



Sleep and dreaming in the light of reactive and predictive homeostasis

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ABSTRACT

Dreams are often viewed as fascinating but irrelevant mental epiphenomena of the sleeping mind with questionable functional relevance. Despite long hours of oneiric activity, and high individual differences in dream recall, dreams are lost into oblivion. Here, we conceptualize dreaming and dream amnesia as inherent aspects of the reactive and predictive homeostatic functions of sleep. Mental activity during sleep conforms to the interplay of restorative processes and future anticipation, and particularly during the second half of the night, it unfolds as a special form of non-constrained, self-referent, and future-oriented cognitive process. Awakening facilitates constrained, goal-directed prospection that competes for shared neural resources with dream production and dream recall, and contributes to dream amnesia. We present the neurophysiological aspects of reactive and predictive homeostasis during sleep, highlighting the putative role of cortisol in predictive homeostasis and forgetting dreams. The theoretical and methodological aspects of our proposal are discussed in relation to the study of dreaming, dream recall, and sleep-related cognitive processes.

1. Introduction: dreaming is relevant but evanescent

The human brain constructs enormous amounts of dreams – approximately 4.8 h during an average (8-hour-long) night of sleep (Nielsen, 2000a), which, if combined would add up to around 1750 h of mental experiences a year. Yet if we asked someone to recall a dream over the past year, hardly any reliable dream reports could be collected. Even if we were Truman Capote's Mr. Revercomb, a fictional character, who purchases dreams for cash every day (Capote, 1949), and we dealt with a rare individual, who can recall dreams every morning, we would (be able to) gather only a collection of vague and fragmented dreams, which would amount to approximately 18 h in a year. In fact, even individuals with a high rate of dream recall only remember 1–2 min of their oneiric experiences upon awakening (Schredl et al., 2019). Still, the peculiar nature of dreams – their bizarreness, vividness, emotional intensity and surprisingly complex narrative structure – has always been a fascinating topic for intellectual inquiry. From ancient religious interpretations (Hughes, 2000; Oppenheim, 1956) and philosophical accounts (Gottesmann, 2010), until recent times, many researchers pondered on the putative functions of dreaming (Crick and Mitchison, 1983; Hobson, 2009; Nielsen and Levin, 2007; Revonsuo, 2000).

Nevertheless, since dreaming can only be indirectly accessed through dream reports (De Gennaro et al., 2012), the number of empirical studies lags behind the study of other cognitive processes by far, such as attention, memory or emotions. Consequently, dreaming remained an overlooked topic in cognitive science (Wamsley, 2013). Perhaps more surprisingly, dream research is also a relatively neglected topic within the field of sleep science (Nielsen, 2011), indicating that, albeit interestingly, it is still considered an epiphenomenal aspect of sleep with limited scientific relevance. However, a closer look at past and ongoing research indicates that dreaming is more than an appendix; it is an integral part of human sleep. For instance, the qualitative aspects of dreams have been shown to reflect key cognitive processes during sleep, such as sleep-related memory consolidation (Picard-Deland and Nielsen, 2022a; Wamsley, 2014; Wamsley et al., 2010) or sensory processing during sleep (Carr et al., 2020; Flo et al., 2011a; Schredl et al., 2009a; Wamsley and Antrobus, 2009a). Moreover, dreams are altered in conditions of disrupted sleep (Schredl, 2009; Siclari et al., 2020), their emotional quality is associated with the perceived quality of sleep (Soffer-Dudek, 2017), and they seem to depict personally relevant thoughts and concerns (Nielsen and Stenstrom, 2005; Van Rijn et al., 2015). The last two points have been dramatically highlighted by the

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impact of the COVID-19 pandemic on sleep and dreaming. A wealth of studies implied that home confinement under stressful environmental conditions had a pronounced influence not only on sleep (Gorgoni et al., 2022; Jahrami et al., 2021; Simor et al., 2021) but also on dreaming (Gorgoni et al., 2022, 2021; Pesonen et al., 2020). More specifically, an increase in dream recall rates and dreams related to the pandemic was evidenced, which, among other factors, was potentially associated with longer sleep durations, delay in rising times (and hence, more time spent in REM sleep), as well as with reduced sleep depth and more nocturnal awakenings (Gorgoni et al., 2022). These studies show that changes in sleep and dreaming go hand in hand, even if memories about dreams are quite evanescent. Moreover, such “pandemic dreams” clearly illustrate how dreaming provides a means to imagine and simulate (i.e., pre-experience) self-relevant life-scenarios, which may or may not happen in the future. The renewed interest in the scientific study of dreaming latches onto the emerging line of studies that focus on subjective experiences, rediscovering a Jamesian “stream of consciousness” for cognitive neuroscience (Smallwood and Schooler, 2015). Instead of being conceptualized as a mental by-product of sleep, dreaming is viewed as a variation of self-generated thought processes. As such, dreaming shares, to some extent, the neural underpinnings, cognitive mechanisms, and functions of daytime mind-wandering (Domhoff, 2011; Fox et al., 2013). In this article we propose a framework that builds upon this view, but extends it by linking dreaming and dream amnesia to the homeostatic processes of sleep. In this theoretical review, we will elucidate the roles of reactive and predictive homeostasis during sleep. The former refers to the corrective actions in response to a change which has already occurred, whereas the latter encompasses corrective responses initiated in anticipation of a future challenge (Moore-Ede, 1986). We will show that reactive homeostasis during the early hours of sleep facilitates a variety of restorative processes at multiple levels (neural, neurohormonal, immune, and cognitive functions), and may also impact the qualitative aspects of dreaming. In addition, we will elucidate the influence of predictive homeostasis on sleep and sleep-related cognitive processes, with a special emphasis on dreaming. Finally, we will highlight the influence of predictive homeostasis on spontaneous self-referent thoughts in wakefulness, and point to the putative effect of goal-directed prospection on morning dream recall and dream amnesia. More specifically, the core arguments of this review are the following: 1) the dreaming mind aligns to the fundamental functions of sleep involving reactive and predictive homeostasis; 2) whereas the first part of sleep is dominated by reactive homeostasis, the second part mobilizes predictive homeostatic functions, and 3) facilitates dreaming as a form of non-constrained self-referent future thinking (prospection); 4) predictive homeostasis and its expression in the form of dreaming is constrained by awakening and goal-directed prospective memory processes initiated upon awakening; 5) the gradual increase in cortisol in the second half of the night initiates behavioral and cognitive processes subserving the predictive homeostatic engagement; 6) whereas the abrupt increase in cortisol upon awakening facilitates waking prospection and contributes to dream amnesia. In the following sections we will argue that dreaming and their forgetting are inherent features of the temporal progression of sleep. In this respect, the present review provides a novel framework for the study of dreaming and dream recall, with implications for the understanding of sleep-related cognitive processes (i.e., learning and off-line memory consolidation).

2. Reactive and predictive homeostasis during sleep

As put forward by Cannon (1929), homeostasis refers to a set of physiological and behavioral mechanisms devoted to maintain stability or balance by keeping the organism within its viable states in response to changes in the environment. Although the usefulness of this concept is undisputable, the theory was significantly enhanced six decades later. While Cannon described and conceptualized the initiation of corrective actions as emerging only *after* the physiological system has been

perturbed (e.g., a decrease in blood glucose level), it became clear that the effects can be manifested with significant time delays for many effector mechanisms (e.g., protein synthesis). Moreover, the self-sustaining nature of circadian and circannual rhythms became more and more evident, whereas their utmost importance in physiological adaptation got strong empirical support (Borbély et al., 2016). Thus, the corrective actions in response to a change which has already occurred were considered as *reactive homeostatic* mechanisms, whereas corrective responses initiated in anticipation of a predictably timed challenge (e.g., temperature and/or light intensity) were included in a new concept of *predictive homeostasis* (Moore-Ede, 1986). In other words, predictive homeostasis is a chronobiological concept focusing on anticipation and preparedness instead of corrective reactions.

