Sleep Advances, 2024, **5**, zpae096
https://doi.org/10.1093/sleepadvances/zpae096
Advance access publication 18 December 2024
Original Article

Festschrift in Honor of Dr. Robert Stickgold

Original Article

Memory updating in dreams

Erin J. Wamsley*, Tempest Trost and Matthew Tucker

Department of Psychology and Program in Neuroscience, Furman University, Greenville, SC, USA

*Corresponding author. Erin J. Wamsley, Department of Psychology and Program in Neuroscience, Furman University, 3300 Poinsett Highway, Greenville, SC 29613-1111, USA, Email: erin.wamsley@furman.edu.

Abstract

Robert Stickgold's research was among the earliest to rigorously quantify the effect of learning on dream content. As a result, we learned that dreaming is influenced by the activation of newly formed memory traces in the sleeping brain. Exactly how this happens is an ongoing area of investigation. Here, we test the hypothesis that participants are especially likely to dream of recent experiences, which overlap with well-established semantic networks. We created an artificial situation in which participants encountered new information about a person with which they have extensive past experience—a favorite celebrity. We tracked the effect of novel information about a favorite celebrity on participants' dream content across 3 consecutive nights and queried participants about other recent and remote memory sources of their dreams. While the celebrity manipulation failed to affect dream content, this dataset provides rich descriptive information about how recent and remote memory fragments are incorporated into dreams, and how multiple memory sources combine to create bizarre, imaginative scenarios. We discuss these observations in light of the proposed "memory updating" function of sleep-dependent memory consolidation, as well as Stickgold and Zadra's NEXTUP (Network Exploration to Understand Possibilities) model of dreaming. This paper is part of the Festschrift in honor of Dr Robert Stickgold.

Key words: sleep; memory; dreams; dreaming; memory consolidation; memory updating; hippocampus

Statement of Significance

Memory consolidation is fundamental to human cognitive functioning, determining which newly learned information is retained over the long term. The research reported here demonstrates how dreams might provide insight into the consolidation of memory in the sleeping brain. Specifically, our data suggest that during sleep, the brain co-activates multiple memories simultaneously, combining the activation of recent experience with the reactivation of remote, long-past memory. This process could function to help the brain update older memory networks with new information over time.

Dreams about recent experience are a promising source of information about how specific memories are reactivated and altered during sleep. The effect of recent experience on dreaming has been systematically studied since at least the 1960's [1–4]. Yet, while it is well established that we dream about experiences, thoughts, and concerns from our everyday lives [5, 6], early studies made little progress in prospectively predicting "which" waking experiences will be incorporated into dreams [7]. The 1960s–1980s saw myraid attempts to experimentally influence dreams, using a range of presleep tasks including exposure to negative emotional images and videos [8, 9], erotic stimuli [10], and manipulation of thirst and hunger [11–13]. However, these studies largely failed to detect unambiguous, statistically significant effects on dream content, and it seemed that the experimental manipulation of dreams might not be a feasible approach. Beginning in the late 1990's, Robert Stickgold's innovative approach to the topic began to change that situation.

Bob Stickgold's approach to measuring dream content combined two key features that together allowed the successful experimental manipulation of dreams. First, he moved away from difficult laboratory studies in which technicians monitor participants all night in order to awaken them for just a handful of dream reports. Instead, Stickgold developed new technologies that automatically awakened participants for a large number of reports in quick succession in the home environment [14–18]. Second, instead of passively exposing participants to stimuli such as images or videos, Stickgold utilized engaging, interactive games as a presleep experience that would more effectively capture participants' attention and drive learning. While experimentally manipulating dreams remains difficult, the use of interactive, game-like tasks combined

Submitted for publication: July 2, 2024; **Revised:** November 9, 2024

with experimental awakenings in rapid succession has enabled scientists to track the incorporation of presleep experience intro dreams in a way not previously possible [19].

Together with work from other labs, Stickgold's research in this area established that interactive, engaging learning tasks reliably affect dreams and that incorporation of these learning experiences into dreaming is associated with enhanced memory consolidation during sleep [18, 20, 21]. These observations have now been confirmed and extended by multiple other laboratories. Today, while it is still unknown whether dreaming about recent learning experiences "causes" changes in memory, it is well established that dreaming about a recent learning experience is positively associated with subsequently improved performance [21].

Yet, the features of everyday experience that cause a particular memory to be incorporated into dreaming over another remain obscure. In retrospective studies, participants are likely to perceive their dream as related to at least one specific past experience [22, 23]. But prospective "prediction of which" everyday waking experiences will appear in subsequent dreams has never been convincingly demonstrated. This speaks to our still poor understanding of the factors that mediate the appearance of particular memories in dreams. While engaging video games and game-like tasks appear to be successful in affecting dream content, the exact reasons for this have not been systematically established. For example, it has often been claimed that the interactive nature of video games accounts for their incorporation into dreams, but few studies have attempted to manipulate this factor, and none have demonstrated its importance. Potentially, the fact that game-like tasks involve learning a new skill could be essential to their effect on dreams, but this too has not been experimentally established. There is, however, some converging evidence that life experiences that are emotional [24] and/or personally significant (e.g. a divorce [25], an upcoming surgery [26]) may be especially likely to be incorporated into dreams, in comparison to less-salient daily activities [27, 28].

One feature of daytime experience insufficiently explored as a driver of dream content is the degree to which a new experience is related to pre-existing semantic memory networks. In the late 2000s, research on memory consolidation during sleep increasingly began to describe how memory is not only "strengthened" during sleep but also "reorganized." One form of memory reorganization thought to be facilitated by sleep is the integration of new, hippocampus-mediated learning into existing cortical networks. For example, a 2010 collaboration between Stickgold's lab and Gareth Gaskell's at the University of York investigated the role of sleep spindles in integrating newly learned words into the mental lexicon [29], a gradual process thought to develop preferentially across periods filled with sleep [30, 31]. This is now just one of several lines of evidence supporting the hypothesis that sleep is involved in updating established cortical representations with new information gleaned from recent episodes [32–36]. For example, new memories that are strongly related to an existing schema are preferentially and rapidly consolidated [37], and there is evidence that this could preferentially occur during sleep—quantitative sleep features including spindles [38] and theta activity [39] have been associated with improved retention of new information that relates to established schemata. Thus, it may be that sleep especially facilitates the consolidation of new information that is strongly related to existing representations.

If schema-congruent experiences are preferentially reactivated during sleep, might they also be preferentially represented in dreams? We know already that dreams can combine fragments of recent and remote episodes together into novel scenarios [23], and that at times, the remote memories referenced in dreams are semantically related to a recent experience. For example, after playing the downhill skiing arcade game *Alpine Racer II*, one participant dreamed, not of the game itself, but of a related remote memory [18]:

> I was picturing stacking wood this time… I felt like I was doing it at… at a ski resort that I had been to before, like five years ago maybe

Similarly, in two studies during which participants played the video game Tetris before sleep, participants reported dreaming of past experiences with this game or similar games, rather than the specific presleep task itself [20, 40].

