Nemeth, D., & Janacsek, K. (2010). The Dynamics of Implicit Skill Consolidation in Young and Elderly Adults. *Journal of Gerontology: Psychological Sciences, 66B(1)*, 15–22, doi:10.1093/geronb/gbq063. Advance Access published on October 7, 2010.

The Dynamics of Implicit Skill Consolidation in Young and Elderly Adults

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Objectives. Implicit skill learning underlies not only motor but also cognitive and social skills; it is therefore an important aspect of life from infancy to old age. We studied aging effects on the time course of implicit skill consolidation.

Methods. Young and elderly adults performed a probabilistic implicit sequence-learning task before and after a 12-, a 24-hr, and a 1-week interval. The task enabled us to separate the components of skill learning and consolidation: (a) general skill and (b) sequence-specific learning (SSL).

Results. We found improvement of general skill for the young adults in all delay conditions. The elderly adults also showed enhancement after the 12-hr period, revealing brain plasticity similar to young adults. This improvement disappeared in the 24-hr and the 1-week delay conditions. Regarding SSL, no improvement was found in either age group and at either consolidation intervals. In contrast, sequences-specific knowledge decreased in the elderly group independently of the delay.

Discussion. These results draw attention to the fact that consolidation is not a single process, rather there are multiple mechanisms that are differentially affected by time course and by aging.

Key Words: Aging—ASRT—Implicit sequence learning—Memory consolidation—Skill learning.

Introduction

Skill learning can be differentiated by phases (rapid and slower), modalities, and whether or not it is conscious (implicit and explicit) (Doyon, Bellec, et al., 2009). Implicit skill learning occurs when information is acquired from an environment of complex stimuli without conscious access either to what was learned or to the fact that learning occurred (Reber, 1993). In everyday life, this learning mechanism is crucial for adapting to the environment and evaluate events unconsciously. Implicit skill learning underlies not only motor but also cognitive and social skills (Lieberman, 2000; Ullman, 2004); it is therefore an important aspect of life from infancy to old age. Implicit skills remain essential to healthy functioning with the advancement of age in various contexts, such as social interactions, everyday habits, or reading skills. Social skills appear in compound behaviors realized in proper sequences and under appropriate circumstances. These skills (e.g., communication of emotions) are needed for normal social functioning in various sorts of situations: in the workplace, in the family, in the neighborhood, during recreation, shopping, or in the context of medical and mental care. Furthermore, these skills are crucial for an effective participation in educational, training, and rehabilitation programs. Most models of skill learning (Doyon, Bellec, et al., 2009; Hikosaka et al., 1999; Hikosaka, Nakamura, Sakai, & Nakahara, 2002; Keele, Ivry, Mayr, Hazeltine, & Heuer, 2003; Kincses et al., 2008) emphasize the role of the basal ganglia and the cerebellum. Skill learning does not occur only during practice, in the so-called "online" periods, but also between practice periods, during the so-called "off-line" periods. The process that occurs during the off-line periods is referred to as consolidation, which means stabilization of a memory trace after the initial acquisition; it can result increased resistance to interference or even improvement in performance following an off-line period (Krakauer & Shadmehr, 2006; Nemeth et al., 2010; Robertson, 2009; Song, 2009). Understanding the time course of skill consolidation can help us reveal the nature of aging memory and age-related changes in brain plasticity.

Recent reviews conclude that off-line changes vary with factors such as the phase and awareness of learning, the formation of contextual associations, the type of information to be learned, as well as the age of the participants (Brashers-Krug, Shadmehr, & Bizzi, 1996; Deroost & Soetens, 2006; Doyon, Korman, et al., 2009; Jiménez, Vaquero, & Lupiáñez, 2006; Keele et al., 2003; Robertson, Pascual-Leone, & Press, 2004; Siengsukon & Boyd, 2008; Song, 2009; Song, Howard, & Howard, 2007). Studies on the time course of skill consolidation indicate that there is a "critical period" after the learning phase, which is necessary for the stabilization of memory traces. This time period depends on the task demand, and it varies from 1 to 2 hr (Robertson, Press, & Pascual-Leone, 2005), to 5 hr (Shadmehr & Brashers-Krug, 1997; Shadmehr & Holcomb, 1997), or 6 hr (Walker, Brakefield, Hobson, & Stickgold, 2003). Using the serial reaction time (SRT) task, which is a widely known sequence-learning paradigm, one study found that the off-line

