations. However, when contrasting these results with an early sleep group that had not received any reward information, there was an interaction between reward and emotion. In the group that received no reward information, memory performance for neutral items was better than for negative items, which was not the case in the group that had received reward information. The authors interpreted this result

as that without reward information, early sleeps mainly benefits neutral material. With the presence of a reward, however, this salience cue can “override” the cue of emotion, making early sleep benefit negative and neutral items equally. This effect was only present for the image-color associations (for which the reward was promised), and not for the images themselves.

Interim Summary

The most replicated finding when it comes to studies on sleep selectively benefitting memories based on their perceived future relevance has been found in the literature on reward, where an interaction between sleep and reward has been found in about half of the studies.

Regarding other ways of manipulating future relevance, results have been more mixed. Regarding test-expectancy, three studies have found sleep to be more beneficial for memory when a re-test is expected (although one of these studies did not have a wake control group), whereas two studies found no such effects. One study actually instead found the opposite effect, when re-categorizing participants post hoc based on subjective ratings of memory test-expectancy (regardless of which instructions were received).

Support for sleep selectively benefitting memories rated by participants to be of subjective relevance has also been quite limited, with only one study clearly finding such an effect. The tasks used in these studies have, however, been highly varied, making it difficult to know how related these findings are to each other.

Regarding sleep and forgetting, the literature has been even more scattered and inconsistent. One study has found sleep to decrease LMDF, thus increasing performance on the list subjected to “Forget” instructions, whereas two studies have not found any effect. Two studies have found sleep to increase IMDF, another has found the effect only for emotional items (whereas the studies finding an effect used neutral items only), and a fourth study found no difference. One exciting recent development is the preliminary findings that DF can be boosted during sleep through TMR. None of the three studies conducted to date have found sleep to have a different effect than wake on SIF using the T/NT paradigm, and the three studies on RIF have shown effects in opposite directions.

Only one of the three studies that have combined sleep with forgetting instructions and emotion has found an interaction. This interaction consisted of sleep increasing

IMDF for negative items only. Sleep studies combining emotion with test-expectancy and/or reward have not found these factors to additionally increase memory performance for emotional items, but rather for neutral ones.

Studies of which sleep variables that are involved in preferentially benefitting certain memories have been equally contrasting. REM sleep has for example been found to be associated with both reducing RIF and decreasing memory performance for low-reward items, while late sleep has been found to increase memory for items subjected to retrieval-suppression. There has, however, been very little replication of findings, even within highly similar paradigms. There are also findings involving spindle-related variables, with spindles increasing the IMDF effect, and increasing memory performance for high-reward items. Percentage of Stage 4 sleep has also been found to be correlated with memory for high-reward items, and to selectively enhance memories when a test was expected. Once again, one should, however, be careful when interpreting these findings considering the lack of replication between studies.

Discussion

Many say that the field of psychology is currently experiencing a replication crisis.¹⁴² As is hopefully evident by this review paper, this seems to be a major issue also in the literature regarding the frequently made claim that sleep preferentially consolidates memories believed to be of future relevance. Such effects are actually only shown in a minority of studies. This does not necessarily mean that it is impossible that there is such an effect, but we do believe it shows that it is too early to make this claim, and that the effects are probably much smaller than is often suggested in the literature. This lack of an effect of sleep on emotional memory bias is also supported by two recent meta-analyses.^{31,32}

The Schäfer et al³¹ meta-analysis showed that REM-rich sleep, as compared to sleep intervals with less REM, selectively benefitted emotional memories. Considering, however, that a correlation between time spent in REM and emotional memories has only been found in a small minority of studies, it is unclear whether REM sleep is the factor causing the effect in these early sleep/late sleep and selective REM deprivation designs.

Results regarding the role of sleep in prioritizing memories based on other factors that predict future relevance (such as test-expectancy, reward, subjective relevance, or forgetting instructions during encoding or retrieval) have

also revealed highly mixed findings. There has been very little overlap between paradigms, and in several cases, highly contrasting results also between studies using the same paradigm.

