Sleep-mediated memory consolidation depends on the level of integration at encoding

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ABSTRACT

There is robust evidence that sleep facilitates declarative memory consolidation. Integration of newly acquired memories into existing neocortical knowledge networks has been proposed to underlie this effect. Here, we test whether sleep affects memory retention for word-picture associations differently when it was learned explicitly or using a fast mapping strategy. Fast mapping is an incidental form of learning that references new information to existing knowledge and possibly allows neocortical integration already during encoding. If the integration of information into neocortical networks is a main function of sleep-dependent memory consolidation, material learned via fast mapping should therefore benefit less from sleep. Supporting this idea, we find that sleep has a protective effect on explicitly learned associations. In contrast, memory for associations learned by fast mapping does not benefit from sleep and remains stable regardless of whether sleep or wakefulness follows learning. Our results thus indicate that the need for sleep-mediated consolidation depends on the strategy used for learning and might thus be related to the level of integration of newly acquired memory achieved during encoding.

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1. Introduction

Consolidation of declarative memories has frequently been shown to benefit from sleep. Sleep after learning results in better memory performance and increases resistance to interference compared to wakefulness (Diekelmann & Born, 2010; Dumay, 2016; Ellenbogen, Payne, & Stickgold, 2006; Gais, Lucas, & Born, 2006; Schönauer, Pawlizki, Kock, & Gais, 2014; Stickgold, 2013). The underlying mechanisms, however, are still not fully understood. A widely held model proposes that a main function of memory consolidation during sleep is an integration of newly learned information into existing long-term memory networks. This is supposed to generate neocortical representations of information that was initially encoded into the medial temporal lobe (MTL) (Gais & Born, 2004). In line with this idea, a number of experiments find that consolidation of hippocampus-dependent memory is supported by sleep (Albouy et al., 2013; Cai, Shuman, Gorman, Sage, & Anagnostaras, 2009; Inostroza, Binder, & Born, 2013; Marshall & Born, 2007; Robertson, Pascual-Leone, & Press, 2004; Schönauer, Gratsch, & Gais, 2015). A slow shift in neural representation from highly plastic MTL to more stable neocortical networks

can provide fast initial acquisition, a large capacity of long-lasting storage and safe integration of new information into previously acquired schemas without the risk of interfering with older memory traces (Dudai, Karni, & Born, 2015; Frankland & Bontempi, 2005; McClelland, McNaughton, & O'Reilly, 1995; Takashima et al., 2006). If the integration of new memories into existing neocortical networks is indeed one function of sleep, memory tasks that allow immediate neocortical integration already during encoding should benefit less from consolidation during sleep than memory tasks that do not promote immediate integration. This prediction has not yet been tested directly because only few declarative memory tasks allow neocortical integration already during encoding. One task that does, however, is Fast Mapping (FM).

FM is a learning method thought to underlie the rapid extension of vocabulary in children at young age (Bion, Borovsky, & Fernald, 2013; Bloom & Markson, 1998; Carey & Bartlett, 1978). Using systematic rejection mechanisms, a single mention of a new name in presence of an unknown object within a known context can suffice to learn this new association without the connection between object and word ever being explicitly and consciously established (Halberda, 2006). Sharon, Moscovitch, and Gilboa (2011) developed a paradigm that mirrors this process in a simplified way by presenting images of unknown animals, fruit and flowers to

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patients along with a known image and a question that mentions the name of the unknown object. Patients with severe hippocampal lesions are able to acquire declarative knowledge using FM despite showing memory impairments in explicit encoding (EE) tasks (Merhav, Karni, & Gilboa, 2014; Sharon et al., 2011; however, see Smith, Urgolites, Hopkins, & Squire, 2014; Warren, Tranel, & Duff, 2016). Functional imaging studies in healthy adults investigated neural contributions to FM learning and retrieval. They show that subsequent memory relies on a more widespread neocortical network during encoding using FM than using EE (Atir-Sharon, Gilboa, Hazan, Koilis, & Manevitz, 2015). Similarly, memory retrieval is supported by a larger neocortical network for FM memory than for EE memory, shortly after learning as well as on the following day (Merhav, Karni, & Gilboa, 2015). This extensive recruitment of neocortical areas early in the learning process suggests that new associations learned via FM are more rapidly integrated into known schemas than those learned by EE. FM has also been shown to lead to higher lexical integration of words than EE immediately after learning (Coutanche & Thompson-Schill, 2014). Lexical integration of newly learnt words has been demonstrated to benefit from sleep (Dumay & Gaskell, 2007; Tamminen, Payne, Stickgold, Wamsley, & Gaskell, 2010) and to coincide with shifts from hippocampal to neocortical memory representations (Davis, Di Betta, Macdonald, & Gaskell, 2009). This further strengthens the notion that FM provides a mechanism for rapid integration into preexisting networks that can be observed in both brain activity and behavior.

FM creates declarative, consciously retrievable memories after only few learning repetitions. This makes FM an ideal model to investigate whether the degree of neocortical integration at encoding can modulate the effect that sleep has on memory consolidation. In our experiment, two groups of participants used either EE or FM as a method for encoding an identical set of word-picture associations. We compared memory performance between FM and EE immediately after encoding as well as after intervals spent awake or asleep (see Fig. 1). If a main function of sleep is neocortical integration of previously learnt information, we hypothesize that sleep should be more beneficial for the retention of associations encoded by EE than by FM.

