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Contribution of night and day sleep vs. simple passage of time to the consolidation of motor sequence and visuomotor adaptation learning

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Abstract

There is increasing evidence supporting the notion that the contribution of sleep to consolidation of motor skills depends on the nature of the task used in practice. We compared the role of three post-training conditions in the expression of delayed gains on two different motor skill learning tasks: finger tapping sequence learning (FTSL) and visuomotor adaptation (VMA). Subjects in the **DaySleep** and **ImmDaySleep** conditions were trained in the morning and at noon, respectively, afforded a 90-min nap early in the afternoon and were re-tested 12 h post-training. In the **NightSleep** condition, subjects were trained in the evening on either of the two learning paradigms and re-tested 12 h later following sleep, while subjects in the **NoSleep** condition underwent their training session in the morning and were re-tested 12 h later without any intervening sleep. The results of the FTSL task revealed that post-training sleep (day-time nap or night-time sleep) significantly promoted the expression of delayed gains at 12 h post-training, especially if sleep was afforded immediately after training. In the VMA task, however, there were no significant differences in the gains expressed at 12 h post-training in the three conditions. These findings suggest that “off-line” performance gains reflecting consolidation processes in the FTSL task benefit from sleep, even a short nap, while the simple passage of time is as effective as time in sleep for consolidation of VMA to occur. They also imply that procedural memory consolidation processes differ depending on the nature of task demands.

Keywords

Memory consolidation; Motor learning; Sleep; Passage of daytime; Visuomotor adaptation; Motor sequence

Introduction

The acquisition of new motor skills is a multi-step process occurring on a time-scale of hours, days and even weeks (Korman et al. 2003, 2007; Walker et al. 2003). At least two distinct stages are present: first, a fast learning phase associated with considerable within-session improvement, and second, a slow phase in which further gains can be observed across several sessions of practice (Doyon and Ungerleider 2002; Doyon 2008; Karni et al. 1995, 1998). Recently, an intermediate stage of consolidation, in which spontaneous increases in performance that evolve following a latent interval of more than 6 h after the initial training session, or in which resistance to interference by a competitive experience is observed as a function of time, has also been reported for a variety of procedural tasks (e.g., Korman et al. 2007; Krakauer et al. 2005; Roth et al. 2005). During the consolidation process, synaptic and

systemic changes in neuronal representation of learning are believed to take place, hence leading to a strengthening of the memory trace (McGaugh 2000; Dudai 2004).

Sleep has been shown to play a critical role in the consolidation of a variety of skills that involve the visual (Stickgold et al. 2000), auditory (Gaab et al. 2004) and motor systems (Huber et al. 2004; Fischer et al. 2002; Korman et al. 2007; Walker et al. 2002). For example, studies have shown that delayed gains in performance on a motor sequence task (Korman et al. 2007; Walker et al. 2002) are triggered after a period of sleep, but not following an equivalent period of day-time. However, despite accumulating evidence supporting such a notion (see Smith et al. 2004; Rauchs et al. 2005, for reviews), an increasing number of reports showing off-line memory improvements in the absence of post-training sleep are departing from this exclusive sleep-dependent consolidation hypothesis. Indeed, studies examining motor sequence learning using an implicit task (Press et al. 2005; Robertson et al. 2004), a probabilistic paradigm (Song et al. 2007), or a task necessitating to distinguish between the goal and the movement components of a motor skill (Cohen et al. 2005) have revealed delayed spontaneous increases in performance after the simple passage of day-time, hence suggesting that time alone may be sufficient to consolidate a previously learned skill. Other studies that investigated motor procedural learning using a force-field adaptation paradigm have also reported delayed increases in performance after the simple passage of time (Donchin et al. 2002; Shadmehr and Brashers-Krug 1997). Altogether, these findings suggest that sleep may not be necessary to induce consolidation in all forms of motor procedural learning.

Thus, the aim of the current study was to compare directly the role of sleep, either day-time or night-time, with the simple passage of day-time in the expression of delayed, consolidation phase, gains in two different motor skills: motor sequence learning and kinematic visuomotor adaptation. To this end, we studied the evolution of delayed performance increases in these two forms of learning using identical protocols in terms of time of training, time of sleep and time of re-test. We hypothesized that the expression of sleep-dependent delayed gains in performance would be task-specific: i.e., that motor sequence learning would be sleep-dependent, whereas time per se would suffice to promote consolidation in the VMA task.

