

## How Sleep Enhances Motor Learning – a Review

by

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*There is a fast growing body of research in the area of neuropsychology and the behavioral sciences addressing consolidation and optimization of internal representation in the course of motor learning. Only recently it has been shown that, after initial learning, elapse of time preserves, but sleep enhances performance in procedural motor skills. In this paper, we review the most recent findings on the relation of specific sleep stages, associated brain activity, and sleep-related improvements in performance. Here, different activity states seem to correspond to different learning stages. It is argued that certain sleep associated processes could enhance local neural connectivity and thereby re-structure (motor) memory representations in a more proficient way as compared to their state at the end of (initial) skill acquisition on the day before. We will also discuss the impact of expertise level on sleep associated processes of memory optimization. We will conclude in highlighting some promising methodological approaches in the analysis of motor learning and REM sleep intensity.*

**Key words:** *sleep, sleep stages, motor skills*

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## ***Introduction***

For more than a decade it has been known that elapse of time is required for consolidating of a newly acquired motor skill (Brashers-Krug, Shadmehr, & Bizzi, 1996). If another, similar skill is practiced during this consolidation period, on the next day retention of the skill learned at first will be degraded. Such retroactive interference can be avoided only if the two skills learned in close succession are free of any conflicting control requirements. Thus, after initial learning, a rest period (wake) of 5,5 h at minimum seems to be essential for stabilizing the central nervous representation of the respective motor skill, or, in terms of Jordan (1994), its “internal model”.

Consolidation, however, is only one of the salient components affecting motor memory formation in the course of motor learning: While time *preserves* motor memory and prevents performance from deteriorating, *sleep* following physical practice and memory consolidation repeatedly has been shown to result in additional *enhancements* of performance (cf. e.g. Plihal & Born, 1997; Walker, 2005).

Altogether these findings on consolidation and sleep-associated enhancement of movement representations make understandable the fact that motor learning procedures render better results when practice is spread over several days or even weeks (Shea, Lai, Black, & Park, 2001). Particularly recall considerably improves after retention intervals ranging from one day to several weeks. Essential to this is always to distribute practice trials over several days; as opposed to this the sheer amount of practice is of minor importance (Baddeley & Longman, 1978; Savion-Lemieux & Penhne, 2005).

These sleep-associated enhancements in motor learning, however, cannot be attributed to the experience of sleep as such, but are obviously associated with specific processes confined to certain sleep stages a person passes through repeatedly in the course of a night. In the following sections of this paper, we will discuss the relation of sleep stages and motor memory formation in greater detail.

## ***Sleep improves motor performance***

Five sleep stages are distinguished physiologically as well as functionally (see table 1). Certain biochemical processes in the central nervous system associated with REM sleep and stage 2 sleep during the second half of the night support efficacy and consolidation of newly established neural connections. With respect to motor learning, these processes seem to be of predominant importance, since sleep associated enhancements in performance have been

proved to be proportional to the time spent in REM sleep altogether (Fischer, Hallschmidt, Elsner, & Born, 2002), and (particularly during the last quarter of the night) in stage 2 sleep of NREM sleep (Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002; Walker, Brakefield, Seidmann et al., 2003).

**Table 1**

*Sleep state characteristics (modified, from Smith, Aubreys, & Peters, 2004).*

Sleep-State	EEG-Activity	EOG-Activity	EMG-Activity	Biochemistry	
				Aminergic	Cholinergic
<i>Stage 1</i> (about 5 % of night of sleep)	Alpha-frequencies give way to 7-9 Hz.	Slow rolling eye movements	Muscle tension reduced compared to waking	Low	Low
<i>Stage 2</i> (about 50 % of night of sleep)	5-8 Hz theta-activity, interrupted by low-frequent K-complexes & 12-14 Hz Spindles.	No eye movements	Muscle tension more reduced than in Stage 1	Low	Low
<i>Stages 3 &amp; 4</i> (about 20 % of night of sleep)	3-5 Hz activity; Stage 3, if 20% of epoch in delta (0,5-3 Hz); Stage 4, if at least 50% of epoch in delta.	No eye movements	Muscle tension more reduced than in Stage 2	Low	Very low
<i>REM</i> (comprises 20-25 % of night of sleep)	7-9 Hz activity.	Rapid eye movements	Complete atonia of large muscle groups except for small phasic twitches of the extremities	Very low	Very high

While most of the studies addressing sleep-related improvements in motor learning so far incorporated mirror drawing, or continuously repeated finger movement sequences as criterion tasks, Buchegger, Fritsch, Meier-Koll and Riehle (1991) also found a proportional increase in REM sleep after initial learning of a discrete, gross motor trampoline skill.

