ORIGINAL RESEARCH

Time rather than sleep appears to enhance off-line learning and transfer of learning of an implicit continuous task

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Abstract: There is increasing evidence that sleep promotes off-line enhancement of a variety of explicitly learned motor tasks in young adults. However, whether sleep promotes off-line consolidation of implicitly learned motor tasks is still under question. Furthermore, the role of sleep in promoting transfer of learning remains unknown. This study examined the role of sleep in learning and transfer of learning of an implicit continuous motor task. Twenty-three neurologically intact individuals (mean age 26.4 years) were randomly assigned to either a sleep group or a no-sleep group. The sleep group practiced a continuous tracking task in the evening and underwent retention and transfer testing the following morning, while the no-sleep group practiced the tracking task in the morning and underwent retention and transfer testing in the evening. The results show that in both the sleep and no-sleep groups, performance improved off-line without further practice for both the general skill and the sequence-specific skill. The results also indicate that sleep and time promote transfer of learning of both sequence-specific and general skill learning to a spatial and temporal variation of the motor task. These findings demonstrate that sleep does not play a critical role in promoting off-line learning and transfer of learning of an implicit continuous motor task.

Keywords: sleep, off-line learning, implicit learning, transfer, continuous task

Introduction

Behavioral and imaging studies demonstrate that learning a motor skill occurs in at least two distinct phases, ie, a fast learning phase which takes place during or soon after the training period, and a slow latent phase which occurs for a period of time following training and includes a process of memory consolidation.[1–5] Memory consolidation refers to either the stabilization or the enhancement of a memory (also known as off-line learning).[2,5,6] Special attention has been given to the role of sleep in off-line motor skill learning. Many studies have demonstrated that performance on a motor task has greater improvement when the off-line period (ie, period between the practice session and the retention session) includes sleep than when it does not.[7–12] However, the benefit of sleep to promote off-line motor skill learning appears to depend on several factors, including the type of task utilized[3,13] and an individual's awareness of the task regularities.[4,14,15]

Awareness about the regularities of the task to be learned has emerged as a likely factor in determining if sleep-dependent memory consolidation occurs following practice of the task.[12,15] Two types of awareness, explicit and implicit, have been distinguished.[16–18] Explicit awareness refers to when participants are aware of the regularities of the task to be learned. Explicit awareness often occurs through

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instruction provided to the participant prior to task practice (ie, the participant is instructed on the pattern of a repeating sequence) or can occur when the participant figures out the task regularities during task practice. On the other hand, implicit awareness refers to when a participant does not have conscious awareness of the regularities of the task to be learned and does not become aware of the task regularities during task practice.[15–17,19] Researchers can manipulate awareness by providing instruction to participants about the task regularities or withholding these instructions.

Robertson et al[15] was the first to demonstrate that awareness of task regularities impacts sleep-dependent off-line motor learning. In this study,[15] participants who had no awareness of the sequence to be learned (implicit condition) demonstrated improvement in their performance, as indicated by a faster response time after a 12-hour interval regardless of whether or not it contained a period of sleep. In contrast, when another group of participants was instructed on the sequence pattern to be learned and then practiced the sequence (explicit condition), an improved performance as demonstrated by a faster response time was observed only when training was followed by a period of sleep. The findings of this study suggest that memory consolidation of an implicitly learned task is time-dependent, while memory consolidation of an explicitly learned task is sleep-dependent.

While the findings of Robertson et al[15] and of many other studies[3,11,12,20–23] concur that explicitly learned tasks undergo sleep-dependent off-line enhancement, there is less consensus as to whether implicitly learned tasks benefit from sleep or the passage of time. A few studies have demonstrated a critical role of sleep for implicit motor learning.[24–27] Using a sleep deprivation paradigm, Maquet et al[24] found that performance on an implicitly learned pursuit task was impaired in participants following a night of sleep deprivation compared with those participants who were allowed to sleep. The functional magnetic resonance imaging data from this study further revealed that participants allowed to sleep during the first post-training night experienced increased brain activity in critical regions typically activated by performing learned motor tasks. In addition, increased functional connectivity was observed between these regions and other regions known to participate in improved control of eye movements. Using a probabilistic version of the Serial Reaction Time Task, Fischer et al[26] demonstrated that, in adults, the difference between response times to grammatical and nongrammatical trials (ie, implicit learning) was enhanced after a retention period containing sleep in comparison with a retention period of daytime wakefulness.

The behavioral data from a study by Peigneux et al[27] supported the findings of Fischer et al,[26] and found that brain regions involved during learning the probabilistic Serial Reaction Time Task were reactivated during subsequent rapid eye movement sleep. Furthermore, Huber et al[25] found that participants demonstrated less error in performance on an implicit motor reaching adaptation task following a night of sleep, but not following an equivalent period of wake. Enhanced performance was positively correlated with an increase in time spent in slow wave sleep.

While the findings from the abovementioned studies[24–27] demonstrate sleep-dependent enhancement of implicitly learned motor tasks, other studies have reported conflicting results.[4,15,28–31] The participants in studies by Doyon et al[3] and Debas et al[31] demonstrated a reduction in performance error on an implicit visuomotor adaptation task both following sleep and following a period of being awake, suggesting, as did Robertson et al,[15] that off-line learning of an implicitly learned task is time-dependent rather than sleep-dependent. These findings by Doyon et al[3] and Debas et al[31] appear to refute the findings of Huber et al[25] that sleep is essential for the consolidation process in an implicit motor adaptation task. Providing further discordant results, participants in a study by Reith et al[29] failed to demonstrate improvement in performance on an implicitly learned version of a pursuit task regardless of whether they slept or stayed awake between practice and retention testing.