Received October 4, 2009; Accepted July 31, 2010
Decision Editor: Elizabeth Stine-Morrow, PhD

enhancement increased with the length of delay (Press, Casement, Pascual-Leone, & Robertson, 2005). In this SRT study, no enhancement was found 1 hr after the learning phase, but significant enhancement was observed after 4 hr, which further increased after 12 hr. These results suggest that off-line learning may be a dynamic process. However, this study examined only a shorter stretch of time, so the question can be raised, what happens in skill consolidation after more than 12 hr.

The modified version of SRT is the alternating serial reaction time (ASRT) task (Howard & Howard, 1997), which enables us to separate general skill learning and sequence-specific learning (SSL). In the ASRT task, repeating events alternate with random ones in an eight-element sequence so that the location of every second stimulus in the stream is determined randomly (e.g., 1*R*2*R*3*R*4*R*, where the numbers represent the repeating events, and *R* represents random stimulus events). This sequence structure has been termed "probabilistic second-order dependency" (Remillard, 2008), because to predict stimulus "n," we need only to remember stimulus $n - 2$ in the sequence, regardless of stimulus $n - 1$. The repeating sequence in the ASRT task is better hidden than in the classical SRT task (e.g., Press et al., 2005), so that the task relies more on implicit mechanisms of learning (Howard & Howard, 1997; Song et al., 2007). Why are the properties of the ASRT interesting in everyday life in aging? The key factor is the implicit nature of the task. In everyday life, we use explicit, conscious, and implicit, nonconscious processes at the same time to do a task (e.g., typing on the computer or learning a foreign language). These processes interact in cooperative and sometimes competitive ways (Brown & Robertson, 2007; Poldrack & Packard, 2003; Song, Marks, Howard, & Howard, 2009) in order to optimize the memory performance (Ullman, 2004). It has long been known that there is age-related decline in explicit memory and executive functions (Cowan, Naveh-Benjamin, Kilb, & Saults, 2006; Craik & Bialystok, 2006; Craik & Salthouse, 2000; Einstein & McDaniel, 1990). It is therefore possible that the efficiency of acquiring new skills decreases in older ages because of these weaker explicit processes and not because of the impairment of pure implicit skill learning. In the ASRT task, explicit memory processes and conscious awareness on sequence learning are almost totally eliminated. That is why it can model implicit learning better than other tasks. So, finding intact learning in the ASRT task could suggest that everyday difficulties regarding skill learning are mainly due to weak explicit processes.

Several studies using the ASRT task demonstrated that older adults show age-related deficits in online skill learning (Curran, 1997; Howard et al., 2004; Howard & Howard, 1997). However, little is known about the effects of aging on skill consolidation and its time course (Siengsukon & Boyd, 2009; Spencer, Gouw, & Ivry, 2007).

Previous studies using the ASRT task focused primarily on whether sleep affects skill consolidation and have concluded that these processes are not influenced by sleep (Nemeth et al., 2010; Song et al., 2007). For example, in a recent ASRT study, Nemeth and colleagues investigated implicit skill learning after 12-hr off-line period. The novelty of this research compared with previous studies of consolidation in older adults (Siengsukon & Boyd, 2009; Spencer et al., 2007) was that (a) it used probabilistic second-order sequences and (b) it dealt separately with general skill and SSL (relatively faster responses to repeated patterns). They showed that general skill learning, as assessed via overall reaction time (RT), improved off-line in both the young and older groups, with the young group improving more than the old group. However, the improvement was not sleep dependent, in that it was not relevant whether the 12-hr off-line period included sleep or not. They did not find sequence-specific off-line improvement in either age group, and similarly to general skill learning, it was not influenced by sleep. However, this study did not examine the consolidation of skills after more than 12 hr in healthy aging.

