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RESEARCH NOTE

Sleep has no critical role in implicit motor sequence learning in young and old adults

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Abstract The influence of sleep on motor skill consolidation has been a research topic of increasing interest. In this study, we distinguished general skill learning from sequence-specific learning in a probabilistic implicit sequence learning task (alternating serial reaction time) in young and old adults before and after a 12-h offline interval which did or did not contain sleep (p.m.–a.m. and a.m.–p.m. groups, respectively). The results showed that general skill learning, as assessed via overall reaction time, improved offline in both the young and older groups, with the young group improving more than the old. However, the improvement was not sleep-dependent, in that there was no difference between the a.m.–p.m. and p.m.–a.m. groups. We did not find sequence-specific offline improvement in either age group for the a.m.–either p.m. or p.m.–a.m. groups, suggesting that consolidation of this kind of implicit motor sequence learning may not be influenced by sleep.

Keywords Implicit sequence learning · Alternating serial reaction time task · Aging · Sleep · Memory consolidation

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Introduction

Most models of motor skill learning (Doyon et al. 2009a; Hikosaka et al. 1999, 2002) emphasize the role of the basal ganglia and the cerebellum, while the role of hippocampus remains inconclusive (Albouy et al. 2008; Schendan et al. 2003). Motor skill learning can be differentiated into phases (first rapid phase, second slower phase), into modalities (motor, visual, visuomotor, auditory, etc.) and into consciousness types (implicit and explicit) (Doyon et al. 2009a).

Skill learning does not occur only during practice, in the so-called online periods, but also between practice periods, during the so-called offline periods. The process that occurs during the offline periods is referred to as consolidation, and is typically revealed either by increased resistance to interference, and/or by improvement in performance, following an offline period (Krakauer and Shadmehr 2006). Special attention has been given to the role of sleep; for instance, references are made to sleep-dependent consolidation (Walker and Stickgold 2004) suggesting that performance improves more when the offline period includes sleep than when it does not. Several studies showed the critical role of sleep in skill learning consolidation (Fischer et al. 2002; Stickgold et al. 2000; Walker et al. 2002).

Nonetheless, the results concerning offline improvements have been mixed, and recent reviews (Doyon et al. 2009b; Robertson et al. 2004; Siengsukon et al. 2008; Song

2009; Song et al. 2007) indicate that whether or not offline improvements occur at all, and whether they are sleep-dependent, varies with factors, such as phase of learning, awareness, the formation of contextual associations and type of information to be learned, as well as the age of the participants. For example, a recent study by Doyon et al. (2009b) found offline sleep-dependent consolidation for a finger tapping sequence-learning task, but no sleep-dependent consolidation for a visuomotor adaptation task in young people. In another study, which used a sequence-learning task, Spencer et al. (2007) showed that while young adults revealed sleep-dependent offline improvements, healthy older adults did not.

The present study focuses on another distinction that has received little attention in the literature on offline learning, i.e., on separating general skill learning from sequence-specific learning. General skill learning refers to increasing speed as the result of practice with the task, while sequence-specific learning refers to acquisition of sequence-specific knowledge, which results in relatively faster responses for events that can be predicted from the sequence structure versus those that cannot. Most research, including the Doyon and Spencer studies cited above, has not distinguished these, because the tasks used make it difficult to do so.

Here, we use a modified version of the serial response time (SRT) task, the alternating serial reaction time (ASRT) task (Howard and Howard 1997) which enables us to separate general skill learning, and sequence-specific learning. General skill learning is reflected in the overall reaction time (RT), whereas sequence-specific learning is reflected in the difference between the RT of unpredictable, random, and predictable, sequence events. In classical SRT tasks, the structure of a sequence is deterministic with the stimuli following a simple repeating pattern as in the series 213412431423, where numbers refer to distinct events. In contrast, in the ASRT task (Howard and Howard 1997; Remillard 2008) repeating events alternate with random elements. This means that the location of every second stimulus on the screen is determined randomly. If, for instance, the sequence is 1234, where the numbers represent locations on the screen, in the ASRT the sequence of stimuli will be 1R2R3R4R, with R representing a random element. The sequence is thus better hidden than in the classical SRT task and it is also possible to track sequence-specific learning continuously by comparing responses to the random and sequence elements. This structure is referred to as a probabilistic second-order dependency (Remillard 2008). The structure is second-order in that for pattern trials, event $n - 2$ predicts event n. It is probabilistic in that these pattern trials occur amidst randomly determined ones. In addition, participants do not generally become aware of the alternating structure of the sequences even after extended practice, and sensitive recognition tests indicate that people do not develop explicit knowledge of which event-sequences are more likely to occur (Howard and Howard 1997; Howard et al. 2004a, b; Song et al. 2007). Thus, even the predictable alternate events appear unpredictable to the participants.