Noteworthy indeed are the proportions of sleep-dependent learning enhancements, when comparing performance at the end of acquisition to performance on a retention test twelve hours later after one night of sleep: With respect to speed and accuracy of finger movement sequences, Fischer et al.

(2002), for example, report improvements in performance of over 30 % following a night of sleep. And Walker and his associates consistently report on sleep induced enhancements between 12 % and 30 %. Moreover, these effects are strictly specific to the skill being practiced. I. e. they do not generalize, not even when identical movement segments have to be produced just in a different sequence, or when the movement pattern of a visual target on a computer screen that continuously has to be tracked with a curser is simply rotated by 90° (Fischer et al., 2002; Fischer, Nitschke, Melchert, Erdmann, & Born, 2005; Maquet, Schwartz, Passingham, & Frith, 2003; Walker, 2005).

Is a newly acquired finger movement sequence (sequence 1) consolidated over time and, after a night of sleep, shortly reproduced the next day during recall, and is another, similar finger movement sequence (sequence 2) learned immediately thereafter, then after one more night of sleep sequence 1 will suffer clear performance decrements (retrograde interference) (Walker, Brakefield, Hobson et al., 2003). Obviously, loading an already consolidated skill into motor short term memory temporarily renders the respective neuronal network “plastic” and labile, and requires its subsequent consolidation again.

Such a mechanism is definitely useful in that it allows for continuous re-organization and optimization of already learned motor skills in the context of current new experience. From a neuro-cybernetic perspective this could be interpreted as an opportunity for “up-dating” the internal model responsible for movement control. Thus in the course of motor learning consolidation and optimization of neuronal networks proceeds along four process levels, which differ in function, and which are characterized by specific phenomena (cf. table 2).

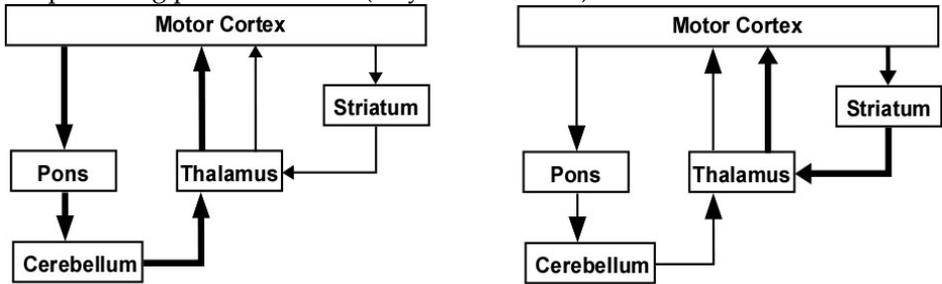
**Table 2**

*Process components of consolidation (mod. according to Walker, 2005). IM: Internal Model; STM: Short Term Memory; LTM: Long Term Memory.*

Phenomenon	Condition	Process
<b>Acquisition</b> (performance improves)	<b>Wake</b>	<b>Formation</b> of an IM in STM
<b>Stabilization</b> (performance is preserved)	<b>Time</b> (wake)	<b>Transfer</b> of IM into LTM
<b>Enhancement</b> (performance improves)	<b>Sleep</b> (REM-or stage-2 sleep)	<b>Modification</b> of IM in LTM
<b>Labilization</b> (performance improves or deteriorates)	<b>Wake</b> (recall)	<b>„Up-Dating“</b> of IM in STM

## *Sleep allows for learning-related changes of the brain's activity patterns*

In addition, fMRI-studies on the acquisition of finger movement sequences recently established evidence on sleep-dependent plastic changes in brain areas usually associated with initial learning (see figure 1): Early in learning, especially in the cerebellum activity shifts from cerebellar cortex to dentate nucleus, and, more generally, as amount of practice increases, from a cortico-cerebellar to a cortico-striatal network (Doyon, Song, Karni, Lalonde, Adams, & Ungerleider, 2002; Smith, Aubrey, & Peters, 2004). Later on, during sleep specific experience-related re-activations of this cortico-striatal network take place, which are proportional in their intensity to the level of performance reached at the end of the preceding practice session (Doyon et al., 2002).



