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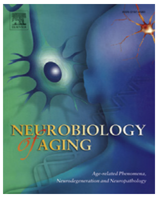

Sleep-dependent motor memory consolidation in older adults depends on task demands

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ABSTRACT

It is often suggested that sleep-dependent consolidation of motor learning is impaired in older adults. The current study challenges this view and suggests that the degree of motor consolidation seen with sleep in older age groups depends on the kinematic demands of the task. We show that, when tested with a classic sequence learning task, requiring individuated finger movements, older adults did not show sleep-dependent consolidation. By contrast, when tested with an adapted sequence learning task, in which movements were performed with the whole hand, sleep-dependent motor improvement was observed in older adults. We suggest that age-related decline in fine motor dexterity may in part be responsible for the previously described deficit in sleep-dependent motor consolidation with aging.

1. Introduction

The formation of memories in humans is underpinned by highly specialized processes of encoding, consolidation, and retention. Initially labile new memory traces undergo postencoding processing, which aids in stabilizing and integrating learned material over time (Diekelmann et al., 2009; Rasch and Born, 2013; Stickgold, 2009) and frequently enables further postlearning improvements associated with off-line consolidation (Doyon et al., 2009; Robertson et al., 2004; Trempe and Proteau, 2010). Depending on the type of material being learned, these off-line gains may occur during wakefulness and/or during sleep.

After a single session of learning a novel motor sequence, healthy young adults consistently show off-line gains in performance and in the case of explicit sequence learning particularly after an off-line period of sleep (Fischer et al., 2002; Robertson et al., 2004; Walker et al., 2002, 2003). By contrast, a growing number of studies have found that such improvements, immediately after a period of sleep, are lacking in healthy older adults (Fogel et al., 2013; Spencer et al., 2007; Wilson et al., 2012). Tucker et al. (2011) found a decline in performance of a motor sequence in older adults after a 12-hour period of wakefulness, in contrast to maintained performance after a 24-hour period containing both sleep and wake. Although this interesting result could be interpreted as consistent with the possibility of consolidation during sleep, the authors did not find improvements in performance after sleep but rather just a smaller decrement in performance. In addition, the design did not control for the passage of time (24 hours in the sleep condition compared with 12 hours in the wake condition), and so it remains unclear whether sleep-dependent consolidation of motor sequence learning occurs in older adults.

Multiple factors may contribute to this age-related discrepancy. It is well established that sleep architecture changes with age (e.g., Colrain et al., 2010; Crowley et al., 2002; Mander et al., 2013; for meta-analysis see Ohayon et al., 2004). Studies in younger adults have shown significant associations between specific sleep characteristics (e.g., sleep spindle and slow-wave activity) and motor consolidation (Huber et al., 2004; Landsness et al., 2009). It is therefore possible that age-related changes to sleep architecture and activity contribute to a reduced capacity for consolidation of motor learning during sleep (Fogel et al., 2013; King et al., 2013).

However, another issue that has been overlooked previously is the degree to which decline in movement dexterity may contribute to observed differences. There is evidence to suggest significant reductions in fine motor skill, including speed, dexterity, and finger

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strength with older age (Ashendorf et al., 2009; Dayanidhi and Valero-Cuevas, 2014; Marmon et al., 2011; Ranganathan et al., 2001; Soer et al., 2012). Such effects are thought to partly reflect age-related changes in cortical inhibitory processes important for fine motor performance (e.g., by suppressing coactivation of agonist and antagonist muscles; Heise et al., 2013; Klass et al., 2007; Marneweck et al., 2011). The sequence learning tasks that are typically used to assess sleep-dependent motor consolidation require rapid, individuated finger movements. Therefore, it is possible that age-related changes in fine motor dexterity impact on performance during training, which in turn could influence off-line consolidation in older adults. However, one previous study that required older adults to perform an explicit sequence-tracking task using a hand-operated joystick, which would not require individual finger movements, did not find clear evidence for sleep-dependent consolidation (Siengsukon and Boyd, 2009). Nevertheless, in contrast to the evidence on consolidation of fine motor tasks, which tend to show a lack of improvement in performance immediately after sleep in older adults (Fogel et al., 2013; Spencer et al., 2007; Wilson et al., 2012), the joystick tracking task did produce improvements in performance after sleep in older adults, but these did not differ significantly from the gains seen after a comparable period of wakefulness. It is possible that individual task demands may influence the degree to which consolidation of motor learning after sleep can be detected in older adults.

