



Sleep and memory consolidation: Motor performance and proactive interference effects in sequence learning



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ABSTRACT

That post-training sleep supports the consolidation of sequential motor skills remains debated. Performance improvement and sensitivity to proactive interference are both putative measures of long-term memory consolidation. We tested sleep-dependent memory consolidation for visuo-motor sequence learning using a proactive interference paradigm. Thirty-three young adults were trained on sequence A on Day 1, then had Regular Sleep (RS) or were Sleep Deprived (SD) on the night after learning. After two recovery nights, they were tested on the same sequence A, then had to learn a novel, potentially competing sequence B. We hypothesized that proactive interference effects on sequence B due to the prior learning of sequence A would be higher in the RS condition, considering that proactive interference is an indirect marker of the robustness of sequence A, which should be better consolidated over post-training sleep. Results highlighted sleep-dependent improvement for sequence A, with faster RTs overnight for RS participants only. Moreover, the beneficial impact of sleep was specific to the consolidation of motor but not sequential skills. Proactive interference effects on learning a new material at Day 4 were similar between RS and SD participants. These results suggest that post-training sleep contributes to optimizing motor but not sequential components of performance in visuo-motor sequence learning.

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1. Introduction

Motor learning is at the root of many daily activities, requiring coordination between afferent multimodal stimulations and the production of appropriate efferent motor commands (Wolpert, Ghahramani, & Flanagan, 2001). Successful motor learning is a long-term process whereby a rapid improvement of performance is observed within the first trials, then followed by slower performance gains achieved through sustained repetition (Karni et al., 1998). Motor schemas progressively become more stable and resistant to interference with practice, disclosing a memory consolidation process (Krakauer & Shadmehr, 2006). Besides, motor memories continue to be consolidated after actual practice has ended, i.e. during so-called offline periods. In particular,

post-learning sleep might contribute to the consolidation of novel motor representations, eventually leading to performance stabilization or improvement (Stickgold & Walker, 2007). However, this assumption is disputed by studies suggesting that post-training sleep and wakefulness periods might equally benefit the consolidation of motor skills (Al-Sharman & Siengsukon, 2014; Nemeth et al., 2010; Song, Howard, & Howard, 2007), or alternatively that sleep-related improvements in motor memory consolidation might be due to confounding factors such as massive practice and circadian confounds (Rickard, Cai, Rieth, Jones, & Ard, 2008).

Delineating how and to what extent sleep contributes to consolidating novel motor representations is complicated by several factors. First, sleep might actually subtend stabilization or improvement of performance for specific components of motor memories, or in definite contexts of acquisition. Accordingly, sleep-related improvement or stabilization in performance has been repeatedly reported using a motor finger-tapping task (FTT) in which subjects continuously reproduce the same short sequence of five-finger movements (Albouy et al., 2013; Debas et al., 2010; Doyon et al., 2009; Wilhelm et al., 2011). Visuo-motor sequence

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learning tasks feature both progressive visual and motor adaptation to the settings of the task and the integration of sequential regularities embedded in the material (e.g. a repeated sequence of button presses corresponding to the stimuli's locations on a screen in the paradigmatic serial reaction time task [SRT; Nissen & Bullemer, 1987]). In these kind of tasks, sleep-dependent consolidation was reported for the goal-related, but not for the movement-related components of the learned sequences (Cohen, Pascual-Leone, Press, & Robertson, 2005) or when a cue indicates the presence of the sequence (Robertson, Pascual-Leone, & Press, 2004). In contrast, several studies found equal performance after sleep or wakefulness in sequence learning tasks when the succession of elements was embedded in noise (ASRT) or in probabilistic sequence learning paradigms, thus making sequence learning essentially implicit (Nemeth et al., 2010; Song et al., 2007). These latter results are in apparent contradiction with other studies having showed sleep-related performance changes (Cajochen et al., 2004), neuronal reactivation during post-learning sleep (Maquet et al., 2000; Peigneux et al., 2003) and sleep-dependent plasticity processes (Urbain et al., 2013) for implicitly learned sequences.

In a related domain, performance improvement on non-sequential motor learning tasks such as continuous tracking (Siengsukon & Al-sharman, 2011; but see Maquet, Schwartz, Passingham, & Frith, 2003) or motor adaptation to deviated trajectories was claimed to be non-sleep-dependent (Debas et al., 2010; Doyon et al., 2009). Alternatively, sleep was found to help to prevent a decrease of performance as compared to the end of learning (Albouy, Sterpenich, et al., 2013). Although these studies may suggest that post-training sleep is not beneficial for the consolidation of simple motor adaptation skills, high-density EEG data in adults disclosed a local increase in slow wave activity (SWA) during NREM sleep after task practice in learning-related areas, that was correlated with performance improvement (Huber, Ghilardi, Massimini, & Tononi, 2004). Also in children in whom it was claimed that sleep does not benefit procedural learning at all (Wilhelm, Diekelmann, & Born, 2008), sleep-dependent consolidation for the same motor adaptation task was exhibited looking at proactive interference effects (Urbain, Houyoux, Albouy, & Peigneux, 2014). In this latter study, although performance for the learned motor deviation was identical after an episode of sleep or of wakefulness, like in prior studies (Al-Sharman & Siengsukon, 2014; Siengsukon & Al-sharman, 2011), the presentation of the opposite motor deviation resulted in markedly higher proactive interference effects on performance in participants having slept after learning than in the wake condition. This suggests that the learned deviation was in fact more automatized after the post-training sleep episode, paradoxically resulting in more difficulties to adapt to a novel, opposite motor deviation (Urbain et al., 2014).