In a previous study using a different version of the ASRT, Song et al. (2007) studied offline learning in young adults. People were tested on three sessions with an equivalent period of wake or sleep between sessions. Results showed evidence of offline improvement of general skill learning after a period of wakefulness, but no evidence of improvement following sleep. In contrast, there was no evidence of offline improvement in sequence-specific learning following either a period of sleep or wake.

Few studies have examined skill consolidation in older adults. Several studies have shown that old adults show implicit sequence-specific learning comparable to young adults for simple repeating patterns in the SRT task (Frensch and Miner 1994; Howard and Howard 1989, 1992). However, more recent studies have reported that although older adults can learn higher-order sequence structure, they show age-related deficits in doing so (Curran 1997; Howard and Howard 1997; Howard et al. 2004a). It was interesting to find that in one study using a version of the ASRT task, old persons were able to learn even third-order dependencies (1RR2RR3 where R refers to random), although they learned less than the young control group (Bennett et al. 2007). The few studies that have investigated offline learning in old persons (Siengsukon and Boyd 2009a, b; Spencer et al. 2007) did not find offline improvement. Spencer et al. (2007) used an implicit deterministic SRT in order to examine the effect of sleep specifically. Neither offline improvement, nor a sleep effect was shown in elder subjects. However, neither Siensukon et al. (2009b) nor Spencer et al. (2007) distinguished general skill learning from sequence-specific learning in their tasks. The ASRT task has been shown to yield offline general skill learning, but not offline sequence-specific learning in young adults (Song et al. 2007), and so it is important to distinguish between these two aspects of skill learning in older adults. The aim of the current study is to compare offline learning and the role of sleep in young and old adults (1) in implicit sequence-specific learning and (2) in general skill learning separately.

Materials and methods

Participants

The Young group consisted of 25 right-handed subjects (between 19 and 24 years of age, average age: 21, SD 1.2; 9 male/16 female) randomly assigned to the Day group ($n = 11$) or the Night group ($n = 14$). The Aged group consisted of 24 older right-handed subjects (between 60 and 80 years of age, average age: 69.75, SD 7.25; 8 male/16 female) randomly assigned to the Day group ($n = 13$) or the Night group ($n = 11$). Subjects did not suffer from any developmental, psychiatric or neurological disorders did not have sleeping disorders, and all reported having 7–8 h of sleep a day. All subjects provided signed informed consent agreements and received no financial compensation for their participation.

All participants completed a short sleep questionnaire, which was adapted from the one used in Song et al. 2007. It consisted of four questions regarding sleep quantity and quality ("How many hours did you sleep?", "How would you rate your sleep quality?", "How long does it take you to fall asleep?" and "How often do you wake up in the middle of the night or early morning?"), and each question was asked separately for sleep in general, and for the previous night's sleep. Each question could be scored between 0 and 3 (the larger the score, the worse the sleep characteristic). A sleep score was calculated for general sleep and for previous night's sleep for each subject by summing across the four questions (so the sum scores could vary between 0 and 12). Across all participants, the overall mean sleep score for general characteristics was 3.49 (SD 1.28), and that for previous night's characteristics was 2.38 (SD 1.09). There were no significant differences among the groups (Day and Night, Young and Aged; all $P > 0.48$).

Procedure

All groups completed two sessions: a learning phase (Session 1) and a testing phase (Session 2). These sessions were separated by a 12-h interval. For the Day group, the first session was in the morning (between 7 and 8 a.m.) and the second session was in the evening (between 7 and 8 p.m.), with the opposite for the Night group (see Fig. 1a).

Alternating serial reaction time task

We used a modification of the original ASRT task (Howard and Howard 1997) in which a stimulus (a dog head) appeared in one of the four empty circles on the screen and the subject had to press the corresponding key when it occurred (see Fig. 1b). The computer was equipped with a special keyboard with four heightened keys (Y, C, B, and M), each corresponding to the circles. Before beginning, people were read detailed instructions as they followed along on the screen. We emphasized that the aim was to try to respond as quickly and as correctly as possible.