Few studies have examined whether sleep only enhances certain characteristics of the implicit task and may be a possible reason behind the disparity of findings between the studies of Nemeth et al[4] and Song et al,[30] both of which utilized an implicit probabilistic sequence learning task to assess the role of sleep in promoting off-line general motor skill learning compared with sequence-specific motor skill learning. Nemeth et al found that sleep enhanced off-line general skill motor learning, whereas participants in the study by Song et al failed to demonstrate sleep-dependent off-line general skill learning. Participants in both studies failed to benefit from sleep to enhance off-line sequence-specific motor learning. Both found that general skill learning occurred off-line over the day, but off-line enhancement of sequence-specific motor learning did not occur over the day. The findings of Nemeth et al and Song et al suggest that sequence-specific motor skill learning and general motor skill learning are consolidated by different mechanisms.

In addition to the debate surrounding the role of sleep in promoting off-line learning of an implicit motor task, little is known about whether sleep enhances the transfer of learning of one task to variations of the task. Generalization or transfer

of motor learning refers to individuals applying what has been learned in one context to another context with shared similar characteristics.[32–34] For example, a person who has never been to the beach will likely be able to generalize his or her ability to walk in the sand; the stepping pattern or timing may be different from walking on a smooth floor, but he or she will be able to walk successfully across the beach.

Only a few studies have addressed whether sleep facilitates the transfer of motor learning in young individuals.[1,12,33] In studies by Cohen et al[1] and Witt et al,[33] participants practiced a motor sequence task with one hand. At retention testing following either a period of sleep or a period of being awake, transfer was tested by assessing the participants' ability to perform the sequence task with the opposite hand. Researchers in both studies examined whether sleep enhances spatial (or goal) transfer so that the same sequence of button presses was performed but with a different sequence of finger movements and motor (or movement) transfer so that the same sequence of finger movements was used but a different configuration of the buttons were pressed. Both studies found that sleep enhanced the transfer of sequence learning to the spatial variation but not the motor variation of the task. The study by Cohen et al[1] did find that the motor transfer was enhanced after a period of wakefulness. Fischer et al[12] found that off-line learning did not generalize to a sequence containing the same finger movements in a mirror-reversed order, supporting the results reported by Witt et al[33] and Cohen et al[1] showing that sleep does not enhance the transfer of the motor variation of a skill. These studies suggest that sleep promotes generalization of a learned skill to variations of the skill, but only certain variations are enhanced.

Due to the conflicting evidence on the role of sleep in off-line learning of implicit motor tasks, the purpose of this study is to assess the influence of sleep on learning an implicitly learned version of a continuous tracking (CT) task. Furthermore, due to the limited evidence suggesting that sleep promotes transfer of motor skill learning, the secondary purpose of this study is to examine if sleep enhances transfer of learning to variations of the CT task. We hypothesized that sleep will promote off-line learning and transfer of learning of the CT task. The CT task is a well-used sequence learning task[14,19,35–38] and is well suited to assess the influence of sleep on implicit learning because detecting the imbedded sequence within the task is more difficult than with a shorter finger tapping task. The CT task is also well suited to exploring the effect of sleep on generalizability because variations of the CT task can be easily constructed.

Materials and methods
Participants
Participants were recruited from the community as well as among employees and students at the University of Kansas Medical Center. Twenty-three individuals participated in the study (mean age 26.4 years, 12 women). All of the subjects except three were right-handed as assessed by the Edinburgh Handedness Inventory.[39] Fourteen individuals participated in the sleep condition and nine individuals participated in the no-sleep condition. Subjects were instructed to record their sleep pattern during the week prior to the practice session and the night between the practice and retention session using a sleep log. The Stanford Sleepiness Scale[40] was used to assess level of sleepiness prior to practice and retention testing. Participants were instructed to refrain from recreational drugs, alcohol, or caffeine use for 24 hours prior to and during testing. Participants were excluded if they presented with acute medical problems, uncorrected vision loss, previous history of psychiatric admission or neurological disease, or scored below 26 on the Mini-Mental State Examination.

Procedure
All interested subjects were initially screened for eligibility in the study. If determined eligible to participate, subjects provided their written informed consent. The study was conducted according to the regulations and with approval from the Human Subjects Committee at the University of Kansas Medical Center. Participants were randomly assigned to either the sleep or no-sleep group. Both the sleep and no-sleep groups completed two sessions of a CT task. The first session was a practice session which consisted of performing the CT for eight blocks, and the second session, conducted 12±1 hours later, was a retention session which consisted of performing the CT for three blocks. For the no-sleep group, the practice session was performed in the morning (8 am ±1 hour) and the retention and transfer session was performed in the evening (8 pm ±1 hour). The no-sleep group participants were instructed to perform their normal daily activities and to avoid taking a nap between sessions. For the sleep group, the practice session was performed in the evening (8 pm ±1 hour) and the retention and transfer session was performed in the morning (8 am ±1 hour) following a night of sleep at home.

For the CT task, participants were required to control a joystick using their dominant arm to track a target on the computer screen that moved vertically in a sinusoidal wave pattern.[35,38] Only the target (white box on a black background) and the participant's cursor position (red circle) were visible to the participant; there was no residual trace of the wave on

the screen. Each participant practiced the CT task for eight blocks (from block 1 to block 8) of ten trials, each for a total of 80 iterations. Each trial consisted of three segments, ie, one repeating segment imbedded between two random segments (Figure 1).[41] Each segment was 12 seconds in duration for a total trial length of 36 seconds with a 3-second stable baseline trial divider. Participants were instructed to try to keep the cursor as close to the target as possible; they received no instruction on the presence of the repeating segment. Off-line motor learning was assessed by asking participants to complete one block (ten trials) of the CT task at a retention test 12±1 hours after practice. To assess whether off-line consolidation contributes to the process of generalization, participants performed another two blocks following the retention test, one block to assess spatial transfer (the sensitivity of the joystick was changed from 40% sensitivity to 60% sensitivity resulting in the alteration of the spatial requirements of performing the movement) followed by another block to assess temporal transfer (a faster speed was used, and the target speed was changed from 40 Hz to 50 Hz, thereby changing the temporal requirements of the movement).

