

Awareness Modifies the Skill-Learning Benefits of Sleep

Edwin M. Robertson,^{1,*} Alvaro Pascual-Leone,^{1,2} and Daniel Z. Press¹

¹Laboratory for Magnetic Brain Stimulation
Behavioral Neurology Unit
Beth Israel Deaconess Medical Center
330 Brookline Avenue
Boston, Massachusetts 02215

²Institut Guttmann Hospital de Neurorehabilitaco
08916 Barcelona
Spain

Summary

Behind every skilled movement lies months of practice. However, practice alone is not responsible for the acquisition of all skill; performance can improve between, not just within, practice sessions. An important principle shaping these offline improvements may be an individual's awareness of learning a new skill. New skills, such as a sequence of finger movements, can be learned unintentionally (with little awareness for the sequence, implicit learning) or intentionally (explicit learning). We measured skill in an implicit and explicit sequence-learning task before and after a 12 hr interval. This interval either did (8 p.m. to 8 a.m.) or did not (8 a.m. to 8 p.m.) include a period of sleep. Following explicit sequence learning, offline skill improvements were only observed when the 12 hr interval included sleep. This overnight improvement was correlated with the amount of NREM sleep. The same improvement could also be observed in the evening (with an interval from 8 p.m. to 8 p.m.), so it was not coupled to retesting at a particular time of day and cannot therefore be attributed to circadian factors. In contrast, in the implicit learning task, offline learning was observed regardless of whether the 12 hr interval did or did not contain a period of sleep. However, these improvements were not observed with only a 15 min interval between sessions. Therefore, the practice available within each session cannot account for these skill improvements. Instead, sufficient time is necessary for offline learning to occur. These results show a behavioral dissociation, based upon an individual's awareness for having learned a sequence of finger movements. Offline learning is sleep dependent for explicit skills but time dependent for implicit skills.

Results and Discussion

We are all familiar with dedicating hours of practice to acquiring new skills. However, performance can improve between, not just within, practice sessions [1]. These "offline" improvements can require a few minutes to many waking hours to develop [1, 2], while on occasion sleep is required for their development [3–8]. Why

sleep is essential for some but not all offline improvements is unknown.

An individual's awareness of learning a new skill, such as a sequence of finger movements, has proven useful to understanding the acquisition of skill during practice [9, 10] and may also be an important factor in offline improvements. Learning new skills with practice can be accomplished unintentionally, with little awareness (implicit learning), or intentionally, with an individual's awareness (explicit learning). Any procedural task has an uncertain blend of both implicit and explicit components [11]. Nonetheless, the distinction between implicit and explicit learning has given important insights into the biological basis of skill acquisition during practice [12]. Here, we use a procedural task, in which awareness of learning a new sequence of finger movements can be manipulated, to determine whether the implicit-explicit distinction influences offline learning.

The serial reaction time task (SRTT) uses visual cues to guide the acquisition of a sequence of finger movements (Figure 1). A visual cue appears on a screen at one of four possible positions within a horizontal array. Each screen position corresponds to a button on a response box. A trial begins when a cue appears on the screen and ends once a subject has selected the appropriate response button. In this task, a series of sequential trials are immediately followed by random trials [13]. The difference in response time between sequential and random trials gives a sensitive and widely used measure of sequence skill learning (e.g., [13–15], Figure 1). Subjects can develop awareness of the underlying sequence either as a consequence of prolonged training [16] or by using a cue to signal the introduction of the sequence [17, 18]. This latter approach allows awareness to be manipulated independently of practice. Applying this strategy, we promoted explicit learning by informing a group of subjects that a change in the color of the visual cues would mark the introduction of a repeating sequence. In contrast, a second group of subjects were instructed that the SRTT was a four-choice reaction time test, the cues remained the same color throughout the trials, and the possibility of a sequence was never mentioned, giving implicit procedural learning. Subjects within these two groups, called the explicit and implicit groups, respectively, learned the same 12-item finger movement sequence. However, the different instructions promoted a relative difference in subjects' awareness for the sequence. Despite this difference, both implicit and explicit learning support improvements in skill and consequently fall within the domain of procedural learning [19].