The most widely accepted and empirically supported model of sleep-wake regulation that integrates the interplay of reactive and predictive homeostasis is undisputedly the two-process model proposed by Alexander Borbély (Borbély, 1982). According to the model, the timing, the depth, the continuity, and the duration of sleep are determined by the interaction of homeostatic sleep pressure (process S) and circadian drive (process C). While the former accumulates during wakefulness and declines over the course of sleep, the latter reflects the sinusoidal oscillation of the circadian drive, a stable biological rhythm aligned with environmental timing cues (e.g., light-dark cycles and social time cues). Process S depends on the “history” of preceding time spent asleep and in wakefulness (Borbély, 2022), a form of “need-fulfilment” (Borbély, 1982), anchored to individual-specific setpoints of slow wave EEG activity fed by use-dependent, plasticity-related changes in the central nervous system (Borbély et al., 2016). In turn, the timing of sleep provided by Process C supports the optimization of metabolic processes at the appropriate phase of the 24-h cycle (Borbély et al., 2016). Thus, the two processes are well cohering with the concepts of reactive and predictive homeostasis, ensuring corrective actions after the perturbation of the system by use-dependent processes and anticipation of environmental changes by ensuring appropriate sleep timing, respectively. In this regard, processes S and C of the Borbély model are two specific instances of the reactive and predictive homeostasis, respectively.

The validity of the mathematical formulation of the model was extensively studied and independently confirmed by a large body of data, and a variety of markers was introduced to quantify both processes (Achermann et al., 1993; Borbély et al., 2016; Borbély and Achermann, 1992; Daan et al., 1984; Reid, 2019). Amongst these, low frequency electroencephalographic (EEG) oscillations, also known as slow wave activity (SWA), emerged as the most powerful indices of sleep pressure. Indeed, SWA (contributing to Slow Wave Sleep, SWS) dominates the first part of the night and decays through consecutive sleep cycles, and its magnitude increases after extended wakefulness (Hung et al., 2013), sleep deprivation (Achermann et al., 1993), and demanding pre-sleep activity such as physically challenging activities, learning, or novel experience (Horne and Minard, 1985; Ribeiro et al., 2004; Tononi and Cirelli, 2006). SWA in the beginning of the night reflects the restorative properties of sleep, providing the organism with a period to recover from the “burden of wakefulness” preceding sleep; that is, it allows the body’s biological resources that were depleted during wakefulness to repair and to replenish (Bódizs, 2021).

2.1. Reactive homeostasis: the restorative functions of sleep

The restorative function of sleep, which parallels reactive homeostatic mechanisms, especially during the first, SWS-dominated part of the sleep period was evidenced at multiple levels (Fig. 1/A, B). For instance, the widespread central and peripheral effects of the somatotrophic axis are well known for facilitating neural growth, neuroprotection, overall anabolic processes, protein synthesis and cellular repair. Indeed, several key molecules of the somatotrophic axis were shown to be critical endocrine/paracrine sleep regulatory factors, with hypothalamic growth hormone releasing hormone (GHRH) being

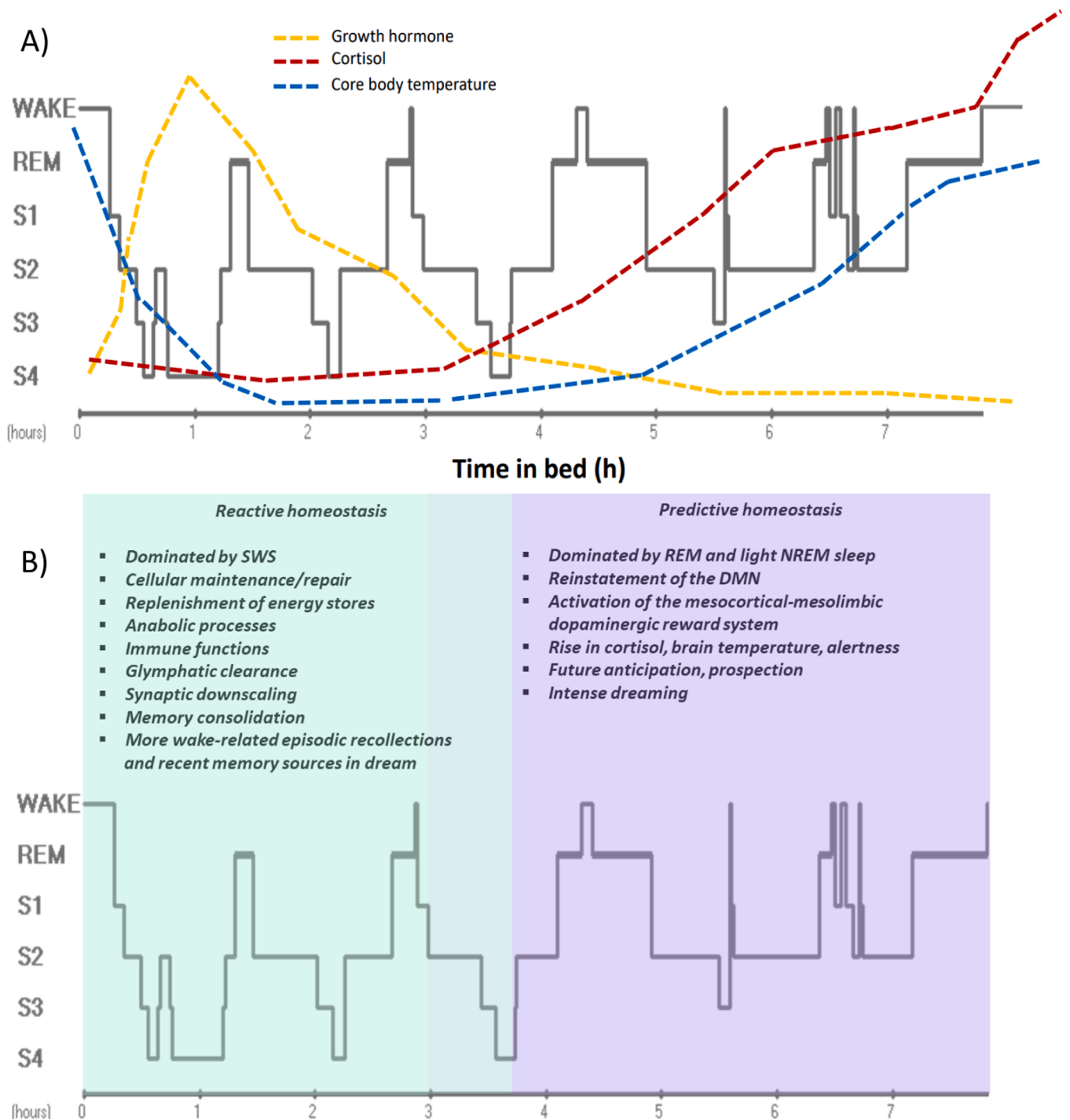


Fig. 1. Reactive and predictive homeostasis in sleep I. A) The reactive homeostatic functions of sleep during the first part of the night coincide with the predominance of slow waves sleep (SWS), and the secretion of growth hormone, whereas in the second part of the night the secretion of growth hormone is attenuated while cortisol levels and core body temperature rise gradually. B) Reactive and predictive homeostasis seem to facilitate a variety of physiological functions and neurocognitive processes, that are also reflected at the phenomenological, mental level. The hypnogram, reflecting the succession and distribution of sleep stages is depicted in the background. S1-S4: Stage 1-Stage 4 sleep. Note that S3 and S4 are called SWS in current nomenclatures; however, in this illustration we differentiate S3 and S4 to indicate more precisely the overnight decrease of SWS.

involved in NREM sleep promotion (Obal and Krueger, 2004). Besides, the secretion peaks of growth hormone (GH) associate with the rise of SWS (Davidson et al., 1991; Van Cauter and Plat, 1996), whereas GH itself promotes the increase of subsequent REM sleep (Obal and Krueger, 2004)(Fig. 1/A). Furthermore, SWS was shown to facilitate the replenishment of energy stores (Benington and Craig Heller, 1995), as well as to promote cellular maintenance to overcome cellular stress induced by

synaptic and spiking activity during wakefulness (Vyazovskiy and Harris, 2013). Recent findings indicate that glymphatic clearance (i.e., the elimination of metabolic waste products from the interstitial space) is markedly increased in sleep (Xie et al., 2013), particularly during SWA (Fultz et al., 2019). Additionally, the first part of the night dominated by SWS plays a key role in cognition. Experimental and field studies point out that frontal cortical functions are characterized by heightened