Following performance of the retention and transfer blocks, the acquisition of explicit awareness about the presence of the repeating wave pattern was assessed in three steps. Participants were first asked an open-ended question of "Did you notice anything about the task?" If the participants said "Yes", a follow-up question of "What did you notice?" was asked. All participants then underwent a forced-choice recognition test. Ten iterations of a trial segment were displayed on the computer screen while the participants watched the screen. Three of the segments displayed were the repeating wave pattern used in the practice session while seven
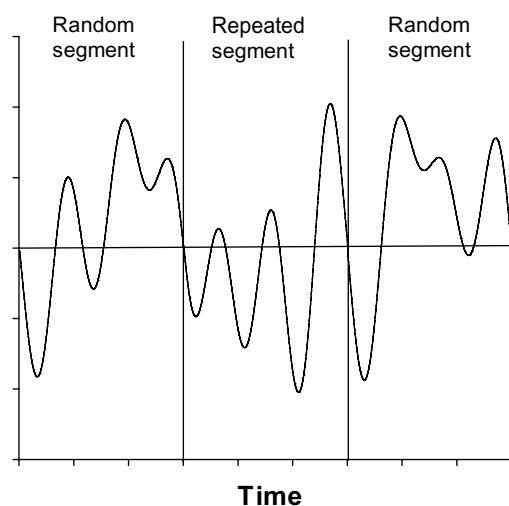

Figure 1 An example of one 36-second trial. Each segment is 12 seconds in length.

of the segments were a random foil segment. Participants had to decide (forced choice) if the segment was one they recognized or not. Participants were deemed to have gained explicit awareness if they were correct on more than five of the ten trials and correctly identified the repeating segment on at least two of the three occasions. Five individuals in the sleep group and one individual in the no-sleep group gained explicit awareness and was removed from data analysis.

Statistical analysis

Performance on the CT task was evaluated by calculating the root mean square error (RMSE) for each segment in each trial. The average RMSE for the first random segment of each trial was calculated and one standard deviation was added to the average. Any trial (random or sequence) with an RMSE above this score was removed from data analysis to eliminate outlying data. The first random segment of each trial was used to determine general skill learning and the repeated segment of each trial was used to determine sequence-specific skill learning. The median RMSE was calculated for each block as a summary score for tracking accuracy of the tracking task.[14,35,36,38,42] A two factor (segment [sequence, random] × block [1–8]) repeated-measures analysis of variance with RMSE as the dependent variable was used to assess general skill and sequence-specific practice performance for both the sleep and no-sleep group. Off-line learning was assessed for both the sleep and no-sleep group using a two factor (segment [sequence, random] × block [last practice block, retention block]) repeated-measures analysis of variance with RMSE as the dependent variable. For analysis of transfer of general skill learning and sequence-specific skill learning at retention for each group, a one-way analysis of variance was performed with RMSE at retention as the dependent variable with post hoc analysis to assess for differences between the six conditions at retention (sequence segment, spatial sequence transfer, temporal sequence transfer, random segment, spatial random transfer, and temporal random transfer). Transfer of learning was determined to occur if there was no statistically significant difference between the sequence segment and the spatial or temporal variation of the sequence segment or between the random segment and the spatial or temporal variation of the random segment.

Results

There were no differences between the sleep and no-sleep group for age ($P=0.829$), amount of sleep the week prior to practice ($P=0.211$), level of sleepiness at practice ($P=0.620$), or retention and transfer testing ($P=0.969$, Table 1).

Table 1 Data for 17 individuals who completed the study

	Age, years	Sleep week prior to testing, hours	Stanford Sleepiness Scale at practice	Stanford Sleepiness Scale at retention
Sleep group (n=9)	27.0±3.12	7.16±0.65	2.38±0.74	1.88±0.64
No-sleep group (n=8)	27.5±5.98	7.50±0.37	2.56±0.73	1.89±0.78

Notes: Data are shown as the mean ± standard deviation. Sleep week prior is the average amount of sleep the week prior to testing determined by sleep log.