After carefully reviewing the literature, we have not been able to detect any specific factor determining when effects are found and when they are not. Our aim has been to present these findings in the hope of making it easier for other researchers to be able to detect whether such patterns exist. As discussed in the following section, larger sample sizes will be crucial for obtaining replicable findings. In addition, novel methodologies, such as multiverse analyses,¹⁴³ may prove helpful in determining which experimental factors, if any, are crucial in accounting for the heterogeneity of results observed to date. There are many factors that might, in combination, bias results toward finding or not finding domain-specific (eg emotional versus neutral) effects of sleep-dependent memory consolidation. As an example, the intensity of the emotional stimuli might be important, as it is possible that a certain intensity is necessary to recruit specific processes during sleep that would further enhance memory consolidation. Other such factors might be the type of sleep manipulation (eg naps versus full nights of sleep), how much time has passed between encoding and the memory test, the kind of memory test used, or the type of stimuli (eg verbal versus pictorial).

A recent meta-analysis showed that a major contributing factor when it comes to replicability issues in psychology research is low statistical power.¹⁴⁴ Sleep research certainly suffers from this problem, as the need for sleep labs and PSG equipment often limits laboratories to run only one participant per day, making it difficult to amass the large sample sizes needed for robust and replicable results. Button et al¹⁴⁵ argue that the risk of spurious findings is larger in underpowered studies, as effect sizes that yield significance in such studies are likely to be among the largest possible by chance alone (the “winner’s curse”), with subsequent attempts at replication having smaller effect sizes and often failing to reach significance. This becomes additionally problematic in correlational studies on sleep and memory, as there are so many sleep variables that can be entered into a correlation matrix, and often several different outcome measurements of memory performance as well. This means that, in the absence of correction for multiple comparisons, one is always very likely to find some significant correlation, based on just the sheer number of tests that can be conducted. This is

probably one factor contributing to the picture we are seeing here, with a lot of significant findings, but none that are replicated in more than a small minority of studies, as well as significant findings in opposite directions.

So where do we go from here? We believe that the first main step is to increase the power in our studies. This is, of course, not a problem that can be easily solved by sleep research itself as the low-powered studies seen in the literature (our own of course no exception) are part of a structural problem in science. Incentive structures reward having many publications rather than a few well-powered ones, and much work is conducted by doctoral, or pre-doctoral, students who often have limited time and resources to complete their studies. One solution is to increase collaboration between labs so that data collection becomes more of a joint effort. What is urgently needed now is large-scale collaborations allowing hundreds of participants per group in order to replicate basic paradigms together, instead of individually working on new advanced paradigms with limited power. We also call for more standardization on how we report our results, so that not only the significant findings are reported and discussed. This is another problem related to problematic incentive structures, where high-impact publishing depends on making one’s results appear as interesting as possible. As a result, researchers tend not to focus on findings they were unable to replicate, making it difficult to get a sense of how common certain findings are in the literature.

We should also agree on some standards for analyzing data, and especially for correcting for multiple tests. One method for handling multiple tests, as suggested by Mantua,¹⁴⁶ is entering all variables into single regression models, instead of performing multiple tests of correlations. Furthermore, it would be beneficial if more correlations were done with the difference score between the two memory measurements of interest (as in the example of using emotional memory bias when testing the role of sleep in emotional memory). This would be the best way of knowing whether a certain sleep variable affects one type of memory more than another rather than merely saying that the sleep variable was correlated with one type of memory but not the other. This would also decrease the total number of tests conducted. We would also call for more pre-registration, which would allow for less “researcher degrees of freedom” to analyze the data in ways that makes the results appear as interesting as possible.

Finally, it is important to remember that even if sleep does not strengthen certain memories more than others, sleep does have an established effect on increasing memory performance in general.¹ This is also supported by the many studies in this review paper showing a main effect of sleep. Thus, sleeping after a learning experience is still highly recommended for better memory consolidation, even if it will not help to sort out which memories that are important from those that are not, at least not to the degree that is so frequently suggested in the literature.

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