vulnerability to extended wakefulness, while the recovery of these functions occurs during human SWS (Horne, 1993). In addition, SWS plays an important role in the consolidation of previously encoded information (i.e., memory consolidation; see Rasch and Born, 2013 for an extensive review). The two most influential models of sleep-related memory consolidation are the synaptic downscaling or synaptic homeostasis hypothesis (SHY) (Tononi and Cirelli, 2006) and the memory reactivation theory (Buzsáki, 1998; Rasch and Born, 2013). The SHY postulates that sleep facilitates learning by locally renormalizing synaptic weights saturated by prolonged wakefulness experience inducing synaptic plasticity. The elimination of weak synaptic links and the strengthening of stronger and functionally relevant (learning-related) synaptic connections increase the signal to noise ratio and optimize information processing (Tononi and Cirelli, 2006). The reactivation hypothesis claims that newly acquired memories are reactivated during sleep and reorganized into widely distributed cortical networks (Buzsáki, 1998; Rasch and Born, 2013). Whereas the two theories provide different mechanistic explanations for the role of sleep in consolidating memories, they are not mutually exclusive, and can be combined into one model (Genzel et al., 2014; Lewis and Durrant, 2011). Notably, both assume that SWS provides a window to process the ‘neurocognitive impact’ of previous, pre-sleep experience. The processing of pre-sleep experience might not be limited to the neurocognitive domain: a growing number of studies indicate that SWS facilitates immunological functions especially in the presence of antigens requiring the adaptive immune response (Westermann et al., 2015). In sum, the first part of the night serves to restore homeostatic balance at multiple scales; in other words, it is dedicated to process the ‘personal past’ of the organism (Fig. 1/B). In the next section we will briefly consider how reactive homeostasis might influence the nature of dream experiences during early-night slow wave sleep.

2.2. Mental activity during early slow wave sleep

Mental (dream) experiences during the first part of the night might also reflect the influence of early night sleep on the consolidation of previously encoded information (Wamsley and Stickgold, 2011). Despite the long-standing belief that dreaming occurs mainly in REM sleep, it is widely accepted nowadays that dreaming can occur also in NREM sleep, including the deepest sleep states of SWS (Scarpelli et al., 2022). Although the rates of the so-called white dreams (i.e., the impression of having dreamt, but being unable to recall it) do not appear to vary across early and latenight dreams (Noreika et al., 2009), successfully recalled dreams do exhibit qualitative differences: early night dreams were rated as less bizarre, and were more strongly associated with previous waking-life events, while late night dreams were considered more emotional, personally important, and hyperassociative-metaphorical (Malinowski and Horton, 2021). Moreover, cognitive activities resembling the waking state, such as thinking, planning, and making decisions are more frequent in dreams that occur in the beginning of the night, whereas dreams become more hallucinatory-like and dominated by sensorimotor experiences as the night progresses (Fosse et al., 2004). As a reminder, early night sleep is dominated by SWS, while REM sleep is much more abundant in the late part of the night. Interestingly, however, studies investigating the differences between the content and the memory sources of NREM and REM dreams were not that conclusive (Cavallero et al., 1992; Scarpelli et al., 2022), suggesting that different sleep states may not be the major determinant of the nature of dream reports. A circadian factor also appears to influence the qualitative aspects of dreaming: mental experiences during the first part of the night are dominated by past-oriented dreams and episodic recollections compared to dreams that occur in the second half of the night (Malinowski and Horton, 2021; Wamsley, 2022), and NREM dreams are more similar to REM dreams in the late compared to the early part of the night (Fosse et al., 2004). In any case, studying the content of dreams is methodologically challenging, as

forced awakenings may bias the natural process of dreaming, and the memory of a specific dream might not necessarily originate from the preceding minutes, but potentially from other parts of the night, especially if the dreamer is forced to wake up and access dream content several times during the night. In this respect, parasomnias with dream enacting movements (e.g., SWS sleepwalking or REM behavior disorder) offer a unique opportunity to study dreaming in relation to memory consolidation. Although such studies are still relatively scarce, a groundbreaking study reported the case of a patient who showed the re-enactment of previously learned motor movements during a sleepwalking episode (Oudiette et al., 2011). Systematic studies on dream enacting behaviors in sleep disordered patients may open new avenues to unravel the links between dreaming and memory consolidation.

2.3. Anticipation of wakefulness: predictive homeostasis during sleep

The dissipation of reactive homeostasis in the first half of the night does not terminate sleep. As the influence of process S decays and the system is relieved from homeostatic sleep pressure, SWS dissipates and sleep becomes dominated by Stage 2 and REM sleep (Carskadon and Dement, 2005). Under optimal nocturnal sleep timing conditions, the decay of process S coincides with the rising phase of process C (Borbély, 2022), which facilitates REM sleep and boosts predictive homeostasis that precedes awakening (Borbély et al., 2016). This aspect is well exemplified by the density of eye movement bursts during REM sleep, which reflects sleep satiety, more REM eye movements indicating higher satiety (Aserinsky, 1973, 1969). Whereas REM sleep exhibits a strong circadian modulation with a clear peak positioned shortly after the minimum of the core body temperature (Dijk and Czeisler, 1995), the modulation of REM density is dominantly sleep-dependent. The relationship between sleep satiety and REM density was corroborated by a forced desynchrony protocol, in which 20 consecutive sleep opportunities were scheduled over the full circadian cycle. This study showed that REM density was the highest when sleep pressure was low, regardless of the circadian phase; however, an additional boost of REM density was observed if the end of the sleep period coincided with the wake maintenance zone (Khalsa et al., 2002). Moreover, sleep deprivation-induced lowering of sleep satiety was shown to reduce the intensity and the overnight increase of REM eye movement density (Marzano et al., 2011). Thus, the attenuation of SWS during the course of a night of sleep, marking the diminished influence of restorative processes, associates with a build-up of peak REM eye movement density, a measure known to be related to the vividness of dream imagery and dream recall frequency (Hong et al., 1997) (Fig. 2/A). In sum, physiological processes that facilitate reactive homeostasis recede and give room for predictive homeostasis, with important consequences. Indeed, if reactive homeostasis is dedicated to process the ‘personal past’, the function of predictive homeostasis is to envision the ‘personal future’.

Predictive homeostasis entails a set of physiological mechanisms dedicated to anticipate future challenges, which, in the context of sleep, prepare the organism for upcoming wakefulness (Moore-Ede, 1986; Riede et al., 2017). Among these processes the activation of the mesocortical-mesolimbic-dopaminergic system (MMDS) stands out, comprising the ventral tegmental area, diencephalic structures, in particular the nucleus accumbens, and parts of the prefrontal cortex (Alcaro et al., 2007). The MMDS is part of the more extensive *Seeking system* dedicated to process exploratory and approach behaviours in anticipation of rewards (Panksepp, 2004). Several lines of evidence indicate that the MMDS is involved in the processing of future rewards, punishments and signals of novelty (Fibiger and Phillips, 1988; Perogamvros and Schwartz, 2012; Reichardt et al., 2020). The activity of the key regions of the MMDS is enhanced during REM periods, and even before the onset of REM sleep, indicating the involvement of REM sleep in anticipatory processes (Perogamvros and Schwartz, 2012). Although REM periods are more abundant during the second part of the night, it is