During the first session (learning phase) the ASRT consisted of 25 blocks, with 85 key presses in each block: the first 5 button pressings were random for practice purposes, then the 8-element alternating sequence (e.g., 1R2R3R4R) was repeated 10 times. Following Howard and Howard (1997), stimuli were presented 120-ms following the previous response. As one block took about 1.5 min, the first session took approximately 30–35 min. Between blocks, the subjects received feedback about their overall RT and accuracy on the screen, and then they had a rest of between 10 and 20 s before starting a new block. The second session (testing phase) lasted approximately 10 min as the ASRT consisted only of five blocks to examine the offline changes of previously acquired knowledge. The number of key presses per block and the event timing were the same as Session 1.

The computer program selected a different ASRT series for each subject based on a permutation rule such that each of the six unique permutations of the four repeating events occurred. Consequently, six different sequences were used across subjects, but the sequence for a given subject was identical during Session 1 and Session 2.

To explore how much explicit knowledge subjects acquired about the task, we administered a short questionnaire (the same as Song et al. 2007) after the second session. This questionnaire included increasingly specific questions such as "Have you noticed anything special regarding the task? Have you noticed some regularity in the sequence of stimuli?" The experimenter rated subjects' answers on a 5-item scale, where 1 was "Nothing noticed" and 5 was "Total awareness". None of the subjects in either

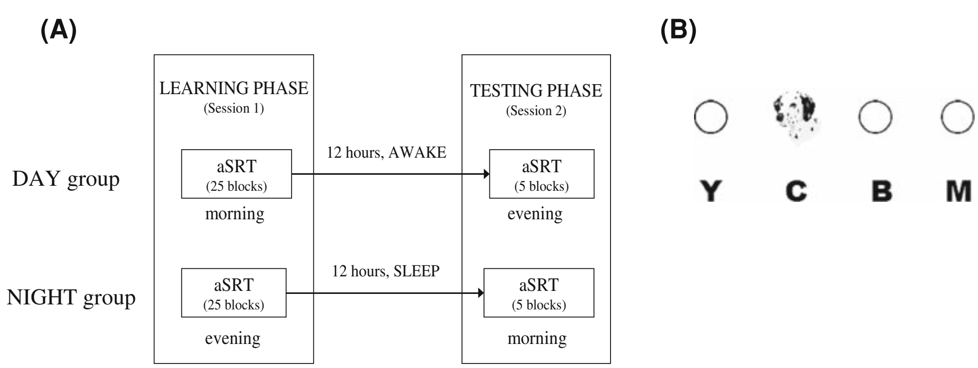

Fig. 1 **a** Design of the experiment: the DAY group stayed awake between the two sessions, whereas the 12 h delay included sleep in the NIGHT group. **b** Example of stimulus displayed on the screen (*top*), and the corresponding keys (*below*)

the young or the older groups reported noticing the sequence in the task.

Statistical analysis

As there is a fixed sequence in the ASRT with alternating random elements (for instance 1R2R3R4R), some triplets or runs of three events occur more frequently than others. For example, in the above illustration 1×2, 2×3, 3×4, and 4×1 would occur often whereas 1×3 or 4×2 would occur infrequently. Following previous studies, we refer to the former as high-frequency triplets and the latter as low-frequency triplets. For the analyses reported below, as in previous research (e.g., Howard et al. 2004b; Song et al. 2007), two kinds of low frequency triplets were eliminated; repetitions (e.g., 222, 333) and trills (e.g., 212, 343). Repetitions and trills are low frequency for all subjects, and people often show pre-existing response tendencies to them (Howard et al. 2004a; Soetens et al. 2004), so eliminating them ensures that any high versus low frequency differences are due to learning and not to pre-existing tendencies. Thus, pattern trials are always high frequency, whereas one-fourth of random trials are high frequency by chance. Of the 64 possible triplets, the 16 high frequency triplets occurred 62.5% of the time and the 48 low frequency triplets occurred 37.5% of the time. Thus, each low-frequency triplet occurs on approximately 0.8% of the trials whereas each high-frequency triplet occurs on approximately 4% of the trials, about 5 times more often than the low-frequency triplets. Note that the final event of high-frequency triplets is, therefore, more predictable from the initial event compared to the low-frequency triplets.