Practice performance

Performance improved across practice for both the general skill and sequence-specific skill as shown by a main effect of block for both the sleep group ($F_{7,112}$=2.109, P=0.048; Figure 2A) and no-sleep group ($F_{7,98}$=5.965, P=0.000;
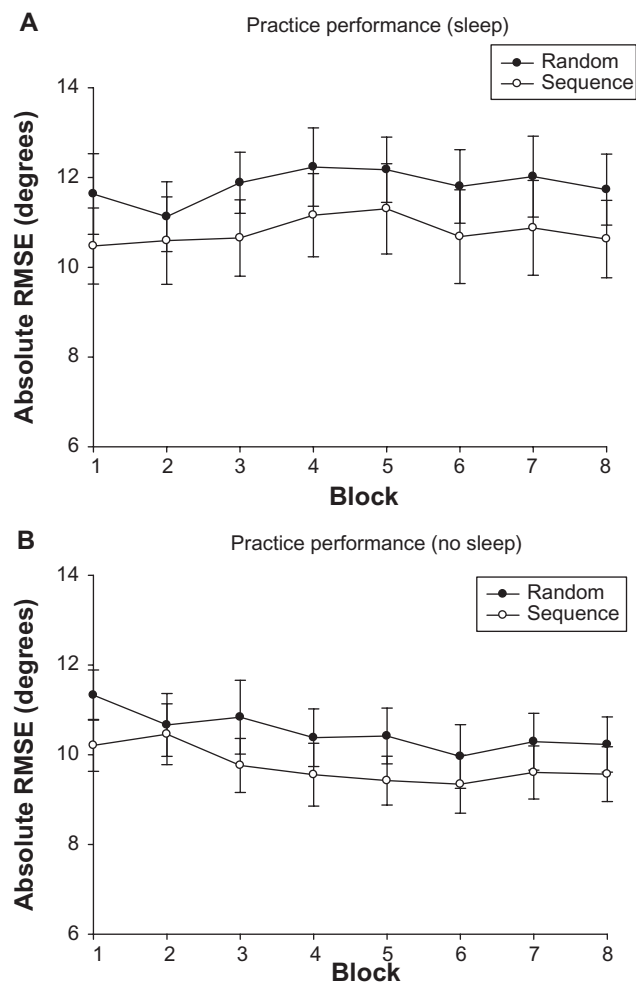
Figure 2B), but there was no difference between the general skill or sequence-specific skill across practice as shown by a lack of main effect of segment for both the sleep group ($F_{1,16}$=0.581, P=0.457) and the no-sleep group ($F_{1,14}$=0.608, P=0.448) indicating that both the general skill and sequence-specific skill improved with practice regardless of the time of day performed. The interaction of block X segment was not statistically significant for either the sleep group ($F_{7,112}$=0.291, P=0.956) or the no-sleep group ($F_{7,98}$=0.930, P=0.487).

Off-line motor learning

Performance improved off-line without further practice from the last practice block to retention for both the general skill and sequence-specific skill as shown by a main effect of block for both the sleep group ($F_{1,16}$=7.475, P=0.015; Figure 3A)
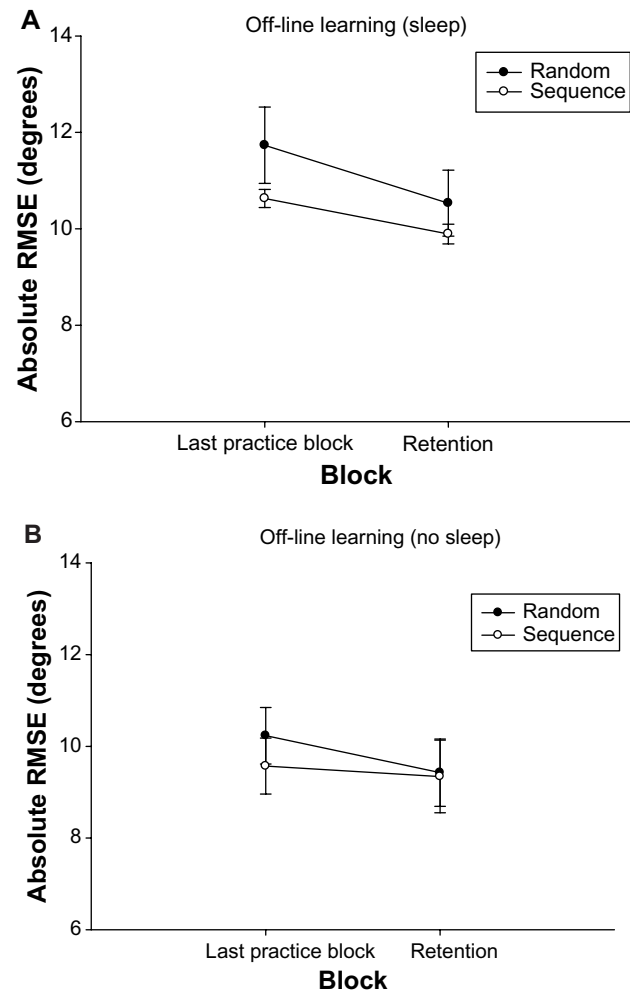

Figure 2 (**A**) Sleep group performance on the general skill and sequence-specific skill of the CT task across the practice. (**B**) No sleep group performance on the general skill and sequence-specific skill of the CT task across the practice. Errors are shown as the standard error of the mean.
Abbreviations: CT, continuous tracking; RMSE, root mean square error.

Figure 3 (**A**) Sleep group off-line learning between the last practice block and the retention test for the general skill and sequence-specific skill. (**B**) No sleep group off-line learning between the last practice block and the retention test for the general skill and sequence-specific skill. Errors are shown as the standard error of the mean.
Abbreviation: RMSE, root mean square error.

and no-sleep group ($F_{1,14}$=4.665, P=0.049; Figure 3B), but there was no difference in off-line learning between the general skill or sequence-specific skill, as shown by a lack of main effect of segment for both the sleep group ($F_{1,16}$=0.482, P=0.497) and the no-sleep group ($F_{1,14}$=0.118, P=0.736), indicating that general skill and sequence-specific skill undergo off-line enhancement both following a period of sleep and following a period of being awake. The interaction of block X segment was not significant for either the sleep group ($F_{1,16}$=0.426, P=0.523) or the no-sleep group ($F_{1,14}$=0.1.467, P=0.246).

Transfer of temporal and spatial variations of motor task

Least significant difference post hoc analysis did not show any statistical differences between the sequence segment or random segment and the corresponding spatial or temporal variation of the sequence or random segment for either the sleep group or no-sleep group (sleep group, sequence segment versus spatial sequence transfer, P=0.626, sequence segment versus temporal sequence transfer, P=0.359, random segment versus spatial random transfer, P=0.480, and random segment versus temporal random transfer, P=0.451, Figure 4A; no-sleep group, sequence segment versus spatial sequence transfer, P=0.821, sequence segment versus temporal sequence transfer, P=0.392, random segment versus spatial random transfer, P=0.568, and random segment versus temporal random transfer, P=0.236, Figure 4B). This indicates that sleep and time promotes transfer of learning of both sequence-specific and general skill learning to a spatial and temporal variation of the motor task.