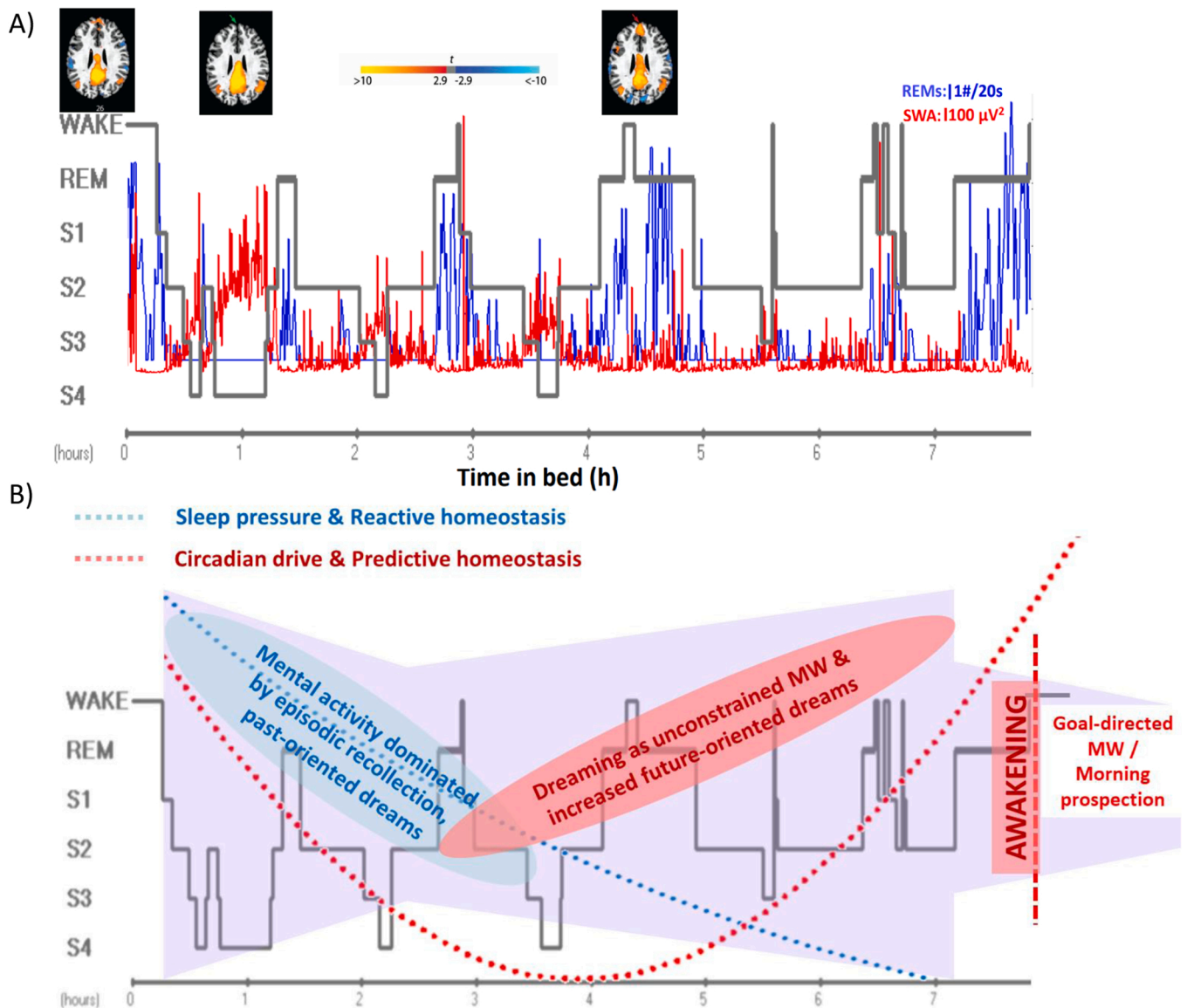


Fig. 2. Reactive and predictive homeostasis in sleep II. A) The intensity of SWS and Rapid Eye Movements (REMs) show inverse patterns: the occurrence of REMs is enhanced when the pressure of SWS dissipates. The key nodes of the Default Mode Network (DMN), i.e., the medial prefrontal and posterior/parietal nodes are decoupled in the first and deepest sleep cycle, but are active again the second half of the night when SWS dissipates and sleep is dominated by REM periods and shallow stage 2 sleep (Chow et al., 2013). B) The phenomenological aspects and memory sources of dreams conform to the dynamic interplay of reactive and predictive homeostasis, and dream recall is constrained by goal-directed morning prospection upon awakening. The hypnogram, reflecting the succession and distribution of sleep stages is depicted in the background. S1-S4: Stage 1-Stage 4 sleep. Note that S3 and S4 are called SWS in current nomenclatures; however, in this illustration we differentiate S3 and S4 to indicate more precisely the overnight decrease of SWS.

not clear whether the activation of the MMDS is limited to REM periods, or also to Stage 2 sleep, which alternates with REM sleep in the second part of the night. Nevertheless, the MMDS was shown to play a significant role in dreaming regardless of REM sleep (Solms, 2000), implying that the reward-related activity of the *Seeking system* goes beyond REM sleep, and may characterize sleep whenever dreaming is more intense (i.e., in the second part of the night).

The activity of the HPA (hypothalamus-pituitary-adrenal) axis, which secretes cortisol from the adrenal cortex, is another key process in maintaining predictive homeostasis during the second half of the night (Born et al., 1999). Nocturnal cortisol secretion (the end product of the HPA axis) shows an inverse pattern with that of growth hormone, as it reaches its lowest level during the first half of the night (when growth hormone secretion peaks) and progressively increases towards the morning (Weitzman et al., 1971) (Fig. 1/A). A specific role of cortisol in anticipating wakefulness was demonstrated in a study involving the

continuous assessment of the hormone adrenocorticotropin (ACTH, the trophic hormone of cortisol) during the night. ACTH gradually increased after the middle of the night, and a sharp rise in ACTH was evidenced in a subgroup who expected to be woken up early in the morning. Such steep rise in nocturnal ACTH was not observed if participants were allowed to wake up spontaneously, or did not expect to be awakened by the experimenters (Born et al., 1999). Above this gradual increase in nocturnal cortisol, a further and even sharper increase in cortisol secretion occurs after awakening, also known as the cortisol awakening response (CAR) (Wilhelm et al., 2007). Noticeably, the CAR is larger if the upcoming day involves stressful challenges (e.g., workdays versus weekends, job interview, sport competition, etc.), suggesting that the morning rise in cortisol reflects anticipatory predictive homeostasis mechanisms that help to prepare the organism to face anticipated future demands (Clow et al., 2010; Fries et al., 2009). Evidently, cortisol is not the only regulator of predictive homeostasis. Other

time-of-day-dependent physiological changes were also shown to serve an important function in the anticipation of and coping with wakeful demands. Beyond cortisol, the decrease in pineal melatonin production, as well as a consequent increase of core body temperature contribute to increased efficiency in maintaining wakefulness and an appropriate level of arousal (Moore-Ede, 1986; VanSomeren, 2000; Wright Jr et al., 2002) (Fig. 1/A).

2.4. Predictive homeostasis and mental simulations

2.4.1. Mind-wandering as dream-like mental simulations

Humans spend about one third of their time by engaging in mind wandering during wakefulness, which involves a variety of self-generated mental contents such as simulations of personally relevant past episodes, imagined events, and planned behaviours (Buckner and Carroll, 2007). Mind-wandering was already recognized by ancient Greek philosophers and modern founders of psychological science. For instance, William James himself described in his *Principles of Psychology* (James et al., 1890) frequent ebbs and flows in attention eventually leading to a mind vacancy state, during which the individual's mind escapes its ongoing activity focus. Hence, mind-wandering is characterized by the spontaneous occurrence of mental contents in the awake state that appear to be independent of the ongoing context, which makes it at least partially akin to the dreaming activity experienced in the sleep state. Another common characteristic of mind-wandering and dreaming is that they are both subjective in nature, and only accessible through the individual's self-report. In mind-wandering, the most common data collection method is experience sampling: participants are unexpectedly asked to report on their thoughts at various time points while completing a cognitive task (Jubera-Garcia et al., 2021). Similarly, it is possible to sample dreams during sleep by awakening participants at various time points in their night of sleep and asking them to report on their dream content. In both cases, an inherent limitation is that verbal reports are often only distorted and abbreviated versions of the participant's train of thoughts, for various reasons ranging from partial amnesia to reconstruction mechanisms. Mind-wandering also arguably differs from mind-blanking, in which we also experience attentional lapses but are unable to report any mental content; rather, we have the feeling of an empty mind. This could partially parallel the frequently reported feeling experienced at awakening: having dreamt during the night but being totally unable to report the content or even the topic of the dream (*white dreams*). What mind-wandering and mind-blanking have in common, however, is that their frequency tends to increase with accumulated sleep pressure (Andrillon et al., 2019; Poh et al., 2016), and attentional out-of-focus experiences are associated with local neuronal lapses (Nir et al., 2017), suggesting that they reflect (or at least, correlate with) local brain exhaustion in continuously facing a task that demands cognitive focus. In this respect, the occurrence (mind-wandering) or not (mind-blanking) of a mental content during attentional drifts was also shown to be associated to local sleep-like activity in the awake state with spatio-temporally localized slow waves distinguishing mind-blanking from mind-wandering. More precisely, mind-wandering was globally associated with an increased number of slow waves and slow-wave amplitude over frontal electrodes, and an increased slope of downward and upward slow waves over centro-frontal electrodes, mind-blanking differentiating from mind-wandering by reduced slow-wave amplitude over frontal electrodes and increased upward slope over parietal electrodes (Andrillon et al., 2021). How and to what extent variations in the topography and temporal organization of local brain oscillations both during sleep and wakefulness could similarly explain the presence vs. absence of reported mental content in mind-wandering/mind-blanking and dreaming is a hypothesis that remains to be investigated.