Earlier results have shown that as people practice the ASRT task, they come to respond more quickly to the high- than low-frequency triplets revealing sequence-specific learning (Howard and Howard 1997; Howard et al. 2004a; Song et al. 2007). In addition, general skill learning is revealed in the ASRT task in the overall speed with which people respond, irrespective of the triplet types. Thus, we are able to obtain measures of both sequence-specific and general skill learning in the ASRT task.

To facilitate data processing, the blocks of ASRT were organized into epochs of five blocks. The first epoch contains blocks 1–5, the second epoch blocks 6–10, etc. (Barnes et al. 2008; Bennett et al. 2007).

Subjects' accuracy remained very high throughout the test (average over 97% for all groups), as is typical (e.g., Howard and Howard 1997), and so we focus on RT for the analyses reported. For RT, we calculated medians for correct responses only, separately for high- and low-frequency triplets and for each subject and each epoch.

Results

Online learning during Session 1

To investigate learning during the first session (learning phase), a mixed design ANOVA was conducted on the first 5 epochs of the data shown in Fig. 2a, b with (Triplet: high vs. low) and (Epoch: 1–5) as within-subjects factors, and Age group (young vs. old) and Day group (day vs. night) as between-subjects factors. There was significant sequence-specific learning (indicated by the significant main effect of Triplet: $F(1,45) = 93.08$, MSE = 89.57, $P < 0.0001$) such that RT was faster on high- than low-frequency triplets (Bennett et al. 2007). There was also general skill learning (shown by the significant main effect of Epoch: $F(4,180) = 42.49$, MSE = 1,928.87, $P < 0.0001$), such that RT decreased across epochs.

The only significant effect involving Day group was an interaction with Age group: $F(1,45) = 5.89$, MSE = 24,677.52, $P = 0.02$. Subsequent t tests revealed that the young group who had been tested first in the a.m. had overall faster RTs than those tested first in the p.m. (389 vs. 414 ms): $t(23) = 2.09$, $P = 0.048$, whereas the older groups showed the reverse pattern, even though the difference was not significant for the older groups (614 vs. 574 ms), $t(22) = 1.59$, $P = 0.12$. It is not clear why these differences occurred, but they are not important for interpreting the offline results in that they do not involve learning. Importantly, no other effects involving Day group approached significance (all $P > 0.26$).

The ANOVA also revealed three significant age differences, all consistent with previous findings. First, young people responded faster overall than older (shown by the main effect of Age group: $F(1,45) = 192.87$, MSE = 24,677.52, $P < 0.0001$). Second, young people revealed greater sequence-specific learning than older (shown by the Triplet × Age group interaction: $F(1,45) = 7.68$, MSE = 89.57, $P = 0.008$). Third, old people showed more general skill learning than young people (shown by the Epoch × Age group interaction: $F(4,180) = 16.41$, MSE = 1,928.87, $P < 0.0001$). Older adults' RT decreased from 675 ms in Epoch 1 to 550 ms in Epoch 5, while young subjects' decreased from 420 to 380 ms. Subsequent Triplet × Epoch × Day group mixed design ANOVAs, conducted separately for each age group confirmed that when examined alone, each age group showed both general skill learning and sequence-specific learning. For the young group, there was a main effect of Epoch, $F(4,92) = 6.54$, MSE = 32.53, $P < 0.0001$, and of Triplet, $F(1,23) = 124.00$, MSE = 56.65, $P < 0.0001$, and an Epoch × Triplet interaction, $F(4,92) = 6.54$, MSE = 32.54, $P < 0.0001$. For the old group, there were main effects of Epoch, $F(4,88) = 28.21$,