Performance in the SRT task was measured prior to and following a 12 hr interval (Figure 1). The 12 hr interval either did (evening [8 p.m.] to morning [8 a.m.]) or did not (morning [8 a.m.] to evening [8 p.m.]) include sleep. With these two interval types (sleep or no-sleep) and the two modes of learning (explicit or implicit), there were four study groups: (1) sleep/explicit, (2) sleep/implicit, (3) no-sleep/explicit, and (4) no-sleep/implicit.

*Correspondence: emrobert@bidmc.harvard.edu

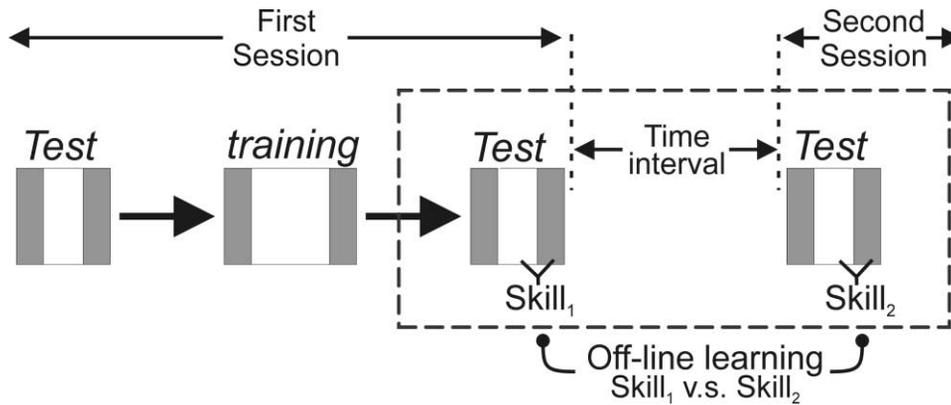


Figure 1. Experimental Design

The first session consisted of a single *training* block sandwiched between two *test* blocks. The second session consisted of a single *test* block. A 12 hr interval with or without sleep separated the sessions (8 p.m. to 8 a.m., or 8 a.m. to 8 p.m., Experiment 1). Alternatively, the sessions were separated by only 15 min (Experiment 2) or by 24 hr (8 p.m. to 8 p.m., Experiment 3). The development of skill over these intervals was measured by comparing the skill in the final test block of the first session ($Skill_1$) against the skill shown in the test block of the second session ($Skill_2$). When $Skill_2$ was significantly greater than $Skill_1$, offline learning had occurred. A standard measure of skill in this task is to calculate the difference between the response times of the sequential (white blocks) and the following random (gray blocks) trials [13, 14, 15].

A mixed repeated measures ANOVA explored offline skill improvements within and among these groups.

Immediately prior to the interval, there was no significant difference in skill (i.e., in $Skill_1$, Figure 1) across the four groups (ANOVA, $F(3,36) = 1.145$, $p = 0.344$). However, the change in skill over the 12 hr interval differed significantly across the groups (ANOVA, $F(3,36) = 3.50$, $p = 0.025$) with only a trend toward a change in the random response times (ANOVA, $F(3,36) = 2.25$, $p = 0.1$). Skill increased significantly between the sessions in both implicit groups (ANOVA, $F(1,18) = 17.112$, $p = 0.001$, an average increase of 45 ms, Figures 2 and 3), unaffected by whether the subjects had slept or not (ANOVA, $F(1,18) < 1$, $p = 0.391$). In contrast, for subjects

in the explicit groups, having slept or not made a substantial difference to offline learning (ANOVA, $F(1,18) = 5.73$, $p = 0.028$). Subjects in the sleep/explicit group showed a significant increase of skill over the 12 hr interval (ANOVA, $F(1,8) = 7.215$, $p = 0.025$, an increase of 35 ms, Figures 2 and 3) while those in the no-sleep/explicit group failed to show offline learning (ANOVA, $F(1,8) < 1$, $p = 0.458$). This contrast between the implicit and the explicit groups was preserved even when only the correct trials were included in the analysis. The overnight improvement, in the explicit group, showed a significant positive correlation with the duration of non-rapid eye movement (NREM) sleep ($R = 0.729$, $F = 9.1$, $p = 0.017$, Figure 4) and a negative correlation with the