Discussion

The results of this study demonstrate that both general skill learning and sequence-specific skill learning of an implicitly learned motor task improve off-line regardless of whether participants slept or stayed awake between practice and retention testing. Furthermore, this study demonstrates that both general skill learning and sequence-specific skill learning transfer off-line to spatial and temporal variations of the task following sleep and following a period of being awake.

The results of this study appear to support the awareness theory of Robertson et al,[15] which proposes that off-line learning of implicit motor sequence tasks depends on the passage of time rather than requiring sleep. The results of the current study also largely confirm the results of Doyon et al[3] and Debas et al,[31] ie, that time rather than sleep is sufficient to promote consolidation of an implicitly learned task.
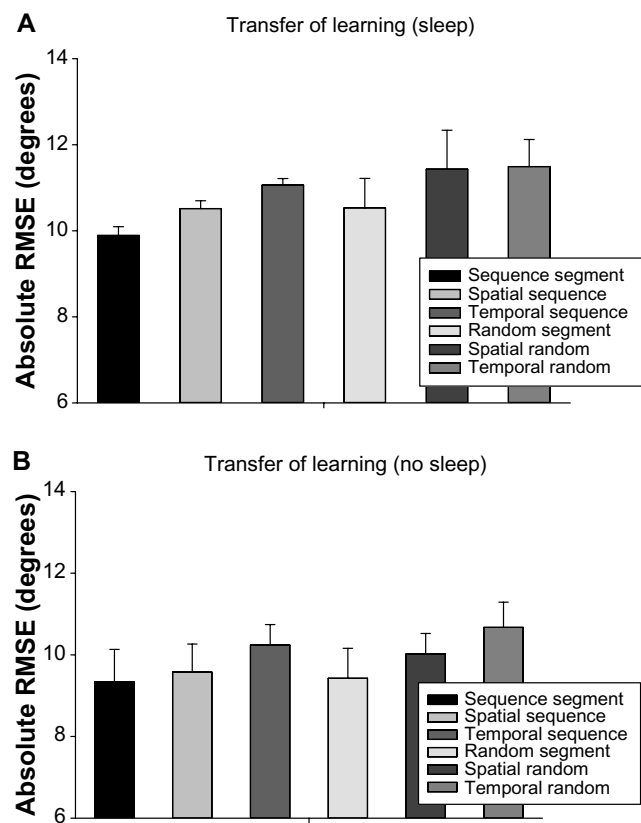
Figure 4 (**A**) Sleep group transfer of learning of sequence-specific and general skill learning to a spatial and temporal variation of the motor task. (**B**) No sleep group transfer of learning of sequence-specific and general skill learning to a spatial and temporal variation of the motor task. Errors are shown as the standard error of the mean.
Abbreviation: RMSE, root mean square error.

Interestingly, the studies by Doyon et al[3] and Debas et al[31] do not corroborate the study of Huber et al[25] despite the fact that all three utilized a visuomotor adaption task. Huber et al[25] demonstrated a reduction in directional errors occurred exclusively across a night of sleep, but not across an equivalent period of wakefulness. The disparity of findings between Huber et al[25] and the studies by Doyon et al[3] and Debas et al[31] may be explained by methodological differences, including amounts of practice, demands on upper arm effectors, and extent of kinematic adaptations performed.

The findings of the current study demonstrating that sleep is not critical for implicit motor skill learning contrast with the results of studies by Fischer et al,[26] Peigneux et al,[27] Huber et al,[25] and Maquet et al,[43] who found that sleep rather than time strengthens learning of an implicit task. There are several possible explanations for the different outcomes. A task-related difference between the current study and previous studies is a likely reason for the lack of consistent findings between these studies. The current study used a continuous tracking task, while Fischer et al[26] and

Peigneux et al[27] used a discrete task. The evidence suggests that the consolidating effect of sleep differs between discrete tasks and continuous tasks,[13] likely due to differences in motor control.[44–46] On the other hand, Huber et al[25] used a visuomotor adaptation task while the current study used a motor sequencing task, and perhaps sleep preferentially enhances implicit adaption tasks but not implicit sequencing tasks. Studies suggest motor adaptation tasks rely more on perceptual abilities,[3,30] and perceptual processes undergo sleep-dependent enhancement.[47–50]

Interestingly, despite using an implicit pursuit task with characteristics similar to those of a continuous motor task (a segment of the pursuit tasks was repeated during practice), the finding of Maquet et al[24] that sleep produces off-line performance enhancement of an implicit task conflict with the findings of the current study. The many differences in the experimental design between the current study and the study by Maquet et al[24] likely explain the conflicting results. Whereas participants in the current study practiced the CT task for eight blocks and the length of each block was 5 minutes, for a total practice time of 40 minutes, the pursuit task by Maquet et al was practiced for 19 blocks and the length of each block was 18 seconds, for a total practice time of 5.7 minutes. The evidence suggests that skills practiced for less time may benefit more from sleep for enhancement.[51] In addition to the large difference in time practicing, practice in the study by Maquet et al[24] was interspersed with 18 seconds of rest. Due to the short block length followed by a similar period of rest, we believe the task used by Maquet et al[24] has characteristics more closely resembling a discrete task, not a continuous task, and thus benefit from sleep to enhance learning.[13] Taken together, due to multiple tasks and methodological differences, comparing the results of the current study with those of the Maquet et al,[24] as well as other previous studies, is very difficult.