This suggests the hypothesis that, among the multitude of new memories we form each day, those congruent with well-established cortical schemata might be especially likely to reactivate during sleep and be incorporated into dream content. But as in the above example, the result may often be a dream more clearly related to remote memories stored in cortical networks, rather than to the recent experience that triggered the dream.

In the current study, we hypothesized that dreams are most likely to incorporate new information when it is strongly related to well-learned existing representations of high personal significance to the dreamer. We tested this by experimentally introducing research participants to novel information about a well-learned concept of personal significance to them—a favorite celebrity. Our goal was to test how exposure to new information about an established semantic concept would affect dreams. It is challenging to identify categories of pre-existing knowledge common across participants with diverse interests and backgrounds. In this case, the use of celebrity information leveraged a category of semantic knowledge common to most young adult college students, many of whom have a strong interest in at least some celebrities.

In this study, participants read novel information regarding a favorite celebrity of theirs and then were repeatedly awakened to report dreams across the subsequent 3 nights in their home environment. Our primary hypothesis was that exposure to novel information about a favorite celebrity would cause participants to dream about remote memories related to this individual. Morning questionnaires additionally queried participants about other recent or remote episodic memories that they believe influenced their dream. We expected that, independent of dreams about the celebrity, participants would also report dreams that combined features other recent experiences with fragments of semantically related remote memory.

Materials and Methods

Participants

Participants were $N = 34$ undergraduate students at Furman University (94.12% female, mean age = 20.0 ± 1.39 *SD*, age range: 18–24 years).

Procedures

Overview

This study was conducted remotely during the COVID-19 pandemic, utilizing Zoom for participant–researcher meetings, a smartphone app for dream sampling (Expiwell, www.expiwell.com), and Qualtrics for administration of surveys and delivery of stimuli. This research was approved by the Furman University Institutional Review Board.

Participants read a mix of real and fabricated entertainment news articles. The critical manipulation was that experimental group participants read a fabricated entertainment news story created specifically for them, containing novel information about a favorite celebrity they had listed on a screening survey >2 weeks earlier.

Following exposure to the entertainment news articles, participants were experimentally awoken using their smartphone across the next 3 nights, reporting up to 5 dreams per night. Each morning, participants completed a questionnaire asking for detailed reports of the memory sources for each dream reported the night before.

Screening

Interested participants completed a screening survey, which included demographic questions, the Mindful Attention and Awareness scale [41], the daydream frequency subscale of the Imaginal Processes inventory [42], and a 40-question "Media Preferences Inventory" created specifically for this study. This lengthy survey was for the sole purpose of distracting attention from the critical question of interest, which asked participants whether they had "favorite" celebrities, and if so, to list up to three favorites. To be invited to complete the remainder of the study, participants had to indicate at least one favorite celebrity on the screening survey. The celebrity was required to be an entertainment or sports figure with at least 100-k followers on Twitter. It was also permitted that the "celebrity" could be a group (e.g. a band or sports team). It was required that participants not list any favorite celebrities that were planned to appear in the standard set of news articles given to all participants later in the study. Participants were also required to report that they typically recall at least one dream per month and to indicate that they have a smartphone with at least 15 MB of free space to download and install the Expiwell experience sampling app.

Experimental manipulation

The next phase of the study began a minimum of 2 weeks after participants submitted the screening survey. This was designed to minimize the probability that participants would become aware that study materials intentionally incorporated information about their specific favorite celebrities, as supplied on the screening survey. Participants first completed a ~1-hour video call with the project manager (T.T.), who explained study procedures, walked participants through installing the Expiwell experience sampling app on their phone, led them through a series of practice dream reports, and explained how to complete the dream questionnaire each morning. The 3 experimental nights were then scheduled at a time of the participants' choosing, during a time when they expected to be keeping a regular sleep schedule.

The evening before the first night of dream collection, participants completed a Qualtrics survey in which they read and answered questions about 10 different tabloid entertainment news articles, including a mix of 6 real and 4 fabricated celebrity news stories. The real articles were taken from web sources (including TMZ, NME, ET, and SkyNews), and the fake articles were fictitious creations which used the same website headers, fonts, and advertisements to create the illusion of a genuine article. Both real and fabricated articles were short-format and fit on a single screen, with a word count between 150 and 200, excluding text in the headline and advertisements (mean word count = 170.1, *SD* = 9.9). Screenshots of the full set of articles can be found with our publicly posted study materials on Open Science Framework at https://osf.io/mj43y/.

Control participants each saw a standard set of 10 articles. Experimental participants saw the same set of articles, except that one of the fake articles in the standard set was replaced with an article about their favorite celebrity, individually created for that participant. The story about their favorite celebrity was always either about a TikTok video they had just posted following the "Wipe it Down" dance trend, or a donation they had just made to the Red Cross, depending on which would be most realistic for that particular celebrity. We used a fabricated instead of a real story to ensure that the information was novel for the participant. Other fabricated news stories were also included, to ensure that the fabricated article about a favorite celebrity did not stand out stylistically. In the control group, no articles mentioned a favorite celebrity.

After reading each article, participants responded to 4 questions. The first was a multiple-choice question testing comprehension of and memory for the content of the article. Participants performed well on these questions (mean 81.07% correct, ±12.86% *SD*). Participants also rated their level of interest in the article, whether they had previously heard of the celebrity discussed in the article, and their level of interest in that celebrity.

Dream collection

Across the next 3 nights, participants were awoken via a text alarm 4 times during the night, at which point they were prompted to record their dream experience using the Expiwell app. The timing of awakenings was individualized for each participant's self-reported sleep schedule. During the experimental nights, participants reported a mean bedtime of 00:23 ± 74.37 min (*SD*) and a mean wake time of 09:11 ± 105.99 min (*SD*). After excluding the first hour after their normal bedtime and the last hour before their normal wake time, alarms were scheduled to occur 34%, 55%, 70%, and 85% through the remaining interval of participants' self-reported habitual sleep phase. This schedule, focusing on sleep during middle portion of the night, was selected to maximize the probability that participants would be asleep at the time of the alarm, and to cause reports to be collected from a variety of sleep stages, including REM sleep, during which rates of dream recall are high [43]. Participants were additionally encouraged to record one further report upon awakening in the morning if they had any additional content to report. This led to a maximum of 5 opportunities per night to report a dream experience. However, participants usually did not provide this many reports, as during this challenging pandemic-era field study, it was common that participants not wake up in response to some of the alarms, did not respond to some of the alarms, or did not successfully complete and upload the experience sampling form. In total, 149 reports were collected, including 58 on night 1, 55 on night 2, and 36 on night 3. The reasons for the lower number of dreams contributed on night 3 are uncertain, but this could have been driven by a decline in participant motivation across the course of this 3-day study. Figure 1 describes the number of successfully collected reports by night and awakening number.

