Published in final edited form as:

Behav Brain Res. 2009 January 23; 196(2): 180–186. doi:10.1016/j.bbr.2008.09.034.

Consciousness and the Consolidation of Motor Learning

Sunbin Song

Interdisciplinary Program in Neuroscience, Department of Psychology, Georgetown University, Washington, DC, USA

Abstract

It is no secret that motor learning benefits from repetition. For example, pianists devote countless hours to performing complicated sequences of key presses, and golfers practice their swings thousands of times to reach a level of proficiency. Interestingly, the subsequent waking and sleeping hours after practice also play important roles in motor learning. During this time, a motor skill can consolidate into a more stable form that can lead to improved future performance without intervening practice. Though it is widely believed that sleep is crucial for this consolidation of motor learning, this is not generally true. In many instances only day-time consolidates motor learning, while in other instances neither day-time nor sleep consolidates learning. Recent studies have suggested that conscious awareness during motor training can determine whether sleep or day-time plays a role in consolidation. However, ongoing studies suggest that this explanation is also incomplete. In addition to conscious awareness, attention is an important factor to consider. This review discusses how attention and conscious awareness interact with day and night processes to consolidate a motor memory.

Index Words

Consciousness; Consolidation; Motor Learning; Procedural; Sleep; Off-line; Attention

Introduction

Learning and memory are directed to one output system: the motor system. Sensory inputs and cognitive decisions combine to direct appropriate motor behavior. With this in mind, a beginning student of psychology would be perplexed to discover that motor skill learning has been relegated as a subset of a subset (“procedural learning”) of a subset (“non-declarative learning”) in the standard classifications of memory (Figure 1A) [42]. Furthermore, he would see that non-declarative learning is defined not by what it is, but what it is not. It is not “declarative” memory which can be understood as conscious memory, as conscious awareness confers the ability to “declare” (i.e. give a subsequent verbal report of) the memory [42]. If this student were asked on an exam to use this traditional schema to classify a consciously learned motor skill such as an intentional series of button presses on a piano keyboard, how should he reply? If this student turned to an expert on motor learning for the answer to this question, he would receive an alternative classification schema that relied on a more intuitive (but poorly defined) concept of procedural motor learning which included both conscious and

Mailing Address: Dept. of Psychology, Georgetown University, 3700 O St NW, Washington DC 20057, Email Address: sss35@georgetown.edu, Phone Number: 202-687-4099, Fax Number: 202-687-6050.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

non-conscious processes (Figure 1B) [2; 29; 32]. All of this confusion would be irrespective of the difficulties this student would have in finding a definition for “consciousness” or “conscious awareness” [18].

This student is not alone in his confusion. Though it has become widely accepted that sleep consolidates procedural learning [48], few are certain as to what procedural learning actually refers to in this context. This is because, this sleep-dependent consolidation theory is based on a task in which subjects consciously learn a motor sequence. Hence, though this theory claims to use a traditional schema similar to Figure 1A, it actually uses a schema more along the lines of Figure 1B for its definition of procedural learning.

Consolidation in the context of this theory, also refers specifically to what is now termed “off-line enhancement” [32]. This sleep-dependent enhancement is seen as follows: After initial training, with an intervening night of sleep, subjects become additionally faster and more accurate at tapping sequences the next morning. For these consciously learned sequences, this practice-independent enhancement does not occur if the intervening 12 hours did not contain sleep [48]. Strangely, when conscious awareness of the sequence is removed from motor sequence learning such that sequence learning now occurs in a non-conscious manner, in addition to over-night improvement, off-line enhancement also occurs over the course of the waking day [30;32]. Further, when slight variations such as divided attention or complex sequence structure are added to the task, learning now demonstrates only day-time enhancement [5;6;39] or no offline enhancements of any kind [17].

Let us return now to the hapless student who was formerly faced with a trick question about procedural learning. This time, he receives a question on an exam which asks if sleep, day-time, both, or neither consolidates for procedural motor learning. After wracking his brain, he will discover he can give any answer and still find evidence to back up his claim.

Even to this beginning student, it is clear that previous models of procedural motor learning are inadequate to explain the current state of knowledge. Alternative schemas of motor learning which use dividing lines based on attention rather than conscious awareness may provide solutions to this predicament (Figure 1C) [22]. Issues of attention and conscious awareness and their relevance to various classification schemas for motor skill are discussed in the first of three sections which comprise this review. The second section suggests that sleep and day-time each mediate consolidation for attention-dependent learning but not for attention-independent learning. The third section discusses how conscious and non-conscious processes may or may not interact to affect motor consolidation.