2. Material and methods

2.1. Participants and general procedure

All experimental procedures were approved by the ethics committee of the LMU Munich and were carried out according to the stated guidelines. 76 healthy young adults took part in the study and received monetary compensation. All participants gave written, informed consent before participating in the experiment. They were native German speakers, reported to be non-smokers, had no jetlag in the previous six weeks, and reported to take no medication other than oral contraceptives. All had a regular sleep schedule of 6–9 h. On the days of the experiment, participants were prohibited to consume caffeine. All subjects were randomly assigned to 1 of 4 groups: EE + wakefulness after learning, EE + sleep after learning, FM + wakefulness after learning, or FM + sleep after learning. A between-subjects approach was chosen for this study, as FM tasks are only performed by incidental learning as long as healthy participants are unaware that the task requires memorizing associations and can therefor only be applied once.

Because they napped during their wake interval, 2 subjects were excluded from all analysis (one from EE group, one from FM group). Additionally, participants who performed at chance level (33%) or worse in their immediate recall were excluded from all analyses (2 subjects, one from each FM group). This resulted in n = 72 participants (22 male, age: range = 18–32, m = 22.71, SD = 2.69), with 20 (7 male), 18 (5 male), 18 (4 male), and 16 (6 male) participants in the EE/wake, EE/sleep, FM/wake and FM/
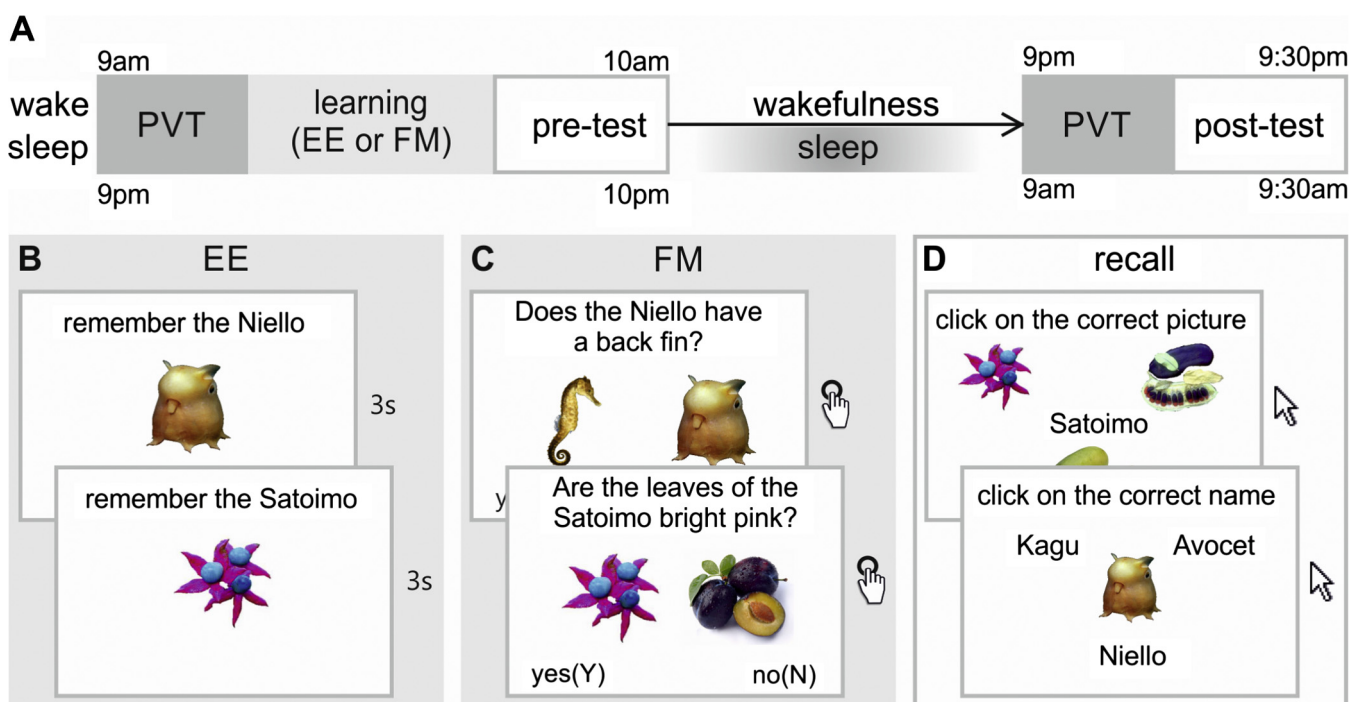
Fig. 1. General procedure, tasks and stimuli. (A) Participants visited the laboratory for two sessions and either slept or stayed awake during the intervening 11-h interval. Fatigue was assessed with the psychomotor vigilance performance task (PVT) and a questionnaire before memory tasks in both sessions. Learning by either fast mapping (FM) or explicit encoding (EE) took place during the first session. Memory performance was assessed in both sessions. (B) Example of EE learning trials with previously unknown targets. (C) Examples of FM trials with previously unknown target objects and comparable known objects. (D) Memory testing procedures for both EE and FM groups.