Materials and methods

Participants

A total of 82 young healthy subjects aged between 19 and 30 years (mean age: 23.6 ± 2.8 years, 46 women) participated in the present study. All subjects were strongly right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield 1971). They were either assigned to a **DaySleep** ($n = 29$), **NightSleep** ($n = 26$) or **NoSleep** ($n = 27$) condition, using a quasi-random procedure in order to match subjects according to their age and gender. Seven days prior to and during the study, subjects were instructed to maintain a regular sleep schedule as determined by their preferred bedtime and wake time (± 30 min), and their compliance was verified using sleep diaries. All subjects reported to sleep between 7 and 9 h per night, and none had any disruption of their regular sleep-wake cycle 4 weeks prior to their participation. Subjects were excluded if they worked night shifts, were engaged in a trans-meridian trip in the 3 months preceding the study, were regular nappers or were extreme evening and morning-type individuals (assessed by Morningness–Eveningness Questionnaire from Horne and Östberg 1976). For the **DaySleep** groups, only “morning” to “moderate morning” type persons were included to ensure that they would fall asleep during the day-time nap. To be accepted in the study, participants also had to be in good health, to present no obesity problem (body mass index < 27), and to report no medication intake, no sleep complaint, and no psychiatric or neurological illness. All subjects had a score lower than 4 on the short version of the Beck Depression Scale (Beck and Steer 1987), and all women were tested in their follicular hormonal cycle. Subjects were non-smokers, and were asked to be alcohol and caffeine-free at least 12

h before each experimental session. Finally, musicians, professional typists and video games players were excluded to avoid subjects with previous expertise on motor sequence and motor adaptation types of task. This study was approved by the Ethics Committee of the Hôpital du Sacré-Coeur de Montréal, and by the Ethics Committee of the C. Sheba Medical Center. All subjects provided written informed consent and received financial compensation for their participation.

Procedure

Groups of subjects were trained either on a finger tapping sequence learning task (FTSL, Fig. 1a) or a visuomotor adaptation learning task (VMA, Fig. 1b). They were assigned to one of the following experimental conditions (see Fig. 1c): (1) FTSL task, **DaySleep** condition ($n = 10$, 4 men); (2) FTSL task, **NightSleep** condition ($n = 14$, 6 men); (3) FTSL task, **NoSleep** condition ($n = 13$, 4 men); (4) FTSL task, **ImmDaySleep** condition ($n = 9$, 4 men); (5) VMA task, **DaySleep** condition ($n = 10$, 6 men); (6) VMA task, **NightSleep** condition ($n = 13$, 4 men); (7) VMA task, **NoSleep** condition ($n = 13$, 4 men). In conditions 1 (FTSL-**DaySleep**), 4 (FTSL-**ImmDaySleep**) and 5 (VMA-**DaySleep**), subjects spent two consecutive days in the laboratory. These included an adaptation night, an experimental day and a post-training night. To facilitate napping, the experiment was scheduled so as to time the nap interval early into the afternoon. Accordingly, all participants in the **DaySleep** and **ImmDaySleep** groups woke up at 6:30–7:00 AM. Half an hour after lunch, i.e., at 2:00 PM, participants afforded a 90 min nap. Performance of the trained sequence was then re-tested at 9:00 PM on the same day, and again at 9:00 the next morning following a night of recorded sleep. In the **ImmDaySleep** condition, subjects were trained at 12:00 PM immediately before the afternoon nap to test for the possible effect of the long intervening post-training delay that subjects in the FTSL **DaySleep** experienced before napping. In conditions 2 (FTSL-**NightSleep**), 3 (FTSL-**NoSleep**), 6 (VMA-**NightSleep**) and 7 (VMA-**NoSleep**), subjects were tested according to their habitual sleep-wake cycle. Morning sessions started 2 h after their usual wake time. Subjects in the **NightSleep** conditions began their training session in the evening around 09:00 PM, and were re-tested on the same task 12 h later in the morning following a night of recorded sleep. They were submitted to a screening night in the sleep laboratory 7 days prior to the experiment. By contrast, participants assigned to the **NoSleep** conditions were trained in the morning around 09:00 AM, and were re-tested in the evening, i.e., 12 h after the simple passage of time without sleep (see Fig. 1). In order to control for eating times, lighting and motor activities that could possibly interfere with learning (caffeine consumption, keyboard typing, etc.), subjects stayed in the laboratory for the whole period between the training and re-test sessions, and a research assistant was present at all time. Two minutes before each testing session, the participant's level of subjective alertness was assessed using a 10-cm visual analog scale (from “very sleepy” to “very alert”).