When participants were awoken by the alarm, they opened the Expiwell app and made an audio recording of "everything that was going through their mind" just before the alarm, in as much detail as they could remember. They were assured that it was alright if the dream had very little content, or if they could not remember anything they had been dreaming, but they were encouraged to take a moment and remember the dream before they attempted a recording. Once they completed the recording, they were asked if they felt they had been asleep or awake when they heard the alarm go off.

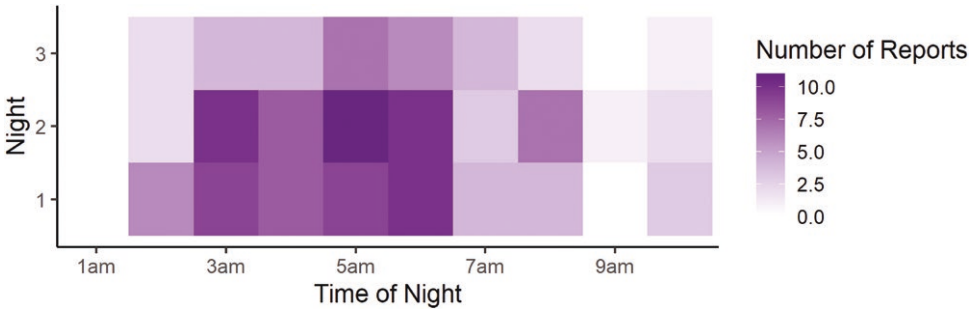

Figure 1. Reports submitted by night and time of night. Number of reports successfully submitted across each of the 3 nights of the study, by the time of night.

Morning dream survey

Participants received a follow-up survey about their dreams within an hour of their habitual wake time each morning and were asked to complete it as soon as possible. This survey asked about their sleep schedule the previous night and then showed the transcript of each of the previous nights' dreams, one by one. For each dream, participants were asked whether "this dream, or any part of it, originated in a specific past experience of yours?" Participants were specifically instructed that "we are interested in specific experiences that happened at a particular place and time. For example, taking a biology final exam last Tuesday is a specific experience that happened at a particular place and time. However, the general idea of being worried about your grades is not a specific experience that happened at a particular place and time." If they answered this question in the affirmative, participants then described up to 3 episodic memory sources for each dream, described which specific part of the dream they felt the source was related to, indicated how long ago the experience occurred (yesterday/in the last week/in the last month/in the last year/>1 year ago/do not know), how certain they were that the dream was caused by this experience, as well as how important and how emotional the experience was. When more than one experience was listed as the origin of a single dream, the participant also rated how strongly related these experiences were to each other (separately for each pair of experiences).

Exit questionnaire

Finally, after 3 nights of dream reporting were completed, participants completed an exit questionnaire. This questionnaire asked participants whether they suspected that any of the articles they read were fictitious, if they noticed that a favorite celebrity of theirs was discussed in one of the articles, and if they had looked up information about the articles during the study. Debriefing information was also included at the end of this questionnaire.

Dream report scoring

Transcribed dreams were scored by three independent raters, blind to experimental condition. Alongside reports from the current study, raters also scored a set of reports from a similar prior study in our lab, in which participants were not shown any news articles. This set of reports (referred to as the "Nonexposure" group) served as a control for exposure to entertainment news in general.

For each report, raters first determined whether it contained content. Dreams were considered to be "content-filled" if participants described any mental content at all, as opposed to indicating that they could not remember or were not dreaming. For all content-filled reports, raters then determined whether the report included the following:

1. Content that was *directly celebrity-related*. This included direct mention of specific celebrities, including:
   (a) The participant's specific, target favorite celebrity.
   (b) Another specific celebrity from the entertainment news articles.
   (c) Other celebrities not among those mentioned in the articles.
2. Content that was *indirectly celebrity-related*, without mention of any specific celebrity. (Example provided to raters: "I was talking to a famous person, but I can't remember who it was").
3. *Article-related content*. This could include images or sensations directly or indirectly related to any other element of the news articles. (Example provided to raters: "I was playing golf with a friend and he ripped his pants, like in the articles you had me read").
4. *Study-related content*. This could include images or sensations directly about the study procedures (the experience sampling app, the alarms, reporting dreams) or more indirectly related content of persons, objects, locations, or actions similar to those in the study. (Example provided to raters: "I was recording something").
5. Mention of *remote episodic memories* related to the task or experiment. This included content referencing participants' personal past experiences with celebrities, research studies, or article-related content. (Example provided to raters: "I was thinking about the last time I did a dream study like this").

To allow raters to know which target favorite celebrity should be considered in scoring, reports were scored in triads, with raters receiving all reports from one experimental condition participant, one control group participant, and one nonexposure group participant as a set (unlabeled), along with a copy of the target favorite celebrity article that had been read by the experimental participant.

Interrater reliability was high, with 95.1% agreement on whether a report contained content, 80.4% agreement on determining the presence of celebrity-related content (encompassing categories 1–4 above), 84.8% agreement on article-related content, and 87.0% agreement on study-related content. Agreement on the mention of past experiences related to celebrities, research studies, and article content was 99.4%, 99.1%, and 99.4%, respectively. Final scores for analysis were based on a two-thirds majority. Three-way disagreements were resolved through discussion and consensus.

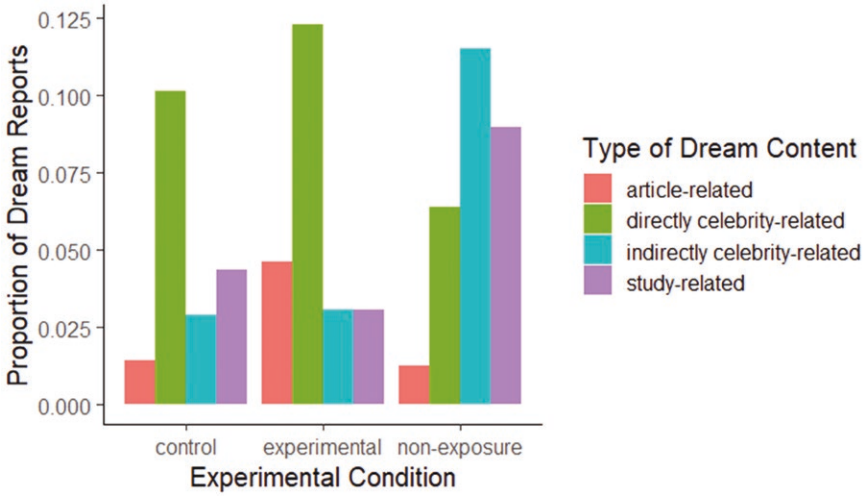

Figure 2. Effect of condition on incorporation of entertainment news articles into dreaming. Experimental condition had no significant effect on dreaming about celebrities (either those specifically represented in the news articles or other celebrities) and no effect on dream content related to other aspects of the entertainment news articles. Dreams in the nonexposure group contained more content judged to be indirectly related to celebrities. Dream content related to the study itself also did not differ by experimental condition.

