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Review article

Sleeping on the motor engram: The multifaceted nature of sleep-related motor memory consolidation

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ABSTRACT

For the past two decades, it has generally been accepted that sleep benefits motor memory consolidation processes. This notion, however, has been challenged by recent studies and thus the sleep and motor memory story is equivocal. Currently, and in contrast to the declarative memory domain, a comprehensive overview and synthesis of the effects of post-learning sleep on the behavioral and neural correlates of motor memory consolidation is not available. We therefore provide an extensive review of the literature in order to highlight that sleep-dependent motor memory consolidation depends upon multiple boundary conditions, including particular features of the motor task, the recruitment of relevant neural substrates (and the hippocampus in particular), as well as the specific architecture of the intervening sleep period (specifically, sleep spindle and slow wave activity). For our field to continue to advance, future research must consider the multifaceted nature of sleep-related motor memory consolidation.

1. Introduction

Sleep has long been thought to play a beneficial role in memory consolidation, the process by which newly acquired, relatively labile memories are transformed into enhanced and more stable memory traces [e.g., see (Diekelmann et al., 2009; Frankland and Bontempi, 2005; McClelland et al., 1995) for reviews]. Although the role of sleep in memory consolidation was traditionally associated with the declarative memory system, a plethora of studies has extended these findings into the procedural, and more specifically motor, memory domain [e.g., (Fischer et al., 2002; Karni et al., 1994; Maquet, 2000; Plihal and Born, 1997; Smith and MacNeill, 1994; Walker et al., 2003)]. The influence of post-learning sleep on both the behavioral and neural correlates of motor memory consolidation is the focus of the current review.

Motor learning is known to not only take place online (i.e., during task practice) but also offline (i.e., between training sessions) in the absence of any further practice (Karni et al., 1998, 1995). This offline period is thought to offer a privileged time window for motor memory consolidation to occur. It has been approximately 20 years since the earliest studies demonstrated that post-learning sleep benefited motor memory consolidation processes (Plihal and Born, 1997; Smith and MacNeill, 1994). Since these seminal experiments, research examining the relationship between sleep and motor memory consolidation has continued to increase. This beneficial effect of post-learning sleep has been frequently replicated in subsequent experiments; however, there have also been numerous studies demonstrating no such sleep-related enhancement. Moreover, examinations into the roles of REM and NREM sleep – and specific sleep features such as spindles and slow wave activity – on motor memory processing have also produced inconsistent findings. Thus, the sleep and motor memory story is currently equivocal. Accordingly, the overarching aim of this paper is to offer an exhaustive review of the effect of sleep on motor memory consolidation at both the behavioral and neural levels. A point of emphasis in this review is the multifaceted nature of sleep-dependent memory consolidation, as whether or not sleep affords performance benefits is heavily influenced by particular features of the motor task, the involvement of specific task-related neural substrates and post-training sleep characteristics.

Given that the effects of sleep on motor memory consolidation vary based on the motor task (see Inset 1 for a brief overview of the various motor learning paradigms), our review, when possible, will decompose the available literature based on the motor task examined. It is critical

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to emphasize that the vast majority of sleep and motor memory studies are based on variants of motor sequence learning paradigms and thus our review and primary conclusions reflect this lack of balance in the literature.

2. Influence of sleep on the behavioral correlates of motor memory consolidation

2.1. Does sleep enhance performance as compared to wakefulness?

In this section, we describe how sleep and wake periods after initial training on various motor learning tasks influence performance at delayed retests (see Inset 2 for a description of the different experimental designs). We only report the studies in which the effect of sleep was *statistically* compared to the effect observed in a matched-control wake group. Thus, assessing whether or not a sleep group exhibited performance enhancement or maintenance from the end of the initial training session to the post-sleep retest provides little valuable information (when not compared to an appropriate wake control group), as it has recently been argued that such within-group statistical comparisons are confounded by non-learning and −memory related factors such as the averaging of performance across multiple blocks, fatigue, etc. [see (Adi-Japha and Karni, 2016; Pan and Rickard, 2015; Rickard and Pan, 2017) for detailed discussion of these issues]. Consequently, *sleep-enhanced consolidation* here refers to an advantage in performance (i.e., either enhancement or maintenance) or by a reduction in the susceptibility to interfering experiences (i.e., stabilization; see Section 2.2.2) after a period of sleep as compared to an equivalent period of wakefulness.

Please note that the purpose of this first section is simply to provide a systematic review of the effect of sleep, as compared to wakefulness, on subsequent motor behavior and thus predominantly discusses the literature in terms of whether or not a sleep-related benefit was demonstrated (i.e., a binary decomposition). This initial section is vital for readers to assess the state of the sleep and motor memory literature before proceeding to the more integrated perspectives presented in subsequent sections.

2.1.1. Motor sequence learning

It has been proposed that consolidation processes differ based on the awareness of the sequential material to learn (Robertson et al., 2004b); thus, we will review findings separately for explicit and implicit motor sequence learning (MSL) tasks.