Polysomnographic recording

EEG electrodes were applied to the subject's head according to the International 10-20 System, using a referential montage with linked ears, a right and left electrooculogram (EOG), and three chin electromyograms (EMG). Signals were recorded using a digital ambulatory sleep recorder (Vitaport-3 System; TEMEC Instruments, Kerkrade, Netherlands). EEG signals were filtered at 70 Hz (low pass) with 1-s time constant and digitized at a sampling rate of 256 Hz using commercial software (Colombus). Sleep stages were visually scored according to standard criteria and modified to 20 s epochs (Rechtschaffen and Kales 1968) using an EEG layout (C3 derivation) displayed on a computer screen (Luna, Stellate System, Montreal, Canada).

Finger tapping sequence learning (FTSL) task

A computerized version of the sequential finger-tapping task initially developed by Karni et al. (1995) was used in the present study (Fig. 1a). This task was chosen because of its well known sleep-dependent consolidation effect (Walker et al. 2002; Korman et al. 2003, 2007). Four numeric keys, disposed in an ergonomic position on a standard computer keyboard were used (with keys-to-number assignment: B[1], F[2], D[3], Z[4]). Similar to the protocol employed by Walker et al. (2002, 2003), the task consisted to repeat, as quickly and accurately as possible, a sequence of five finger movements using the left, non-dominant hand for a period of 30 s. To familiarize the participants with the sequence of finger movements, brief practice that included repetition of the sequence (4–1–3–2–4) was displayed on a computer screen. Visual feedback—green or red dots after each key pressing—were shown on the screen under the sequence numbers to indicate whether the response was “correct” or “wrong”. When three consecutive correct sequences were executed, indicating that the subjects knew the sequence explicitly, the training session began. In the **NightSleep** and **NoSleep** groups, the training consisted of twelve 30-s blocks of trials interspersed with 30-s rest periods (total of 12 min). The first four blocks were used as the pre-training performance test (Pre-test), and the final four blocks were used as the immediate post-training performance test (0 h PT). At re-test 12 h post-training (12 h PT), subjects were required to perform four 30-s blocks of the same sequence, separated by 30-s rest periods. At the beginning of each block during the training and re-test sessions, all subjects were instructed to continuously tap the sequence as quickly and accurately as possible, immediately after hearing a “start” auditory signal, and until given a “stop” auditory signal. During the test and training sessions, the screen stayed black and no feedback was provided. Participants were instructed that occasional errors should not be corrected, and were required to continue with the task without pause. In the **DaySleep** and the **ImmDaySleep** groups, each participant underwent a pre-training performance test (Pre-test), a training session, and an immediate post-training performance test (0 h PT). Re-test sessions were carried out at 09:00 PM. A slightly different procedure was used in the training session for those groups in order to control for the number of repetitions of the sequence during practice (as opposed to the training of the **NightSleep** and **NoSleep** groups, where session consisted of self-initiated performance of the sequence during twelve 30-s blocks): the training session consisted of 160 repetitions of the assigned sequence that were divided into 10 training blocks. During training, the initiation of each sequence was cued by an auditory signal at a rate of 0.4 Hz (2.5 s per sequence). Yet the procedure used for the test and re-test blocks were similar to those employed in the **NightSleep** and **NoSleep** groups, as they consisted of four blocks of 30 s each, spaced by a period of 30 s rest between blocks.

The timings of key presses were recorded. The number of correctly and incorrectly executed sequences per 30-s block was scored; average speed and accuracy of performance for each block of individual subjects were calculated.