Results

A total of 149 dream reports were collected across the course of the study, with each participant contributing an average of 5.52 ± 2.68 *SD* reports. Of these, 134 (89.93%) were content-filled, with the remainder consisting of inability to recall (e.g. "There was nothing"/"I don't remember"). Upon awakening, participants indicated that they had been asleep in 75.18% of cases, awake in 15.6% of cases, and unsure in 9.22% of cases. As "awake" responses may have been the result of sleep state misperception, all reports are considered together in the following, regardless of subjective evaluation of sleep state [44].

No effect of celebrity news exposure on dream content

The experimental manipulation did not significantly affect dream content (Figure 2). Dreams that mentioned specific celebrities were rare. No participant dreamed about the target "favorite" celebrity, and only one (in the control group) dreamed about a specific celebrity from the news articles. Because of this, the statistical analysis considered dreams with a specific mention of any celebrity under the single category of "directly celebrity-related" (see Matherials and Methods).

Chi-squared tests revealed no effect of experimental condition on directly celebrity-related dreams ($\chi^2 = 1.39$, $p = .513$, Cramer's $V = 0.08$). Dreams from the nonexposure group were more often judged as indirectly related to celebrities than dreams form in the current study ($\chi^2 = 6.29$, $p = .043$, Cramer's $V = 0.16$), but the control and experimental groups did not differ from each other on this measure ($\chi^2 = 0$, $p = 1.000$, Cramer's $V = 0$). There was no effect of experimental condition on dreams about other aspects of the articles ($\chi^2 = 1.96, p = .470,$ Cramer's $V = 0.09$) or about the research study itself ($\chi^2 = 2.68$, $p = .293$, Cramer's $V = 0.11$). No dreams contained mention of "remote episodic memories" related to celebrities, the entertainment news articles, or the experiment.

On the exit questionnaire, a handful of participants reported suspecting that some of the news articles they viewed might be fake ($n = 4$ in the Control group and $n = 3$ in the Experimental group). Participants in the Experimental group were likely to notice that one of the articles mentioned a favorite celebrity of theirs ($n = 12$), but only $n = 4$ reported suspecting that this article was created specifically for them. $N = 5$ participants in each group reported looking up information about the news articles during the 3-day study.

Other episodic memory sources of dreams

While the news article manipulation had little if any effect on dreams, participants frequently identified other past episodic memories as sources of their dream content. On the morning dream survey, participants identified 59.7% ($n = 80$) of content-filled reports as originating from at least one specific past episode. Each participant identified a memory source for an average of $n = 3.33 \pm 1.83$ *SD* dreams.

As illustrated in Figure 3, recent episodes from the previous day or week were more commonly identified as a dream source, relative to remote episodes. While the association between temporal origin of the episode and participants' confidence in its connection to the dream did not reach significance ($F(4,111) = 2.37$, $p = .057$, $\eta_p^2 = 0.08$), confidence was numerically higher for recent memory sources (mean certainty for sources from yesterday = 80.18, *SD* = 24.75; last week = 71.81, *SD* = 19.27; last month = 67.47, *SD* = 26.36; last year = 61.00, *SD* = 33.77; >1 year = 62.50, *SD* = 27.52). Temporal origin was not related to the perceived emotion ($F(4,111) = 0.55$, $p = .701$, $\eta_p^2 = 0.02$) or importance ($F(4,111) = 1.47$, $p = .215$, $\eta_p^2 = 0.05$) of an episode.

Confidence in memory source identification

The distribution of certainty ratings was strongly left-skewed, with a modal rating of 100% confidence in the association between a memory source and a dream. Experiences more confidently associated with a dream were also rated as more important life experiences ($r = .19$ (116), $p = .035$). In contrast, the emotional valence of an experience was unrelated to how confidently participants associated it with a dream ($r(116) = -.02$, $p = .804$).

Co-occurrence of multiple episodic sources in the same dream

Of dreams with at least one identified waking source, 38.75% ($n = 31$) were associated with 2 or more memories, as shown in

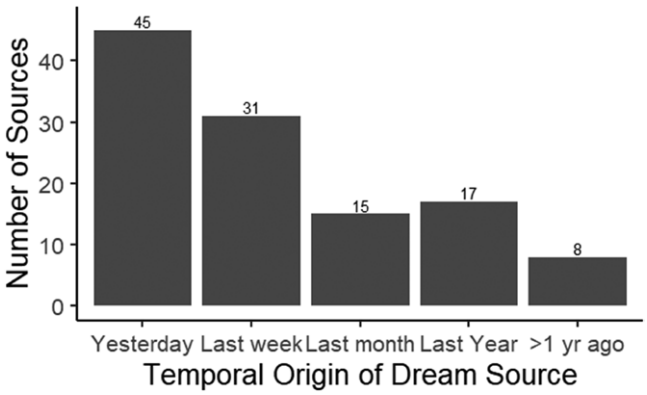

Figure 3. Temporal origin of participant-identified dream sources. Participants were asked to identify the probable episodic memory sources of each dream. For each source, participants indicated when the episode had occurred. Recent episodic sources were more commonly identified than remote episodic sources.

Figure 4A. In just over half of these dreams ($n = 16$), participants reported a semantic relationship between the co-occurring memory sources Figure 4B.

Dreams with multiple memory sources sometimes combined past episodes originating from different time points, for example combining a recent with a more remote memory (Figure 4C). Most commonly, dreams were described as originating both from an episode from yesterday and from a separate episode within the past week. This particular combination of temporal sources was also the one with the highest rating for semantic similarity (Figure 4D). As one example of a dream that combines multiple semantically related sources from different time points, one participant reported the following:

> *Dream:* I had dreamt that I was home, and I looked outside in our yard and uh, there were a ton of turkeys, uh, and I was just having a conversation with my dad about, um, hunting turkeys for Thanksgiving, um, and that was pretty much it.
> *Experience 1, yesterday:* Yesterday night, before bed, I was on the phone with a friend, I shared how when I was little I used to call "cookies" "turkeys"
> *Experience 2, in the last week:* Last week, my dad and I were hiking behind our house and saw turkeys like we always do. We had a conversation about hunting around Thanksgiving.
> *Experience 3, in the last week:* Two days ago, I was at my grandparents'. They talked about how they had heard there would be a turkey shortage at Thanksgiving. They made dinner for my brother and I, they were looking for a turkey to fix, but couldn't find one when they to the store, we had chicken instead.