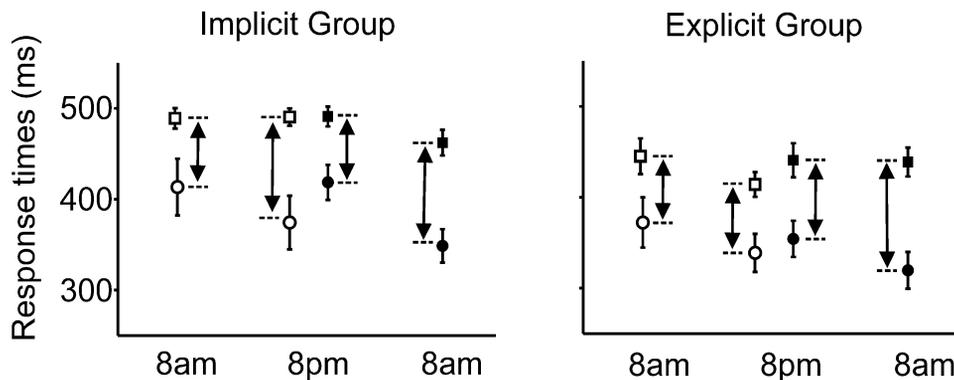


Figure 2. Mean Response Times in the Implicit and Explicit Groups

Skill was measured as the difference between sequential (circles) and random (boxes) response times. In the implicit group, this difference increased significantly when the 12 hr interval went from morning to evening (8 a.m. to 8 p.m., open symbols) and when it went from evening to morning (8 p.m. to 8 a.m., filled symbols). When participants were informed that they would be learning a sequence of finger movements (explicit group), this pattern changed: skill improvements were only observed overnight (8 p.m. to 8 a.m.), not over the day (8 a.m. to 8 p.m.). During the day (8 a.m. to 8 p.m.), there was a parallel decrease in both sequential and random response times. This parallel decrease may reflect a general improvement in task performance. Previous studies have noted that response times, even to random stimuli, decrease with practice (for example, [29]). Fatigue and the time of day also affect response times. Together, these influences can cause response times to rise or fall, making isolated response times difficult to interpret. The symbols (circles and boxes) show the mean response time and the associated whiskers the standard error.

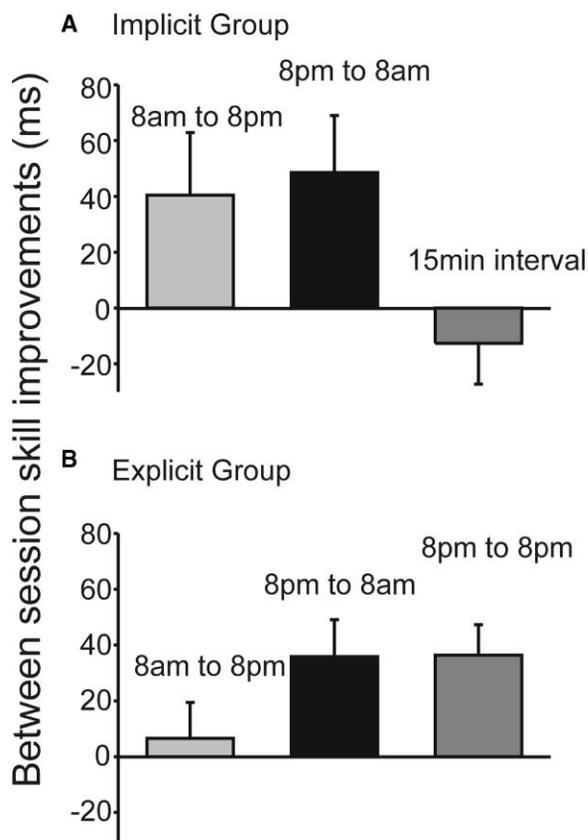


Figure 3. Time-Dependent and Sleep-Dependent Skill Improvements

Between-session skill improvements (with standard errors) are shown. Skill was measured before ($Skill_1$) and after ($Skill_2$) a variable interval (Figure 1). When the difference ($Skill_2 - Skill_1$) between these was significantly greater than zero, skill had been enhanced.

