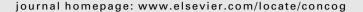
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Cognitive and emotional processes during dreaming: A neuroimaging view *

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ABSTRACT

Dream is a state of consciousness characterized by internally-generated sensory, cognitive and emotional experiences occurring during sleep. Dream reports tend to be particularly abundant, with complex, emotional, and perceptually vivid experiences after awakenings from rapid eye movement (REM) sleep. This is why our current knowledge of the cerebral correlates of dreaming, mainly derives from studies of REM sleep. Neuroimaging results show that REM sleep is characterized by a specific pattern of regional brain activity. We demonstrate that this heterogeneous distribution of brain activity during sleep explains many typical features in dreams. Reciprocally, specific dream characteristics suggest the activation of selective brain regions during sleep. Such an integration of neuroimaging data of human sleep, mental imagery, and the content of dreams is critical for current models of dreaming; it also provides neurobiological support for an implication of sleep and dreaming in some important functions such as emotional regulation.

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1. Introduction

Dreaming represents a major facet of human experience. Yet, the nature of the dream-state is highly subjective and a genuinely personal experience making a scientific analysis of dreaming somewhat prohibitive. Dreaming is a state of consciousness characterized by internally-generated sensory-motor, verbal, cognitive and emotional experiences, which may unfold in actions and events forming imaginary plots. Sensory content predominantly involves visual and auditory modalities. Dreamed motor behaviors are frequent and diverse, including physical activities like self-motion (walking, running, jumping) and interacting with objects. Verbal content might include written and spoken language (heard or produced by the dreamer). Cognitive content also encompasses several aspects of executive functions (planning, reasoning, thinking, etc.), memory (elements in dreams involve retrieval from recent or more remote memory), as well as spatial navigation abilities, among others. Emotional experiences in dreams are frequent, intense, and possibly biased toward negative emotions. Yet, probably all the categories of dream experience described above are also subject to many alterations and distortions that are unlikely to occur in real waking life (Hobson, Stickgold, & Pace-Schott, 1998; Schwartz & Maquet, 2002). Despite the implausibility of many dream elements with respect to the real world, the dreamer usually remains unaware of being in

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a dream and experiences the dream as a world analog (Johnson, Kahan, & Raye, 1984). Because of these distinctive properties, the study of dreaming offers a fascinating opportunity to better understand the varieties of conscious experiences across common, daily but dramatic changes in brain states.

Below, we first provide some historical background for a neuroscience approach to dreaming. We then review the available functional neuroimaging data that describe regional cerebral activity during normal human REM sleep, as well as the likely neurophysiological source for such spontaneous patterns of activity. We also review brain imaging of mental imagery and sensory imagery. We also discuss how brain activity during sleep might be interpreted in neurocognitive terms based on common dream features. In sum, this integrated view on the neural correlates of dreaming provides fundamental elements for the understanding of the organization and functions of dreaming.

1.1. Modern history of dream research

In the modern occidental era, pioneering scientific experimentations on dreaming emerged during the second half of the 19th century (Delboeuf, 1885/1993; Macario, 1857/1978; Maury, 1862; Saint-Denys, 1867/1977; Schwartz, 2000). In those days (as nowadays), introspective dream reports were considered as a valuable material for scientific enquiry, yielding unique information about what was perceived, felt, or thought in a dream. Very ingenuous experiments were designed to determine what factors might influence the dream content and what rules may determine the dream scenario. For example, the French sinologist and man of letters Hervey de Saint-Denys designed the following experiment to test the influence of memory associations on the formation of dreams (Hervey de Saint-Denys, 1867/1977). During a trip that lasted a few weeks, he used a new perfume and hermetically closed the bottle of perfume before traveling back home. A few months later, he asked one of his servants to put a few drops of the perfume on his pillow, but he also asked his servant not to tell him what night that would be. Ten days later, Hervey de Saint-Denys suddenly dreamt that he was back in the same place that he visited during his trip – on that night the servant had put some of the perfume on his master's pillow. The same experiment was successfully repeated for different perfumes, different places, and different time lags, thus corroborating Hervey de Saint-Denys' hypothesis that the stream of dreams is guided by associations or what he called "psychological affinities". A similar use of odors as cues for memory replay during sleep was recently reported in an elegant brain imaging study (Rasch, Buchel, Gais, & Born, 2007).