I. Procedural and Declarative learning: The grey line of consciousness

Although conscious awareness divides declarative from procedural learning in the traditional classification of memory [42] (Figure 1A), the ability to assign learning to one of these two mutually exclusive categories is not always clear. This distinction is perhaps most perplexing when applied to movement. Before we try to define what a consciously learned motor skill is, let us even try to define what a consciously willed movement is. Evidence suggests that though we may experience the qualia of “voluntary” movement, the conscious wish to move is more of an afterthought of movement rather than the cause [18;25]. In 1983, Libet et al. conducted a now classic experiment in which subjects viewed a clock which had a spot moving rapidly around the face of it to demarcate the time. Subjects were told to move at will, and to record when they first experienced a conscious wish to move, and when they were aware they were actually moving. To check whether subjects were able to successfully time events, they were also stimulated at random times and told to record what time they felt a skin stimulus. Simultaneously, movement-related cortical potentials were recorded. It was found that subjects were able to successfully time events, and that the conscious wish to move preceded the

movement. However, the movement-related cortical potential preceded the conscious wish to move. Hence, the subject had non-consciously prepared to move before he had consciously willed it [25]. The qualia of “conscious will” was simply an illusion created by a brain which desired to attribute causation to correlation [49]. This dissociation between movement and the qualia of conscious intention is further exemplified by patients with psychogenic movement disorder. These patients make movements that have the neurological signatures of voluntary movements, but claim that these same movements are involuntary [18]. Nevertheless, studies show that conscious awareness of a sequence can alter the speed with which a series of movements can be made [50] and change how these movements are affected by consolidation [33]. Hence, one is faced with a paradox: conscious will in movement may be just an illusion, and yet conscious awareness of a sequence of movements clearly has a significant impact on movement behavior.

For these reasons, it appears somewhat of a lost cause to try to bin various types of motor learning based on conscious awareness. Nonetheless, attempts have been made to do so, due to the fact that historically, conscious awareness has been the official dividing line between the two main memory systems in the standard classification of memory (Figure 1A, [1]). Often more intuitive definitions of these two types of memory are used, one in which declarative memory refers to knowing “how to” while procedural memory refers to being “able to” [7].

The use of conscious awareness to classify memory arose out of work in amnesiacs like the famous patient H.M., who after bilateral removal of regions of the medial temporal lobe (MTL) was unable to form new conscious memories (declarative) but could still acquire new memories of which he was not conscious (non-declarative) [12;42]. Included in these preserved abilities, amnesiacs could acquire new motor skills and procedures through repetition (categorized as procedural skills). From this history, an anatomical understanding of declarative learning emerged in addition to the conscious/non-conscious distinction: declarative memories were those which relied on intact structures within the MTL [42]. Though initially, these two conceptualizations of declarative memory seemed largely synonymous, over the years, the behavior-based versus the anatomy-based definitions have proven to be increasingly tricky for experts. For example, it is impossible to define declarative learning in animal models for whom consciousness cannot be assessed [51], and difficult to define procedural learning in humans for learning which is non-conscious but relies on MTL structures [4]. Hence, in order to separate the anatomical definition inherent in the declarative/procedural terminology from the consciousness-based definition, experts turned to a different terminology (explicit/implicit). Explicit learning refers to conscious learning while implicit learning refers to non-conscious learning, and neither term is associated with anatomical correlates [31]. Historically, the understandings of implicit learning has also varied, including one definition based on inattentiveness, and another based on lack of intention [15]. The conceptualization used in this review, however, is the one in which “explicit” and “implicit” only refer to whether or not conscious awareness is present [31].

These two classes of terminologies (declarative/procedural and explicit/implicit) are important ones when trying to understand the vast literature on motor learning as each researcher has employed different definitions for these terms. The route many if not most researchers have taken is to classify all motor skills which are acquired through practice as examples of procedural skill regardless of conscious awareness (Figure 1B) [14; 21; 23; 26; 29; 43; 45; 46]. For example, in the finger tapping task, subjects tap out a known sequence such as “41324” repetitively. Healthy subjects get faster and more accurate over time in reproducing the sequence with motor practice. Amnesiacs such as H.M. do not show improvements in performance with practice, suggesting that MTL structures are necessary for learning during this task [10]. By the traditional schema, learning on this task should be placed under the

heading of declarative learning. However, it has been termed a procedural skill by most experts in motor learning [23; 46; 48].