(A) When skill was acquired unintentionally (implicit learning), this enhancement was observed whether (8 p.m. to 8 a.m.) or not (8 a.m. to 8 p.m.) the 12 hr interval included a period of sleep. Accelerated learning during the second session may have been responsible for this ubiquitous improvement. This is not a sufficient explanation, because a 15 min interval between sessions was unable to support any skill improvement. The improvements observed over the 12 hr intervals reflect the offline development of skill.

(B) When skill was acquired intentionally (explicit learning), a substantially different pattern emerges. Skill enhancement was only observed when the 12 hr interval included (8 p.m. to 8 a.m.) a period of sleep. This improvement can still be observed in the evening (24 hr interval, 8 p.m. to 8 p.m.). These skill improvements appear to depend upon sleep, a notion consistent with the relationship these overnight improvements have with NREM sleep (Figure 4).

duration of REM sleep ($R = 0.715$, $F = 8.34$, $p = 0.02$, see Supplemental Data).

When interpreting these results, the effects of repeated practice, resolution of fatigue, and circadian influences need to be considered. Before and after the 12 hr interval, both explicit groups had the same amount of practice, but only the sleep/explicit group showed a skill improvement between sessions. Consequently, skill enhancement is not an inevitable consequence of repeated performance of the explicit task after a 12 hr interval. But repeated practice could be responsible for the skill improvements seen in both the implicit groups.

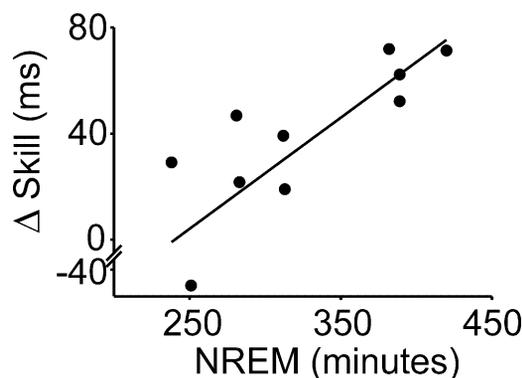


Figure 4. Overnight Skill Improvements and NREM Sleep

There was a correlation between the amount of NREM sleep and the overnight improvement of skill in an explicit sequence-learning task ($R = 0.729$, $F = 9.1$, $p = 0.017$). The solid line is a linear regression fit. Recent studies have also found a relationship between the amount of overnight skill improvement and the length of REM [7] and NREM sleep [8]. Both these sleep components may make an important contribution to enhancing skill [30, 31]; further studies are needed to explore this issue.

We tested the possibility that the second practice session might provide sufficient further practice in the implicit task to lead to a dramatic increase in skill. Eight subjects (Supplemental Experimental Procedures, Experiment 2) performed the implicit version of the SRT task but were tested with an interval between practice sessions of only 15 min. This short interval was not associated with an enhancement of skill between sessions (ANOVA, $F(1,6) < 1$, $p = 0.73$, Figure 3), despite the number of trials within the test blocks remaining the same as in the previous experiment when skill improvement had been observed. Repeated practice is therefore not a sufficient explanation for the between-session skill improvements observed in the implicit groups.

Fatigue is another potential confound that is largely eliminated by Experiment 2. Fatigue could accumulate during practice, masking the acquired skill. It could then dissipate with rest during the interval between sessions, and performance would improve [1]. However, we observed a negligible change in performance (Figure 3) over an interval of 15 min that is sufficient to dissipate fatigue in other procedural tasks [1]. Furthermore, our measure of skill, based upon the difference between response times for sequential and random trials, should not be affected by fatigue ([20], Figure 1).