**Fig. 1**

*Model relating certain sleep stages to different stages of motor learning (modified, from Smith et al., 2004). Left: When a task is completely new, mainly the cortico-cerebellar system is involved in “on-line” information processing during initial learning as well as in “off-line” information “re-processing” during REM sleep. Right: In already well accomplished tasks, mainly the cortico-striatal system is involved in the terminal “off-line” processing and storage of information in a persistent memory during stage 2 sleep.*

Also, sufficient sleep provided after initially learning a finger movement sequence, compared to initial acquisition a considerable decrease in neural activity has been reported in prefrontal, cingular, and premotor cortex, while at the same time activity in parietal cortex, and in the caudate nucleus (a part of the basal ganglia) increases. These changes, too, are associated with relevant performance enhancements, which incrementally add up over several nights of sleep without any further physical practice (Walker, Brakefield, Hobson, & Stickgold, 2003). None of these effects ensue after sleep deprivation. Moreover, sleep loss cannot be compensated by just “catching up” in sleep 24 h later. Instead, under such conditions reproduction of finger movement sequences is

accompanied by an additional increase in activity in prefrontal brain regions (Fischer et al., 2005). According to these authors' opinion, sleep induced reduction in central nervous activity levels generally are associated with decreasing conscious control, while sleep induced increases in neural activity levels are associated with an increasing incorporation of automatic movement control mechanisms.

Similar sleep and performance related changes in neural activity have also been reported in parameter learning, and in optimizing continuous, feedback-controlled visuo-motor skills. Here, too, sleep-dependent performance enhancements are accompanied by task-specific increases in activity in cortical areas (the supplementary motor area (SMA), and the upper temporal sulcus), in the cerebellum (dentate nucleus), and in the tissue connecting temporal sulcus and cerebellar nuclei. All these effects are stable for retention intervals of more than 48 h (Maquet, Schwartz et al., 2003).

### ***Sleep furthers enhancement of local neural connectivity***

The above mentioned changes in performance and neural activity clearly resemble sleep dependent modifications of internal models in motor long term memory. These modifications are brought forth by certain processes on different biological levels, namely electrophysiological, neurochemical, molecular, and cellular. These processes, too, can be attributed to different sleep stages. There they essentially contribute to changes in local neuronal connectivity, and thus to plastic changes in neural networks. During stage 2 sleep, for instance, in the thalamo-cortical network higher frequency oscillations of about 14 Hz (also referred to as "sleep spindles") can be evidenced. Their occurrence is thought to exert strong depolarizing effects in (motor) cortical areas. The resulting pronounced influxes of calcium ions into pyramidal cells could considerably increase long-term synaptic excitability (long term-potential, LTP) of these cells (Sejnowski & Destexhe, 2000; Steriade, 1999, 2001). Similar LTP-facilitating effects are attributed to so-called PGO-waves, which occur during REM sleep. These, too, are high frequency (300-500 Hz) bursts of synchronized neural activity in the midbrain (pons), in the Thalamus (geniculate nuclei), and in the occipital cortex (Datta, 2000).

There are also lower frequency oscillations during stage 3 and stage 4 sleep in the first half of the night. These, too, could contribute to sleep-dependent plasticity of neural networks which previously have been involved in initial learning, but they might do so in quite a different way: Such low-frequent activity bursts possibly induce synaptic de-potentialization (Benington & Frank, 2003; Kourrich & Chapman, 2003). This de-potentialization is based on sub-threshold

excitation of NMDA-receptors, a specific receptor category respondent to the neurotransmitter glutamate, which plays a key-role in changing connectivity patterns of neural networks (cf. Kandel, 2000). Thus this low-frequent brain activity could induce long-term depression (LTD). This would allow for a targeted resolution of superfluous and possibly impeding neuronal connections, which have been established before during active practice, and have been consolidated during a subsequent period of wake. As a result, only those connections absolutely necessary for efficient use would remain. Exactly these connections then during stage 2 sleep and REM sleep later on at night would be amenable to the LTP-facilitating processes mentioned above.

Discussed are also model conceptions regarding (REM)sleep-dependent activation of intracellular gene-expression (Igaz, Vianna, Medina, & Izquierdo, 2002; Ribeiro, Goyal, Mello, & Pavlides, 1999; Ribeiro, Mello, Velho, Gardner, Jarvis, & Pavlides, 2002), and (NREM)sleep-dependent intensification of cerebral protein synthesis (Frank, Issa, & Stryker, 2001; Nakanishi et al., 1997; Ramm & Smith, 1990). While gene-expression is responsible for rapid production and proliferation of synaptic molecules, protein synthesis is necessary for cellular plasticity (e. g. dendrite sprouting).