Due to this difficulty in categorizing finger tapping as a procedural task, researchers have turned to an alternative motor sequencing task in which subjects are unaware of the sequence [33]. In the serial reaction time task (SRTT), subjects press buttons in response to spatial events (targets which appear in one of four locations on the screen) which follow a sequence. As sequence learning is stimulus driven rather than consciously driven, subjects can remain unaware of the sequence but still become faster and more accurate on blocks in which the event sequence is fixed as compared to random. Hence, sequence learning on the SRTT task can be non-conscious and more easily classified as procedural according to the traditional definition [28]. Even for the SRTT however, this procedural distinction is not absolute, as MTL structures can be involved in implicit sequence learning. For example, although amnesiacs show equivalent learning as controls on the SRTT, closer examination reveals subtle deficits when sequences have more complexity [8].

For this reason, the explicit/implicit terminology (which makes no reference to anatomical correlates) has proven more amenable for characterizing learning on these tasks. However, this has resulted in terms such as “explicit procedural learning” (Figure 1B) [2; 29; 32]. For a beginning student of psychology, using the traditional definition of procedural memory (Figure 1A), this is akin to saying “conscious non-conscious learning.” These terms makes sense only if one defines procedural learning as somewhat synonymous with motor skill learning (skills which have been acquired via repetition regardless of the extent of conscious awareness) – with conscious awareness being subsequently delineated by the explicit/implicit terminology (Figure 1B) [29].

One other option has been experiment-based models of motor sequence learning, which classify motor learning based on attention requirements (Figure 1C) [22]. In the particular model proposed by Keele et al. used in this review, conscious awareness is a secondary characteristic to define learning within attention-independent and attention-demanding networks. This model uses the explicit/implicit terminology to delineate conscious engagement while forgoing any mention of procedural/declarative terminology. Attention-demanding networks can be accessed by conscious awareness and hence, can support both implicit and explicit learning (Figure 1C). Using explicit knowledge of a sequence to drive motor behavior from the beginning of training as in the finger tapping task can also engage attention-demanding networks as it immediately brings attention to the movement. The attention-independent network can never be assessed or engaged by conscious awareness and hence learning in this stream is always implicit [22]. As will be reviewed in the next section, this latter experiment-based model can be used to decipher the otherwise confusing pattern of findings on motor memory consolidation.

II. Off-line consolidation of motor learning

In the literature, the term “consolidation” can have several meanings. Although in general, consolidation refers to the process by which a fragile memory acquired via practice or exposure is consolidated into a more permanent, stable, and long-term form [36], consolidation is thought to have several behavioral manifestations. For example, when it is found to occur in the hours post-practice, it is said to occur “off-line” [32]. One behavioral manifestation of off-line consolidation is an improvement in performance which is seen after a delay (*enhancement*) [32;48]. The first part of this section reviews studies which have used *off-line enhancement* as their definition for consolidation.

Another behavioral manifestation however is stabilization against retroactive interference [24]. Retroactive interference describes a case in which learning a second task after a first task

interferes with the retention for the first task. Two types of retroactive interference have been described. The first type interferes with the retention of the initially learned skill [17;27;36]. In other words, post-train performance on the initial skill is not maintained because of the interfering second task. Another type of retroactive interference interferes with enhancement only [23;34;45]. In other words, post-train performance on the initial skill is maintained, but the skill does not undergo the characteristic off-line enhancement otherwise seen because of the interfering second task. The passage of daytime and sleep have both been shown to stabilize learning from both types of retroactive interference [23;27;34;36;45] and this has been termed *off-line stabilization*. The second part of this section considers evidence from studies which use off-line stabilization as their definition for consolidation.

Motor consolidation as Off-line enhancement—For the finger tapping task earlier described where subjects tap out a known sequence repetitively, Karni et al. first suggested that learning consolidated post-practice [20]. Walker et al. subsequently demonstrated that off-line enhancement depended on a night of sleep [46]. This benefit was seen as an improvement in both reaction time and accuracy over-night while a comparable time awake led to no benefit [46]. Diurnal control subjects showed equivalent amounts of enhancement as those who were tested before and after a night of sleep. This suggested that circadian factors could not account for the effects seen. Sleep deprivation the night following training prevented the formation of any enhancement although subsequent nights of sleep continued to enhance the memory provided that the first night was not sleep deprived [14;47]. In one study, Stage-2 NREM sleep duration during late sleep correlated with off-line enhancement [46] although in another study of a similar design, a correlation with REM sleep was found [14]. Regardless, this body of work quite convincingly demonstrates that off-line enhancement for explicit motor sequence learning is dependent on certain sleep-stages.

Consolidation studies using the SRTT task display a different pattern of results. Robertson et al. found that when motor sequence learning was implicit, off-line enhancement occurred over the course of the day-time in addition to over-night [33]. In other words, significant improvements in performance were found after 12 hours during the day-time, or after 12 hours over-night. Another study found that this day-time enhancement increased with the passage of time [30]. In other words, if one hour passed between train and retest, no enhancement was found at retest. If 4 hours passed, significant enhancement is found. After 12 hours, even greater enhancement occurred. Hence, day-time enhancement is also time-dependent.