Time of night effects on memory sources

As shown in Figure 5, the temporal origin of dream sources did not vary significantly by time of night ($F(4,78.45) = 0.24$, $p = .917$, $\eta_p^2 = 0.01$). However, among dreams with multiple memory sources, there was a trend for sources to be more strongly related to each other later in the night (Spearman's rho = 0.36, $p = .057$; Figure 6).

Discussion

Experimental manipulation

Encountering information about a favorite celebrity did not trigger-related dreams. Only a single participant dreamed about a celebrity represented in the study materials, and given the nonzero rate of celebrity dreams in the nonexposure set, this may have been a chance occurrence. Thus, in this paradigm, we found no evidence that exposure to new information about an established concept triggers dream incorporation.

Other approaches of presenting updates to an established semantic memory might be more successful. It could be that the short, simple articles used here did not drive new learning intensely enough to impact dreams. Alternatively, participants may not have been as personally invested in the information as we expected, causing overall attention to and engagement with the materials to be lower than in prior studies showing successful incorporation of presleep learning tasks. Future studies might pursue other ways of introducing updates to established semantic memory that leverage engaging game-like tasks, involve more intensive learning, or increase the emotional and personal significance of study materials in other ways.

Memory source combinations

Still, these data provide useful information about how recent and remote memory fragments are incorporated into dreams. As expected, participants traced the majority of dreams to at least one past episodic memory, and often to more than one distinct episode. In about half of dreams with multiple sources, the component memories were perceived as at least somewhat semantically related to each other. These sources most often were drawn from different time frames, for example being traced to both an experience from the night before and an experience from the previous weeks, months, or years. We interpret this as evidence that recent experiences from the previous days can trigger dreams that incorporate related remote and semantic memory fragments via a spreading activation process.

In wake or sleep, recalling a memory requires that a neural representation of that memory be "reactivated" in the brain. It remains unknown whether the form of reactivation that causes dreams of recent experience is the same, or even similar to the form of memory reactivation thought to account for sleep's mnemonic benefits [45]. But still, we presume that dreams incorporating elements of recent experience signify that neural networks encoding those memory elements must be in some way active in the sleeping brain. Thus, our current data suggest that during sleep, neural ensembles representing elements of participants' recent experience become co-activated with those representing features of related remote and semantic memory. Speculatively, this could be a functional process relevant to the integration of new information into existing cortical networks during sleep.

These observations are consistent with Stickgold and Zadra's NEXTUP (Network Exploration to Understand Possibilities) model of dreaming [46]. A core feature of NEXTUP is the proposal that the sleeping brain strengthens connections between memories, including between recent experiences and remote memories, as well as semantic memories, concerns, thoughts, and feelings. Together with other recent studies [23, 47], our current data support the notion that during dreaming, the sleeping brain activates connections between distinct-related memory networks. This can be seen in cases where participants identify multiple semantically related memory sources for a single dream. Speculatively, in such cases, overlap between the memory representations may have driven their co-activation. Of course, this speculation is tempered by the fact that cases of strong semantic similarity between co-occurring memory sources were found only in a minority of dreams. Participants frequently perceived only a weak

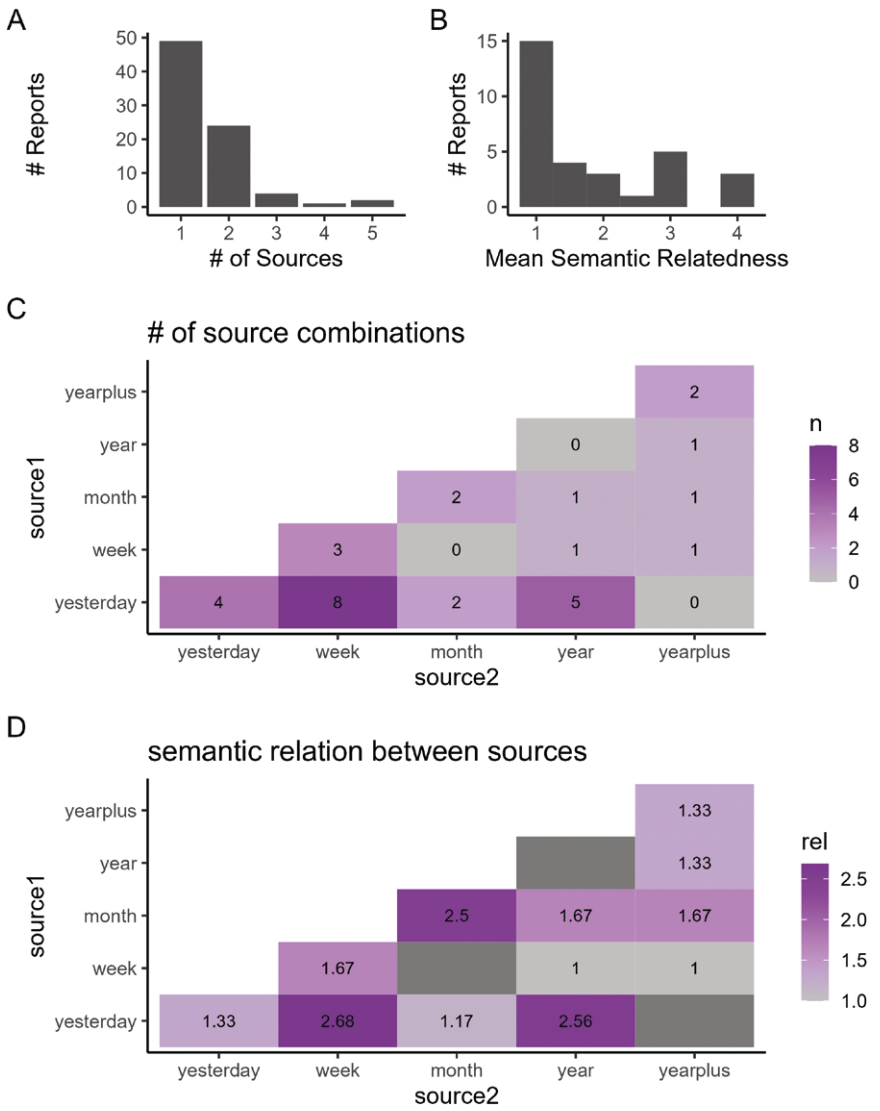

Figure 4. Co-occurrence of multiple memory sources within single dreams. (A) While dreams were most commonly traced to a single episodic memory source, 39% incorporated multiple past episodes. (B) When multiple past episodes appeared together in a dream, participants most often perceived these experiences as unrelated to each other. However, there were notable exceptions, as discussed below. (C) Raw number of dreams referencing multiple episodic memory sources originating from different time points. (D) Mean semantic relatedness of memory source combinations by temporal origin. Numbers are the average participant rating of semantic relatedness for all possible pairs of memory sources appearing together in a single dream. yearplus = memory sources from more than 1 year ago.

relationship between the memories contributing to a dream, and about half the time, they thought that the co-occurring memories were entirely "unrelated" to each other.