2.4.2. Predictive homeostasis instigates self-referent mental simulations

Mind-wandering mainly features self-referent and personally

relevant mental contents (D'Argembeau, 2018). Self-referent mental processes appear to be associated with the coordinated activity of a large-scale neural network known as the default mode network (DMN) (Raichle and Snyder, 2007). The DMN encompasses a set of brain regions including a frontal network along the midline (medial prefrontal cortex, mPFC), a network of lateral and medial parietal regions (inferior parietal lobule, lateral temporal cortex, angular gyrus), and medial temporal lobe structures (hippocampus, parahippocampus) that feature correlated blood oxygen level dependent (BOLD) fluctuations during periods of non-directed, internally generated thoughts (Buckner and Carroll, 2007; Raichle and Snyder, 2007; Smallwood and Schooler, 2015). Although self-generated cognition encompasses a mixture of past, present- and future-directed thoughts, research findings indicate that (especially under non-demanding task conditions) people tend to engage more in future-related themes depicting personally relevant goals, plans and future behaviors (Baird et al., 2022, 2011; Smallwood et al., 2011; Smallwood and Schooler, 2015). These findings led to the speculation that one of the adaptive functions of self-generated thoughts may be to promote personally relevant mental simulations to anticipate and evaluate future scenarios (Buckner et al., 2008). Notably, the DMN partly overlaps with the reward processing system of the mesolimbic-dopaminergic system (in the mPFC) considered to be critical in the anticipation of relevant and salient stimuli (reward, punishment and novelty, see Perogamvros and Schwartz, 2012).

If self-generated thoughts associated with the DMN reflect predictive homeostatic functions at a neurocognitive level, we expect them to vary throughout the course of sleep. In fact, conscious mental activity is largely diminished early in the night during periods of deep sleep (i.e. during the predominance of the reactive homeostatic processes), as reflected by the relative absence of elaborate, intense, and vivid forms of dreaming (Nielsen, 2000b). In contrast, mental experiences become more intense later (i.e. during the predictive homeostatic period) yielding to more complex, story-like, and vivid forms of dreaming with a mixture of sensory hallucinations, emotions and cognitive content (Nielsen, 2000b; Siclari and Tononi, 2016). The fading of mental experiences is associated with connectivity changes in the DMN. Whereas increased connectivity between the nodes of the DMN is not restricted to wakefulness and conscious mental experiences (Buckner and Carroll, 2007), the synchronized activity between its key areas undergoes considerable changes during the first hours of sleep. The combined analysis of electroencephalography (EEG) and functional magnetic resonance imaging (fMRI) signals has opened up new avenues for exploring the activity of brain networks during various stages of sleep. One of the primary areas of interest in these studies has been the default mode network (DMN). Early EEG-fMRI studies revealed that the correlated activity of the DMN nodes is not restricted to wakefulness but is also present during light sleep (Fukunaga et al., 2006; Horowitz et al., 2008). Subsequent research, however, has shown that as sleep deepens, the connectivity within the DMN progressively diverges from that seen in both resting wakefulness and light sleep. More specifically, a gradual decoupling between the medial prefrontal and posterior/parietal DMN nodes was observed in the first sleep cycle as sleep deepened (Horowitz et al., 2009; Sämann et al., 2011). That is, the observed pattern indicating reduced connectivity within the DMN is in line with the observation of impoverished and less elaborate oniric (dream) activity during the deepest states of sleep (Nielsen, 2000b) and almost completely reduced processing of environmental inputs (Andrillon et al., 2016). Moreover, these findings are in line with the observations of a general breakdown of large-scale fronto-parietal connectivity and the shift towards more localized (modularized) networks during the deepest stage of sleep (Ferri et al., 2008; Spormaker et al., 2012, 2010; Tononi and Massimini, 2008). In contrast, as the first sleep cycle and the deepest period of sleep dissipate, the subregions of the DMN appear to recouple during REM sleep (Chow et al., 2013; Wu et al., 2012). For instance, Chow and colleagues found that whereas the main nodes of the DMN (mPFC and posterior cingulate cortex) showed reduced coupling in SWS

compared to wake, interregional connectivity was restored in REM, and was not different from wake. Moreover, correlated activity between the posterior cingulate cortex and the dorsal portions of the mPFC, and the dorsal IPLs were even stronger during REM than during wakefulness (Chow et al., 2013). Another study (Wu et al., 2012) also observed reduced connectivity in deep NREM sleep between sensorimotor regions and the nodes of the DMN, but re-established connectivity in both networks when participants entered into REM sleep. These findings indicate that the transition from restorative to predictive homeostasis involves the recoupling of the key nodes of the DMN. The reinstatement of the DMN does not seem to depend on specific sleep stages, but rather on the circadian phase: connectivity among the DMN core regions was maintained in NREM sleep including periods of SWS in a study where sleep was scheduled after 3.00 a.m. (Koike et al., 2011), corresponding to the rise of predictive homeostasis during sleep.

In line with the increased coupling in the DMN, the recall and vividness of dreaming are intensified with the rise of the circadian drive boosting predictive homeostasis (Nielsen, 2004). The initiation of REM sleep itself is under strong circadian influence related to the activity of the circadian (C)-process (Borbély, 1982). Consistently, findings indicate that the subsystems of the DMN constitute neural substrates for dreaming (Fox et al., 2013). For instance, lesions in widespread regions of the DMN, such as the white matter of the mPFC (that is part of the mesolimbic dopaminergic reward system) and the temporoparietal junction (TPJ), appear to lead to the cessation of dream experiences (Solms, 1997). Furthermore, healthy participants with high dream recall show increased cerebral blood flow in the mPFC and TPJ during REM sleep and resting wakefulness, and increased white matter density in the mPFC as compared to low dream recallers (Eichenlaub et al., 2014b; Vallat et al., 2018). In a meta-analysis, Fox and colleagues (2013) examined the neural correlates of REM sleep and waking rest based on data from functional neuroimaging studies. Since the chance of detectable dreaming is very high during REM sleep, such as the occurrence of mind-wandering during waking rest, the researchers used these datasets as proxies for dreaming and mind-wandering. From eight identified clusters showing enhanced activity in REM sleep, seven overlapped with the key regions of the DMN. Parts of these key regions, such as the mPFC, the retrosplenial, and the posterior cingulate cortex (Fox et al., 2013) were implicated in self-referential processing in a variety of studies (D'Argembeau et al., 2007; Kurczek et al., 2015; van Buuren et al., 2010; Whitfield-Gabrieli et al., 2011). The authors noted the certain brain regions, such as the dorsolateral PFC and the anterior cingulate gyrus, were relatively inactive during REM, leading them to conclude that dreaming may be a heightened form of mind-wandering with attenuated goal-directed thought processes (Fox et al., 2013). We should note however, REM sleep is rarely observed in the MRI environment due to noise and vibration (Sämann et al., 2011; Wehrle et al., 2007), making neuroimaging studies on REM sleep limited by low sample size and in need of further data.

Beyond the shared neural substrates, first-person reports of dream experiences share strong resemblance to daytime mind-wandering with respect to emotionality, social interactions, personally relevant topics and temporal focus (Fox et al., 2013). Dream reports are organized around a self-referent narrative related to personally relevant events, goals, and emotional concerns. Similarly to daytime mind-wandering, dreams also seem to exhibit a prospective (future-oriented) bias often depicting events and activities that may (or may not) happen in the future (Wamsley, 2013). These findings argue against a sharp division between the phenomenology of dreams and spontaneous daytime thoughts, and suggest that dreaming is a night-time variation of daytime mind-wandering, or vice versa (Gross et al., 2021). Despite the continuity between waking and dream mentation, however, differences are also noticeable: whereas dreams appear to revolve around recent and remote past experiences and future goals (Nielsen and Stenstrom, 2005; Wamsley, 2013, 2014), they rarely contain specific episodic memories or specific (well-circumscribed) future goals (Baird et al., 2022; Gross

et al., 2021). Dreams rather combine fragments of past experiences and anticipated future events. In this sense, dreams feature less constrained simulations of past experiences and imagined future scenarios than spontaneous daytime thoughts (Gross et al., 2021). Whereas waking rest and REM sleep feature partly overlapping patterns of neural activity (Chow et al., 2013; Fox et al., 2013; Nir and Tononi, 2010), and spontaneous thought processes sampled during daydreaming (at wake), and dreaming in NREM and REM sleep showed overlapping EEG correlates, more specifically a reduction in slow frequency power – indicating activation – over the midcingulate cortex (Perogamvros et al., 2017), attenuated activity in frontoparietal networks distinguishes REM and NREM sleep from resting wakefulness (Maquet et al., 2005, 2000; Nir and Tononi, 2010). Reduced activity in the frontoparietal network limiting access to executive resources might explain the difficulties in recalling and focusing on specific memories and future plans during dreaming (Baird et al., 2022, 2011; Gross et al., 2021). Moreover, spontaneous thoughts during wakefulness were associated with a more extended network along medial prefrontal regions, which was linked to increased metacognitive processes (Perogamvros et al., 2017). In sum, the transition from restorative to predictive homeostasis is associated with the reinstatement of connectivity between the key nodes of the DMN. The reinstatement of the DMN may associate with self-referent mental simulations similarly to daytime, spontaneous thought processes. Nevertheless, night-time mental simulations are not constrained by specific events or future plans to the same degree as daytime thoughts.