Though implicit sequence learning can undergo over-night and day-time gains, studies suggest that these gains are not generally time-dependent. Rather, over-night and day-time enhancements reflect two different processes. Behaviorally, Cohen et al. demonstrated that inter-manual transfer of the original sequence (based on an allocentric coordinate frame) only underwent over-night enhancement while inter-manual transfer of the mirror sequence (based on an egocentric coordinate frame) only underwent day-time enhancement. Using repetitive transcranial magnetic stimulation (rTMS), another study showed that disruption of the primary motor cortex (M1) immediately following training only disrupted day-time enhancement, but not over-night enhancement [34]. Still other motor sequencing studies find that over-night enhancement does not occur for sequence learning. In a study which used frequency-modulated (probabilistic) sequences instead of fixed sequences, sleep did not enhance sequence learning [39]. Significant daytime enhancement was found but for general motor skill rather than sequence-specific skill, as both high and low frequency sequences underwent equal day-time enhancement. Sleep had no effect on general skill. Experiments which use fixed sequences but divided attention also find no evidence for over-night enhancement. A secondary task during training such as tone counting is typically used to disrupt attention. In these studies, neither over-night nor over-day enhancements were found to occur for sequence learning [17;41].

These latter studies indicate how attention can modulate off-line enhancement. For fixed sequences, subjects often notice the presence of a pattern, even when they are unable to consciously recall it. Hence, attention to the sequence is piqued. A secondary task prevents such engagement of attention. For probabilistic sequences, the presence of sequences goes unnoticed even with extended training. Hence, it is likely that attention to the sequence is necessary for off-line enhancement of sequence learning to occur.

In sum, sleep-dependent enhancement occurs for explicit motor sequence learning and attentive implicit motor sequence learning in an M1-independent manner, but does not occur for non-attentive implicit motor sequence learning or for general skill (Figure 2). Day-time enhancement may also affect attention-demanding networks but in a different and more general manner. Day-time enhancement is not found for explicit motor sequence learning, but can occur for attentive implicit motor sequence learning. The role of day-time in explicit and implicit sequence learning is further discussed in Section 3. Day-time enhancement can also occur for general motor skill and depends on M1 post-training (Figure 2).

Another curious phenomenon has been reported in the literature which may provide some descriptive insight into sleep-dependent processes and that is, the spontaneous development of explicit awareness over a night of sleep. For example, in one study, subjects were instructed to solve math problems and unbeknownst to them, the answers followed a pattern. Time spent in sleep but not in wake was shown to lead to explicit awareness of the hidden pattern [44]. In another study by Fischer et al. using the SRTT task, sleep increased spontaneous explicit awareness of the implicitly acquired sequence [13]. As the attention-demanding learning network is accessible to conscious awareness, stronger associations within it could result in more explicit awareness of implicitly learned information.

Motor consolidation as Off-line stabilization—Off-line stabilization from interference has mainly been demonstrated in studies of dynamic visuomotor transformations. Dynamic transformation refers to the calculation of muscle forces necessary to complete a motion [37]. For example, through repeated exposure we learn to deftly make movements on earth but, suppose one is an astronaut. The absence of gravity would require a recalculation of the forces necessary to move an arm towards an object in a space station. With repeated exposure, this movement would also become natural. The average brain does this recalculation with relative ease, as demonstrated by studies which impose force-fields on a subject's arm. In these force-field learning tasks, subjects grip a robotic arm and move it towards a target. For some trials however, a velocity-dependent force-field is imposed on the robotic arm as it is moved and the trajectory of the subject's arm becomes skewed. Nonetheless, with practice, this skewed trajectory becomes straighter as the subject's arm starts to exert compensatory forces to adapt to the force-field (termed "dynamic adaptation"). When the force-field is removed at baseline, subjects show after-effects and have to "de-adapt" to return back to normal. Both adaptation and de-adaptation are indicative of learning. Amnesiacs including H.M. can learn during this task which suggests conscious awareness and MTL structures are not necessary for such learning [35].