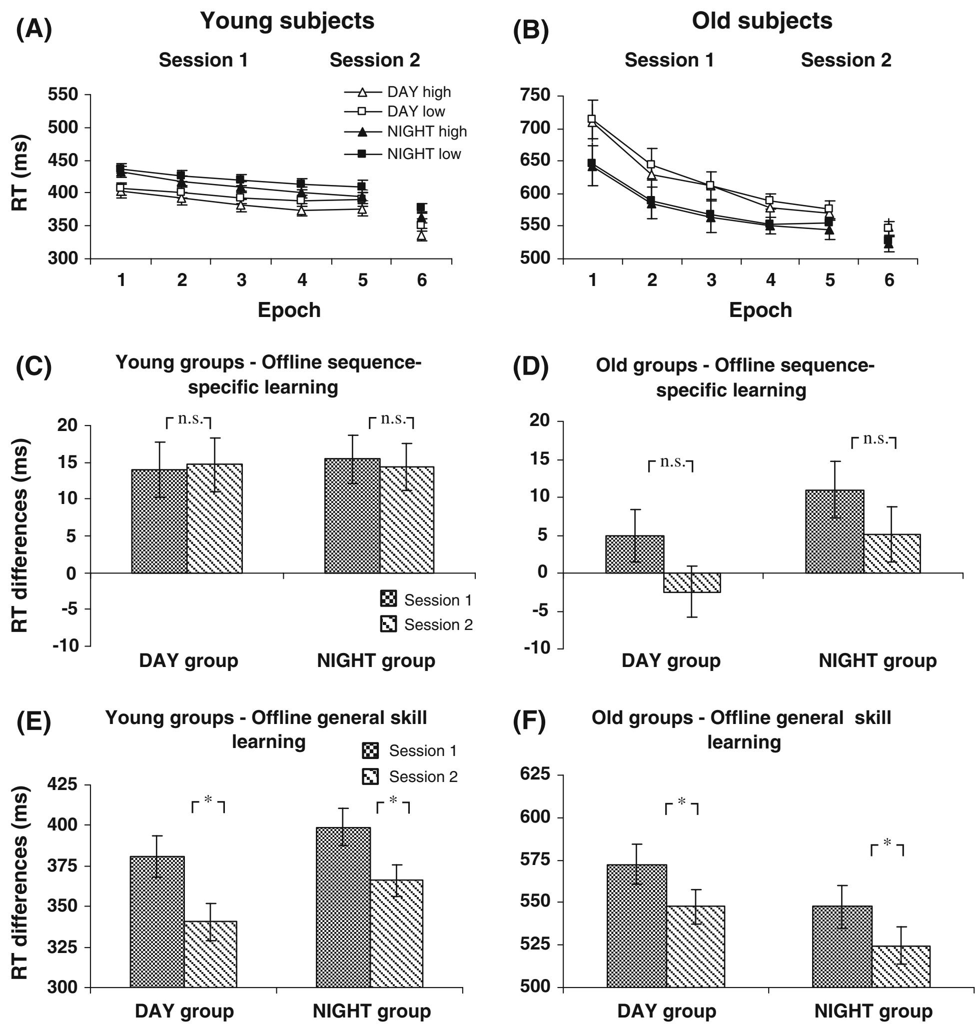

Fig. 2 **a**, **b** Results of Session 1 (Epoch 1–5) and Session 2 (Epoch 6) for young (**a**) and old (**b**) subjects. The differences between the high (*open* and *filled triangles*) and low frequency (*open* and *filled squares*) triplets indicate sequence-specific learning, whereas the *decrease* of *RT* (regardless of triplet types) indicates general motor skill learning. In Session 1 all groups showed significant sequence-specific and general motor skill learning, but the extent of sequence-specific learning was smaller for old subjects than for young ones. **c**, **d** Results of offline sequence-specific learning for young (**c**) and old adults (**d**). The learning index of the last epochs of Session 1 does not differ significantly from that of the first epochs of Session 2 neither in young (**c**) nor in old groups (**d**), suggesting that there is no offline sequence-specific improvement (*n.s.* non-significant). There were no differences between DAY and NIGHT groups (no sleep effect). **e**, **f** Results of offline general motor skill learning for YOUNG (**e**) and OLD groups (**f**). Offline general motor skill learning (calculated by the difference between the last epoch of Session 1 and the first of Session 2, regardless of triplet types) appeared both in young (**e**) and old (**f**) groups (*stars* mark the significant differences). There were no differences between DAY and NIGHT groups (no sleep effect). *Error bars* indicate SEM

MSE = 3,749.98, $P < 0.0001$, and of Triplet, $F(1,22) = 16.80$, MSE = 123.99, $P = 0.0005$.

