

Neural representations during sleep: From sensory processing to memory traces

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Received 26 August 2006; revised 20 October 2006; accepted 26 October 2006
Available online 18 December 2006

Abstract

In the course of a day, the brain undergoes large-scale changes in functional modes, from attentive wakefulness to the deepest stage of sleep. The present paper evaluates how these state changes affect the neural bases of sensory and cognitive representations. Are organized neural representations still maintained during sleep? In other words, despite the absence of conscious awareness, do neuronal signals emitted during sleep contain information and have a functional relevance? Through a critical evaluation of the animal and human literature, neural representations at different levels of integration (from the most elementary sensory level to the most cognitive one) are reviewed. Recordings of neuronal activity in animals at presentation of neutral or significant stimuli show that some analysis of the external world remains possible during sleep, allowing recognition of behaviorally relevant stimuli. Event-related brain potentials in humans confirm the preservation of some sensory integration and discriminative capacity. Behavioral and neuroimaging studies in humans substantiate the notion that memory representations are reactivated and are reorganized during post-learning sleep; these reorganizations may account for the beneficial effects of sleep on behavioral performance. Electrophysiological results showing replay of neuronal sequences in animals are presented, and their relevance as neuronal correlates of memory reactivation is discussed. The reviewed literature provides converging evidence that structured neural representations can be activated during sleep. Which reorganizations unique to sleep benefit memory representations, and to what extent the operations still efficient in processing environmental information during sleep are similar to those underlying the non-conscious, automatic processing continually at work in wakefulness, are challenging questions open to investigation.

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Keywords: Sensory representations during sleep; Single unit recordings during sleep; Event-related potentials during sleep; Functional imaging during sleep; Expression of learning-induced plasticity during sleep; Dynamics of memory representations during sleep

1. Introduction

Although the concept of representation has been questioned, in particular by cognitive psychologists (O'Regan & Noe, 2001) and neurophilosophers (Maturana & Varela, 1987; Thompson & Varela, 2001), in the field of neurosciences the notion of neural representation has become so popular over the last thirty years that it has now come into common use (see reviews by Andersen, Snyder, Bradley, &

Xing, 1997; Knudsen & Brainard, 1995; Logothetis, 1998; Maunsell, 1995; Phillips, 1993; Roland & Gulyas, 1994; Singer, 1998). This is not surprising: albeit may be naive, it is traditionally considered that brain's function is to integrate features of the external world and to build internal representations so as to generate a "model" of the world enabling complex sensory–motor interactions and cognitive functions. However, the notion of neural representation is not univocal. From one article to another, there is a very large diversity in the level and complexity of what is represented, as well as in the type of neural code supposed to underlie the neural representations. Beyond the classical topographic representations of the sensory epithelium

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described at the cortical (Covey & Ellis, 1969; Kaas, Nelson, Sur, Lin, & Merzenich, 1979; Merzenich, Knight, & Roth, 1975) and subcortical (Covey & Casseday, 1986; Malpeli & Baker, 1975; Merzenich & Reid, 1974) levels, neural representation ranges from simply a neuronal signal that has a content and performs a function (deCharms & Zador, 2000), to a response pattern obtained over a cortical area at presentation of a natural stimulus (Wang, Merzenich, Beitel, & Schreiner, 1995), and to widely distributed neuronal assemblies whose firing rate is synchronized across various brain areas in the millisecond scale (Engel, Fries, & Singer, 2001). The smallest common denominator to all these views is the idea that a neural representation contains information. The questions addressed in the present paper are thus: Do neuronal signals emitted during sleep carry information? Have they a content? Have they any functional relevance?