Visuomotor adaptation (VMA) task

Kinematic visuomotor adaptation was measured using a computer-generated eight-target tracking task (Fig. 1b). In this task, subjects were required to use a joystick with their right (dominant) hand in order to move a cursor to a target following an elliptical trajectory instead of a straight line. Target reaching on each trial was achieved using an “Inverted mode” in which the relation between movements of the joystick and direction of the cursor was inverted by 180°, such that moving the joystick to the right and up caused the cursor to move to the left and down. On each trial, a starting point represented by a white square (1.5 cm in diameter), and a small green-square cursor (0.2 cm²) superimposed on the starting point, were displayed at the center of the screen. At the same time, both a square target (1.5 cm in diameter) located 10 cm away from the starting point, and a curved line (0.2 cm in thickness; 3 cm of radius) joining the starting point and the target were presented on the screen. Also on each trial, the

target appeared in one of eight locations situated 45° apart around the center, thus producing a regular circular shape. In order to prevent anticipation of the next movement, targets were displayed in a random order. Subjects were instructed to reach each target as quickly as possible, while following the elliptical trajectory as accurately as possible. They had a 2,500 ms time limit to reach each target, and had to keep the cursor on target for a period of 100 ms. Successful trials were indicated by a color change of the target (from red to blue). After each trial, the target disappeared and subjects had to move the cursor back to its original position with the joystick. To familiarize subjects with the apparatus at the beginning of the training session, they were first asked to perform 16 trials in a “Direct mode” (no 180° rotation), followed by another 16 trials in the “Inverted mode”. The training session consisted of 10 blocks of 64 trials each, for a total of approximately 40 min of practice, whereas the re-test session was composed of only four blocks of 64 trials. Between each block, subjects were allowed to take a pause, if needed.

Performance on the VMA task was assessed using a global performance index measuring both speed and precision of the subject's movement when reaching targets. This performance index (PI) varied between 0 and 1 (1 being a perfect score), and was calculated for each trial. It was then averaged for each block using this formula:

$$PI = \left[\text{success} \times e^{-(DS/S)(TT-500)/2500} \text{ ms} \right]$$

where “DS” represents the difference (in term of the area under the curve) between the trajectory traced by the subject and the proposed trajectory, “S” is the proposed trajectory, “TT” is the total time taken by the subject to reach the target and “2,500 ms” is the maximum time allowed to reach the target. Successful and failed trials were given a value of 1 and 0, respectively. Only successful trials where the target was reached and the trial time was less than 2,500 ms were included in the statistical analysis.

Statistical analysis

For the FTSL and VMA tasks, the extent of learning in the initial training session was statistically measured using repeated measures ANOVAs [group (**DaySleep/NightSleep/NoSleep** and **ImmDaySleep** for FTSL) X block]. Post-hoc paired *t* tests comparing the first and the last block of trials were also carried out to look at learning efficiency. Motor consolidation was assessed using two factors repeated measures ANOVAs [group (**DaySleep/NightSleep/NoSleep** and **ImmDaySleep** for FTSL) X session (post-training/re-test scores)]. Post-hoc paired and unpaired *t* tests on the post-training and re-test scores, as well as on the percentage of consolidation, were also calculated for each group. A *p* value < 0.05 was considered significant. Two participants in the FTSL task (one in the **NightSleep** and one in the **NoSleep** group) showed no learning during the initial training session, and were thus excluded from the statistical analysis.

PSG parameters of either nap or night sleep [Sleep latency (min), Total sleep time (min), Sleep efficiency (%), Stages 1, 2, 3–4 and REM sleep] were used in independent *t* tests to compare differences in sleep parameters between the two Night Groups (FTSL vs. VMA) and the two Day Groups (FTSL vs. VMA).

Results

Motor sequence learning

Training on the sequence of movements resulted in occurrence of early, within-session, improvements in performance speed in the four groups tested ($F_{(2,13)} = 48.04, p < 0.01$,

NoSleep; $F_{(2,12)} = 30.6$, $p < 0.01$, **NightSleep**; $F_{(2,9)} = 48.04$, $p < 0.01$, **DaySleep**; $F_{(2,8)} = 48.04$, $p < 0.01$, **ImmDaySleep**, Pre-test vs. 0 h PT, see Fig. 2a–d). The extent of learning from Pre-test to 0 h PT (the first four blocks compared to the last four blocks of practice) revealed no significant difference between the **NoSleep**, **NightSleep**, **DaySleep** and **ImmDaySleep** groups (main effect of Group: $p = 0.83$; Group X Test interaction: $p = 0.95$), suggesting that the subsequent differences observed in the pattern of delayed gains between groups did not result from possible circadian effects. Importantly, all groups also showed asymptotic performance at the end of the training session, as no significant improvement in performance was observed in the last four blocks of practice (p , non-significant; **NoSleep**, **NightSleep**, **DaySleep** and **ImmDaySleep** groups, 0 h PT).