Findings using dynamic adaptation show a pattern of day- and time-based, sleep-independent consolidation, MTL independent consolidation. Retention on dynamic adaptation tasks are measured by *savings* in learning, which is defined in terms of accelerated adaptation to the learned perturbation at a delay [24]. The pioneering studies in motor memory consolidation were conducted using this dynamic adaptation task. When force-field A and force-field B are learned in close succession, retroactive interference prevents savings for force-field A at a one week delayed retest but this retroactive interference lessens as the time between A and B is increased. This finding points to time-dependent stabilization [36]. Time-dependent stabilization of this skill also occurs in amnesiacs, suggesting that this day-time process occurs

via an MTL-independent mechanism [35]. Sleep deprivation has no effect on savings, which suggests that consolidation is sleep-independent [11]. In summary, for force-field adaptation, the passage of time over the day consolidates learning [36], with savings relying on a sleep-independent [11], and MTL-independent [35] process. Ballistic pinch force learning, which is also a kind of dynamic learning, displays a similar pattern. Retention is disrupted by rTMS to M1 immediately after training, but not if rTMS is delivered to M1 six hours after training [27]. The similarities between day-time enhancement for implicit motor sequencing tasks and day-time stabilization for dynamic transformation may indicate that both off-line enhancement and off-line stabilization can result from the same process, although this has not yet been proven. This similarity would be consistent with the interpretation that day-time can consolidate for general motor skills as well as for motor sequences (Figure 2).

Off-line stabilization studies in motor sequencing tasks have also been conducted. On the finger tapping task, retroactive interference on off-line enhancement has been reported to occur [23;45]. In other words, learning sequence B immediately after learning sequence A prevents sleep-dependent enhancement of A, although sequence B undergoes the usual sleep-dependent enhancement. If however, 6 hours separate training on sequences A and B, then both sequence A and sequence B undergo sleep-dependent enhancement [45]. Korman et al. further demonstrated that a one hour nap was as effective as the passage of several hours during the day-time for stabilizing learning on this task [23]. Though both day-time and sleep can stabilize learning from interference, this stabilization may be through different mechanisms [10]. For implicit sequence learning, rTMS to M1 post-train disrupts day-time enhancement, but not if two hours is allowed to pass between training and rTMS disruption suggesting that 2 hours is sufficient to stabilize learning from interference [34]. For implicit sequence learning under conditions of divided attention, no off-line enhancements are seen and retroactive interference disrupts retention [17]. Even with a delay of up to 24 hours in between sequence A and B, retention of sequence A is impaired by learning on sequence B. This finding suggests that for non-attentive sequence learning, waking-day and sleep both fail to stabilize from interference, whereas for attention-based sequence learning, both time over waking-day and sleep can stabilize from interference. This pattern of results is compatible with findings from enhancement studies (Figure 2).

III. Explicit/Implicit interactions in motor learning and performance

The discussion on the consolidation of motor memories can not be fully addressed without considering interactions between explicit and implicit systems at the time of performance, rather than during the learning process. This interaction may be a related issue to the role attention can play in engaging different brain systems during a task [22]. In a PET study, sequence learning was initially associated with activity in the premotor cortex (PMC) and the dorsolateral prefrontal cortex (dlPFC), but after extended practice, activity shifted to the supplementary motor area (SMA). However, if subjects were instructed to explicitly “think about their movements,” this led to an immediate return of activation in the dlPFC and reduction of activation in the SMA [19]. In another experiment, cortical mapping in M1 was assessed during implicit sequence learning on the SRTT. As reaction times fell, the M1 cortical output maps to the muscles involved in the task became progressively larger. However, when explicit knowledge of the sequence was achieved, these M1 maps returned to their baseline topography [29].

Behavioral studies show that while explicit/implicit systems compete to control performance, learning within these networks can occur in parallel [9;38;50]. In Willingham et al., “Intentional” learners were told that sequenced trials would always have red targets while randomly ordered trials would have black targets. Unbeknownst to them, some sequenced trials were given black targets – hence, these covertly hidden sequence trials could remove the

explicit driver to reveal the implicit one. “Incidental” learners saw the same stimuli but were not told to look for a sequence in the red targets. Though Intentional subjects showed greater sequencing ability on red sequence trials than Incidental subjects, on these hidden black sequence (Probe) trials, sequence learning between Intentional and Incidental subjects was identical. Difficulties in establishing the implicitness of fixed sequence learning motivated another experiment which used frequency-modulated probabilistic ones. Nonetheless, the same conclusion was reached in a study by Song et al. [38], which used Probe trials at various points during training. Hence, in both studies, the implicit system had been slowly logging in sequential information independent and simultaneous to the differential engagement of the explicit system, showing that both systems could operate in parallel.

