Sleep and Motor Skill Learning

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The improvement of a perceptual or motor skill continues after training has ended. The central question is whether this improvement is just a function of time or whether sleep, a certain circadian phase, or their interaction (sleep occurring in a particular circadian phase)isfavorabletothe reprocessingof recent memory traces.Inthis issue of *Neuron*, Walker et al. provide behavioral evidence that most of the improvement of a motor skill depends on nocturnal sleep.

Using the texture discrimination task described by Karni and Sagi (1991), it was previously shown that *perceptual* learning depends on sleep. This task has the interesting feature that the acquisition of the perceptual skill is thought to rely on plastic changes in the primary visual cortex. Learning this task is disrupted by total sleep deprivation (Stickgold et al., 2000) and by rapid-eye-movement (REM) sleep deprivation (Karni et al., 1994) during the first post-training night. In contrast, another recent study reports that subjects' performance significantly improves if they are allowed to sleep at least in the first part of the night (composed mainly of slow-wave sleep [SWS]) (Gais et al., 2000). Furthermore, their performance is optimal only after a complete night of sleep, i.e., after the succession of SWS in the first part of the night and REM sleep in the second part of the night (Gais et al., 2000).

Walker and collaborators (2002 [this issue of *Neuron*]) have now switched to *motor* skill learning. They chose a task in which the acquisition of the motor skill relies mainly on the plasticity of the primary motor cortex (Karni et al., 1995). In this sequential finger-tapping task, the subjects are requested to repeat the same five-element sequence as fast and as accurately as possible with the fingers of the non-dominant hand for 30 s. The performance is estimated as the number of times the subject can repeat the sequence within this time frame.

The authors trained different groups of subjects and retested the subjects up to 24 hr later. They cleverly manipulated the number of training sessions on a single day (group A), the arousal state during the delaybetween the training and testing sessions (12 hr of wakefulness or sleep, groups B and D), and the subjects' activity during the waking interval (group C). In doing so, they provided answers, at the behavioral level, to the following issues.

Does the Motor Skill of the Subjects Improve Just Because Time Passes By?

This question is at the center of the literature examining the role of sleep in memory. Various paradigms were used in different tasks to demonstrate the effects of sleep on recent memory traces (Maquet, 2001). For instance, total and partial sleep deprivation were shown to alter subsequent performance to both explicit and implicit memory tasks (Peigneux et al., 2001). Conversely, training subjects to various tasks could modify the structure of their subsequent sleep (Maquet, 2001; Peigneux et al., 2001). Walker et al. use still another experimental paradigm to provide evidence that the acquisition of motor skill is sleep dependent. They show that subjects trained either in the morning or in the evening demonstrate an improvement after a night of sleep. However, they show no such improvement after 12 hr of daytime wakefulness following either the first practice (for the group trained in the morning) or the overnight retest (for the group trained in the evening).

Do All Sleep Stages Matter?

The question remains open as to whether SWS or REM sleep or their succession throughout the night are necessary for memory consolidation. REM sleep could be particularly useful for implicit learning, while SWS could be more critical for explicit learning (Peigneux et al., 2001). In a fifth group, Walker etal. obtained polysomno-graphic recordings from the subjects during the post-training night. They show a significant positive regression between the subjects' performance and the amount of stage 2 sleep, especially late in the night.

Stage 2 is a newcomer in the discussion of the influence of sleep on memory. The role of stage 2 sleep in motor skill learning has originally been inferred indirectly. The performancein the pursuit rotor task, another procedural learning task, was shown to be insensitive to REM sleep deprivation but nevertheless to be sensitive to the deprivation of sleep in the second part of the night. This led to the conclusion that learning this task was sensitive to deprivation of stage 2 sleep (Smith and MacNeill, 1994). This hypothesis had never been confirmed, although preliminary data had already suggested that sleep spindles—an EEG pattern characteristic of this sleep stage—increase after training to several other procedural tasks (Fogel et al., 2001).

The experimental evidence of the influence of stage 2 sleep on the acquisition of motor skill has a special importance, given the recent proposal that spindles would promote cerebral plasticity (Sejnowski and Des-texhe, 2000). Spindle activity is associated with an important dendritic depolarization. This would cause a strong calcium influx into the pyramidal dendrites, triggering the activation of a cascade of intracellular processes and eventually leading to some permanent experience-dependent synaptic changes.

Is There a Circadian Modulation of Motor Skill Learning?

The circadianrhythmsbythemselves and independently of sleep processes might modulate neuronal function. While cognitive performance (Dijk et al., 1992) and the generation of sleep spindles (Dijk, 1999) have both been shown to be modulated in a circadian manner, it is still unknown if the same applies for memory processes.

Walker and collaborators argue that their experiment rules out the expression of learning after 12 hr of wake-fulness. First, the rate of learning was the same whether the subjects were trained in the morning or in the evening. Second, repeated testing across the day showed a linear improvement of performance, a finding interpreted as inconsistent with a circadian regulation. These arguments speak against a significant circadian effect upon the acquisition of motor skill during the training session. They do not rule out a circadian effect on consolidation during nighttime nor an interaction between circadian and sleep processes for consolidation processes. For instance, would sleep rhythms (especially spindles) have the same influenceonsubsequent performance after a daytime nap or in a condition of forced desynchrony between endogenous circadian rhythms and sleep/wake cycles?

In conclusion, the recent data confirm the impact of sleep on recent memory traces. They show that sleep has a favorable effect not only on perceptual but also on motor skill learning. They also stress the importance of stage 2 sleep in the processing of certain types of memory traces. Future research will have to characterize, at the cellular and systems levels, the mechanisms underlying these effects.

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