istered after a night of sleep, showed significant improvements. On the other hand, subjects trained in the evening already showed improvements in the first (morning) test, and no further improvements were demonstrated in the second (evening) test. This led Walker to conclude that a consolidation-based enhancement of performance, leading to a significant improvement, occurred only after a night of sleep. It is not fully clear to me, however, what exactly consolidation-based enhancement implies. Is there an experimental design, which can discriminate between predictions related to consolidation-based stabilisation and those related to consolidation-based enhancement?

Walker rejects the classical time-dependent second stage model of memory formation, but on what grounds? Putting aside that a circadian rhythm in performance cannot fully be excluded in the previously mentioned experiment, the good old interference theory also seems able to explain these results. Let me try to give a comparison: the role of sleep in food digestion. After food intake the process of digestion starts, independent of sleeping and waking. But sleep provides a more beneficial condition for digestion than waking. During waking, activity interferes with digestion, but during sleep bodily activity is restricted, providing a minimal interference, and the process of digestion is faster. The effect of sleep on this digestive process is variable: It depends on factors such as the kind and amount of food, the circadian time of eating, and the timing of sleep after food intake. In all, the effect of sleep on digestion is generally positive, but indirect and variable. In this way it is an interference theory, like the one which explains the positive effect of sleep on memory. Consolidation starts immediately after acquisition; it is a slow running process in which information is first stored in a labile trace, and then remodelled into a stabile memory trace. It seems unnecessary to accept that sleep has a direct and active role in memory stabilisation, simply because it creates a favourable condition for storage by preventing gross disturbances caused by newly incoming information. Retroactive interference is a main factor in inadequate memory formation and minimising interference might improve memory organisation. In this way the outcomes of the afore-mentioned experiments can also be explained.

Therefore, I do not see the necessity for a two-stage model to explain the positive effects of sleep on memory. The one-stage time-dependent model of memory formation, with fluctuating amounts of interference dependent on sleeping and waking, is simpler and, in my opinion, also able to explain the highly variable effects of sleep on memory, as described in the literature.

Motor memory: Consolidation-based enhancement effect revisited

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Abstract: Following Karni's seminal work, Walker and other researchers have recently provided gradually convincing evidence that sleep is critical for the consolidation-based enhancement (CBE) of motor sequence learning. Studies in our laboratory using a motor adaptation paradigm, however, show that CBE can also occur after the simple passage of time, suggesting that sleep effects on memory consolidation are task-related, and possibly dependent on anatomically dissociable circuits.

In this target article, Walker proposes a well-documented account of the role of sleep in both acquisition and consolidation phases of procedural memory formation. We applaud his effort to better define the nature of sleep's contribution to the consolidation of motor and perceptual learning by proposing a new model that separates this process into two stages: a consolidation-based stabilization (CBS) phase and a consolidation-based enhancement (CBE) phase. Although enlightening, we believe, however, that this model needs further refinement, especially with respect to the specificity of sleep on CBE effects in the motor domain and the possible functional neuroanatomical systems mediating this motor memory process.

First, using skill learning paradigms initially developed by Karni and colleagues (Karni & Sagi 1993; Karni et al. 1994; 1995; 1998), Walker, Stickgold, and other investigators have recently reported compelling evidence that sleep is indeed necessary after initial training to observe spontaneous gains (i.e., consolidation) in performance without additional practice on the same task (Fischer et al. 2002; Stickgold et al. 2000a; 2000b; Walker et al. 2002; 2003b). In the motor domain, for example, Walker and colleagues have elegantly demonstrated that CBE is elicited only after a period of sleep, and not after an equivalent period of time awake following the acquisition of a new sequence of finger movements (i.e., motor sequence learning). The results of a recent study in our laboratory suggest, however, that time alone is sufficient for observing CBE effects when testing for the consolidation of skills based on the capacity to compensate for environmental changes (i.e., motor adaptation) (Simard 2004). In the latter experiment, motor adaptation was measured using a version of the eight-target tracking task in which subjects were required to use a joystick to move a cursor from the center of a screen to one of eight targets following an elliptical trajectory within a time limit (see Fig. 1A). Target reaching on each trial was accomplished in a reversed mode, where the relation between movements with the joystick and direction of the cursor had been inverted. In a parametric experimental paradigm, three distinct groups ($n = 12$) of healthy volunteers were first given enough practice trials in the morning (i.e., 16 blocks of 16 trials each) to reach asymptotic performance within this training session. Without additional practice, subjects were then retested 5, 8, or 24 hours later to measure their level of performance gains on this task. Importantly, subjects in the 5-hour and 8-hour-delay conditions were told to refrain from taking a nap between the two testing sessions, while subjects in the 24-hour delay group were allowed a normal night of sleep. The results (see Fig. 1B) revealed that unlike subjects in the 5-hour delay group, those who were tested 8 hours later the same day, or 24 hours later the next day, showed a significant increase in performance between testing sessions. Furthermore, the level of between-session improvement on the task did not differ between these two groups, hence suggesting that the simple passage of time is sufficient to elicit spontaneous performance gains in a motor adaptation task, and therefore that sleep-dependent CBE effects are not universal, but task-dependent.

