



Local sleep spindle modulations in relation to specific memory cues



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ABSTRACT

Sleep spindles have been connected to memory processes in various ways. In addition, spindles appear to be modulated at the local cortical network level. We investigated whether cueing specific memories during sleep leads to localized spindle modulations in humans. During learning of word–location associations, words presented in the left and right visual hemifields were paired with different odors. By presenting a single odor during a subsequent nap, we aimed to selectively reactivate a subset of the studied material in sleeping subjects. During sleep, we observed topographically restricted spindle responses to memory cues, suggesting successful reactivation of specific memory traces. In particular, we found higher amplitude and greater incidence of fast spindles over posterior brain areas involved in visuospatial processing, contralateral to the visual field being cued. These results suggest that sleep spindles in different cortical areas reflect the reprocessing of specific memory traces.

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Introduction

Memories appear to be reprocessed during sleep, leading to consolidation and reorganization of previously acquired information (Cox et al., 2014; Takashima et al., 2009; Talamini et al., 2008). In recent years, sleep spindles have attracted considerable attention as potential neurophysiological markers of such reprocessing (Fogel and Smith, 2011; Lüthi, 2013). Short bouts of cortical oscillatory activity generated by the thalamus, sleep spindles occur in the electroencephalogram (EEG) during both light sleep and slow wave sleep (SWS). Due to their thalamic dependence, spindles have classically been viewed as suppressing the flow of incoming sensory information, a view that is supported by recent evidence (Dang-Vu et al., 2011). Furthermore, spindles may be classified as either slow (10–13 Hz) or fast (13–16 Hz). Slow and fast spindles have different EEG scalp topographies (Zeitlhofer et al., 1997), and are co-active with hemodynamic responses in different cortical regions (Schabus et al., 2007).

Notwithstanding a potential gatekeeping role for spindles, recent evidence has strongly implicated spindle rhythms in the reprocessing of previously encoded information. Besides having plasticity-inducing capabilities *in vitro* (Rosanova and Ulrich, 2005), sleep spindles are affected by prior learning (Gais et al., 2002) and have been associated with systems-level memory consolidation processes (Buzsáki, 1996;

Diekelmann and Born, 2010), as evidenced by their correlation with memory retention across sleep (Cox et al., 2012; Griessenberger et al., 2013; Nishida and Walker, 2007; Schabus et al., 2004). Moreover, pharmacologically induced increases in spindle occurrence lead to improved memory, providing even stronger support for a mechanistic role of spindles in memory consolidation (Mednick et al., 2013). Of special relevance are findings suggesting that the scalp topography of memory-related spindle involvement reflects the nature of the pertaining memory traces. In particular, retention of verbal material is related to spindles recorded over frontal brain regions (Clemens et al., 2005), while parietal spindles correlate with spatial memory (Clemens et al., 2006). In the procedural realm, unilateral motor memory consolidation depends on the balance between spindle occurrence over contra- and ipsilateral premotor cortices (Nishida and Walker, 2007). Combined with evidence demonstrating that spindles may be locally regulated (Nir et al., 2011), these distinct topographies raise the possibility that spindles constitute instances of memory trace reactivation that are tied to the regional cortical networks harboring the specific memories being reprocessed. This suggestion is based, however, on separate studies employing different study materials. Moreover, given the low surface electrode coverage in the pertaining studies, the allocation of recorded signals to specific cortical areas remains speculative.

To test the hypothesis of local memory-related spindling directly, we adopted an approach in which subjects were required to learn word–location associations. The associations were presented in blocks that were spatially biased to either the left or the right visual field. Each associational category (i.e., each block) was paired, during learning, with an odor that served as a reactivation cue during subsequent sleep. During sleep, we recorded high-density EEG for post-hoc sleep spindle analysis. We used odors for cueing because they have been

Abbreviations: EEG, electroencephalography; SWS, slow wave sleep; REM, rapid eye movement; NREM, non-rapid eye movement; CSD, current source density; fMRI, functional magnetic resonance imaging.

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applied successfully in the past (Diekelmann et al., 2011; Rasch et al., 2007), because odor cue effects are very specific (Rihm et al., 2014), and because odors carry a limited risk of waking the participant relative to auditory stimulation (Carskadon and Herz, 2004).

With this setup we aimed to assess whether the two cueing conditions induce differential topographies of spindle modulations. This would support the notion that spindles respond in a local and memory-specific manner to reactivation cues. More specifically, we expected responses over parieto-occipital brain areas contralateral to the hemifield bias of the cued word block. We predicted involvement of these regions because they are known to process visuospatial aspects of stimuli (Kravitz et al., 2011). Importantly, these areas show contralateral activity to unilaterally encoded (Kuo et al., 2012; Vogel and Machizawa, 2004) or attended visual information (Capilla et al., 2014; Händel et al., 2011), as well as during retrieval of spatially lateralized stimuli in working memory (Medendorp et al., 2005; Sereno et al., 2001; Van Der Werf et al., 2013) and long-term memory tasks (Takashima et al., 2007). Thus, lateralized parieto-occipital spindle responses to hemifield-related odor cues would support the hypothesis that spindles reflect the nature of reactivated representations.