We also considered whether circadian factors could offer a viable explanation for our results. However, circadian factors seem unlikely to have played a role. In the implicit groups, the same increase in skill was observed regardless of whether the 12 hr interval extended from morning to evening (8 a.m. to 8 p.m., an increase of 41 ms) or from evening to morning (8 p.m. to 8 a.m., an increase of 49 ms; ANOVA, $F(1,18) < 1$, $p = 0.391$, Figure 3). In the explicit groups, only one time of day (8 a.m.) was associated with skill enhancement. A follow-up experiment allowed circadian factors to be excluded as a possible explanation for our findings. We examined eight further subjects (Supplemental Experimental Procedures, Experiment 3) who performed the explicit ver-

sion of the SRT task, with a 24 hr interval between practice sessions (evening [8 p.m.] to evening [8 p.m.]). Despite the different time of day, we again observed a significant increase of skill over an interval (8 p.m. to 8 p.m.) that included sleep (ANOVA, $F(1,6) = 11.4$, $p = 0.012$, an increase of 36 ms, Figure 3). Therefore, the overnight improvement of skill is not coupled to retesting at a particular time of day.

In summary, we found that the development of skill without practice can be either time dependent or sleep dependent. Whether or not sleep was required for this between-session skill improvement was dependent upon the instructions given to the subjects. The different instructions were designed to manipulate a subject's awareness for the sequence. For the implicit group, the task was introduced as a choice reaction time test, while subjects allocated to the explicit group were told that there was an underlying sequence. We used both subjective and objective measures to test whether the instructions were able to manipulate a subject's awareness of the sequence [21].

First, subjects were given a free recall test to assess their awareness for the sequence at the end of the second session. If they thought there was an underlying sequence, subjects were asked to reproduce it as a sequence of finger movements. Recalling more than five items was defined as having achieved explicit awareness of the sequence, because five items is approximately the guessing rate of subjects exposed to random stimuli [15]. Members of the implicit group stated at most four items, with most (17 subjects) unable to recall any of the 12-item sequence. This low rate of recall, below that of even the average guessing rate, was because those with greater recall were removed from the implicit group to ensure that the remaining individuals had little or no awareness of the sequence. In contrast, seven subjects in the explicit group were able to recall all 12 items of the sequence (average of eight items, for the 20 subjects).

Second, we analyzed the response times to identify trials in which subjects may have anticipated the next visual cue. Explicit learning is marked by an ability to anticipate the next item of a sequence, and this is expressed as a reduction in response time to less than a visual reaction time (approximately 200 ms, [14]). During implicit learning, very few of the sequential response times (<2%) were shorter than 200 ms. In contrast, during explicit learning, 16% of the response times were faster than 200 ms. Neither this objective measure nor the free recall test provides a pure measure of explicit learning. The former is contaminated by guesses, and free recall has possible implicit contributions. This is a problem for many, if not all, tests of awareness [11].

Nonetheless, these measures confirm that subjects' awareness of the sequence differed across the implicit and explicit groups. This is not to suggest that subjects in the implicit group had no awareness of learning a sequence of finger movements, nor that those in the explicit group did not develop some implicit knowledge of the sequence. Few, if any, tasks have purely explicit or implicit characteristics [11], and behavioral and functional imaging studies provide evidence for the parallel development of implicit and explicit skills [15, 18]. Never-

theless, this has not prevented the dissociation of implicit and explicit learning [12, 17, 22–24]. In our study, a subtle change in the instructions given to participants modified their awareness of the underlying sequence and was sufficient to transform offline learning from being sleep independent to being sleep dependent.

The nature of this dissociation is surprising. Those who learned the task explicitly could mentally rehearse some or all of the known sequence during the day. Despite this opportunity, these participants only showed skill improvements following sleep. Participants who learned the task implicitly were not even aware that there was a skill to be mentally practiced. However, it was these individuals who showed offline learning during the day. This makes it unlikely that either covert practice or mental rehearsal could be responsible for the observed skill improvements [25].

Overnight improvements have been observed in other sequence-learning tasks [7, 8]. Participants in these studies were instructed to learn a short sequence of finger movements. In this respect, these tasks are comparable to our explicit sequence-learning task. From these studies and our own observations, a consistent picture emerges: when sequences of finger movements are learned intentionally, the development of further skill without practice is sleep dependent [7, 8]. These studies showed an 18% overnight improvement in performance, compared to the 38% we describe. This greater effect size may be attributable to differences in the task demands (only in the SRT task does a visual cue guide sequence learning) or to the sensitivity of the skill measure we used.