Addressing these questions may surprise given that loss of consciousness, loss of sensory awareness, and unresponsiveness to stimuli from the external world are among the major features defining sleep. However, sleep does not bring a little death. The neuroscience community no longer conceives of the sleeping brain as simply dormant, fully disconnected from the environment and completely quiescent. In particular, the relations between sleep and cognition have attracted considerable interest in the last decade, as attested by the recent spate of publications on that topic. In the field of sleep and cognition, now called “the cognitive neuroscience of sleep” (Hobson & Pace-Schott, 2002), it is explicitly or implicitly assumed that neural representations can be activated or can be spontaneously active and eventually modified during sleep. The present review presents some aspects of that literature, posing as many questions as it answers. Starting with the issue of sensory representations in the first two sections, we will progress by evaluating whether learned representations are accessible and can be expressed during sleep, to finally address, in the last section, the question of the dynamics of memory representations during sleep. Despite partial overlaps, the review does not cover the fields of “information processing during sleep” (see Aton, Cantero, & Escera, 2001; Bonnet, 1982; Coenen & Drinkenburg, 2002), nor that of “sleep and memory” (see Maquet, Smith, & Stickgold, 2003b, as well as Gais & Born, 2004a; Rauchs, Desgranges, Foret, & Eustache, 2005; Walker & Stickgold, 2006). Lastly, though dreaming is the clearest evidence of the activation of internal representations during sleep, the special field of “dreams” is not tackled at all. Dreaming has long been the object of a neurobiological approach (Hobson & McCarley, 1977), but linking the subjective mental experiences of dreams with any neural representation is a challenge that is far from being achieved, if ever (see Fagioli, 2002; Hobson, Pace-Schott, & Stickgold, 2000; Nielsen, 2000, 2004; Revonsuo, 2000; Schwartz & Maquet, 2002; Solms, 2000).

Classically, two states of sleep are distinguished, paradoxical sleep (PS; also known as rapid-eye movement sleep or REM sleep) and slow-wave sleep (SWS; also referred to

as non-REM sleep). In animals, the terms SWS and non-REM sleep are synonymous, and the former is generally used. In humans, the two terms are not synonymous; non-REM sleep is subdivided into a continuum of four stages reflecting the depth of sleep: sleep onset period (stage 1), light sleep (stage 2), and SWS (stages 3 and 4). Because many of the reported data are from animal studies, the term SWS is used here in its more global acceptance (i.e., the whole non-REM sleep).

Contrary to waking and PS which are both associated with fast rhythms of brain electrical activity, SWS is characterized by large-amplitude, low-frequency (<15 Hz) oscillations reflecting a massive synchronization of neuronal activities in thalamocortical networks. Spindles, delta waves, and slow oscillation are the three brain rhythms defining SWS. The neuronal patterns prevailing in thalamocortical systems, a burst-silence mode during SWS versus a sustained single-spike activity during waking and PS, are under the control of generalized modulatory systems originating in the brainstem, the hypothalamus, and the basal forebrain (review in Jones, 2005; Pace-Schott & Hobson, 2002; Steriade, 2003; Steriade & McCarley, 1990). But none of the natural states of vigilance is uniform. It is well known that within the waking state, the level of arousal modulates sensory responses (e.g., Foote, Berridge, Adams, & Pineda, 1991; Hubel, Henson, Rupert, & Galambos, 1959; Morrow & Casey, 1992), and that attentional processes strongly influence sensory processing, either facilitating responses to target stimuli or suppressing responses to non-target stimuli (review in Desimone & Duncan, 1995). Qualitatively different epochs, and thereby differences in sensory processing, also exist within a given sleep state. This is the case of the epochs with or without ocular saccades in PS (e.g., Baust, Berlucchi, & Moruzzi, 1964; Cairns, Kiang, McErlane, Fragoso, & Soja, 2003). This is also the case of the depolarizing and hyperpolarizing phases of the slow oscillation in SWS (Massimini, Rosanova, & Mariotti, 2003). Indeed, during SWS, the membrane potential of cortical neurons oscillates between depolarized and hyperpolarized levels with a periodicity of about 1 s. This cyclic alternation is reflected in the electroencephalogram (EEG) by a slow (<1 Hz) oscillation: cortical neurons are depolarized and fire spikes during depth-negative EEG waves, while they are hyperpolarized during depth-positive EEG waves (Steriade, Timofeev, & Grenier, 2000; Timofeev, Grenier, & Steriade, 2001). Lastly, some factors independent of the sleep process per se modulate sensory processing during sleep: to take only one example in human, differences in stimulus processing were observed between the first and second part of the night for the same sleep stage (Plihal, Weaver, Mölle, Fehm, & Born, 1996).

2. Sensory representations during sleep: Neuronal activity in sleeping animals

From which literature can it be inferred that sensory representations are or are not maintained during sleep? If we

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