The current experiment was designed to study the effects of aging on the off-line time course of implicit skill learning. The present study goes beyond Nemeth and colleagues (2010) and other previous studies (Press et al., 2005; Siengsukon & Boyd, 2009; Spencer et al., 2007) by comparing the performance after 12-, 24-hr, and 1-week delays from the initial learning session. We focused on the consolidation of implicit SSL and, separately, general skill learning between young and elderly adults. Despite the results of previous studies that found greater improvement after longer off-line periods (more after 12 hr compared with 4 hr, see Press et al.), it is less plausible that this is true for 12-, 24-hr, and 1-week delays as well. Therefore, we aim to determine a time point in a longer stretch of time at which improvement can still be observed in skill consolidation and analyze its possible age-related differences.

Methods

Participants

Seventy-one young and 58 elderly right-handed adults participated in the experiment. They were randomly assigned to the 12-, 24-hr, or 1-week delay group (70% of the 12-hr groups were also presented in the study of Nemeth et al., 2010). The age and education of participants were controlled (for detailed data, see Table 1). Participants did not suffer from any developmental, psychiatric, or neurological disorders, did not have sleeping disorders, and all reported having 7–8 hr of sleep a day. Participants were recruited from Szeged and Bekescsaba (Hungary). They gave informed written consent after the aims and procedures of the experiment were explained to them and received no financial compensation for participation.

Table 1. Mean Age, Education, and Sex of Young and Elderly Groups

Group		Age (years)	Education (years)	Sex
Young	12 hr (n = 23)	20.83 (1.11)	13.48 (1.27)	8 men/15 women
	24 hr (n = 31)	21.74 (4.15)	14.77 (2.13)	12 men/ 19 women
	1 week (n = 17)	19.88 (1.27)	13.65 (1.32)	3 men/14 women
Elderly	12 hr (n = 23)	66.43 (6.18)	12.90 (3.26)	7 men/14 women
	24 hr (n = 22)	67.36 (5.30)	13.84 (2.44)	5 men/17 women
	1 week (n = 13)	65.15 (4.14)	14.23 (2.00)	6 men/7 women

Procedure

There were two sessions in the experiment to examine the off-line changes of implicit skill learning: a learning phase (Session 1) and a testing phase (Session 2) separated by a 12-, 24-hr, or 1-week interval off-line period (see Figure 1). Previous studies with similar tasks and experimental designs showed no time of day effect either on general RTs or on learning measures (Nemeth et al., 2010; Press et al., 2005; Robertson et al., 2004; Song et al., 2007); the time of testing was however controlled in our study.

ASRT Task

We used a modification of the original ASRT task (Howard & Howard, 1997) in which a stimulus (a dog head) appeared in one of the four empty circles shown all the time on the screen (Nemeth et al., 2010). Participants were instructed to press one of four possible response keys on an IBM PC keyboard as fast as they could to indicate the location of the stimulus. Each response key (Y, C, B, or M on Hungarian keyboard) was assigned to one of the four stimulus locations on the screen.

During Session 1 (learning phase), the ASRT task consisted of 25 blocks, with 85 stimuli in each block. For practice purposes, the locations of the first five stimuli of each stimulus block were always random. These were followed by the eight-element sequence (e.g., 1*R*2*R*3*R*4*R*) repeating

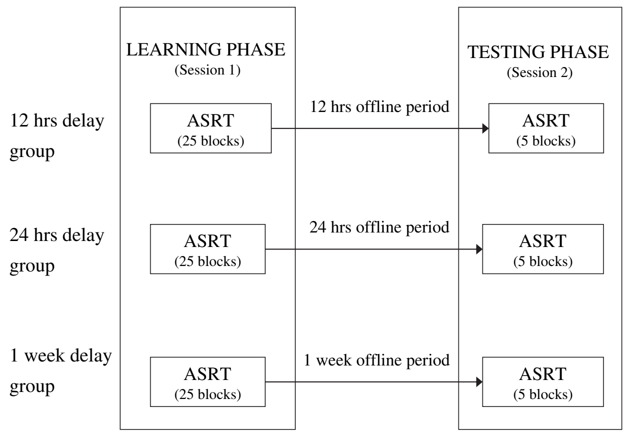

Figure 1. The design of the experiment.

10 times. Following the design of Howard and Howard (1997), stimuli were presented 120 ms after the response to the previous stimulus. Between stimulus blocks, the subjects received feedback about their overall RT and accuracy presented on the screen, and then they had a rest period of between 10 and 20 s before starting the next stimulus block. Session 2 (testing phase) consisted of only five stimulus blocks of the same type as in Session 1.