2.4.3. Reactive and predictive homeostasis and the temporal dimension of dreams

Research findings suggest that the dynamic balance between reactive and predictive homeostasis has a major impact on nocturnal mental simulations. Sleep deprivation leading to increased reactive homeostatic pressure almost completely abolishes dream recall during the recovery night (De Gennaro et al., 2010), whereas high sleep duration as well as extending the duration of sleep are associated with higher rates of dream recall (Leproult et al., 2015; Schredl and Reinhard, 2008). (A similar phenomenon might explain the sudden rise of dream reports during the first wave of the COVID-19 pandemic (Bottary et al., 2020)). While the transition from reactive to predictive homeostasis is not an all-or-none phenomenon, but is rather highly dynamic depending on several factors (e.g., external noise, abrupt awakenings) affecting sleep throughout the night, the influence of reactive homeostasis gradually diminishes, and predictive homeostasis unfolds throughout the night under normal conditions. Notably, the “takeover” of predictive over reactive homeostasis later in the night is not absolute, but relative, as restorative processes still may take place to some extent at later hours, and similarly, predictive homeostasis might also play a more prominent role in early night sleep in some cases (for instance, in case of disturbed sleep in insomnia disorder). The qualitative features of dreaming seem to reflect the shift from reactive to predictive homeostasis to some extent. Early-night dreams as compared to late-night dreams are more continuous with waking activities, probably reflecting memory processing related to waking life events (Malinowski and Horton, 2021). Moreover, the incorporation of recent versus distant memory sources into dreams also appeared to vary across the night. The proportion of recent to distant memory sources was relatively higher in early night than in late night dreams, which in turn, featured more remote memory sources (Picard-Deland et al., 2022b). In another study, past-related memory sources were less common in dreams reported in the last quartile of the night compared to dreams in the first quartile (Wamsley, 2022). Three recent studies applying serial awakenings and dream collection, systematically examined if future-oriented dreams were more frequent at later times of the night regardless of the stage of sleep (i.e., time of night effects). One study reported a relatively higher incidence of future temporal orientation in dream content in dreams that were recalled later (Picard-Deland et al., 2021), and two studies observed upward trends in

the proportion of future-oriented dream content in late versus early-night dreams (Picard-Deland et al., 2022b; Wamsley, 2022). While the relative increase in future-oriented dream themes should be corroborated in further studies, serial awakening protocols may introduce a systematic bias in the incorporation of memory sources. Since participants are awakened multiple times during the night, their recalled dreams may be incorporated into later-night dream reports (Picard-Deland et al., 2022b); hence, the memory sources of early-night dreams may be overrepresented in late-night dreams. Future studies assessing dream reports at different time points over multiple nights may reduce the potential bias induced by serial awakenings.

2.4.4. The future in sleep and dreams

In this section we will highlight the relevance of prospection during sleep and dreaming by focusing on three research domains: sleep-related memory consolidation, dreaming about future challenges, and the incorporation of external stimuli into dreams.

Sleep-related memory processing can be conceptualized as an adaptive mechanism to consolidate past experiences (Ellenbogen et al., 2006); however, it can also be viewed as a kind of preparatory process in order to anticipate future events and regulate future behavior (Diekelmann et al., 2013). A variety of studies demonstrates that sleep selectively facilitates the consolidation of the memories that are “tagged” as relevant (for the future) (Blaskovich et al., 2017; Rauchs et al., 2011; Saletin et al., 2011; Wilhelm et al., 2011). For instance, post-sleep memory consolidation was more pronounced if the memory was associated with an anticipated future reward (Fischer and Born, 2009; Oudiette et al., 2013), or if it was emotionally salient (Payne et al., 2008; Sterpenich et al., 2009, 2007; Wagner et al., 2006), and supposedly self-relevant (Saletin and Walker, 2012). In addition, prospective memory performance (assessed as intentions to be implemented in the future) also benefits from sleep (Hoedlmoser et al., 2022), and according to a recent study appears to be associated specifically with REM sleep (Scullin et al., 2019). Recent and more remote waking life experiences are often incorporated into the content of dreams that likely reflect memory processing during sleep (Fogel et al., 2018; Schoch et al., 2019). While dream reports reflecting pre-sleep learning may reflect processes of memory reactivation (replay), task-related dreams can also be viewed as forms of future anticipation (pre-play), especially when participants expect to be re-tested on the task after sleep. Interestingly, despite the long-standing popular belief that dreams provide insights into the future, the anticipatory or future-oriented quality of dreams was only scarcely subjected to scientific scrutiny. Former studies imply that dreams with and without assumed precognitive references do not differ in statistical terms (Schriever, 1987), and precognitive dreams were indeed modeled as meaningful coincidences (Houran and Lange, 1998). Although dreams are probably not mental crystal balls, different approaches indicate that the constructive simulation of future goals, planned actions and expected events are some of the most remarkable features of dreaming (Wamsley, 2013). In fact, one of the first theorists about the function of dreams, Sigmund Freud (1899) already emphasized the role of dreams in allegorically depicting repressed desires, motivations and goals that have happened yet, but may point towards (usually socially and morally unacceptable) future behaviors or events. Early empirical studies by Klinger and colleagues (see Klinger, 2013) showed that dream content can be efficiently manipulated if pre-sleep dream suggestions (instructions to dream about specific topics) or goal-related acoustic stimuli (words or phrases) delivered during sleep are related to the participants’ personal concerns or goals (Klinger, 2013). Whereas participants often dream about tasks that they engaged with before falling asleep (Stickgold et al., 2000; Wamsley et al., 2010; Wamsley and Stickgold, 2019), task-related dreams were observed even before participants had any experience with the task, but had known (and presumably anticipated) that they would be tested later (Wamsley, 2013). Apart from experimental manipulations, the high prevalence of anticipatory dream content was also witnessed in natural settings,

especially during emotionally intense periods such as giving birth to a child or preparing for an important exam (Arnulf et al., 2014a; Nielsen and Paquette, 2007). For instance, Arnulf and colleagues (Arnulf et al., 2014a) examined the dreams of medical students who had to pass a high-stakes entrance examination. Around 60% of the responders reported to have dreamt about the test the preceding night. The dreams mainly depicted negative scenarios of being late or having difficulties to answer the questions. In spite of these dreamt failures, dreaming about the examination the previous night, and having examination-related dreams during the preparatory period predicted higher scores on the test. The authors conclude that examination-related dreams irrespective of their emotional valence, might have helped the students to prepare for the situation by simulating different aspects of the stressful event (Arnulf et al., 2014b). This finding indicates that although dreams are generally less constrained mental simulations of future concerns than waking thoughts, stressful experiences and challenges might narrow the array of envisioned future scenarios. Alternatively, dreams that cohere with waking prospection (such as concerns about the examination in the same morning) might be more salient and easier to remember than dreams that are unrelated to specific goals recalled after awakening. Apart from personal concerns, dreams are also influenced by the present environment of the sleeper. Although the incorporation of external inputs into dreams is rare, and environmental stimuli are not represented in dreams in a realistic manner (Oudiette and Paller, 2013), the emotional quality of external inputs impacts dream content. For instance, pleasant and unpleasant odors delivered during sleep resulted in emotionally positive and negative dream experiences, respectively (Schredl et al., 2009b), and aversive conditioning before sleep resulted in dysphoric dream reports when the conditioned stimuli were presented during post-learning sleep (Flo et al., 2011b; Wamsley and Antrobus, 2009b). The incorporation of the relevant features of the environment into dreams might help to anticipate proximate events that the sleeper may face with upon awakening. The association between dreaming and such environmental sampling during sleep is exemplified by findings showing enhanced cortical responses to external inputs in high versus low dream recallers (Eichenlaub et al., 2014a).