Methods

Participants

This study was approved by the local ethics committee of the University of Amsterdam and all subjects provided written informed consent. Twenty-eight right-handed subjects (25 female, age: 20.1 [mean] \pm 2.3 [SD], range: 18–29 years) who reported no history of psychiatric or neurological disorders participated in the study. All were good habitual sleepers and were asked to wake up no later than 8.30 AM on the day of participation. Furthermore, they reported not taking any psychoactive substances in the 24 h before the experiment, or more than one caffeine-containing beverage in the 6 h before participation. Participants were rewarded with either course credits or monetary compensation.

Procedure overview

Fig. 1A shows an overview of the experimental procedure. Subjects reported to the sleep laboratory at noon and filled out questionnaires regarding sleep habits and sleep on the prior night, before being prepared for EEG registration. Next, they performed a practice run of the memory task (see Supplementary methods). Participants were then fitted with a nasal cannula that was connected to an odor dispenser and were asked to perform an odor detection task. This task served to ensure that the odors used as reactivation cues were perceived by all subjects. Next, subjects performed the main memory task with odor stimulation and subsequent retrieval. During the ensuing two-hour sleep opportunity with high-density EEG registration, odor cueing of hemifield-biased associations was carried out in a between-subject fashion. That is, each sleeping subject was cued with only one of the odors presented during encoding. Upon waking, participants were allowed to recover from sleep inertia for about 45 min before starting the delayed memory retrieval session around 6 PM. The interval between the first and second retrieval sessions was kept constant at 3 h. Finally, an exit questionnaire probed issues regarding learning strategy, odor delivery and sleep cueing. Total duration of the experimental session was approximately 6.5 h. All tasks were presented using Presentation software (Neurobehavioral Systems, Albany, CA), while subjects were seated approximately 50 cm away from a 17" screen.

Odor delivery and detection

Four distinct odors were used during the encoding phase of the main task. Two milliliters of each of the single-molecule odorants ionone beta, silvial, tetrahydro linalool and undecavertol (Perfumer's Apprentice, Capitola, CA), was mixed with 1 ml odorless dipropylene glycol. A custom-built odor dispenser located outside the experimentation room forced air through one of five glass jars; four containing diluted odor and an empty one to keep total resistance constant when administering neutral air. Odors were delivered via ~5 m long polytetrafluoroethylene tubing to the nasal cannula worn by the subject. Participants quickly adapted to the constant, light air flow.

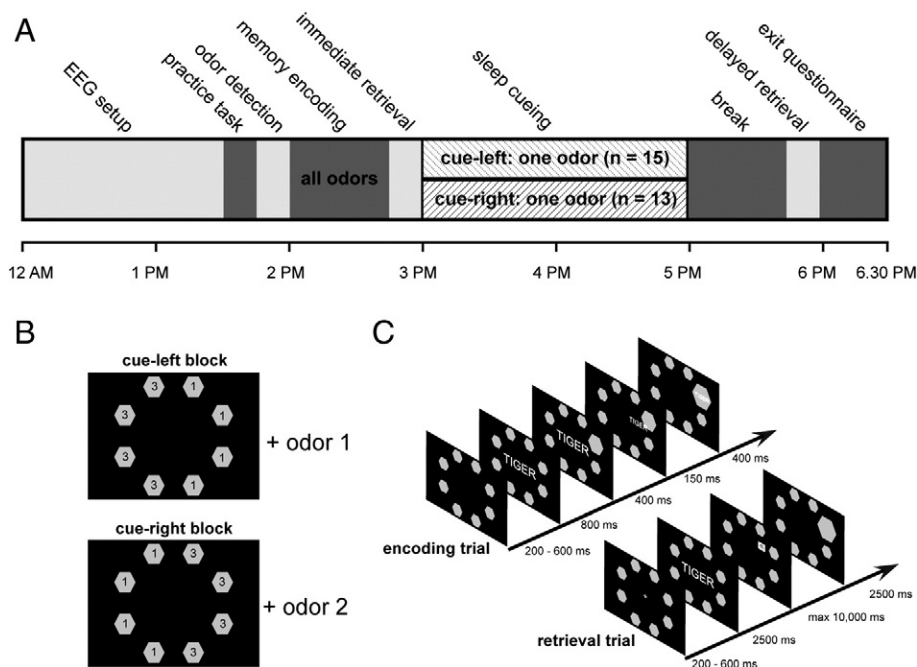


Fig. 1. Experimental procedure. (A) Timeline showing approximate timing of the various parts of the experimental procedure. (B) Schematic representation of word–location assignments for cue-left (top) and cue-right (bottom) word blocks. The numbers in each of the 8 locations indicate how many words were associated with that position. A block consisted of 16 words in total and was consistently paired with one odor. (C) Encoding (top) and retrieval (bottom) trial timing.

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