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PHYSIOLOGICAL REVIEW

Beyond the neuropsychology of dreaming: Insights into the neural basis of dreaming with new techniques of sleep recording and analysis

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SUMMARY

Recent advances in electrophysiological [e.g., surface high-density electroencephalographic (hd-EEG) and intracranial recordings], video-polysomnography (video-PSG), transcranial stimulation and neuroimaging techniques allow more in-depth and more accurate investigation of the neural correlates of dreaming in healthy individuals and in patients with brain-damage, neurodegenerative diseases, sleep disorders or parasomnias. Convergent evidence provided by studies using these techniques in healthy subjects has led to a reformulation of several unresolved issues of dream generation and recall [such as the inter- and intra-individual differences in dream recall and the predictivity of specific EEG rhythms, such as theta in rapid eye movement (REM) sleep, for dream recall] within more comprehensive models of human consciousness and its variations across sleep/wake states than the traditional models, which were largely based on the neurophysiology of REM sleep in animals. These studies are casting new light on the neural bases (in particular, the activity of dorsal medial prefrontal cortex regions and hippocampus and amygdala areas) of the inter- and intra-individual differences in dream recall, the temporal location of specific contents or properties (e.g., lucidity) of dream experience and the processing of memories accessed during sleep and incorporated into dream content. Hd-EEG techniques, used on their own or in combination with neuroimaging, appear able to provide further important insights into how the brain generates not only dreaming during sleep but also some dreamlike experiences in waking.

Introduction

Dreaming (also termed "sleep mentation", "dream experience" or "mental activity during sleep") is a state of consciousness occurring in a physiological condition different from that in which it becomes available for investigation via its recall (and possibly report). Because of the asynchrony between its generation during sleep and recall after awakening, dreaming has traditionally been considered difficult to study through the conceptual apparatus applied to investigate the states of consciousness experienced in wakefulness (for review [1,2]). This (often implicit) assumption has deeply influenced the experimental investigation of dreaming, first developed in the 1950s after the discovery of the cyclic architecture of sleep and the identification of rapid eye movement (REM) sleep as a possible neurophysiological marker of dreaming. However, recent neuroimaging and neurophysiological studies on resting state and mind wandering in wakefulness have shown a wide overlap of phenomenological features and underlying brain mechanisms [3,4] with dreaming. This has led to a conceptualization of dreaming as a "natural" extension of waking consciousness [5], namely, a state characterized by internally generated multisensorial (overall visual and auditory), motor (sometimes dramatic), cognitive and emotional experiences, inserted as fairly coherent events into an imaginary story-like plot [3,6–8].

In this review, we will examine the deepening of our knowledge of the neurobiological basis of dreaming made possible by recent advances in electrophysiological and neuroimaging methods of sleep recording and analysis. To facilitate the understanding of the theoretical relevance of the findings obtained through these

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Abbreviations

(f)MRI	(functional) magnetic resonance imaging
dl/dm/l/m/vmPFC	dorsolateral/dorsomedial/lateral/medial/ventromedial prefrontal cortex
DTI	diffusion tensor imaging
EEG	electroencephalography
Hd-EEG	high density EEG
HDR/LDR	high/low dream recaller
MEG	magnetoencephalography
NIRS	near-infrared spectroscopy
NREM	non rapid eye movement
P300	P3 wave (event-related potential)
PET	positron emission tomography
PTSD	post-traumatic stress disorder
PuM	medial pulvinar nucleus
RBD	REM sleep behavior disorder
REM	rapid eye movement
SEEG	stereo-EEG
SOREM	sleep onset REM sleep
SWS	slow wave sleep
tACS	transcranial alternating current stimulation
tDCS	transcranial direct current stimulation
TMR	targeted memory reactivation
TMS	transcranial magnetic stimulation
TP(O)	temporoparietal (occipital)
V1/V4/V5	visual area one/four/five
video-PSG	video-polysomnography

methods, we will start from an updated characterization of dreaming, as results from over 60 years of laboratory and clinical research.