Temporal origin of memory sources did not change across the night

A handful of influential early studies reported that early night dreams are likely to reference recent memories, whereas late night dreams are likely to reference memories originating the longer past [48]. This has suggested to contemporary researchers that the engagement of memory systems might change systematically across the course of the night, and indeed, similar observations have been reported in at least one recent study [47].

In the current study, we found no evidence that the temporal origin of dream memory sources varied by the time of night. However, if there is a true association between time-of-night and the temporal origin of memory sources, we could have been ill-positioned to detect it because our data do not include many early-night dreams. In fact, recent observations from Picard-Deland et al. [47] suggested that the time-of-night effect is driven specifically by a high proportion of recent memory sources in the 1st third of the night, a time frame underrepresented in the current data. Additionally, if the effect of time of night on dream memory sources varies by sleep stage, the fact that the sleep stage of dream reports in the current study is unknown could have obscured our ability to detect this effect.

Future directions

Determining the features of a presleep task that causes its incorporation into dream content

The particular features of a presleep learning task, which mediate its incorporation into subsequent dreams, remain poorly understood. This is highlighted by the failure of our experimental manipulation to affect dream content, which is not unique among

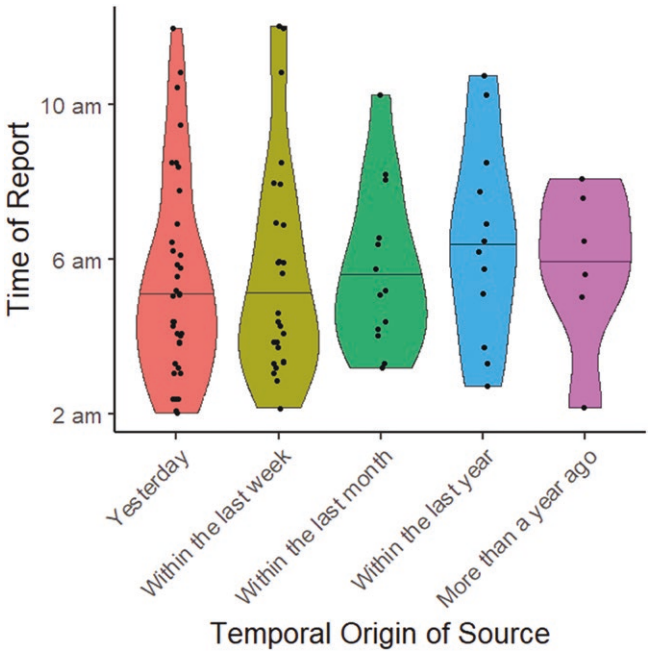

Figure 5. Temporal origin of dream sources by the time of night. The temporal origin of dream sources did not vary by the time of night from which the dream was reported. Each point represents an individual memory source within a dream report.

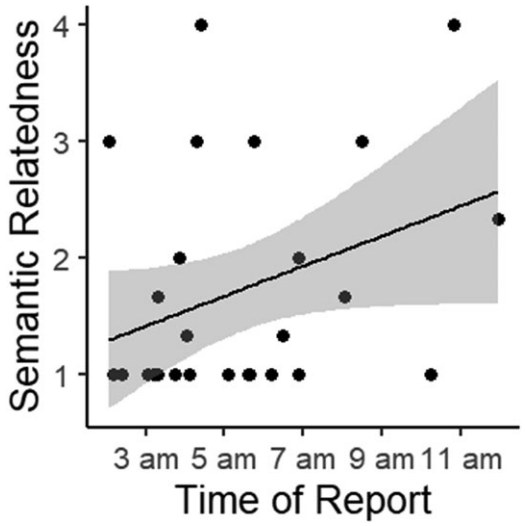

Figure 6. Semantic relatedness of dream sources by time of night. There was a trend for sources co-occurring within the same dream to be more strongly semantically related to each other later in the night.

similar investigations. In addition to the older literature reviewed in the introduction, a number of more recent investigations have also found limited or no direct incorporation of presleep tasks into dream content [49–52]. It remains unclear whether the particular experimental tasks employed in these studies lack some key feature that drives incorporation, or alternatively, whether these null results can be attributed to more general factors such as sampling error, measurement error, or the participant populations under study.

In part, our understanding has been hampered by a lack of a systematized, consistent approach. Remarkably, no studies cited in the current paper have been subject to a direct replication, nor have two utilized the exact same learning task. Thus, the stability of incorporation rates across samples remains unknown. To remedy this situation, further rigorous experimental studies that systematically manipulate the features of presleep tasks are required. It is often proposed that features of a task such as the amount/type of new learning, or the level of interactivity, emotion, or personal relevance account for its incorporation into dreaming. But none of these features have yet been isolated and demonstrated to reliably affect dreaming across multiple studies.

Does the coactivation of multiple memories in dreaming serve a function?

Potentially, coactivating recent and semantically related remote memories during sleep could facilitate the integration of new information into existing knowledge structures, a hypothesized function of sleep-dependent memory consolidation [29–36, 38, 39]. To test whether dreams that combine multiple memories reflect, this function would require measuring changes in a remote memory after participants dream about it in association with related recent experiences. This approach presents many methodological challenges, too numerous to list here. But potentially, these could be overcome with the help of creative techniques that boost the reliability with which presleep experiences trigger dreams of remote memory, using targeted memory reactivation [53] and/or volitional control of dreaming in experienced lucid dreamers [54–56]. Future studies should continue to explore whether memory representations, and the connectivity between them, may be altered as a consequence of their coactivation during dreaming.

Effect of sleep stage on memory source activation

A limitation of the current study is that, because we were unable to use polysomnography, the stage of sleep during which dreams occurred is unknown. It is likely that some reports were collected during wakefulness. Within sleep, these at-home awakenings may have been biased toward collecting dreams from lighter sleep stages, from which participants were more likely to successfully awaken. The sleep stages from which dream reports were collected may have influenced the results we present here, as there is reason to believe that the activation of memory sources during sleep varies by sleep stage [23]. Future studies should continue to examine this. For example, the NEXTUP model predicts that weakly associated memory networks should be especially likely to become coactive during REM, as opposed to NREM sleep.