The computer program selected a different ASRT sequence for each subject based on a permutation rule such that each of the six unique permutations of the four repeating events occurred with equal probability (Howard & Howard, 1997; Nemeth et al., 2010). The repeating sequence was identical between Session 1 and Session 2 for each participant.

To explore how much explicit knowledge subjects acquired about the task, we administered a short questionnaire (the same as Song et al., 2007 and Nemeth et al., 2010) 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 the participants' answers on a 5-point scale, where 1 meant *Nothing noticed* and 5 meant *Total awareness*. None of the participants reported noticing the repeating sequence of the stimulus locations.

Statistical Analysis

Because in ASRT a repeating sequence alternates with random events, some runs of three consecutive events (termed triplets) occur more frequently than others. For example, with the 1*R*2*R*3*R*4*R* sequence, 1x2, 2x3, 3x4, and 4x1 (where "x" denotes any location) would occur more often than e.g., 1x3 or 4x2. We refer to the former as "high-frequency" triplets and the latter as "low-frequency" triplets. The triplets including two consecutive repeating-sequence stimuli were always of high-frequency triplets, whereas one-fourth of the triplets that included two consecutive random stimulus events were high-frequency by chance, the rest being low frequency. 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. Note that the final event of high-frequency triplets is therefore more predictable from the initial event compared with the low-frequency triplets. Previous results showed that as participants practice the ASRT task, they come to respond more quickly to the high- than to low-frequency triplets, thus revealing SSL (Howard et al., 2004; Howard & Howard, 1997; Song et al., 2007). Therefore, SSL is reflected in the RT difference between low- and high-frequency triplets (Song, Howard, & Howard, 2008; Song et al., 2007). The larger this SSL score, the greater the SSL is. In addition, general skill learning is revealed in the ASRT task in the improving overall response speed, irrespective of the triplet types. To facilitate data processing, stimulus blocks were organized into larger clusters (called epochs); where the first epoch contained blocks 1–5, the second epoch blocks 6–10, etc. (Barnes et al., 2008; Bennett, Howard, & Howard, 2007). Consequently, Session 1 consisted of 5 epochs, whereas Session 2 consisted of 1 epoch.

The accuracy of responses remained very high throughout the test (average over 97% for all groups), as is typical (e.g., Howard and Howard, 1997 and Nemeth et al., 2010). Therefore, we analyzed the median RT for correct responses only, calculated separately for high- and low-frequency triplets and for each epoch.

Results

Online Learning—Session 1

To be able to investigate the off-line changes, the learning in Session 1 must be similar in the groups. From this point of view, the end of Session 1 is crucial (Nemeth et al., 2010; Press et al., 2005; Song et al., 2007). Therefore, SSL score was computed for RTs on low- minus high-frequency triplets in Epoch 5 (Song et al., 2007, 2008). The larger this difference, the greater the SSL was. This score was submitted to a univariate analysis of variance (ANOVA) with age group (young versus older) and delay (12, 24 hr, or 1 week) as between-subject factors. The ANOVA revealed significant SSL (F(1,123) = 136.69, mean square error (MSE) = 157.95, $\eta_p^2 = .53$, $p < .00001$). Neither the main effects of age group and delay nor the Age group × Delay interaction was significant (p's > .19); thus, there were no differences in SSL among age groups or delays at the end of Session 1(see Figure 2A,B).

Regarding the general skill, a univariate ANOVA was conducted on overall RTs of Epoch 5 (collapsed across triplet types) with age group (young versus older) and delay (12, 24 hr, or 1 week) as between-subject factors. The only significant effect was the main effect of age group (F(1,123) = 409.89, MSE = 1784.08, $\eta_p^2 = .77$, $p < .001$) reflecting longer RTs for the elderly group (537 ms) compared with the younger participants (381 ms). The main effect of delay and Age group × Delay interaction did not approach significance (all p's > .41). Thus, participants responded with similar overall RTs in all delay conditions (see Figure 2C,D).