2.1.1.1. Explicit motor sequence learning. A beneficial effect of sleep as compared to wakefulness on motor performance has predominantly been observed for explicit finger sequence learning tasks (Debas et al., 2010; Doyon et al., 2009b; Fischer et al., 2005, 2002; Fischer and Born, 2009; Gregory et al., 2014; Korman et al., 2003; Nettersheim et al., 2015; Nishida and Walker, 2007; Rickard et al., 2008; Robertson et al., 2004b; Schönauer et al., 2015, 2014; Siengsukon and Al-Sharman, 2011; Spencer et al., 2007; Tucker et al., 2016; Wilson et al., 2012). A similar beneficial effect of sleep was also observed for grosser explicit MSL involving sequential movements of the hand (Kvint et al., 2011), the arms (Kempler and Richmond, 2012; Malangré et al., 2014) as well as the whole body (Genzel et al., 2012b). This positive impact of sleep on motor sequence memory consolidation was demonstrated with a variety of tasks (i.e., finger tapping tasks, finger opposition tasks, serial reaction time tasks) and experimental designs, including diurnal and nocturnal sleep (as compared to matched wake control groups).

It should be emphasized that a smaller number of studies using finger (Albouy et al., 2013c; Backhaus et al., 2016; Cai and Rickard, 2009; Genzel et al., 2015; Landry et al., 2016; Schönauer et al., 2014) as well as grosser [i.e., arm movements; (Gudberg et al., 2015)] explicit MSL tasks did not replicate such a beneficial effect of sleep on consolidation processes. Among the cited studies, it has been argued that this lack of an effect could be attributed to subsequent sleep episodes occurring between the sleep/wake manipulation and the retest [i.e., 2 post-sleep-deprivation recovery nights before retest; (Albouy et al., 2013c)], the time window during which sleep occurs after learning [(Cai and Rickard, 2009), but see Section 2.2.1 below], the duration of the sleep episode [i.e., 3 h vs. 8 h; (Schönauer et al., 2014)] or the intake of oral contraception (Genzel et al., 2015). Collectively, however, the majority of studies on explicit sequence learning including both fine and grosser tasks show a positive effect of sleep on consolidation processes as compared to wakefulness.

2.1.1.2. Implicit motor sequence learning. The picture is less clear regarding implicit motor sequence learning. While some studies report a beneficial effect of sleep on consolidation processes (Albouy et al., 2006; Ertelt et al., 2012; Spencer et al., 2007, 2006), others show no differential influence of sleep and wake on changes in motor sequence performance (Borragán et al., 2015; Nemeth et al., 2010; Robertson et al., 2004b; Song et al., 2007; Urbain et al., 2013). It is worth noting however, that studies showing positive effects of sleep on implicit motor sequence memory consolidation often used specific versions of the serial reaction time task including: (a) a greater spatial component in which the sequence of ocular movements followed a pattern of spatial locations in two dimensions (Albouy et al., 2006); (b) a contextual dimension where a sequence of color-cued movements was presented in the context of a sequence of spatial locations (Spencer et al., 2007, 2006); or, (c) a modulation of the declarative component of learning, as participants simultaneously completed a declarative word pair association and sequence learning tasks (Ertelt et al., 2012). Interestingly, these three aspects are thought to trigger sleep-related consolidation processes due to their dependency on the hippocampal system (see Sections 2.2.5 and 3.1.3). Based on these latter results, it appears that sleep-dependent consolidation can be observed for implicit motor sequence learning for specific task variants (but see Section 3.1 for additional discussion of this issue). Thus, certain features of the task, rather than solely the traditional explicit vs. implicit dissociation appear to influence the contribution of sleep in motor memory consolidation processes. The remaining sections in this review will predominantly collapse across implicit and explicit sequence learning paradigms; but, for the sake of completeness, we will note the type of task employed.

2.1.2. Motor adaptation

The seminal paper by Plihal and Born (1997) was one of the first to demonstrate that sleep following an initial session of a motor adaptation (MA) task (mirror tracing) increased performance in a subsequent retest. Moreover, their results indicated that this effect was specific to sleep towards the end of a night, which consists of a higher proportion of REM as compared to NREM sleep (see Inset 3). Since this first formative study, the beneficial effect of sleep on MA consolidation has been replicated on multiple occasions with different task variations and experimental designs (Albouy et al., 2013d; Backhaus and Junghanns, 2006; Huber et al., 2004; Javadi et al., 2011; Mantua et al., 2015; Schönauer et al., 2015; Seeck-Hirschner et al., 2010). However, and analogous to implicit motor sequence learning, sleep-dependent enhancements following MA have not been consistently replicated as multiple studies reported no differences between sleep and wake control groups (Backhaus et al., 2016; Debas et al., 2010; Donchin et al., 2002; Doyon et al., 2009b; Tucker et al., 2006).

It is worth mentioning that the majority of previous research that has employed a mirror tracing task has indeed demonstrated sleep-dependent performance enhancements [(Backhaus and Junghanns, 2006; Javadi et al., 2011; Mantua et al., 2015; Plihal and Born, 1997; Schönauer et al., 2015; Seeck-Hirschner et al., 2010); but see (Tucker et al., 2006) for no effect of sleep]. As the mirror completely flips the available visual information and adults typically have ample prior experience in their daily lives with mirrors, performance may depend,