Sleep contribution, day-time or night-time, to the post-training gains in performance speed is underscored in Fig. 2a–d (upper panels). Significant changes in performance within each group at different times following training are denoted by asterisks. No gains in speed performance were found ($p = 0.14$, 0 h PT vs. 12 h PT) (Fig. 2a) in the **NoSleep** group. By contrast, the pattern of results for the participants in the **NightSleep** group (Fig. 2b) was qualitatively different, as subjects experienced significant additional over-night improvements in speed performance by 12 h PT ($F_{(1,12)} = 50.24$, $p < 0.01$, 0 h PT, 12 h PT). Interestingly, there was also a significant additional over-day delayed improvement in speed performance in the **DaySleep** and the **ImmDaySleep** groups ($F_{(1,9)} = 5.27$, $p < 0.05$, **DaySleep**; ($F_{(1,8)} = 20.89$, $p < 0.05$, **ImmDaySleep**, 0 h PT, 12 h PT) (Fig. 2c, d).

Given the small number of errors overall, a decrease in the absolute number of errors in the time-window of 12 h PT was non-significant in the four groups ($p = 0.75$, **NoSleep**; $p = 0.4$, **NightSleep**; $p = 0.20$, **DaySleep**; $p = 0.14$, **ImmDaySleep**, Pre-test, 0 h PT, 12 h PT). The near zero slope values of the regression lines fitted to all data points reflect that absolute accuracy remained unchanged during the consolidation period (Fig. 2a–d, lower panels). These results indicate that there was no speed-accuracy trade-off during the consolidation period following training. Moreover, relative to the number of correct sequences, the accuracy by 12 h PT improved in all four groups.

To characterize the effects of post-training conditions (wake, night sleep, nap 4 h post-training and immediate post-training nap) on the course of consolidation, a pair-wise comparison between groups was conducted for the post-training time window (0 h PT vs. 12 h PT). The data was analyzed using a repeated measures ANOVA with four groups as categorical values, and with post-training re-tests time points (0 h PT, 12 h PT) and four blocks, as within-subject factors. The results are summarized in Table 1. Delayed post-training improvements in speed occurred in all four groups. Yet, sleep and training experience did differentially interact in the time-window of 12 h after training, depending on the kind of sleep (day-time or night-time) and when, relative to the training experience, sleep was afforded. Indeed, night sleep induced significant beneficial post-training effects on speed performance as compared to the absence of sleep. Even a 90 min nap, as in the **DaySleep** and the **ImmDaySleep** groups, resulted in consistent group delayed gains by 12 h PT. In contrast, when no nap was afforded, as in the **NoSleep** group, the latter did not reveal any significant effect for the expression of the delayed gains by 12 h PT, see Fig. 2a. However, as apparent from the group \times gains interaction analysis between the **NoSleep** and the **DaySleep** groups (Table 1), the delayed post-training gains attained by these groups were not significantly different from one another, p , non-significant.

Although subjects in the **NightSleep** and **DaySleep** groups showed significant delayed gains, direct comparisons between these conditions (see Table 1) revealed that night sleep produced greater increases in performance than day sleep, a finding slightly inconsistent with results from one of our recent study (Korman et al. 2007). In the latter study, we found that day-time sleep elicited performance gains similar to those achieved after a night of sleep when the nap

was afforded immediately after training. An **ImmDaySleep** group trained at noon instead of 09:00 AM (i.e., just before the nap) was thus used to test the possibility that timing of the post-training nap relative to the training may be an important factor in the processes mediating the development of delayed performance gains. All participants showed delayed gains at 09:00 PM re-test (see Fig. 2d). A group \times gains interaction analysis on performance data in the time-window 0 h PT vs. 09:00 PM re-test revealed that there was no difference in gains attained by the **ImmDaySleep** and **NightSleep** groups ($p = 0.234$), hence suggesting that time between the training and nap is an important factor to consider in this type of study.