Frequency of dream recall and dream generation processes

The collection of dream reports after provoked awakening in the laboratory has provided both reliable estimates of the frequency of dream experience developed in the different sleep stages and useful insights into the underlying cognitive processes, while the clinical observation of sleep and dream recall of patients with acute brain lesions has offered important evidence of the anatomical correlates of dream alteration and dream loss.

Frequency of dream recall

Early laboratory studies using electropolygraphic recordings of sleep [9–11] reported a much more frequent association of fairly long, perceptually vivid and complex ("dreamlike") mental experiences after awakening from periods of sleep with heightened and desynchronized cortical activity (i.e., high-frequency/low-amplitude electroencephalographic [EEG] activity) accompanied by REMs, muscle atonia and increased variability in heart rate and respiratory activity, compared to other non-REM (NREM) periods of sleep (for review, see [7,8]).

The originally postulated close (if not exclusive) association of REM sleep and dreaming, however, was rapidly disproved by studies carried out using more complex designs and interview techniques (for review, see [8,12]), which yielded several crucial findings.

1) Dream recall is also fairly frequent (about 50%) after awakening from nighttime [13–15] and daytime (in particular, stage-2) NREM sleep [13,16] relative to REM sleep (more than 80%).
2) One or more dreamlike characteristics (such as perceptual vividness, bizarreness, emotional tone and story-like organization) are enhanced in reports collected after late night NREM sleep (relative to the early night) [15,17,18] and in the morning [19,20], as well as after periods of total or partial sleep deprivation [21,22], restriction [23] or with multiple awakenings [24].
3) Neither dreaming nor REM and NREM sleep are stable, homogeneous and distinct states irrespective of terminology (for dreaming) and taxonomy (for sleep stages). Indeed, not only perceptual, but also cognitive contents (such as planning, reasoning and thinking) are common, as are emotional experiences (often intense and negatively toned [25,26]), in dream reports. Moreover, whole reports can rarely be classified as "dreams" or "thoughts", but are better described along a continuum ranging from "thought-like" (overall in NREM sleep of early night [15,18]) to "dreamlike" content (overall in REM sleep of late night [17,18,27] and under higher sleep pressure [21]). Finally, 5–10% of NREM reports after stage 2 [28] and stages 3 and 4 [29] cannot be distinguished from REM reports solely on the basis of the perceptual and emotional features of their contents.
4) The stage- and cycle-related variations in recall frequency and in the perceptual, emotional, motor and story-like features of dream reports are influenced by large differences not only between (trait-like), but also within subjects (state-like). For example, there are opposite trends in the length and complexity of reports according to whether the time-in-stage pertains to REM or NREM sleep [15] and whether it is in the first or second half of the night [18,30].
5) The frequency and characteristics of dream reports (and, thus, their within-subject variability) are influenced, in particular, by situational and individual factors (for reviews [31,32]). Situational factors concern the modalities of awakening (abrupt/gradual [33]) and dream reporting (free recall [31]/questionnaire [32]/affirmative probes [34]/guided recall [35]), and the presence/absence of interfering tasks upon awakening [36]. Individual factors concern gender, age, personality traits (openness to experience, psychological boundaries and absorption [37]), the tendency to suppress negative thoughts and emotions [38] and the attitude toward dreams, motivation, emotional reactivity, and cognitive styles [39].
6) Individuals with normal or high recall frequency (once or more per week [32,40]) usually fail to report any dream after 5–30% of REM awakenings [8], and some (so-called non-recallers) cannot even report any dream after REM awakenings [31,41].
7) Dream recall can be modulated by dopamine agonists [42,43], or even suppressed by brain lesions (see below) located at the temporoparieto-occipital (TPO) junction and ventromedial prefrontal cortex (vmPFC) [44,45], without any appreciable effect on REM sleep frequency and duration or REM density [46].

The evidence that a more or less dreamlike mental activity is also developed during NREM sleep prompted researchers to reconcile the observed differences not only by postulating a continuum (ranging from purely thought-like to dreamlike features) of