In the current study, the role of sleep in general skill learning was distinguished from sequence-specific learning because studies suggest that these components of implicit motor skill learning are consolidated by different mechanisms.[4,30] The current study found significant off-line improvement of general skill learning; however, this improvement was not sleep-dependent because both the sleep group and the no-sleep group demonstrated off-line consolidation of general skill learning. These results largely confirm those reported by Nemeth et al,[4] who found evidence of off-line improvement for general skill learning in both the sleep and the no-sleep conditions. Nonetheless, the findings of the current study and the study by Nemeth et al appear to refute the findings of Song et al,[30] who found that general skill learning occurred off-line over the day but not during sleep. In assessing sequence-specific learning, our results indicate that sequence-specific learning improved off-line in both the sleep and no-sleep conditions. These findings contrast with the studies by Nemeth et al[4] and Song et al,[30] which demonstrate that sequence-specific motor learning is not enhanced off-line by sleep or day time. These previous studies[4,30] differ from the present study in many ways, so it is difficult to identify the source of the disparate findings. However, the most distinguished difference is that the current study used a deterministic sequence while Nemeth et al[4] and Song et al[30] used a probabilistic sequence. There is some evidence to suggest that different mechanisms are involved in the consolidating process of probabilistic learning and deterministic learning.[30] More studies would be needed in the future to confirm this contention.

To the authors' knowledge, the current study is the first to assess if sleep facilitates the transfer of learning of an implicitly learned continuous task. The novelty of this study compared with previous studies that have examined the role of sleep in learning transfer[1,12,33] is that we used a continuous task and examined separately the transfer of general skill learning and sequence-specific learning. Furthermore, using the same hand at retest, we assessed both the transfer of learning to a spatial variation (ie, changing the joystick gain) and temporal variation (ie, using a faster speed). We found that both general skill learning and sequence-specific skill learning transfer off-line to spatial and temporal variations of the task both following sleep and a period of wakefulness. These results suggest that off-line transfer of an implicitly learned continuous task is time-dependent.

Our finding that time promotes transfer of learning of the spatial variations of an implicitly learned task differs from those of Witt et al[33] and Cohen et al[1] who found that sleep rather than time produced transfer of learning of spatial variations of a task. However, methodological differences between the current study and those of Witt et al[33] and Cohen et al[1] likely explain the disparate findings. Witt et al[33] utilized an explicitly learned motor task, and there is a lot of evidence suggesting that sleep preferentially enhances explicitly learned tasks[3,11,12,15,20–23] compared with implicitly learned tasks.[3,11,12,15,20–23] While Cohen et al[1] utilized an implicitly learned task, their task was a discrete one, making comparison with the continuous task utilized in the current study difficult because the evidence suggests that sleep acts preferentially on discrete tasks.[13]

One limitation of this study is that the influence of endogenous circadian rhythm or time-of-day of testing on the results cannot be completely discounted. However, we feel that the impact of these factors on the results are limited and are not driving the results of this study because there was no difference between the sleep and no-sleep groups on the Stanford Sleepiness Scale at either the practice session or retention session, regardless of the time of day when the session occurred. Other studies have attempted to control for these factors by including a nap to determine the contribution of sleep to off-line learning (so the practice session and retention session occur at the same time of day regardless of whether participants are in the sleep condition or no-sleep condition), and found that a daytime nap enhances learning of a mirror-tracing task[52] and a finger-tapping task.[49,53] Cohen et al[1] used two diurnal control groups, so that practice and retention testing took place at the same time of day (both at 8 am or both at 8 pm) and found that improvements in their task outcome measures were not associated with the time of day of testing. Walker et al[20] had participants practice a finger-tapping task at either 10 am or 10 pm and then retested them 12 hours and 24 hours later, and found only intervals containing sleep resulted in improved performance. Therefore, the influence of circadian rhythm and time of day of testing does not appear to be the driving factor between the results, although those factors cannot be completely discounted.

Despite the significant main effect of block for both the sleep and no-sleep groups indicating performance improvement across practice, visual examination of practice performance for the sleep and no-sleep groups in Figures 1 and 2 indicates limited performance improvement across practice. While an improvement in the performance curve is generally expected across practice, this largely depends on the task and does not indicate the magnitude of the information learned during practice. Limited improvement in the performance curve may be due to participant fatigue or boredom, neither of which was directly assessed after practice. However, fatigue, boredom, or other practice conditions not accounted for do not prevent motor learning but do impact performance. It is possible that the participants did not encode sufficient information during practice, but if this were the case, neither group would have demonstrated learning of the task at the delayed retention test.

Another limitation is that failure to reject the null hypothesis was used as evidence of transfer of skill learning. Due to the small sample size of this study, future studies should be adequately powered to provide concurrent evidence that sleep and time appear to enhance transfer of skill learning of an implicit motor task.