Off-line SSL

To define the index of off-line SSL, we calculated the SSL score at the first epoch of Session 2 similarly to the learning score in Session 1 (Epoch 5). The greater this score at the beginning of the Session 2 compared with the end of Session 1, the larger the off-line SSL was. These two SSL scores were submitted to a mixed-design ANOVA with session (end of Session 1 versus beginning of Session 2) as within-subject factor and age group (young versus elder) and delay (12, 24 hr, or 1 week) as between-subject factors. Thus, any off-line change of SSL would be revealed by main effects and/or interactions with session.

The main effect of SESSION was not significant (F(1,123) = 2.28, MSE = 178.4, $\eta_p^2 = .02$, $p = .13$). However, the ANOVA revealed significant main effect of age group (F(1,123) = 15.01, MSE = 194.89, $\eta_p^2 = .11$, $p < .001$) and significant Session × Age group interaction (F(1,123) = 5.35, MSE = 178.4, $\eta_p^2 = .04$, $p = .02$) reflecting that age groups differed in off-line SSL. Sequence-specific knowledge decreased in the elderly groups (−6 ms) compared with the young, who retained the previously acquired skill (1 ms). There was no off-line improvement of sequence-specific knowledge in either group.

Regarding the time course, there were no differences among delay conditions (neither the main effect nor the interactions with delay was significant, p's > .38); thus, the consolidation of sequence-specific knowledge was not affected by the elapsed time between the learning and the testing session (see Figure 2E).

Off-line General Skill Learning

Off-line general skill learning was tested by comparing the overall RTs (collapsed across triplet types) between the last epoch of Session 1 and the first epoch of Session 2 (see Figure 2F). The greater the decrease from Session 1 to Session 2, the larger the off-line general skill learning was. These two variables were submitted to a mixed-design ANOVA with session (end of Session 1 versus beginning of Session 2) as within-subject factor and age group (young versus older) and delay (12, 24 hr, or 1 week) as between-subject factors. Similarly to previous analysis, any off-line change of general skill would be revealed by main effects and/or interactions with session.

This ANOVA revealed significant off-line general skill improvement (indicated by the main effect of session: F(1,123) = 27.88, MSE = 399.98, $\eta_p^2 = .19$, $p < .00001$) participants responding faster at the beginning of Session 2 than at the end of Session 1. This off-line improvement was larger for the young group than for the elderly participants (shown by the Session × Age group interaction: F(1,123) = 11.45, MSE = 399.98, $\eta_p^2 = .09$, $p = .001$). In addition, the elapsed time between the two sessions influenced the improvement of general skill improvements as well (indicated by the Session × Delay interaction: F(2,123) = 5.29, MSE = 399.98, $\eta_p^2 = .08$, $p = .006$). Thus, participants' response speed improved more after the 12-hr than after the 24-hr (least significant difference post hoc test: $p = .007$) or 1-week delay ($p = .006$), whereas there was no difference between the 24-hr and 1-week delay conditions ($p = .64$).

The subsequent paired-samples t-tests conducted separately for all age and delay groups revealed that the off-line improvement of general skill was significant in all young groups (all p's < .047), whereas in the elderly groups only the 12-hr delay led to off-line enhancement ($p = .032$).