Offline sequence-specific learning

To define the index for offline sequence-specific learning, we calculated the RT difference for the low- minus high-frequency triplets for the last epoch of Session 1. This index shows the magnitude of learning at the end of the first session. Then, similarly, we calculated the RT difference for the low- minus high-frequency triplets for the first epoch of Session 2. These difference scores (shown in Fig. 2c, d) were submitted to a mixed design ANOVA with Session (1–2) as a within-subject factor and AGE group (young vs. old) and Day group (day or night) as between-subject factors. Thus, any offline consolidation of sequence-specific learning would be revealed by main effects and/or interactions with session. However, the only significant effect obtained was a main effect of Age group, $F(1.45) = 14.57$, MSE = 166.27, $P = 0.0004$, reflecting the smaller magnitude of sequence-specific learning in both sessions in the Old group compared to the Young. No other main effects or interactions approached significance (all $P > 0.15$). Thus, there was no evidence of offline changes (improvement or decrease) of sequence-specific knowledge regardless of Age or Day group.

Offline general skill learning

To examine offline general skill learning, we calculated the overall RT (combined across triplet types) for the last epoch of Session 1 and the first epoch of Session 2; the greater the decrease from Session 1 to 2, the larger the offline general skill learning. These RTs (shown in Fig. 2e, f) were submitted to a mixed design ANOVA with Session (1–2) as a within-subjects factor and Age group (young vs. old) and Day group (day or night) as between subject factors. Thus, any offline consolidation of general skill would be revealed by main effects and/or interactions with session. This ANOVA revealed a main effect of age group, reflecting the overall longer RTs for the old than the young group, $F(1,45) = 257.64$, MSE = 2,933.77, $P < 0.0001$, and an Age group × Day group interaction, $F(1,45) = 4.32$, MSE = 2,933.77, $P = 0.043$. This interaction again reflects the finding from Session 1 that the Young a.m. group has overall faster RT than the Young p.m. group, $t(48) = 2.02$, $P = 0.048$, whereas the Old groups show the reverse pattern (though the a.m./p.m. difference is only marginally significant for the older groups) $t(46) = 1.80$, $P = 0.08$. The fact that this effect does not interact with session ($P > 0.65$) suggests that we happened to assign slightly faster young people to the a.m. group; if this were a true time of day effect then we would not expect it to occur for the Young a.m. group for both of their testing sessions. Further, Song et al. (2007) included diurnal control groups in their study, and were able to rule out time of day effects as explanations for offline changes in the ASRT.

More important for present purposes, this ANOVA revealed evidence of offline improvement of general skill in that the main effect of session was significant, $F(1,45) = 96.76$, MSE = 228.62, $P < 0.0001$, reflecting the faster overall RTs for Session 2 compared to those at the end of Session 1. The Session × Age group interaction was also significant, $F(1,45) = 4.20$, MSE = 228.62, $P = 0.046$, indicating that the Young group (mean improvement of 36 ms) showed more offline improvement than the Old (mean improvement of 24 ms). Importantly, there was no evidence that offline consolidation depended upon sleep, in that no interactions involving session and Day group approached significance (Ps > 0.45). It is also possible that the improvement in RT reflects a release from fatigue rather than consolidation per se. However, studies that have included a fatigue control group (Spencer et al. 2006; Walker et al. 2002) suggest that this interpretation is unlikely.

Subsequent Session × Day group mixed design ANOVAs, conducted separately for each age group confirmed that when examined alone, each age group showed consolidation of general skill learning, in that both groups yielded significant main effects of session: for the Young group, $F(1, 23) = 105.23$, MSE = 156.03, $P < 0.0001$, and for the Old group $F(1,22) = 22.40$, MSE = 304.50, $P < 0.0001$. Thus, although the overall ANOVA had revealed that the young group showed more offline improvement of general skill than the old, the Old group did show significant consolidation of general skill as well.

This evidence for offline consolidation of general skill relies on comparing RT on Epoch 6 to that on Epoch 5, so it is possible that the faster RT on Epoch 6 is simply due to learning that occurred during Epoch 6. To rule out this possibility, we compared the difference in overall RT between the last two epochs within Session 1 (Epoch 4 − 5) versus the change across sessions (Epoch 5 − 6). This difference was significantly greater across sessions than within sessions for both age groups, $t(23) = 6.665$, $P < 0.0001$ for old, and $t(24) = 13.164$, $P < 0.0001$ for young. This suggests that the offline effects we observed were not simply due to continued learning.