Second, although Walker describes potential physiological, neurochemical, molecular, and cellular mechanisms underlying the development of procedural memories, little is said about the neuroanatomical systems thought to support the different forms of motor learning (motor sequence, motor adaptation) discussed in this review paper, and about their possible role in mediating CBE effects in the motor domain. In such a model, Doyon and Ungerleider (2002; cf. Doyon et al. 2003) have recently proposed that both cortico-striatal (CS) and cortico-cerebellar (CC) systems contribute to motor learning and consolidation, and that representational changes within these two systems depend not only on the learning phase, but on the type of motor skilled behaviour acquired. In brief, this model suggests that in the fast (early) learning phase, both motor sequence and motor adaptation tasks recruit the CS and CC systems. When consolidation occurs, the subject has achieved asymptotic performance on the task, and this performance is then automatic. At this point, it is believed that the neural representation of a new motor skill is distributed in a network of structures involving the CS or CC circuit that depends on the type

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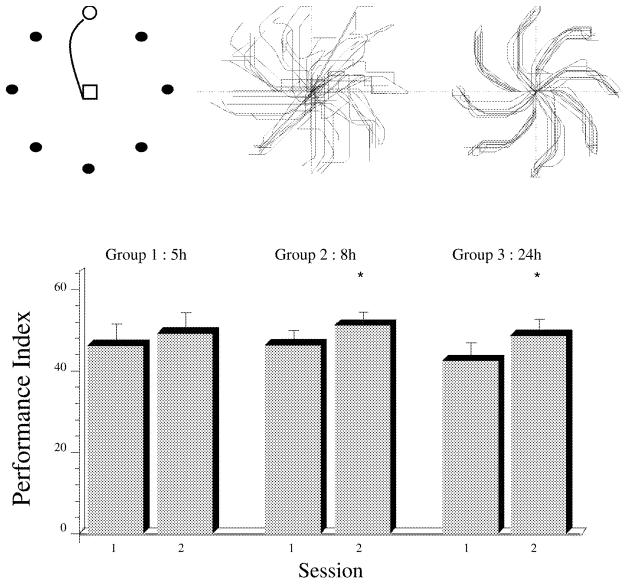


Figure 1 (Doyon et al.). Motor adaptation consolidation in normal control subjects: Method and results. Motor-adaptation learning: (A) Figure illustrates the motor- adaptation task, in which subjects are asked to reach one of the eight targets, following a curved line with a joystick in the inversed mode; that is, the x and y coordinates of the joystick had been reversed. (B) Early in training, movements of the cursor had significant deviations from the elliptical path. (C) Late in the training, movements of the cursor followed essentially a straight elliptical line. (D) Bar graph illustrating the results from Simard and colleagues (Simard 2004). Consolidation was operationally measured by comparing the subjects' performance on the last two blocks of trials in the training session to the second block of the retest session. Only subjects who were retested 8 and 24 hours after initial training revealed significant spontaneous performance gains ($p < .05$). These findings suggest that the simple passage of time is sufficient to observe significant consolidation of a motor adaptation skill, and that this physiological process may occur within a period of 5 to 8 hours after training.