3. Dream recall interferes with goal-directed prospection

Difficulties in dream recall pose perhaps the biggest methodological challenge for dream research.

In the following section, we consider the phenomenon of dream amnesia (and dream recall) within the present framework of reactive and predictive homeostasis during sleep. However, a detailed discussion of dream amnesia and dream recall is far beyond the scope of the present article; therefore, we provide only a brief and focused overview here (for a recent comprehensive review on this topic, see Nemeth, 2022). Despite the individual differences in overall dream recall rates (inter-individual variability) and day-to-day fluctuations (intra-individual variability) in dream recall, dream amnesia is so profound that it seems to be an inherent part of dreaming. In fact, some forms of dreaming are present approximately in more than half of the time during the entire sleep process (Nielsen, 2000a; Schredl, 2007), but even individuals with high dream recall rates may only retain vague fragments lasting a couple of minutes. Classical theories of dream amnesia emphasized personality factors and attitudes towards dreams (Freud, 1899; Hartmann et al., 1991; Schonbar, 1965), phenomenological aspects, such as the salience of dreams (Cohen and MacNeilage, 1974), or cognitive mechanisms (Cohen, 1974) as critical factors of dream forgetting. A more comprehensive theory, the arousal-retrieval model (Koulack and Goodenough, 1976) suggests that the recall of dreams requires some form of wakefulness; therefore, dreams must be followed by short awakenings to be encoded in memory. After encoding, the fate of dreams is dependent on memory retrieval. During retrieval, the salience of dream content (e.g., vividness and bizarreness) as well as interfering memories might affect the consolidation of the dream material. Furthermore, the engagement

in retrieval processes might also vary as a function of personality factors such as introspection or openness to mental experiences (Koulack and Goodenough, 1976; Schredl, 2007).

The first assumption of the model received support from empirical findings. Individuals with high dream recall wake up more often during the night, and presumably spend more time awake when sleep is interrupted (Vallat et al., 2017; van Wyk et al., 2019). Moreover, EEG patterns indicating cortical arousal, wake-like activity, or encoding-related processes predicted successful dream recall upon forced awakenings in laboratory settings (Cipolli et al., 2017; Scarpelli et al., 2020, 2015). Whereas arousals might facilitate dreaming (Siclari et al., 2020, 2017), they may not be sufficient for successful dream recall. Cortical arousals during sleep are usually transient events that do not lead to complete awakening, and hence, the continuity of sleep may hinder the retrieval and consolidation of dream experiences, especially because information encoded shortly before falling asleep was shown to be forgotten later (Wyatt and Bootzin, 1994). Nevertheless, this argument does not explain why the majority of dreams are also forgotten upon final awakening in the morning. In sharp contrast with spontaneous dream recall, laboratory studies applying forced awakenings and the collection of dream reports yield very high recall rates (70–100%) if participants are awakened from Stage 2 and REM sleep (Nielsen, 2000a; Schoch et al., 2019). Nocturnal awakenings by ambulatory devices if properly timed around shallow sleep or arousals also facilitate dream recall in home environment (Carr et al., 2020; Stickgold et al., 1994). In addition, it is a common observation that spontaneous morning dream recall is enhanced when participants are instructed, and more importantly, motivated enough to keep a dream diary and report their dreams upon awakening (Aspy et al., 2015). Effortful dream recall in the morning was believed to facilitate retrieval by reducing interference with distracting thoughts and environmental stimuli after awakening (Cohen and Wolfe, 1973). In the following section we will extend this argument, and propose that the key obstacle of dream recall is goal-directed prospection initiated in the morning upon awakening. More specifically, we suggest that the difficulties in recalling dreams are caused by the competition for resources between dream-related retrospection and goal-directed morning prospection (unrelated to the dream experience). On the other hand, we will also argue that dream recall will be enhanced if the object of morning prospection coincides with the aim to recall dreams.

We argued that predictive homeostasis taking place during the second half of the night facilitates unconstrained self-referent mental simulations that are associated with the reinstated activity of the DMN. In turn, awakening, especially in the morning, sets the stage for focused, goal-directed prospective memory processes. These may include spontaneous, self-referent thought processes that re-establish the coherent sense of the self and its orientation in space and time, as well as cue-driven immediate (e.g., drinking coffee) or future plans (e.g., finishing a manuscript). After awakening, the efficient recoupling of frontoparietal networks with the DMN (Wu et al., 2012) may facilitate executive functions that help to focus (constrain) the scope of morning prospection and select appropriate behaviors in accordance with specific goals (Fig. 2/B). Since self-referent simulations generated during sleep and goal-directed self-referent thoughts rely on overlapping neural networks, they compete for resources: goal-directed prospection inhibits the recall of dreams that fall into oblivion without retrieval. On the other hand, successful dream recall may also inhibit and temporarily delay goal-directed prospective memories (i.e., we are not able to envision future goals while recalling a dream). In other words, we forget our dreams to remember the future.

The competition between goal-directed morning prospection and dream recall may explain why dream recall is enhanced when participants are instructed or motivated to recall their dreams in the morning. When keeping a dream diary and writing down dreams each morning, the object of goal-directed morning prospection coincides with the task to recall dreams. Similarly, laboratory studies on dreaming may also

enhance dream recall, since participants are instructed to recall their dreams after forced awakenings. Therefore, in such settings, the recollections of dream experiences (i.e., dream related retrospection) are assigned as specific goals in prospective memory. Goal-directed morning prospection peaks after complete awakening (when participants do not return to sleep); therefore, longer nocturnal awakenings that do not boost morning prospection may also lead to more frequent dream recall. Accordingly, reduced competition between goal-directed prospection and dream recall may contribute to the association between intra-sleep wakefulness and increased dream recall, as goal-directed prospection is reduced during the night (Ohayon et al., 1997; Schredl, 2009; Vallat et al., 2017; van Wyk et al., 2019). We may also speculate that the likelihood of dream recall will be increased if the content of dreams overlaps with the content of goal-directed morning prospection. The predominantly future-oriented nature of dreams in natural (Gross et al., 2021) and laboratory settings (Picard-Deland et al., 2021) might reflect the selective retrieval of dreams that are related to the contents of morning prospection. Likewise, the relatively high prevalence of dysphoric dreams related to past (traumatic) experiences in patients with posttraumatic stress disorder (PTSD) (Mellman et al., 2007) might be facilitated by the predominance of past-oriented daytime spontaneous thoughts in these patients (Sutherland and Bryant, 2005). Dreams about anticipated daytime challenges such as job interviews, or demanding examinations may not be inhibited, but in contrast, cued by morning prospection. Likewise, more mundane dreams related to immediate goals may also be easily recalled. A trivial example could be the highly frequent ‘toilet dream’, which may coincide with the urge and intention to urinate after awakening (Schredl, 2011). While remembering a dream after awakening competes with morning prospection, the opposite may occur in case of false awakenings. In false awakenings, the sleepers usually dream about their normal morning routine (e.g., going to the toilet, eating breakfast, visiting friends, etc.) and believe they are awake while they are still sleeping. According to our framework, false awakenings provide peculiar examples for the intrusion of goal-directed morning prospection into the stream of otherwise unconstrained dreaming. In such cases, goal-directed prospection competes and interferes with dreaming while individuals are still asleep. Relatedly, false awakenings seem to occur in sleep-state transitions, in a state when unconstrained nocturnal thought processes compete with goal-directed prospection for shared neurocognitive resources (Raduga et al., 2020).