Individual data analyses were also carried out to further explain the results of the group comparisons (see Fig. 3). The data points represent the difference in each participant's average performance from his/her own average 0 h PT performance speed, normalized to the 0 h PT performance at both immediate (0 h PT) and 09:00 PM re-test sessions. Results from the **NoSleep** group reveal that 4/12 (33%) participants had negative gains, while 8/12 participants showed positive gains in performance by 12 h PT that were comparable to the other groups that afforded sleep. Thus, the fact that there were two subpopulations in terms of the expression of delayed gains in performance in the **NoSleep** group suggests that this effect was masked by group data averaging. This also suggests that sleep-independent delayed gains may occur in motor sequence learning (see also, Fischer et al. 2002). By contrast, only two participants in the **DaySleep** group showed some deterioration in PT performance, while none expressed deterioration in PT performance and almost all individuals showed delayed gains in the **NightSleep** and **ImmDaySleep** groups. Thus, individual data analyses demonstrate that inconsistent sleep-independent delayed gains, as well as, some deterioration in performance, may occur in motor sequence learning. Napping after training is advantageous and timing is important. Indeed, scheduling the nap immediately after training had positive effect on the amount of delayed gains expressed on re-testing at 09:00 PM, as compared to the protocol where the training and nap were separated by several hours.

Visuomotor adaptation

Training on the reverse adaptation task resulted in significant within-session gains in speed and accuracy measures in the three groups tested (speed: $F_{(12,9)} = 9.04$, $p < 0.001$, **NoSleep**; $F_{(12,9)} = 4.33$, $p < 0.001$, **NightSleep**; $F_{(9,9)} = 10.83$, $p < 0.001$, **DaySleep**; accuracy: $F_{(12,9)} = 12.62$, $p < 0.001$, **NoSleep**; $F_{(12,9)} = 8.25$, $p < 0.001$, **NightSleep**; $F_{(9,9)} = 32.53$, $p < 0.001$, **DaySleep**; 10 blocks, training), see Fig. 4a–c (white squares, accuracy; black squares, speed). In the three groups, asymptotic performance was reached at the end of the training session, as demonstrated by the absence of significant improvements in the last three blocks of practice (speed: $p = 0.67$, **NoSleep**; $p = 0.3$ **NightSleep**; $p = 0.97$, **DaySleep**; accuracy: $p = 0.55$, **NoSleep**; $p = 0.07$ **NightSleep**; $p = 0.07$, **DaySleep**, 3 (final) blocks, training). There were also no group differences in the amount of learning that subjects reached in the training session, as the group \times block interaction was not significant ($p = 0.12$, 10 blocks, training).

At re-tests 12 h post-training, similar performance in both speed and accuracy were found across the **NoSleep**, **NightSleep** and **DaySleep** groups, as there was no significant group \times session interaction effect for both speed ($p = 0.81$, 4 blocks, 12 h PT) and accuracy measures ($p = 0.13$, 4 blocks, 12 h PT). Furthermore, there was no improvement in speed over the four blocks of trials in the 12 h PT re-test session ($p = 0.73$, **NoSleep**; $p = 0.49$ **NightSleep**; $p = 0.10$, **DaySleep**, 4 blocks, 12 h PT), although accuracy tended to improve with further practice in the re-test session ($F_{(1,4)} = 61.78$, $p < 0.001$, **NoSleep**; $p = 0.07$ **NightSleep**; $p = 0.07$, **DaySleep**, 4 blocks, 12 h PT).

Statistical comparisons were conducted using the last three blocks of trials in the training session and the first three blocks of the re-test session to look at consolidation effects. Significant delayed gains in speed were observed in the **NightSleep** and **DaySleep** groups, but

not in the **NoSleep** group. Yet all three groups showed significant delayed gains in accuracy by 12 h PT (speed: $F_{(1,12)} = 3.78, p = 0.076$, **NoSleep**; $F_{(1,12)} = 5.17, p = 0.042$, **NightSleep**; $F_{(1,9)} = 17.07, p = 0.003$, **DaySleep**; accuracy: $F_{(1,12)} = 5.01, p = 0.045$, **NoSleep**; $F_{(1,12)} = 10.99, p = 0.006$, **NightSleep**, $F_{(1,9)} = 27.43, p = 0.001$, **DaySleep**, 3 last training blocks versus 3 first blocks at 12 h PT). Overall, the delayed improvements relative to the performance at the end of the training session in the VMS task were consistent, but small, as compared to the FTSL task (2–3% vs. 10–14% improvement in the VMS and FTSL tasks, respectively). The within-group distribution of individual gains (Fig. 5) shows that delayed post-training improvements in speed and accuracy occurred in all groups. Yet, sleep did not differentially interact with the amount of gains in the 12 h time-window after training.