Other procedural tasks also show offline improvements that are sleep dependent [4, 26, 27]. In most of these cases, an individual is aware that the task involves acquiring a new skill and is aware of his or her improving performance. For example, in the rotary pursuit task, subjects intentionally improve their ability to maintain the position of a stylus on a rotating target and are aware of their enhanced skill. The intention to learn a new skill and the awareness of improved performance are features of an explicit procedural task. These tasks follow the principle that offline learning of explicit skills is sleep dependent [4, 26]. Nonetheless, within these explicit procedural tasks, there may also be significant implicit components. These components, for example in the rotary pursuit task, may account for the improved performance that also occurs over short intervals without sleep or further practice [1]. These improvements follow the principle that offline learning of implicit skills does not depend upon sleep. Nonetheless, sleep can make an important contribution to memories and skills acquired unintentionally [27].

Nor should there be any pretence that other offline processes adhere to these principles. For example, a memory trace for an explicit procedural task steadily becomes less susceptible to interference following practice, without the benefit of sleep [28]. This type of time dependent offline processing reduces the fragility of an explicit memory, but does not support offline skill improvements. The principles we describe relate only to offline learning, not to other types of offline processing that are responsible for stabilizing memories.

Conclusion

Here, we demonstrate that awareness is an important factor in offline learning. When an individual is aware of having learned a new skill, the development of further skill without practice is dependent upon sleep. This observation complements recent findings that short finger movement sequences learned intentionally are dependent upon sleep for offline learning [7, 8]. In contrast, when skills are learned with little awareness, offline learning occurs independently of sleep. This dissociation suggests that offline learning of implicit and explicit skills is supported by two distinct mechanisms: one time dependent and the other sleep dependent.

Supplemental Data

Supplemental Results and Experimental Procedures are available with this article online at <http://current-biology.com/cgi/content/full/14/3/208/DC1/>.

Acknowledgments

We thank Robert Stickgold for his helpful comments and for use of the Nightcap monitoring system. The National Alliance for Research in Schizophrenia and Depression (E.M.R.) and the National Institutes of Health (MH-65434, D.Z.P.) financially supported this study.