Conclusions

In summary, despite the failure of the main experimental manipulation, we report several theoretically relevant observations surrounding the co-occurrence of memory fragments from multiple waking sources in dreams. Speculatively, dreams that incorporate memories drawn from multiple time frames may reflect sleep's role in updating remote and semantic memory networks with new information gleaned from recent experience, a putative function of sleep.

Acknowledgments

Thank you to Bob Stickgold for everything. Thank you to Megan Collins for technical assistance in preparing the study procedures. This manuscript was prepared using Quarto in R, assisted

by the apaquarto extension by William Joel Schneider https://wjschne.github.io/apaquarto/. Tempest Trost's work on this project was supported by a summer research fellowship from Furman University.

Author contributions

Erin Wamsley (Conceptualization [supporting], Formal analysis [lead], Funding acquisition [lead], Methodology [equal], Resources [lead], Supervision [lead], Visualization [lead], Writing—original draft [lead], Writing—review & editing [equal]), Kathryn Trost (Conceptualization [equal], Formal analysis [supporting], Methodology [equal], Project administration [equal], Writing—original draft [supporting], Writing—review & editing [equal]), and Matthew Tucker (Conceptualization [equal], Writing—review & editing [equal])

Funding

The authors have no financial conflicts of interest to disclose.

Conflict of interest statement

The authors have no other disclosures to make.

Data availability

All raw data and code required to reproduce the analyses described here are publicly available on Open Science Framework at: https://osf.io/mj43y/.

References

1. Dement WC, Kahn E, Roffwarg HP. The influence of the laboratory situation on the dreams of the experimental subject. *J Nerv Ment Dis*. 1965;**140**:119–131. doi:10.1097/00005053-196502000-00002
2. De Koninck JM, Koulack D. Dream content and adaptation to a stressful situation. *J Abnorm Psychol*. 1975;**84**(3):250–260. doi:10.1037/h0076648
3. Fiss H, Kremer E, Litchman J. The mnemonic function of dreaming. *Sleep Research*. 1977;**6**:122.
4. Foulkes D, Rechtschaffen A. Presleep determinants of dream content: Effect of two films. *Percept Mot Skills*. 1964;**19**:983–1005. doi:10.2466/pms.1964.19.3.983
5. Domhoff GW. Dreams are embodied simulations that dramatize conceptions and concerns: The continuity hypothesis in empirical, theoretical, and historical context. *Int. J. Dream Res*. 2011;**4**(2):5062.
6. Hall CS, Nordby VJ. *The Individual and His Dreams*. NY: New American Library; 1972.
7. Wamsley EJ, Stickgold R. *The neuroscience of sleep*. In: London: Academic Press; 2009:330–336.
8. Witkin HA, Lewis HB. *Presleep Experiences and Dreams*. NY: Random House; 1967.
9. Goodenough DR, Witkin HA, Koulack D, Cohen H. The effects of stress films on dream affect and on respiration and eye-movement activity during Rapid-Eye-Movement sleep. *Psychophysiology*. 1975;**12**(3):313–320. doi:10.1111/j.1469-8986.1975.tb01298.x
10. Cartwright RD, Bernick N, Borowitz G, Kling A. Effect of an erotic movie on the sleep and dreams of young men. *Arch Gen Psychiatry*. 1969;**20**(3):262–271. doi:10.1001/archpsyc.1969.01740150006002
11. Dement WC, Wolpert EA. The relation of eye movements, body motility, and external stimuli to dream content. *J. Exp. Psychol*. 1958;**55**(6):543–553. doi:10.1037/h0040031
12. Bokert EG. *The Effects of Thirst and a Related Verbal Stimulus on Dream Reports*. New York, NY: New York University; 1967.
13. Koulack D. Effects of thirst on the sleep cycle. *J Nerv Ment Dis*. 1970;**151**(2):143–145. doi:10.1097/00005053-197008000-00008
14. Rowley JT, Stickgold R, Hobson JA. Eyelid movements and mental activity at sleep onset. *Conscious Cogn*. 1998;**7**(1):67–84. doi:10.1006/ccog.1998.0333
15. Pace-Schott EF, Kaji J, Stickgold R, Hobson JA. Nightcap measurement of sleep quality in self-described good and poor sleepers. *Sleep*. 1994;**17**(8):688–692. doi:10.1093/sleep/17.8.688
16. Cantero JL, Atienza M, Stickgold R, Hobson JA. Nightcap: A reliable system for determining sleep onset latency. *Sleep*. 2002;**25**(2):238–245. doi:10.1093/sleep/25.2.238
17. Stickgold R, Malia A, Fosse R, Propper R, Hobson JA. Brain-mind states: I. *Sleep*. 2001;**24**(2):171–179. doi:10.1093/sleep/24.2.171
18. Wamsley EJ, Perry K, Djonlagic I, Reaven LB, Stickgold R. Cognitive replay of visuomotor learning at sleep onset: temporal dynamics and relationship to task performance. *Sleep*. 2010;**33**(1):59–68. doi:10.1093/sleep/33.1.59
19. Wamsley EJ, Stickgold R. Dreaming of a learning task is associated with enhanced memory consolidation: replication in an overnight sleep study. *J Sleep Res*. 2018;**28**:e12749. doi:10.1111/jsr.12749. https://onlinelibrary.wiley.com/doi/abs/10.1111/jsr.12749
20. Stickgold R, Malia A, Maguire D, Roddenberry D, O'Connor M. Replaying the game: Hypnagogic images in normals and amnesics. *Science*. 2000;**290**(5490):350–353. doi:10.1126/science.290.5490.350
21. Hudachek L, Wamsley EJ. A meta-analysis of the relation between dream content and memory consolidation. *Sleep*. 2023;**46**:1–13. doi:10.1093/sleep/zsad111
22. Fosse MJ, Fosse R, Hobson JA, Stickgold R. Dreaming and episodic memory: A functional dissociation? *J Cogn Neurosci*. 2003;**15**(1):1–9. doi:10.1162/089892903321107774
23. Wamsley EJ. Constructive episodic simulation in dreams. *PLoS One*. 2022;**17**(3):e0264574. doi:10.1371/journal.pone.0264574
24. Malinowski JE, Horton CL. Evidence for the preferential incorporation of emotional waking-life experiences into dreams. *Dreaming*. 2014;**24**(1):18–31. doi:10.1037/a0036017
25. Cartwright R, Agargun MY, Kirkby J, Friedman JK. Relation of dreams to waking concerns. *Psychiatry Res*. 2006;**141**(3):261–270. doi:10.1016/j.psychres.2005.05.013
26. Breger L, Hunter I, Lane RW. The effect of stress on dreams. *Psychol Issues*. 1971;**7**(3):1–213.
27. Schredl M, Hofmann F. Continuity between waking activities and dream activities. *Conscious Cogn*. 2003;**12**(2):298–308. doi:10.1016/s1053-8100(02)00072-7
28. Schredl M. Continuity between waking life and dreaming: are all waking activities reflected equally often in dreams? *Percept Mot Skills*. 2000;**90**(3):844–846. doi:10.2466/pms.2000.90.3.844
29. Tamminen J, Payne JD, Stickgold R, Wamsley EJ, Gaskell MG. Sleep spindle activity is associated with the integration of new memories and existing knowledge. *J Neurosci*. 2010;**30**(43):14356–14360. doi:10.1523/JNEUROSCI.3028-10.2010
30. Dumay N, Gaskell MG. Sleep-associated changes in the mental representation of spoken words. *Psychol Sci*. 2007;**18**(1):35–39. doi:10.1111/j.1467-9280.2007.01845.x
31. Dumay N, Gareth Gaskell M. Overnight lexical consolidation revealed by speech segmentation. *Cognition*. 2012;**123**(1):119–132. doi:10.1016/j.cognition.2011.12.009