These early and promising developments for a scientific approach to dreaming were considerably slowed down at the beginning of the 20th century, because of two major events in the history of psychology. On the one hand, after the publication of Freud's psychoanalytic masterpiece, "The Interpretation of Dreams", studies relying exclusively on the manifest content of dreams were discredited on behalf of a quest for the "true" dream, i.e., the latent content hidden beneath the apparent dream (Freud, 1955/1900). On the other hand, the advent of behaviorism was detrimental to the study of dreaming because of its refutation of the existence of mental experiences such as dreams. Hence, both the emphasis on dream phenomenology and the use of introspective dream reports initiated in the late 19th century were rapidly challenged, the former by psychoanalysis and the latter by behaviorism.

A next turning point for the history of the science of dreaming was in the late 1950s, when (i) an objective indicator of the dreaming state was discovered and (ii) a new cognitive approach to the phenomenology of dreams was developed (for a review, Foulkes, 1996).

Between 1953 and 1957, in a laboratory at the University of Chicago, Nathaniel Kleitman and his two students, Eugene Aserinsky and William Dement made a revolutionary discovery. They observed that dreaming occurred during specific periods of sleep when cortical activity is high (i.e., high-frequency/low-amplitude electroencephalographic [EEG] activity, analogous to resting wake state) and accompanied by rapid eye movements (REM), increased heart rate, and respiratory activity (Aserinsky & Kleitman, 1953; Dement & Kleitman, 1957). These REM periods were also found to be associated with muscle atonia (Jouvet, 1994), thus preventing the dreams from being acted out. Compared to non-REM periods, REM awakenings yielded longer dream reports, which appeared to also be more emotional and perceptually vivid, and contained more bizarre features (Aserinsky & Kleitman, 1953; Hobson, Pace-Schott, & Stickgold, 2000). Thus, REM sleep was considered as a state of high cerebral and low physical activation that would provide a neurophysiological marker of dreaming. Not surprisingly, this discovery was extremely influential because it opened new perspectives for the scientific study of dreaming. Critically, the discovery of REM sleep also demonstrated that sleep is not a homogenous state of mental and cerebral quiescence, but that some sustained periods of elevated neurophysiological activity underlying the production of dream experiences were distributed across the sleep night (Aserinsky & Kleitman, 1953). While the equation "REM sleep = dreaming" effectively reduces the characterization of the neural correlates of dreaming to a comparison between REM sleep and waking or NREM sleep, it is important to keep in mind that neither dreaming nor REM sleep are stable, homogeneous and unique states. Indeed, dreaming might best be described along a continuum, from thought-like mentations typical of early NREM sleep to florid and vivid dreamlike experiences typical of REM sleep (Cavallero, Cicogna, Natale, Occhionero, et al., 1992; Stickgold, Malia, Fosse, Propper, & Hobson, 2001). In addition, some studies suggested the presence of a shift toward more dreamlike hallucinations and fewer directed thoughts both by REM and by time spent in sleep (Fosse, Stickgold, & Hobson, 2001, 2004; Nielsen, 2004; Stickgold, Malia, et al., 2001). These findings suggest that REM sleep might reasonably be considered as a facilitating neurophysiological state for dreaming to occur, even though dreams are not exclusively experienced during this sleep stage.

About the same time as Aserinsky and Kleitman wrote their inaugural article on REM sleep, Hall (1953/1966) published "The Meaning of Dreams" in which he described and classified the phenomenological characteristics of thousands of dreams

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