Discussion

The novelty of the present research compared to previous studies of consolidation in older adults (Siengsukon and Boyd 2009b; Spencer et al. 2007) is that (1) it used probabilistic second-order sequences, and (2) it dealt separately with general skill learning and sequence-specific learning. In our study, we focused on the offline changes and the role of sleep in implicit sequence learning in young and elder adults. In the case of general skill learning, we found significant offline improvement for both the young and older groups, although the effect was significantly smaller in the Old than in the Young. We found no evidence that this improvement was sleep-dependent in that there were no differences between the Day (a.m.–p.m.) and the Night (p.m.–a.m.) groups in the offline consolidation of general skill. In the case of sequence-specific learning, we found no offline improvement, in that the RT difference between low- and high-frequency triplets (i.e., the triplet type effect) did not increase between sessions for any group. This occurred despite the fact that there was significant sequence-specific learning for all groups in Session 1. In addition, the fact that the triplet type effect did not decrease significantly between sessions for any of the groups, suggests that sequence-specific knowledge was well consolidated for all groups. However, circadian effects could still have different effects on the consolidation processes.

The results of the Young group in the current study largely confirm the results of Song et al. (2007) in finding no evidence of any offline improvement of sequence-specific skill, and extend them to older adults. However, Song et al. (2007) found general skill improvement only in the no-sleep condition, whereas, we found it in both conditions. The reason for this difference in findings is unclear. The most notable difference between our and Song's study is that we used less training in the learning phase (5 vs. 9 epochs). The resulting greater skill learning in Song et al. (2007)in the first session may have left less room overall for participants to show offline improvement.

Our results are similar to those of Spencer et al. (2007) and Siengsukon and Boyd (2009b) in showing no sleep-dependent consolidation in older adults. However, unlike these studies, which had detected no offline improvement at all in older adults, the current study shows clear evidence of significant offline improvement of general skill learning in older adults over periods of both sleep and wake. These previous studies differed from the present study in many ways, so it is difficult to identify the source of the different findings. For example, they used deterministic rather than probabilistic sequences and gave less training. Our results do suggest that offline improvement is reduced in old compared to young adults, and this may have made it difficult for the previous studies to detect any offline improvements in the older group.

The differences between our findings and those of earlier studies underscore that the role of sleep in offline consolidation is likely task dependent. This is consistent with the conclusions of Doyon et al. (2009b), who found sleep benefits in a finger tapping sequence-learning task, but not in a visuomotor adaptation task with young adults. Future studies should investigate which of the many task differences influence offline learning and sleep effects. Beyond that, the present findings demonstrate that it will also be important to distinguish general skill from sequence-specific learning. For example, it is possible that the offline improvements reported by Doyon et al. (2009b) in the finger-tapping task reflect consolidation of general motor rather than sequence-specific skill. Given that these components are typically inseparable in finger tapping tasks, offline improvements in such studies might be falsely attributed to sequence learning. The present results from both young and old adults join Song et al.'s findings from young adults in suggesting that, at least in the version of the ASRT task used here, general skill, but not sequence-specific learning undergoes offline improvement. Given the likely importance of task factors mentioned above, future research must investigate whether this conclusion holds under other conditions, such as different amounts of initial training and other levels of sequence structure. It will also be useful to include diurnal control groups to ensure that circadian effects are not influencing consolidation in ways we could not detect.

Our findings well complement motor skill learning models (Doyon et al. 2009a; Hikosaka et al. 1999, 2002), and draw attention to the importance of separating general skill and sequence-specific learning during consolidation, and to the question whether these two factors may be differently influenced by nervous system modifications caused by aging.

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References

Albouy G, Sterpenich V, Balteau E, Vandewalle G, Desseilles M, Dang-Vu T, Darsaud A, Ruby P, Luppi PH, Degueldre C, Peigneux P, Luxen A, Maquet P (2008) Both the hippocampus and striatum are involved in consolidation of motor sequence memory. Neuron 58:261–272

Barnes KA, Howard JH Jr, Howard DV, Gilotty L, Kenworthy L, Gaillard WD, Vaidya CJ (2008) Intact implicit learning of spatial context and temporal sequences in childhood autism spectrum disorder. Neuropsychology 22:563–570

Bennett IJ, James H, Howard J, Howard DV (2007) Age-related differences in implicit learning of subtle third-order sequential structure. J Gerontol Psychol Sci 62(B):98–103

Curran T (1997) Effects of aging on implicit sequence learning: accounting for sequence structure and explicit knowledge. Psychol Res 60:24–41