Received: October 13, 2003

Revised: December 9, 2003

Accepted: December 10, 2003

Published: February 3, 2004

References

1. Eysenk, H. (1965). A three-factor theory of reminiscence. *Br. J. Psychol.* **56**, 163–181.
2. Karni, A., and Sagi, D. (1993). The time course of learning a visual skill. *Nature* **365**, 250–252.
3. Karni, A., Tanne, D., Rubenstein, B.S., Askenasy, J.J., and Sagi, D. (1994). Dependence on REM sleep of overnight improvement of a perceptual skill. *Science* **265**, 679–682.
4. Smith, C., and MacNeill, C. (1994). Impaired motor memory for a pursuit rotor task following Stage 2 sleep loss in college students. *J. Sleep Res.* **3**, 206–213.
5. Maquet, P. (2001). The role of sleep in learning and memory. *Science* **294**, 1048–1052.
6. Stickgold, R., Hobson, J.A., Fosse, R., and Fosse, M. (2001). Sleep, learning, and dreams: off-line memory reprocessing. *Science* **294**, 1052–1057.
7. Fischer, S., Hallschmid, M., Elsner, A.L., and Born, J. (2002). Sleep forms memory for finger skills. *Proc. Natl. Acad. Sci. USA* **99**, 11987–11991.
8. Walker, M.P., Brakefield, T., Morgan, A., Hobson, J.A., and Stickgold, R. (2002). Practice with sleep makes perfect: sleep-dependent motor skill learning. *Neuron* **35**, 205–211.
9. Willingham, D. (1998). A neuropsychological theory of motor skill learning. *Psychol. Rev.* **105**, 558–584.
10. Willingham, D.B. (2001). Becoming aware of motor skill. *Trends Cogn. Sci.* **5**, 181–182.
11. Shanks, D.R., and St John, M.F. (1994). Characteristics of dissociable human learning systems. *Behav. Brain Sci.* **17**, 367–447.
12. Clegg, B., DiGirolamo, G.J., and Keele, S.W. (1998). Sequence learning. *Trends Cogn. Sci.* **2**, 275–281.
13. Nissen, M.J., and Bullemer, P. (1987). Attentional requirements of learning: evidence from performance measures. *Cognit. Psychol.* **19**, 1–32.
14. Willingham, D.B., Nissen, M.J., and Bullemer, P. (1989). On the development of procedural knowledge. *J. Exp. Psychol. Learn. Mem. Cogn.* **15**, 1047–1060.
15. Willingham, D., and Goedert-Eschmann, K. (1999). The relation between implicit and explicit learning: Evidence for parallel development. *Psychol. Sci.* **10**, 531–534.
16. Stadler, M.A. (1994). Explicit and implicit learning and maps of cortical motor output. *Science* **265**, 1600–1601.
17. Boyd, L.A., and Winstein, C.J. (2001). Implicit motor-sequence learning in humans following unilateral stroke: the impact of practice and explicit knowledge. *Neurosci. Lett.* **298**, 65–69.
18. Willingham, D.B., Salidis, J., and Gabrieli, J.D. (2002). Direct comparison of neural systems mediating conscious and unconscious skill learning. *J. Neurophysiol.* **88**, 1451–1460.
19. Sanes, J.N. (2003). Neocortical mechanisms in motor learning. *Curr. Opin. Neurobiol.* **13**, 225–231.
20. Heuer, H., Spijkers, W., Kiesswetter, E., and Schmidtke, V. (1998). Effects of sleep loss, time of day, and extended mental work on implicit and explicit learning of sequences. *J. Exp. Psychol. Appl.* **4**, 139–162.
21. Seidler, R.D., Purushotham, A., Kim, S.G., Ugurbil, K., Willingham, D., and Ashe, J. (2002). Cerebellum activation associated with performance change but not motor learning. *Science* **296**, 2043–2046.
22. Hazeltine, E., Grafton, S.T., and Ivry, R. (1997). Attention and stimulus characteristics determine the locus of motor-sequence encoding. A PET study. *Brain* **120**, 123–140.
23. Honda, M., Deiber, M.P., Ibanez, V., Pascual-Leone, A., Zhuang, P., and Hallett, M. (1998). Dynamic cortical involvement in implicit and explicit motor sequence learning. A PET study. *Brain* **121**, 2159–2173.
24. Dominey, P.F., Lelekov, T., Ventre-Dominey, J., and Jeannerod, M. (1998). Dissociable processes for learning the surface structure and abstract structure of sensorimotor sequences. *J. Cogn. Neurosci.* **10**, 734–751.
25. Lafleur, M.F., Jackson, P.L., Malouin, F., Richards, C.L., Evans, A.C., and Doyon, J. (2002). Motor learning produces parallel dynamic functional changes during the execution and imagination of sequential foot movements. *Neuroimage* **16**, 142–157.
26. Plihal, W., and Born, J. (1997). Effects of early and late nocturnal sleep on declarative and procedural memory. *J. Cogn. Neurosci.* **9**, 534–547.
27. Peigneux, P., Laureys, S., Fuchs, S., Destrebecqz, A., Collette, F., Delbeuck, X., Phillips, C., Aerts, J., Del Fiore, G., and Degueldre, C. (2003). Learned material content and acquisition level modulate cerebral reactivation during posttraining rapid-eye-movements sleep. *Neuroimage* **20**, 125–134.
28. Brashers-Krug, T., Shadmehr, R., and Bizzi, E. (1996). Consolidation in human motor memory. *Nature* **382**, 252–255.
29. Willingham, D., and Dumas, J.A. (1997). Long term retention of a motor skill: implicit sequence knowledge is not retained after a one-year delay. *Psychol. Res.* **60**, 113–119.
30. Giuditta, A., Ambrosini, M.V., Montagnese, P., Mandile, P., Cogtugno, M., Zucconi, G.G., and Vescia, S. (1995). The sequential hypothesis of the function of sleep. *Behav. Brain Res.* **69**, 157–166.
31. Gais, S., Plihal, W., Wagner, U., and Born, J. (2000). Early sleep triggers memory for early visual discrimination skills. *Nat. Neurosci.* **3**, 1335–1339.