In summary, existing studies do not provide clear evidence for sleep-dependent consolidation of motor learning in older adults and have not directly addressed whether the presence of consolidation depends on task demands. To address these questions, we tested off-line consolidation of motor learning in both younger and older adults by using either a classic version of the motor sequence task, requiring individual finger movements, or an adapted version of the same task, using whole hand movements.

2. Methods

2.1. Participants

A total of 49 younger (aged 18–35) and 42 older (50–85) healthy, right-handed participants provided written informed consent to participate in accordance with local ethics committee guidelines. Participants were assigned pseudorandomly to different experimental condition groups (Table 1). Participants had no previous history of neurologic, psychiatric, or sleep disorders or drug or alcohol abuse, and they were instructed to remain free of caffeine, alcohol, and drugs (apart from prescribed medication not expected to have an influence on sleep quality, such as for blood pressure, birth control, and nondrowsy antihistamines) for the duration of the study, as well as for 12 hours before taking part. Participants also were instructed to refrain from napping during the day, confirmed verbally at the relevant posttraining retest session. One participant reported having a nap after initial training, and 1 participant consistently reproduced only the first 4 digits of the number sequence at retest. Behavioral consolidation data from these 2 participants were therefore excluded from further analysis.

Table 1
Participant details

Task (by age group)	Mean age (±SEM)	n	Training group
Younger adults			
Classic	24.50 (±0.89)	13	AM
Classic	24.40 (±0.82)	10	PM
Adapted	24.31 (±0.94)	13	AM
Adapted	25.46 (±0.95)	13	PM
Older adults			
Classic	67.22 (±3.19)	10	AM
Classic	67.90 (±2.99)	11	PM
Adapted	66.30 (±2.77)	10	AM
Adapted	65.18 (±3.22)	11	PM

Key: AM, participants trained in the morning; PM, participants trained in the evening; SEM, standard error of the mean.

Nine participants (from the older groups) took part in 2 conditions. In these cases, different conditions were counterbalanced to control for order effects and tested at least 1 month apart, and different sequences with completely unique grammars were used for each condition. In these circumstances, we would not expect any effect of the earlier condition on the later condition (Walker et al., 2003). However, to guard against the possibility that results from these participants were having a disproportionate effect on our findings we also redid any relevant analyses without data from the second condition of these participants, with very similar results (these are provided in the Supplementary Materials).

2.2. Sequence learning tasks

Depending on the group to which participants were assigned, they performed either a standard sequence learning task (classic; Fig. 1A; Walker et al., 2002, 2003) or an adapted whole-hand sequence task (adapted; Fig. 1B). Tasks were matched on all attributes apart from requiring either fine finger or whole hand movements. For the classic task, button presses were made with the index, middle, ring, and little fingers of the (nondominant) left hand on a standard computer keyboard. For the adapted task, button presses were performed with the (nondominant) left hand, with buttons spaced 22° apart and positioned along a curve with a radius of 27.26 cm (equal to the average adult forearm length; Plagenhoef et al., 1983) to allow comfortable reach of all buttons while keeping the left elbow positioned on a padded mat on the table. A 5-digit numeric sequence (e.g., 4-1-3-2-4) was presented on the screen during the entire period participants performed the sequence to prevent any working memory requirement. To avoid providing accuracy feedback, responses elicited only a white dot, which moved from left to right in accordance with the number pressed to indicate the response had been recorded. Participants were instructed to repeat the sequence as fast and as accurately as possible for 30 seconds followed by a 30-second rest period. Each participant performed 12 blocks (sequence + rest) during training (t0) lasting 12 minutes in total. At the first retest session (t1), participants performed only 2 consecutive blocks to reduce any influence of additional practice or training between retest sessions.

2.3. Procedure

Training (t0) took place between 8:00 and 10:30 AM (for the AM group) or 8:00 and 10:30 PM (for the PM group). The 2 retest sessions took place 12 (t1) and 24 (t2) hours after training (Fig. 1C). For morning sessions, testing took place at least 1 hour after participants woke up. Before the start of each session, participants completed the Stanford Sleepiness Scale to indicate their level of subjective alertness (Hoddes et al., 1973). For the 24-hour period of study participation, participants wore an activity monitor on their nondominant wrist (digital accelerometer; Actiwatch-Light; CamNtech Ltd, Cambridge, UK) and were asked to keep an activity log, which together were used to provide measures of sleep-wake patterns (Rogers et al., 1993; Sadeh and Acebo, 2002). Participants also completed the Pittsburgh Sleep Quality Index (PSQI), which is a measure of self-reported sleep quality over the previous month (Buysse et al., 1989).

2.4. Behavioral measures

Performance rate (number of correct complete sequences per block) was used as the main behavioral measure, as in previous