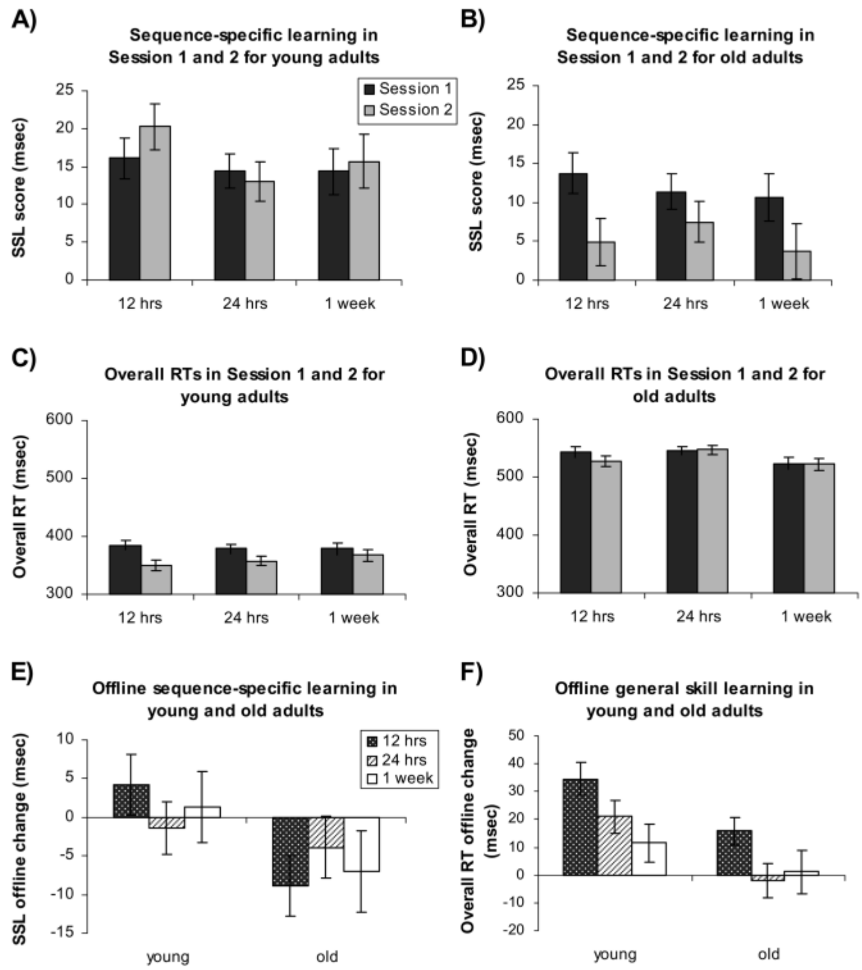

Figure 2. Sequence-specific learning (SSL) (reaction time [RT] on low- minus high-frequency triplets) at the end of Session 1 and at the beginning of Session 2 for young (A) and elderly groups (B). All groups showed significant SSL by the end of Session 1. Overall RTs are also plotted at the end of Session 1 and at the beginning of Session 2 for young (C) and elderly groups (D). Young participants were generally faster than the old ones. Regarding the off-line SSL (measured by the difference of SSL score at the end of Session 1 and the beginning of Session 2), young groups retained the previously acquired sequence-specific skill, whereas the elderly groups showed decrement in this skill compared with the young group. There were no differences across the 12-, 24-hr, and 1-week conditions (E). Off-line general skill learning (measured by the overall RT changes between the end of Session 1 and the beginning of Session 2) was obtained in all young groups and decreased gradually across delay conditions. Older adults showed off-line improvement only after a 12-hr interval (F). These groups responded significantly faster at the beginning of Session 2 compared with the end of Session 1, whereas elderly participants did not speed up after 24-hr or 1-week delay. Error bars indicate standard errors of mean (SEM).

We also compared the performance of young and elderly groups in all conditions separately. Young adults showed larger off-line improvement than the elderly participants in the 12-hr ($t(44) = 2.46$, $p = .019$) as well as in the 24-hr delay period ($t(51)=2.96$, $p = .0060$), whereas there was no significant difference between groups in the 1-week condition ($t(28) = 0.71$, $p = 0.44$).

Discussion

We studied the time course of implicit skill consolidation in young and elderly adults with probabilistic second-order regularity sequences (the ASRT task), which enabled us to separate general skill and SSL. In the young adults, we found off-line improvement of the general skill (overall RT) after the 12-, 24-hr, and 1-week delay as well, with gradual decline among delays. The elderly adults showed off-line improvement of general skill only after the 12-hr off-line period, and this improvement was weaker than that in the young group. Although the pattern in age groups is similar, these results suggest that the off-line course of general skill learning may be affected by aging because we did not find improvement either after 24-hr or 1-week delay in the elderly group. No off-line improvement was found in SSL in either age group with either the 12-, 24-hr, or 1-week consolidation interval. SSL did not decrease significantly between sessions for young participants suggesting that sequence-specific knowledge was well consolidated in this group, whereas the older group showed weaker consolidation in all delay conditions compared with the young. So, according our results, off-line general skill learning is influenced both by the time course and aging, whereas the off-line sequence learning is affected only by aging.