Real life examples also argue for explicit/implicit competition at the time of performance, rather than during learning. For example, the real world is replete with examples of the most highly skilled and specialized implicit learners: professional athletes. Though at most times, the pace of sport prevents conscious engagement, other times, conscious attention can be paid to movements, particularly during times of high pressure. The most notable example is perhaps that of former Pittsburgh Pirates pitcher Steve Blass. Steve Blass who in 1972, led his team to win the World Series, in 1973, inexplicably stopped being able to pitch. This problem was entirely psychological in that as long as there was no batter in front of him, he could pitch just as well as pre-1973 [1]. A similar problem has plagued a number of other professional baseball players since, including Steve Sax, Chuck Knoblauch, and Rick Ankiel. Though there may be other explanations for such a phenomenon, many athletes will say that it comes from “thinking too much” [16]. As in the studies cited above, motor learning may initially rely on more explicit and prefrontal areas, but after extended practice and expertise, shift to more dorsal areas, but thinking about the movement can shift activity back to the less skilled explicit areas. Although many explanations may be derived, one could argue that these athletes show that even when years of practice has given the implicit system an exquisitely fine tuned memory for a movement, the explicit system can interfere at the time of performance and erase all evidence of implicit memory. Lab studies also give indication that explicit engagement can erase implicit memory from performance measures. For example, in one study, subjects were told to look for a pattern during observation-based training. The complexity of the pattern prevented explicit knowledge from being gained such that sequence learning remained implicit in all learners. Half the subjects were then told to stop looking for a pattern during performance when button presses were made for the same pattern as seen during training, while the other half were told to continue to look for a pattern. Only those who stopped looking for a pattern showed evidence of significant observation-based sequence learning [40]. This study demonstrates that continued explicit engagement is enough to disrupt the expression of implicit sequence learning during performance.

In the same way, explicit/implicit interactions at the time of performance may explain why day-time enhancement is not seen for explicit sequence learning and only for implicit sequence learning, even though explicit and implicit learning occurs in parallel [33;46]. One study found that when the explicit system was dis-engaged, daytime enhancement was “induced.” An unrelated declarative task (word-list learning) but not a simple vowel counting task, given right after training on the SRTT impaired spontaneous explicit knowledge, and thereby induced daytime enhancement [3]. Another study suggests this phenomenon is reflective of “unmasking” at the time of performance rather than an active process of induction. In this study, when color cues were present, Intentional subjects had full explicit knowledge of the sequence, but when they were removed in Probe trials, this explicit knowledge was also removed. Incidental learners had no explicit knowledge of the sequence at any point. For Probe trials, Intentional and Incidental learners displayed equal and significant day-time enhancement for general skill [38]. Though in this case, enhancement was for general skill, this study does

demonstrate that the processes of day-time enhancement are not impaired by explicit knowledge if such knowledge is not used to affect performance measures.

Conclusion

For most of us, consciousness takes little notice of the changes yesterday's memories have undergone. Day and night follow each other in seamless cycles, and each have played an important part in transforming yesterday's experiences into more permanent, stable, and enhanced forms. Whether or not we give these processes just recognition, as a pianist, golfer, tennis player, or even a scientist, we rely on them. Though motor skill learning has in the past been regarded in isolation, as a subset of procedural non-conscious learning, consider the pianist for whom the connections between vision, audition, and motor skill becomes increasingly fluid – until even a melody heard on the radio appears in the imagination as notes on a page and sensations of fingers moving across keys. Greater appreciation for the complexities of motor learning and for day and night consolidation processes may one day help improve treatment strategies after brain injury. Luckily, for these patients, and anyone who desires improved motor skills, an improved understanding of motor-memory consolidation is, perhaps, only a matter of time.

Acknowledgements

Support contributed by grant F31NS053388.

References

1. Angell, R. *Five Seasons: A Baseball Companion*. University of Nebraska Press; Lincoln, NE: 2004.
2. Born J, Wagner U. Awareness in memory: being explicit about the role of sleep. *Trends Cogn Sci* 2004;8:242–4. [PubMed: 15165544]
3. Brown RM, Robertson EM. Inducing motor skill improvements with a declarative task. *Nat Neurosci* 2007;10:148–9. [PubMed: 17237776]
4. Chun MM, Phelps EA. Memory deficits for implicit contextual information in amnesic subjects with hippocampal damage. *Nat Neurosci* 1999;2:844–7. [PubMed: 10461225]
5. Cohen DA, Pascual-Leone A, Press DZ, Robertson EM. Off-line learning of motor skill memory: a double dissociation of goal and movement. *Proc Natl Acad Sci U S A* 2005;102:18237–41. [PubMed: 16330773]
6. Cohen DA, Robertson EM. Motor sequence consolidation: constrained by critical time windows or competing components. *Exp Brain Res*. 2006
7. Cohen NJ, Squire LR. Preserved Learning and Retention of Pattern-Analyzing Skill in Amnesia: Dissociation of Knowing How and Knowing That. *Science* 1980;210:207–210. [PubMed: 7414331]
8. Curran T. Higher-order associative learning in amnesia: evidence from the serial reaction time task. *J Cogn Neurosci* 1997;9:522–533.
9. Curran T, Keele SW. Attentional and nonattentional forms of sequence learning. *Journal of Experimental Psychology: Learning, Memory, & Cognition* 1993;19:189–202.
10. Diekelmann S, Born J. One memory, two ways to consolidate? *Nat Neurosci* 2007;10:1085–6. [PubMed: 17726473]
11. Donchin O, Sawaki L, Madupu G, Cohen LG, Shadmehr R. Mechanisms influencing acquisition and recall of motor memories. *J Neurophysiol* 2002;88:2114–23. [PubMed: 12364533]
12. Eichenbaum, H. *The Cognitive Neuroscience of Memory*. Oxford University Press; New York: 2002.
13. Fischer S, Drosopoulos S, Tsen J, Born J. Implicit learning -- explicit knowing: a role for sleep in memory system interaction. *J Cogn Neurosci* 2006;18:311–9. [PubMed: 16602193]
14. Fischer S, Hallschmid M, Elsner AL, Born J. Sleep forms memory for finger skills. *Proc Natl Acad Sci U S A* 2002;99:11987–91. [PubMed: 12193650]