Overall, the differences in experimental paradigms and lack of consistent terminology across studies make comparing the results of previous studies and the current study very difficult. Even studies that use similar paradigms have found different results, possibly due to differences in methodology. For example, Nemeth et al[4] and Song et al[30] used the same task (an implicit probabilistic Serial Reaction Time Task) to assess the role of sleep in promoting general motor skill learning and sequence-specific motor skill learning, but reported different results. As another example, Debas et al[31] and Doyon et al[3] both found that time rather than sleep enhances learning of a visuomotor task, whereas Huber et al[25] found learning was enhanced only following a period of sleep despite using a very similar visuomotor task. Furthermore, the lack of consistent terminology across studies makes interpretation of results and comparison of findings difficult. For example, the implicit–explicit distinction is generally accepted to be based on the participant's awareness of the regularities being practiced; whereas explicit learning refers to having an awareness of the regularities of the environment to be learned, implicit learning occurs without this awareness.[16–18] However, in the study by Reith et al[29] which looked at the effect of sleep on learning an "explicit" and "implicit" version of a pursuit task, they used the term "explicit" to indicate learning of a repeating pattern, but there is no mention of participants receiving instruction about the repeating pattern and no mention of testing participants' explicit awareness either prior to practice or following it. Therefore, defining explicit and implicit learning according to participants' awareness of the pattern, we would consider this to be implicit learning of a sequence-specific task. Furthermore, Reith et al[29] used the term "implicit" to indicate learning of a non-repeating, random, unpredictable pursuit task, which we would consider comparable with implicit general skill learning. The difference in terminology used certainly does not disregard the findings by Reith et al, but it does make comparison between studies much more difficult. We propose that future studies should be cognizant of this terminology issue, and an attempt should be made to use consistent terminology across studies. It is likely that consistent terminology as well as more standardized paradigms would greatly aid in elucidation of the role of sleep in motor skill learning.

Conclusion

Although it is widely accepted that sleep promotes motor learning, our study indicates that this may not always be the case.

In contrast with prior studies reporting a benefit from sleep to enhance implicit motor learning,[25–27,43] we found that participants performed with less error on an implicit continuous tracking task but that this improvement was not specific to sleep. Both general skill learning and sequence-specific skill learning occurred off-line regardless of whether participants slept or stayed awake between practice and retention testing. Furthermore, both general skill learning and sequence-specific skill learning transfer off-line to spatial and temporal variations of the task both following sleep and following a period of being awake. Our findings suggest that sleep does not play a critical role in promoting off-line learning or the transfer of learning of an implicit continuous motor task.

The consolidation process likely differs depending on the nature of the task to be learned. However, when examining the literature that evaluates the role of sleep in motor learning, we have found conflicting results, even between studies that have utilized same task.[3,25,29,43] Therefore, we believe future studies are needed to clarify the role of sleep in motor learning, but a systematic approach using consistent terminology and methodology will allow an improved ability to compare and contrast findings between studies.

Acknowledgments

Disclosure

The authors report no conflicts of interest in this work.

References

1. 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(50):18237–18241.
2. Korman M, Raz N, Flash T, Karni A. Multiple shifts in the representation of a motor sequence during the acquisition of skilled performance. *Proc Natl Acad Sci U S A*. 2003;100(21):12492–12497.
3. Doyon J, Korman M, Morin A, et al. Contribution of night and day sleep vs simple passage of time to the consolidation of motor sequence and visuomotor adaptation learning. *Exp Brain Res*. 2009;195(1):15–26.
4. Nemeth D, Janacsek K, Londe Z, Ullman MT, Howard DV, Howard JH Jr. Sleep has no critical role in implicit motor sequence learning in young and old adults. *Exp Brain Res*. 2010;201(2):351–358.
5. 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(9):1206–1213.
6. McGaugh JL. Memory – a century of consolidation. *Science*. 2000; 287(5451):248–251.
7. Walker MP, Stickgold R, Alsop D, Gaab N, Schlaug G. Sleep-dependent motor memory plasticity in the human brain. *Neuroscience*. 2005;133(4): 911–917.
8. Walker MP, Stickgold R. Sleep, memory, and plasticity. *Annu Rev Psychol*. 2006;57:139–166.
9. Walker MP, Stickgold R. It's practice, with sleep, that makes perfect: implications of sleep-dependent learning and plasticity for skill performance. *Clin Sports Med*. 2005;24(2):301–317, ix.
10. Walker MP, Stickgold R. Sleep-dependent learning and memory consolidation. *Neuron*. 2004;44(1):121–133.
11. 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(4):275–184.
12. Fischer S, Hallschmid M, Elsner AL, Born J. Sleep forms memory for finger skills. *Proc Natl Acad Sci U S A*. 2002;99(18):11987–11991.
13. Siengsukon CF, Al-Sharman A. Sleep promotes off-line enhancement of an explicitly learned discrete but not an explicitly learned continuous task. *Nat Sci Sleep*. 2011;3:39–46.
14. Siengsukon CF, Boyd LA. Sleep to learn after stroke: implicit and explicit off-line motor learning. *Neurosci Lett*. 2009;451(1):1–5.
15. Robertson EM, Pascual-Leone A, Press DZ. Awareness modifies the skill-learning benefits of sleep. *Curr Biol*. 2004;14(3):208–212.
16. Yordanova J, Kolev V, Verleger R, Bataghva Z, Born J, Wagner U. Shifting from implicit to explicit knowledge: different roles of early- and late-night sleep. *Learn Mem*. 2008;15(7):508–515.
17. Yordanova J, Kolev V, Verleger R. Awareness of knowledge or awareness of processing? Implications for sleep-related memory consolidation. *Front Hum Neurosci*. 2009;3:40.
18. Yordanova J, Kolev V, Wagner U, Verleger R. Covert reorganization of implicit task representations by slow wave sleep. *PLoS One*. 2009;4(5):e5675.
19. Shea CH, Wulf G, Whitacre CA, Park JH. Surfing the implicit wave. *Q J Exp Psychol A*. 2001;54(3):841–862.
20. Walker MP, Brakefield T, Morgan A, Hobson JA, Stickgold R. Practice with sleep makes perfect: sleep-dependent motor skill learning. *Neuron*. 2002;35(1):205–211.
21. Walker MP, Brakefield T, Hobson JA, Stickgold R. Dissociable stages of human memory consolidation and reconsolidation. *Nature*. 2003;425(6958):616–620.
22. Smith C, MacNeill C. Impaired motor memory for a pursuit rotor task following Stage 2 sleep loss in college students. *J Sleep Res*. 1994;3(4): 206–213.
23. Plihal W, Born J. Effects of early and late nocturnal sleep on declarative and procedural memory. *J Cogn Neurosci*. 1997(9):534–547.
24. Maquet P, Schwartz S, Passingham R, Frith C. Sleep-related consolidation of a visuomotor skill: brain mechanisms as assessed by functional magnetic resonance imaging. *J Neurosci*. 2003;23(4):1432–1440.
25. Huber R, Ghilardi MF, Massimini M, Tononi G. Local sleep and learning. *Nature*. 2004;430(6995):78–81.
26. Fischer S, Wilhelm I, Born J. Developmental differences in sleep's role for implicit off-line learning: comparing children with adults. *J Cogn Neurosci*. 2007;19(2):214–227.
27. Peigneux P, Laureys S, Fuchs S, et al. Learned material content and acquisition level modulate cerebral reactivation during posttraining rapid-eye-movements sleep. *NeuroImage*. 2003;20(1):125–134.
28. Doyon J, Gaudreau D, Laforce R Jr, et al. Role of the striatum, cerebellum, and frontal lobes in the learning of a visuomotor sequence. *Brain Cogn*. 1997;34(2):218–245.
29. Rieth CA, Cai DJ, McDevitt EA, Mednick SC. The role of sleep and practice in implicit and explicit motor learning. *Behav Brain Res*. 2010;214(2):470–474.
30. Song S, Howard JH Jr, Howard DV. Sleep does not benefit probabilistic motor sequence learning. *J Neurosci*. 2007;27(46): 12475–12483.
31. Debas K, Carrier J, Orban P, et al. Brain plasticity related to the consolidation of motor sequence learning and motor adaptation. *Proc Natl Acad Sci U S A*. 2010;107(41):17839–17844.