Doyon J, Bellec P, Amsel R, Penhune V, Monchi O, Carrier J, Lehericy S, Benali H (2009a) Contributions of the basal ganglia and functionally related brain structures to motor learning. Behav Brain Res 199:61–75

Doyon J, Korman M, Morin A, Dostie V, Hadj Tahar A, Benali H, Karni A, Ungerleider LG, Carrier J (2009b) Contribution of night and day sleep versus simple passage of time to the consolidation of motor sequence and visuomotor adaptation learning. Exp Brain Res 195:15–26

Fischer S, Hallschmid M, Elsner AL, Born J (2002) Sleep forms memory for finger skills. PNAS 99:11987–11991

Frensch PA, Miner CS (1994) Effects of presentation rate and individual differences in short-term memory capacity on an indirect measure of serial learning. Mem Cognit 22:95–110

Hikosaka O, Nakahara H, Rand MK, Sakai K, Lu X, Nakamura K, Miyachi S, Doya K (1999) Parallel neural networks for learning sequential procedures. TINS 22:464–471

Hikosaka O, Nakamura K, Sakai K, Nakahara H (2002) Central mechanisms of motor skill learning. Curr Opin Neurobiol 12:217–222

Howard DV, Howard JH Jr (1989) Age differences in learning serial patterns: direct versus indirect measures. Psychol Aging 4:357–364

Howard DV, Howard JH (1992) Adult age differences in the rate of learning serial patterns: evidence from direct and indirect tests. Psychol Aging 7:232–241

Howard JH Jr, Howard DV (1997) Age differences in implicit learning of higher-order dependencies in serial patterns. Psychol Aging 12:634–656

Howard DV, Howard JH Jr, Japikse K, DiYanni C, Thompson A, Somberg R (2004a) Implicit sequence learning: effects of level of structure, adult age, and extended practice. Psychol Aging 19:79–92

Howard JH Jr, Howard DV, Dennis NA, Yankovich H, Vaidya CJ (2004b) Implicit spatial contextual learning in healthy aging. Neuropsychology 18:124–134

Krakauer JW, Shadmehr R (2006) Consolidation of motor memory. Trends Neurosci 29:58–64

Remillard G (2008) Implicit learning of second-, third-, and fourth-order adjacent and nonadjacent sequential dependencies. Q J Exp Psychol (Colchester) 61:400–424

Robertson EM, Pascual-Leone A, Press DZ (2004) Awareness modifies the skill-learning benefits of sleep. Curr Biol 14:208–212

Robertson EM, Press DZ, Pascual-Leone A (2005) Off-line learning and the primary motor cortex. J Neurosci 25:6372–6378

Schendan H, Searl M, Melrose R, Stern C (2003) An FMRI study of the role of the medial temporal lobe in implicit and explicit sequence learning. Neuron 37:1013–1025

Siengsukon CF, Boyd LA (2009a) Does sleep promote motor learning? Implications for physical rehabilitation. Phys Ther 89:370

Siengsukon CF, Boyd LA (2009b) Sleep to learn after stroke: implicit and explicit off-line motor learning. Neurosci Lett 451:1–5

Siengsukon CF, Siengsukon CF, Boyd LA (2008) Sleep enhances implicit motor skill learning in individuals poststroke. Top Stroke Rehabil 15:1

Soetens E, Melis A, Notebaert W (2004) Sequence learning and sequential effects. Psychol Res 69:124–137

Song S (2009) Consciousness and the consolidation of motor learning. Behav Brain Res 196:180–186

Song S, Howard JH Jr, Howard DV (2007) Sleep does not benefit probabilistic motor sequence learning. J Neurosci 27:12475–12483

Spencer RM, Sunm M, Ivry RB (2006) Sleep-dependent consolidation of contextual learning. Curr Biol 16:1001–1005

Spencer RM, Gouw AM, Ivry RB (2007) Age-related decline of sleep-dependent consolidation. Learn Mem 14:480–484

Stickgold R, Malia A, Maguire D, Roddenberry D, O'Connor M (2000) Replaying the game: hypnagogic images in normals and amnesics. Science 290:350–353

Walker MP, Brakefield T, Morgan A, Hobson JA, Stickgold R (2002) Practice with sleep makes perfect: sleep-dependent motor skill learning. Neuron 35:205–211