15. Frensch, PA. One concept, multiple meanings: On how to define the concept of implicit learning. In: Stadler, MA.; Frensch, PA., editors. *Handbook of implicit learning*. Sage Publications, Inc; Thousand Oaks, CA: 1998. p. 47-104.
16. Gladwell M. *The Art of Failure*. The New Yorker. 2000
17. Goedert KM, Willingham DB. Patterns of interference in sequence learning and prism adaptation inconsistent with the consolidation hypothesis. *Learn Mem* 2002;9:279–92. [PubMed: 12359837]
18. Hallett, M.; Fahn, S.; JJ; LAE; CCR; YSC. *Psychogenic Movement Disorders: Neurology and Neuropsychiatry*. Lippincott Williams & Wilkins; Philadelphia: 2006.
19. Jueptner M, Stephan KM, Frith CD, Brooks DJ, Frackowiak RS, Passingham RE. Anatomy of motor learning. I. Frontal cortex and attention to action. *J Neurophysiol* 1997;77:1313–24. [PubMed: 9084599]
20. Karni A, Meyer G, Rey-Hipolito C, Jezard P, Adams MM, Turner R, Ungerleider LG. The acquisition of skilled motor performance: fast and slow experience-driven changes in primary motor cortex. *Proc Natl Acad Sci U S A* 1998;95:861–8. [PubMed: 9448252]
21. Karni A, Tanne D, Rubenstein BS, Askenasy JJ, Sagi D. Dependence on REM sleep of overnight improvement of a perceptual skill. *Science* 1994;265:679–82. [PubMed: 8036518]
22. Keele SW, Ivry R, Mayr U, Hazeltine E, Heuer H. The cognitive and neural architecture of sequence representation. *Psychol Rev* 2003;110:316–39. [PubMed: 12747526]
23. Korman M, Doyon J, Doljansky J, Carrier J, Dagan Y, Karni A. Daytime sleep condenses the time course of motor memory consolidation. *Nat Neurosci* 2007;10:1206–13. [PubMed: 17694051]
24. Krakauer JW, Shadmehr R. Consolidation of motor memory. *Trends Neurosci* 2006;29:58–64. [PubMed: 16290273]
25. Libet B, Gleason CA, Wright EW, Pearl DK. Time of conscious intention to act in relation to onset of cerebral activity (readiness-potential). The unconscious initiation of a freely voluntary act. *Brain* 1983;106:623–642. [PubMed: 6640273]
26. Mednick S, Nakayama K, Stickgold R. Sleep-dependent learning: a nap is as good as a night. *Nat Neurosci* 2003;6:697–8. [PubMed: 12819785]
27. Muellbacher W, Ziemann U, Wissel J, Dang N, Kofler M, Facchini S, Boroojerdi B, Poewe W, Hallett M. Early consolidation in human primary motor cortex. *Nature* 2002;415:640–4. [PubMed: 11807497]
28. Nissen MJ, Bullemer P. Attentional requirements of learning: Evidence from performance measures. *Cognitive Psychology* 1987;19:1–32.
29. Pascual-Leone A, Grafman J, Hallett M. Modulation of cortical motor output maps during development of implicit and explicit knowledge. *Science* 1994;263:1287–9. [PubMed: 8122113]
30. Press DZ, Casement MD, Pascual-Leone A, Robertson EM. The time course of off-line motor sequence learning. *Brain Res Cogn Brain Res* 2005;25:375–8. [PubMed: 15990282]
31. Reber, AS. *Implicit learning and tacit knowledge: An essay on the cognitive unconscious*. Oxford University Press; New York, NY: 1993.
32. Robertson EM, Pascual-Leone A, Miall RC. Current concepts in procedural consolidation. *Nat Rev Neurosci* 2004;5:576–82. [PubMed: 15208699]
33. Robertson EM, Pascual-Leone A, Press DZ. Awareness modifies the skill-learning benefits of sleep. *Curr Biol* 2004;14:208–12. [PubMed: 14761652]
34. Robertson EM, Press DZ, Pascual-Leone A. Off-line learning and the primary motor cortex. *J Neurosci* 2005;25:6372–8. [PubMed: 16000627]
35. Shadmehr R, Brandt J, Corkin S. Time-dependent motor memory processes in amnesic subjects. *J Neurophysiol* 1998;80:1590–7. [PubMed: 9744966]
36. Shadmehr R, Brashers-Krug T. Functional stages in the formation of human long-term motor memory. *J Neurosci* 1997;17:409–19. [PubMed: 8987766]
37. Shadmehr, R.; Wise, SP. *The Computational Neurobiology of Reaching and Pointing*. MIT Press; Cambridge, MA: 2005.
38. Song S, Howard JH Jr, Howard DV. Implicit probabilistic sequence learning is independent of explicit awareness. *Learn Mem* 2007;14:167–76. [PubMed: 17351140]