Hence, proactive interference effects may be useful markers of behavioral changes. Notwithstanding, only few studies have used interference (Korman et al., 2007; Urbain et al., 2014; Walker, Brakefield, & Hobson, 2003) or transfer (Witt, Margraf, Bieber, Born, & Deuschl, 2010) effects to index or modulate consolidation processes for simple motor tasks, and to the best of our knowledge none tested this effect in the context of visuomotor sequence learning. In the present study, we hypothesized that sleep-dependent memory consolidation processes in visuomotor sequence learning, and more specifically in a SRT paradigm, could be reflected through proactive interference effects. We surmised that even in a case when performance for the learned sequential material seemingly benefits to the same extent from post-training sleep and wakefulness, qualitative reorganization and structuration processes might benefit more from post-training sleep. This would eventually lead to an increased automatization of the learned sequence, which would be expressed by higher proactive interference effects when learning a novel material. In other terms, in line

with Schneider and Shiffrin's (1977) assumption that "once learned, an automatic process is difficult to suppress, to modify, or to ignore", consolidation of motor memories can be measured as a function of the extent to which a consolidated sequence "A" proactively interferes with the learning of a novel sequence "B" (Ghilardi, Moisello, Silvestri, Ghez, & Krakauer, 2009). To test this hypothesis, we administered a tactile adaptation of the deterministic Serial Reaction Time (SRT) task on two different days. On day 1, participants learned a sequence "A". Half of them had a normal night of sleep after learning, whereas the other half was deprived of sleep. After two recovery nights, all participants were first tested on the learned sequence, allowing for the measurement of potential sleep-dependent changes in motor and sequential components of the learned sequence. They had to learn a novel sequence "B", allowing for the testing of proactive interference effects due to the possible sleep-dependent consolidation of the previously learned sequence "A".

2. Methods

2.1. Participants

Thirty-three young healthy adults (28 women, 5 men; mean \pm SD age 21.8 ± 3.36 years) gave their written informed consent to participate in this study conducted in agreement with the Declaration of Helsinki and approved by the Faculty Ethics committee. No participant reported any history of neurological, psychiatric condition or sleeping disorder. Participants were randomly distributed in two groups. There were no significant differences for age ($p > .6$) or sex (Chi-square: .12, $p > .7$) between the two groups.

2.2. Experimental task (tactile SRT)

We used a tactile screen version of the deterministic serial reaction time (SRT) task initially developed by Nissen and Bullemer (1987). Participants were instructed to respond as quickly as possible to the appearance of a stimulus at one of the four screen locations (i.e. corners, see Fig. 1a), by pressing on the stimulus location using a finger of their dominant hand. The non-dominant hand was used irrespective of the participant's laterality because motor dexterity (i.e. precision and speed) is less developed with this hand than with the dominant hand (Francis & Spirduso, 2000), leaving more room for performance improvement. Unbeknownst to participants, the sequence of locations at which successive stimuli appeared was manipulated. A fixed 8-elements sequence was repeated throughout successive blocks of trials, except for one block during which the sequence followed a different order (see Procedure). In the SRT task, reaction time (RT) typically decreases with repeated presentation of a sequence, but presentation of a novel sequence (transfer) elicits slower RTs, indicating anticipation of the next elements in successive trials and successful learning of the trained sequence. Stimuli (i.e. the drawing of a car) were presented using the E-Prime software (Psychology Software Tools) on a computer screen (16 in.; refresh rate 60 Hz) adapted for tactile responses (Magic Touch Add-On Touch Screen, KeyTec, INC). Each stimulus lasted on screen upon subject's response for a maximum of 3000 ms, after which the next stimulus was displayed (response stimulus interval [RSI] 250 ms). Four different sequences were used in this experiment (see Procedure): learning sequences L1 (locations 4 2 1 3 2 4 3 1) and L2 (locations 1 3 4 2 3 1 2 4), reverses of each other (Schmitz, Pasquali, Cleeremans, & Peigneux, 2013) and transfer sequences T1 (locations 2 1 4 3 4 1 2 3) and T2 (locations 3 4 1 2 1 4 3 2). Each SRT block comprised 8 repetitions of the same sequence (i.e. 64 trials). To confirm correct understanding of

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