of learning. Our model proposes that for motor adaptation, the striatum is no longer necessary for the retention and execution of the acquired skill; regions representing the skill are now thought to involve the cerebellum and related cortical regions. By contrast, a reverse pattern of plasticity is believed to occur in motor sequence learning, such that with extended practice the cerebellum is no longer essential, and the long-lasting retention of the skill is now believed to involve representational changes in the striatum and associated motor cortical regions. Most important for this commentary, however, this model also makes predictions about the neural systems mediating the consolidation of these two motor learning modalities. Indeed, based on previous imaging studies (Imamizu et al. 2000; Nezafat et al. 2001; Shadmehr & Holcomb 1997) that have shown that the cerebellum and its related structures are critical for the consolidation and long-term storage of a motor adaptation skill, one would expect that the striatum and its associated structures would play an equally important role in the consolidation of a newly-learned sequence of movements, as this structure contributes to the maintenance of this skilled behaviour over time (Doyon et al. 2002; 2003). Based on this model, one would also predict that sleep-dependent CBE effects observed in motor sequence learning would be associated with representational and cellular changes within the CS system, whereas the time-dependent CBE effects of motor adaptation described above would be mediated by similar changes in the CC system. To date, however, these hypotheses still remain conjectural.

In conclusion, although Walker's notion of CBE in motor learning is informative, it ought to be extended in order to explain that, depending on the type of motor skill acquired, sleep is not necessary for spontaneous performance gains to be observed, and that sleep-dependent and time-dependent CBE effects may be due to plasticity within different neural substrates.

Do words go to sleep? Exploring consolidation of spoken forms through direct and indirect measures

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Abstract: We address the notion of integration of new memory representations and the potential dependence of this phenomenon on sleep, in light of recent findings on the lexicalization of spoken words. A distinction is introduced between measures tapping directly into the strength of the newly acquired knowledge and indirect measures assessing the influence of this knowledge on spoken word identification.

Based on Walker's account, procedural memory and declarative memory seem to have little in common. The two domains would differ not only in their neural substrates and, potentially, the physiological processes underlying learning, but also by the nature of the stages that characterize memory consolidation. For most models of declarative memory (e.g., Buzsaki 1998; Eichenbaum 2000; Hasselmo 1999; McClelland et al. 1995; O'Reilly & Norman 2002), consolidation refers to the integration of newly acquired representations into long-term storage and expresses itself by the fact that decay of memory traces or interference (from another ongoing learning) can no longer be observed. In contrast, in Walker's model of procedural memory formation, integration with pre-existing knowledge is not part of the consolidation process per se; rather, it is an ancillary stage that may take place during or after stabilization or enhanced learning, which are seen as the crucial steps (see Fig. 2B [sect.2.3.2] and Fig. 5 [sect. 2.3.2.2] in the target article). Although procedural and declarative memory tap into different aspects of experience and use presumably different neural implementations, there remains the potential for an isomorphism in the stages of memory formation across the two domains. As Walker points out, little is known about the integration of procedural information, the importance of this stage, and its temporal relationship with respect to consolidation-based enhancement, which affects both perceptual (e.g., Karni et al. 1994) and motor skills (e.g., Brashers-Krug et al. 1996; Walker et al. 2002). In our view, the main reason for this state of affairs is that studies showing memory enhancement have typically used only direct measures of learning, thereby telling us about the strength of the newly acquired representations but not whether these representations would influence the access to more permanent ones. The goal of this commentary is to address the issue of integration, and the potential dependence of this phenomenon on sleep, on the basis of recent results obtained on lexicalization of spoken word forms (i.e., their integration into long-term lexical memory). Whilst the type of knowledge involved in word acquisition is initially declarative, the full lexicalization of this knowledge implies that the newly created representation should affect a well-established perceptual skill: identifying spoken words. Lexicalization of novel words, therefore, represents an ideal test case for bridging the gap between models of consolidation of declarative and procedural memory.

In models of spoken word identification, a key feature of a lexical entry is its ability to be evoked when compatible with the input, and to compete with similar-sounding entities for identifica-

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