39. Song S, Howard JH Jr, Howard DV. Sleep does not benefit probabilistic motor sequence learning. *J Neurosci* 2007;27:12475–83. [PubMed: 18003825]
40. Song S, Howard JH Jr, Howard DV. Perceptual sequence learning in a serial reaction time task. *Exp Brain Res* 2008;189:145–58. [PubMed: 18478209]
41. Spencer RM, Sunm M, Ivry RB. Sleep-dependent consolidation of contextual learning. *Curr Biol* 2006;16:1001–5. [PubMed: 16713957]
42. Squire LR. Memory systems of the brain: a brief history and current perspective. *Neurobiology of Learning and Memory* 2004;82:171–177. [PubMed: 15464402]
43. Stickgold R. Sleep-dependent memory consolidation. *Nature* 2005;437:1272–8. [PubMed: 16251952]
44. Wagner U, Gais S, Haider H, Verleger R, Born J. Sleep inspires insight. *Nature* 2004;427:352–5. [PubMed: 14737168]
45. Walker MP, Brakefield T, Hobson JA, Stickgold R. Dissociable stages of human memory consolidation and reconsolidation. *Nature* 2003;425:616–20. [PubMed: 14534587]
46. Walker MP, Brakefield T, Morgan A, Hobson JA, Stickgold R. Practice with sleep makes perfect: sleep-dependent motor skill learning. *Neuron* 2002;35:205–11. [PubMed: 12123620]
47. Walker MP, Brakefield T, Seidman J, Morgan A, Hobson JA, Stickgold R. Sleep and the time course of motor skill learning. *Learn Mem* 2003;10:275–84. [PubMed: 12888546]
48. Walker MP, Stickgold R. Sleep, memory, and plasticity. *Annu Rev Psychol* 2006;57:139–66. [PubMed: 16318592]
49. Wegner, DM. *The illusion of conscious will*. MIT Press; Cambridge, MA: 2002.
50. Willingham DB, Salidis J, Gabrieli JDE. Direct Comparison of Neural Systems Mediating Conscious and Unconscious Skill Learning. *J Neurophysiol* 2002;88:1451–1460. [PubMed: 12205165]
51. Wise SP, Murray EA. Role of the hippocampal system in conditional motor learning: mapping antecedents to action. *Hippocampus* 1999;9:101–17. [PubMed: 10226772]

1A. Traditional memory classification

1B. Alternative classification often used by experts in motor learning

1C. Experimentally-derived classification

Figure 1. Classifications of Conscious and Non-conscious Motor skill learning

Figure 1A represents the traditional classification of memory familiar to most students of psychology, based largely on works in amnesics [42]. Due to difficulties in classifying consciously learned motor skills, researchers have turned to an alternative classification schema of motor memory as depicted in Figure 1B [2;29;32]. Some experts however, suggest that a better dividing line than that of conscious awareness may be that of attention as seen in Figure 1C [22]. This latter experiment-derived classification schema for motor skill seems to better explain the pattern of results found for memory consolidation as depicted in Figure 2.

Figure 2. Summary of Findings on the Consolidation of Motor Learning

Figure 2 represents a summary of findings on the consolidation of motor learning based on several reports, as summarized in Section 2 of this review.