3.1. Dream recall: trait or state?

Although dream amnesia is a pervasive phenomenon, questionnaire-based studies measuring dream recall frequency (DRF) indicate that individuals differ in their ability to recall their dreams. DRF appears to show a normal distribution between low dream recallers who almost never remember their dreams, and frequent dream recallers who report to recall one or more dreams each morning (Schredl, 2007). Such differences in DRF were associated with a variety of factors including age, gender, personality dimensions, sleep habits, and cognitive functions such as visual memory or creativity (Schredl and Montasser, 1996). Nevertheless, the associations between DRF and dispositional factors (e.g., personality traits) are rather weak and somewhat inconsistent (Nemeth, 2022). Beyond individual differences in DRF, dream recall is also influenced by a number of state factors. Prospective assessments involving multiple laboratory awakenings or home-based assessments with dream logs are used to capture situational factors contributing to intraindividual fluctuations in dream recall. Sleep duration, the sleep stage (REM vs. NREM) preceding awakening, specific cortical activities, and motivation to recall dreams were identified as the most relevant state factors (Nemeth, 2022). Importantly, studies focusing on state factors of dream recall instruct participants to recall their dreams. This is a substantial methodological aspect, since the task to report a dream (e.g., keeping a dream diary) was shown to enhance (and hence

overestimate) dream recall frequency (Aspy, 2016). Reporting dreams after awakening boosts dream recall especially in low dream recallers (Aspy et al., 2015), suggesting that dream recall is also a skill that can be practised and developed. Keeping a dream diary may facilitate memory retrieval after awakening and also increase interest in dreaming (Aspy et al., 2015), the latter being linked to higher DRF (Schonbar, 1965). We argue that prospective memory processes related to specific goals of the upcoming day interfere with dream recall. Relatedly, if individuals are motivated to recall their dreams in the morning, goal-directed prospective memory processes related to the demands of the upcoming day may not immediately interfere with the recollection of dream memories. We assume that recalling a dream will be assigned to prospective memory as a goal to accomplish upon awakening, and hence coincide with goal-directed morning prospection. If morning prospection and dream recall compete for shared neurocognitive resources, individuals with enhanced prospective memory capacity might be more efficient in dream recall. In line with this assumption, high dream recallers compared to low dream recallers exhibited increased functional connectivity in the DMN and between key nodes associated with prospection and episodic memory retrieval after awakening from a daytime nap (Vallat et al., 2020). Nevertheless, the putative link between prospective memory functions and dream recall was not examined to date, and should be tested in further experiments.

3.2. Morning cortisol as a potential modulator of dream amnesia

As discussed above, the gradual increase in nocturnal cortisol reflects predictive homeostasis that prepares the sleeping organism to its imminent awakening. This gradual increase is most often followed by an additional and steeper rise in cortisol 15–45 min after morning awakening, also known as the CAR. The CAR cannot be accounted for by the circadian rise of cortisol that begins in the second half of the night, but is viewed as a distinct physiological marker of the transition from sleep to full alertness (Wilhelm et al., 2007). Compelling evidence indicates that beyond its energetic effect to overcome fatigue and regain arousal, the CAR reflects a rapid anticipation of upcoming demands (Adam et al., 2006; Elder et al., 2014; Fries et al., 2009). Indeed, the CAR is greater on weekdays compared to weekends (Schlotz et al., 2004), and particularly increased if individuals anticipate a busy or challenging day, while attenuated or negative CARs were observed on days off associated with reduced demands (Rohleder et al., 2007; Stalder et al., 2010, 2009). That is, the CAR reflects a stress response that precedes the specific potential stressor. Therefore, the CAR is associated with anticipatory, goal-directed prospective memory processes (Adam et al., 2006; Fries et al., 2009; Wilhelm et al., 2007), and as such, may modulate the recall and the forgetting of dreams. Studies suggest that morning cortisol may impair the recall of episodic and declarative memories and hence, facilitate the forgetting of dreams in the morning (Payne, 2011). Although it was not the specific purpose of the authors, a recent study (Antypa et al., 2021) can be viewed as an experimental model of dream amnesia and dream recall. The focus of the study was the influence of morning cortisol on the ability to recall a specific memory reactivated during the night. The authors found that the pharmacological suppression of morning cortisol facilitated the recall of a previously learned material that was reactivated by a memory cue at 4 a.m., compared to a control condition where the morning rise in cortisol was not inhibited (Antypa et al., 2021). The finding is also in line with other studies showing negative associations between the CAR and memory recall. The CAR was negatively correlated with verbal and visuospatial memory performance in unmedicated depressed patients (showing an elevated CAR compared to medicated patients and controls) (Hinkelmann et al., 2013), and a greater CAR was associated with impaired verbal memory in older individuals (Hidalgo et al., 2016). Nevertheless, correlational studies on the associations between the physiological morning rise in cortisol and declarative/episodic memory functions are somewhat inconsistent (Law and Clow, 2020). More consistent findings emerge

regarding prospective memory: in line with the notion of the CAR as a marker of goal-directed prospection, task performance requiring prospective memory were linked to greater CARs (Bäumler et al., 2014b, 2014a), and morning cortisol facilitated adaptive responses to anticipated stimuli (Brueckner et al., 2019; Meuret et al., 2016).

Day-to-day variations of the CAR indicate that situational factors are more relevant than dispositional ones in determining the morning rise of cortisol (Hellhammer et al., 2007); however, trait-like associations between the CAR and dream recall may exist to some extent. Although the association between dream recall and the CAR was not directly examined, clinical disorders featuring an altered CAR provide some hints in this regard. For instance, a reduced CAR was found in PTSD (de Kloet et al., 2007; Rohleder et al., 2004), a psychiatric condition with intense and dysphoric dreams among the core symptoms (Spoormaker and Montgomery, 2008). Moreover, a blunted CAR was associated with symptom severity, in particular with intrusive recollections in an adolescent group of PTSD patients (Keeshin et al., 2014). A reduced CAR was observed in a variety of clinical conditions such as in Cushing syndrome (Roa et al., 2013), narcolepsy (Kok et al., 2002), attachment anxiety (Quirin et al., 2008), nightmare disorder in females (Nagy et al., 2015), and insomnia disorder (Dressle et al., 2022), all of which feature increased and vivid dream recall (McNamara et al., 2001; Schredl, 2009; Starkman and Scheingart, 1981). State-like variations between the CAR and dream recall were not systematically studied either. State-like changes in sleep patterns, such as sleep at weekends versus on weekdays, late awakening times, or longer sleep duration were associated with increased dream recall (Leproult et al., 2015; Schredl and Reinhard, 2008) and an attenuated CAR (Elder et al., 2014; Randler and Schaal, 2010). We should note, however, that beyond the morning rise in cortisol, other factors, such as longer REM sleep due to extended sleep and late awakenings may also influence dream recall (Schredl and Reinhard, 2008). Future studies are warranted to examine the direct links between dream recall and the CAR, taking into consideration the influence of sleep (e.g., sleep quality and duration, night-time awakenings), as well as the role of homeostatic and circadian factors that affect both variables. The CAR was also associated with executive functions on a trait-and state-like level: older individuals with greater CARs showed better executive functions in general (Evans et al., 2012), and increased CARs predicted better executive functions the same morning in a single case study involving 50 days of daily assessments (Law et al., 2015). We argued that executive functions are reinstated after awakening and facilitate self-referent prospection constrained to specific goals. We speculate here that the CAR boosts goal-directed thoughts and behaviors at the expense of dream recall. Nevertheless, if the recall of dreams is the object of morning prospection (as it is the case in laboratory studies of dream recall or when individuals are highly motivated to keep a dream log), our assumptions imply that the CAR would actually facilitate the recall of dreams. In order to test these assumptions, future studies should aim to manipulate the object of morning prospection or participants' expectations about morning demands to examine the modulatory role of cortisol on memory processes and more specifically, morning dream recall.

4. Concluding remarks

Dreaming is an inherent part of the neurocognitive processes and homeostatic functions of sleep. In this review, we emphasized the role of the dreaming mind in the context of reactive and predictive homeostasis taking place in sleep during the first and second part of the night, respectively. We highlighted the dynamic interplay between reactive and predictive homeostatic functions that facilitate restorative processes and future anticipation. We argued that the dreaming mind aligns with these fundamental functions, and associated with the reinstatement of the DMN, particularly during the second part of the night, unfolds as a special form of non-constrained, self-referent cognition. We hypothesize that more constrained, goal-directed prospection after awakening

interferes with the process of dreaming and dream recall and contributes to dream amnesia. Although dream production and dream recall are usually treated as separate mechanisms, here we aimed to provide a common framework for these processes. In this respect, future studies should consider the critical role of morning prospecting when studying the recall and the forgetting of dreams. Finally, the role of cortisol in future anticipation and dream amnesia, as well as the intimate links between sleep disorders and peculiar dream experiences remain elusive and need to be explored in clinical studies and experimental settings.

Conflict of interest

The authors report no conflicts of interest.

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