### ***Sleep-related processes in motor learning are specific to expertise level***

Moreover, the performance-enhancing contribution of the different sleep-stages seems to depend on the degree of novelty of the motor task, and on a person's learning history and level of expertise. When a task appears to be completely new and unfamiliar, until the basic task requirements are met by the learner predominantly processes associated to REM sleep are required. Further optimization (i. e. "fine-tuning") of the respective task, or acquisition of a skill similar to a previously learned one, do not require REM sleep any more, since the basic movement pattern in question already has been established. Any further improvements instead are linked to stage 2 sleep now, where they are specifically associated with the occurrence of high frequency "sleep spindles" (Peters, Smith, & Smith, 2007; Smith, Aubrey, & Peters, 2004). These findings go along with the fact that in simple structured, procedural motor skills (e. g. the pursuit rotor task) only stage 2 sleep-dependent performance enhancements are reported, while in movement tasks which, however learned implicitly, incorporate certain logical rules (e. g. mirror drawing), in the beginning REM sleep is of prime importance (Fogel, Smith, & Cote, 2007).

## ***REM sleep and initial motor learning – new avenues in research***

As has been pointed out in the previous paragraphs, in initial learning of motor tasks REM sleep appears to play a prominent role. Therefore it is not surprising to find many studies focused on the relationship between REM sleep and motor memory consolidation in humans. So far the reported experimental study designs did so by manipulating REM sleep after learning (e.g. REM sleep deprivation), by comparing time intervals with sleep to matched periods of wakefulness (e.g. day sleep and night sleep), or by correlating REM sleep parameters with improvements in task performance.

An alternative avenue in research here is to measure REM sleep after learning a motor task. This approach is especially promising because it circumvents the typical methodological problems coming along with REM sleep deprivation (e. g. disrupting the natural sleep pattern), comparison of sleep/wake intervals (e. g. circadian variations), and correlational studies (e. g. no experimental manipulation). Smith et al. (2004) reported enhancements in the amount or intensity of REM sleep in 14 out of 16 recording studies that utilized tasks of a procedural nature. While amount was operationalized as minutes spent in REM sleep, intensity was judged by number of eye movements per REM period.

Since the REM-augmenting effect so far has mainly been studied on procedural tasks, the experimental study of gross motor tasks (which can be more apt to the sport domain) should be very promising. Surprisingly, only one of the studies reviewed by Smith et al. (2004) investigated the effect of learning a complex sport activity (trampolining) on REM sleep (Buchegger et al., 1991). In this study sixteen subjects were randomly assigned to an experimental and a control group. The experimental group participated in a basic training course in trampolining whereas the control group practiced a well-known anaerobic sport (dancing or soccer) without motor learning. To ensure motor learning for the experimental group, subjects had to accomplish different skill levels (e.g., tuck-jump, piked-jump, straddle-jump, and somersaults). Progress of motor learning was quantified by an index of performance. Following each practice session, subjects' night sleep was recorded in a sleeping lab. Results showed a marked increase in REM sleep percent for the experimental group in contrast to the control group (from 21% to 30%).

Erlacher and Schredl (2006) tried to replicate these findings with a different motor skill, using a balanced within-design. The participants spent three consecutive nights in a sleeping lab (one adaptation night and two experimental nights). Prior to the experimental nights, subjects had either learned a new motor task (i. e. riding a Snakeboard), or engaged in a control task (i. e. ergometer

riding). In contrast Buchegger's findings, in this study learning the motor task exerted no effect on REM sleep parameters. However, re-analyzing the data revealed a correlational trend between learning rate and different sleep stages: Fast learners showed high correlations with sleep stage 2, whereas slow learners showed high correlations with REM sleep. The authors considered learning rate (fast vs. slow) to reflect different expertise levels, namely in that fast learners had had pre-experience in Snakeboard riding of some sort.

In a recent study by Erlacher, Schredl and Roth (in prep) the effects found in the Buchegger et al. (1991) study should be replicated using the original gross motor skill (trampoline). Again subjects were studied in a balanced within-design with three consecutive nights in a sleep laboratory. In this study only beginners in trampolining were included. This time results showed the expected differences in REM sleep percentage between the motor learning and the control condition, underlining once more the importance of expertise level and sleep stage dependencies. Thus, if sleep significantly contributes to the learning and consolidation processes of motor skills, then sleep following upon learning novel tasks should be of marked interest not only to scientists, but also to athletes in their professional training.

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