The significant off-line general skill improvement after the 12-hr delay period is compatible with the results of Song and colleagues (2007) and Nemeth and colleagues (2010). It is also possible that the improvement in overall RTs after the delay period reflects a release from fatigue rather than consolidation per se. However, studies that have included that a fatigue control group (Spencer, Sunm, & Ivry, 2006; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002) make this interpretation unlikely. The current results confirm those of Song and colleagues and Nemeth and colleagues in finding no evidence of any off-line improvement of sequence-specific performance and extend them to the 24-hr and 1-week consolidation period.

The off-line general skill improvement after 12 hr in the elderly adults contrasts the findings of both Spencer and colleagues (2007) and Siengsukon and Boyd (2009) who obtained no off-line improvement in elderly adults. Due to the different paradigms used in the current and the two previous studies, it is difficult to identify the source of differences. We refer to the point that these previous studies did not distinguish between general skill and SSL, and therefore the signal-to-noise ratio might be reduced making it difficult to detect the off-line improvements for elderly participants.

The differences among the 12-, 24-hr, and 1-week off-line intervals suggest that the consolidation of general skill learning is time dependent. In addition, older participants are more sensitive for this off-line time course in that they showed no off-line improvement even after 24-hr delay. These results are congruent with recent theories of motor skill consolidation (Press et al., 2005; Robertson et al., 2005; Shadmehr & Brashers-Krug, 1997; Walker et al., 2003) that claim that memory stabilization occurs during the first 5–6 hr after learning. The observed strong off-line improvement after 12 hr may reflect this first stabilization process of memory traces, including the previously mentioned critical time period. The differences among 12-, 24-hr, and 1-week consolidation intervals suggest that during new skill acquisition, it could be important to place the training sessions closer to each other for optimal performance, with shorter intervals for elderly participants.

The current results as well as previous findings (Doyon, Korman et al., 2009; Robertson et al., 2004) are compatible with the notion that skill consolidation processes may be different and they could be profoundly dependent on the nature of task demand, such as on the relative proportion of general skill and SSL requirements of the task. Given that these different components of learning are usually not separated in classical sequence learning tasks, off-line improvements in such studies could be falsely attributed to SSL itself. Nevertheless, in the current study consolidation of sequence-specific information was similar in the 12-, 24-hr, and 1-week off-line periods, with a decline for elderly compared with the young, independently of time course. These results suggest that stabilization of sequence-specific memory is a faster process, whereas off-line changes of general skill are more influenced by a longer stretch of time.

On the functional level, there are at least three mechanisms that may underlie the age-related decline in the consolidation of skill learning: (a) cognitive slowing may hinder elderly adults from having multiple representations simultaneously activated (see simultaneity theory of Salthouse, 1996); (b) associative binding deficits may cause impairment in making associations between multiple stimuli or stimulus features and binding these associations into long-term memory traces (Bennett et al., 2007; Harrison, Duggins, & Friston, 2006); and (c) increased sensitivity to interference also can result weaker stabilization of representations (Park, Smith, Dudley, & Lafronza, 1989). On the neuronal level, age-related decrement was observed both structurally and functionally in the basal ganglia (Chen et al., 2005; Dennis & Cabeza, 2010; Erixon-Lindroth et al., 2005; Raz et al., 2005), that is involved in skill learning. Future studies are still needed to systematically examine the background mechanisms of age-related differences in skill consolidation.

Our findings are compatible with skill learning and consolidation models (Cohen, Pascual-Leone, Press, & Robertson, 2005; Doyon, Bellec et al., 2009; Hikosaka et al., 1999, 2002; Song, 2009; Walker et al., 2003) and draw attention to the fact that the consolidation is not a single process; instead there are multiple mechanisms in off-line learning (general skill, sequence-specific processes), which are differently influenced by time course and by aging. Based on these results, therapists can design more effective educational, training, and rehabilitation programs for age-related disorders.

Funding

Bolyai Scholarship Program (to D.N.) and Hungarian National Research Fund (OTKA) K 82068.

Acknowledgments

Thanks to our mentors: Darlene V. Howard, James H. Howard, Jr., and Michael Ullman from Georgetown University. Thanks to Ildikó Vízi, Maria Tarnai, Krisztina Turay, and Anna Rácz for their valuable assistance during data collection and Gábor Csifcsák for his help. István Winkler and Agnes Szokolszky helped us in the final version of the manuscript.

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