32. Krakauer JW, Mazzoni P, Ghazizadeh A, Ravindran R, Shadmehr R. Generalization of motor learning depends on the history of prior action. *PLoS Biol*. 2006;4(10):e316.

33. Witt K, Margraf N, Bieber C, Born J, Deuschl G. Sleep consolidates the effector-independent representation of a motor skill. *Neuroscience*. 2010;171(1):227–234.

34. Criscimagna-Hemminger SE, Donchin O, Gazzaniga MS, Shadmehr R. Learned dynamics of reaching movements generalize from dominant to nondominant arm. *J Neurophysiol*. 2003;89(1):168–176.

35. Wulf G, Schmidt RA. Variability of practice and implicit motor learning. *J Exp Psychol Learn Mem Cogn*. 1997;23(4):987–1006.

36. Siengsukon C, Boyd LA. Sleep enhances off-line spatial and temporal motor learning after stroke. *Neurorehabil Neural Repair*. 2009;23(4):327–335.

37. Boyd LA, Winstein CJ. Cerebellar stroke impairs temporal but not spatial accuracy during implicit motor learning. *Neurorehabil Neural Repair*. 2004;18(3):134–143.

38. Boyd LA, Winstein CJ. Providing explicit information disrupts implicit motor learning after basal ganglia stroke. *Learn Mem*. 2004;11(4):388–396.

39. Oldfield RC. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*. 971;9(1):97–113.

40. Hoddes E, Zarcone V, Smythe H, Phillips R, Dement WC. Quantification of sleepiness: a new approach. *Psychophysiology*. 1973;10(4):431–436.

41. Wulf G, Shea CH. Principles derived from the study of simple skills do not generalize to complex skill learning. *Psychon Bull Rev*. 2002;9(2):185–211.

42. Boyd LA, Winstein CJ. Explicit information interferes with implicit motor learning of both continuous and discrete movement tasks after stroke. *J Neurol Phys Ther*. 2006;30(2):46–57.

43. Maquet P, Peigneux P, Laureys S, et al. Memory processing during human sleep as assessed by functional neuroimaging. *Rev Neurol (Paris)*. 2003;159(Suppl 11):6S27–6S29.

44. Howard IS, Ingram JN, Wolpert DM. Separate representations of dynamics in rhythmic and discrete movements: evidence from motor learning. *J Neurophysiol*. 2011;105(4):1722–1731.

45. Ikegami T, Hirashima M, Taga G, Nozaki D. Asymmetric transfer of visuomotor learning between discrete and rhythmic movements. *J Neurosci*. 2010;30(12):4515–4521.

46. Schmidt RA, Lee TD. *Motor Control and Learning: A Behavioral Emphasis*. 3rd ed. Champaign, IL, USA: Human Kinetics; 1999.

47. Gais S, Plihal W, Wagner U, Born J. Early sleep triggers memory for early visual discrimination skills. *Nat Neurosci*. 2000;3(12):1335–1339.

48. Karni A, Tanne D, Rubenstein BS, Askenasy JJ, Sagi D. Dependence on REM sleep of overnight improvement of a perceptual skill. *Science*. 1994;265(5172):679–682.

49. Mednick SC, Cai DJ, Kanady J, Drummond SP. Comparing the benefits of caffeine, naps and placebo on verbal, motor and perceptual memory. *Behav Brain Res*. 2008;193(1):79–86.

50. Stickgold R, Whidbee D, Schirmer B, Patel V, Hobson JA. Visual discrimination task improvement: a multi-step process occurring during sleep. *J Cogn Neurosci*. 2000;12(2):246–254.

51. Robertson EM. From creation to consolidation: a novel framework for memory processing. *PLoS Biol*. 2009;7(1):e19.

52. Backhaus J, Junghanns K. Daytime naps improve procedural motor memory. *Sleep Med*. 2006;7(6):508–512.

53. Nishida M, Walker MP. Daytime naps, motor memory consolidation and regionally specific sleep spindles. *PLoS One*. 2007;2(4):e341.