32. Stickgold R, Walker MP. Sleep-dependent memory consolidation and reconsolidation. *Sleep Med*. 2007;**8**(4):331–343. doi:10.1016/j.sleep.2007.03.011
33. Stickgold R, Walker MP. Sleep-dependent memory triage: evolving generalization through selective processing. *Nat Neurosci*. 2013;**16**(2):139–145. doi:10.1038/nn.3303
34. Bryant NB, Nadel L, Gómez RL. Associations between sleep and episodic memory updating. *Hippocampus*. 2020;**30**(8):794–805. doi:10.1002/hipo.23178
35. Xia T, Yao Z, Guo X, *et al*. Updating memories of unwanted emotions during human sleep. *Curr Biol*. 2023;**33**(2):309–320.e5. doi:10.1016/j.cub.2022.12.004
36. Calvillo DP, Parong JA, Peralta B, Ocampo D, Van Gundy R. Sleep increases susceptibility to the misinformation effect. *Appl Cogn Psychol*. 2016;**30**(6):1061–1067. doi:10.1002/acp.3259
37. Tse D, Langston RF, Kakeyama M, *et al*. Schemas and memory consolidation. *Science*. 2007;**316**(5821):76–82. doi:10.1126/science.1135935
38. Hennies N, Ralph MAL, Kempkes M, Cousins JN, Lewis PA. Sleep spindle density predicts the effect of prior knowledge on memory consolidation. *J Neurosci*. 2016;**36**(13):3799–3810. doi:10.1523/JNEUROSCI.3162-15.2016
39. Durrant SJ, Cairney SA, McDermott C, Lewis PA. Schema-conformant memories are preferentially consolidated during REM sleep. *Neurobiol Learn Mem*. 2015;**122**:41–50. doi:10.1016/j.nlm.2015.02.011
40. Kusse C, Shaffii-LE Bourdiec A, Schrouff J, Matarazzo L, Maquet P. Experience-dependent induction of hypnagogic images during daytime naps: a combined behavioural and EEG study. *J Sleep Res*. 2011;**21**(1):10–20. doi:10.1111/j.1365-2869.2011.00939.x
41. Brown KW, Ryan RM. The benefits of being present: mindfulness and its role in psychological well-being. *J Pers Soc Psychol*. 2003;**84**(4):822–848. doi:10.1037/0022-3514.84.4.822
42. Huba GJ, Singer JL, Aneshensel CS, Antrobus JS. *Short Imaginal Processes Inventory*. Port Hurson, MI: Research Psychologists Press; 1982.
43. Wamsley EJ, Hirota Y, Tucker MA, Smith MR, Antrobus JS. Circadian and ultradian influences on dreaming: a dual rhythm model. *Brain Res Bull*. 2007;**71**(4):347–354. doi:10.1016/j.brainresbull.2006.09.021
44. Salin-Pascual RJ, Roehrs TA, Merlotti LA, Zorick F, Roth T. Long-term study of the sleep of insomnia patients with sleep state misperception and other insomnia patients. *Am J Psychiatry*. 1992;**149**(7):904–908. doi:10.1176/ajp.149.7.904
45. Picard-Deland C, Bernardi G, Genzel L, Dresler M, Schoch SF. Memory reactivations during sleep: a neural basis of dream experiences? *Trends Cogn Sci*. 2023;**27**(6):568–582. doi:10.1016/j.tics.2023.02.006
46. Zadra A, Stickgold R. *When Brains Dream: Exploring the Science and Mystery of Sleep*. New York, NY: WW Norton; Company, Inc.; 2021.
47. Picard-Deland C, Konkoly K, Raider R, *et al*. The memory sources of dreams: serial awakenings across sleep stages and time of night. *Sleep*. 2023;**46**(4):1–13. doi:10.1093/sleep/zsac292
48. Verdone P. Temporal reference of manifest dream content. *Percept Mot Skills*. 1965;**20**(3c):1253–1268. doi:10.2466/pms.1965.20.3c.1253
49. Beijamini F, Pereira SIR, Cini FA, Louzada FM. After being challenged by a video game problem, sleep increases the chance to solve it. Gilestro GF, ed. *PLoS One*. 2014;**9**(1):e84342. doi:10.1371/journal.pone.0084342
50. Hołda M, Głodek A, Dankiewicz-Berger M, Skrzypińska D, Szmigielska B. Ill-defined problem solving does not benefit from daytime napping. *Front Psychol*. 2020;**11**:559. doi:10.3389/fpsyg.2020.00559
51. Nguyen N, Tucker MA, Stickgold R, Wamsley EJ. Overnight sleep enhances hippocampus-dependent aspects of spatial memory. *Sleep*. 2013;**36**(7):1051–1057. doi:10.5665/sleep.2808
52. Schredl M, Erlacher D. Is sleep-dependent memory consolidation of a visuo-motor task related to dream content? *Int. J. Dream Res*. 2010;**3**(1):7479.
53. Picard-Deland C, Nielsen T. Targeted memory reactivation has a sleep stage-specific delayed effect on dream content. *J Sleep Res*. 2021;**31**(1):e13391. doi:10.1111/jsr.13391
54. Dresler M, Koch SP, Wehrle R, *et al*. Dreamed movement elicits activation in the sensorimotor cortex. *Curr Biol*. 2011;**21**:1833–1837. doi:10.1016/j.cub.2011.09.029
55. Peters E, Golembiewski S, Erlacher D, Dresler M. Extending mental practice to sleep: Enhancing motor skills through lucid dreaming. *Med Hypotheses*. 2023;**174**:111066. doi:10.1016/j.mehy.2023.111066
56. Konkoly KR, Appel K, Chabani E, *et al*. Real-time dialogue between experimenters and dreamers during REM sleep. *Curr Biol*. 2021;**31**(7):1417–1427.e6. doi:10.1016/j.cub.2021.01.026