Sleep quality and subjective alertness

No significant difference in the PSG parameters associated with either night or day sleep were observed after training on the FTSL and VMA tasks (Table 2) (Other EEG results have been previously described in Morin et al. 2008). Moreover, for both tasks, there was no significant difference in the participant's subjective alertness reported by the **NightSleep** and **NoSleep** groups when assessed 2 min before the training session ($t_{(23)} = 1.66, p = 0.11$ for the FTSL task; $t_{(24)} = -0.85, p = 0.4$ for the VMA task), nor before the re-test session ($t_{(23)} = 1.66, p = 0.09$ for the FTSL task; $t_{(24)} = 0.32, p = 0.75$ for the VMA task). Altogether, these findings suggest that the pattern of post-training gains in performance reported above cannot be attributed to differences in the subject's level of vigilance during the different testing phases.

Discussion

In this study, we compared the role of sleep, either day-time or night-time, with the simple passage of time in awake state on the consolidation of two different motor skills: motor sequence learning (FTSL) and kinematic visuomotor adaptation (VMA). To this end, for each task separately, participants afforded either a day-time nap, a night's sleep or no sleep during a 12-h interval following an equivalent training session, and performance was re-tested and compared to that attained immediately post-training. In the FTSL group, robust delayed gains emerged when a night of sleep or a day-time nap was allowed after the initial training session; an equivalent period of time in wakefulness provided no significant benefit. In the VMA group, however, small but significant non-sleep dependent delayed gains were observed subsequent to a single training session.

In both tasks, participants reached asymptotic performance at the end of training. Also there was no within-session learning or relearning at re-test, a pattern of results previously described using both perceptual and motor tasks, and representative of an effective training session apt to lead to the generation of delayed gains (e.g., Karni and Sagi 1993; Hauptmann and Karni 2002; Hauptmann et al. 2005; Korman et al. 2007). This suggests that the amount of practice that subjects were given on either of the two tasks was sufficient to trigger delayed gains in performance.

Although there were clear differences in the initial level of performance between the three experimental conditions of the VMA task with participants training in the evening (**NightSleep**) showing surprisingly better initial performance than those trained in the morning (**NoSleep** and **DaySleep**), all three groups attained similar levels by the end of the training session. Their performance 12 h post-training in all three VMA conditions was also independent of the time of day, and the expression of within-session gains appeared to be independent of circadian effects. Thus, in both tasks, performance at the end of the training was of similar level, regardless of whether the training took place in the evening or in the morning. This suggests that the expression of delayed post-training gains reported here are due

to the memory consolidation process rather than the effects of circadian changes in performance per se.

Group analyses showed that sleep and the type of experience in motor training interact in a time-window of hours after the termination of training. The fine differential effects of sleep on the expression of delayed gains in the two tasks during the post-training interval were evident from the individual analysis (Figs. 3, 5), which revealed additional features of time-dependent memory processes that were otherwise masked in group analyses (Korman et al. 2007). In all experimental groups, some participants attained robust delayed gains in performance speed, even in the FTSL **NoSleep** group, in which the average group data indicated no significant delayed gains. Moreover, in both tasks and in all experimental conditions, a few participants showed no or negative delayed gains, even in the sleep groups in which the average group data revealed highly significant delayed gains (e.g., the FTSL **DaySleep** and **Night Sleep**). These observations are important, as they highlight the fact that robust delayed gains in performance may occur without sleep, not only in VMA task but also in the FTSL task. Also, no improvement or even some deterioration in performance may occur in spite of the affordance of sleep, regardless of the type of motor skill learned. This suggests that in some tasks, the affordance of sleep may constitute an important promoting factor in triggering the consolidation process, but that it is not the only critical factor (see also, Fischer et al. 2002, Maquet et al. 2003, Korman et al. 2007). Indeed, post-training sleep may either have a promoting or neutral effect on the timing as well as the magnitude of delayed gains. Yet the reasons for such behavioral dissociations are conjectural (Roth et al. 2005; Krakauer and Shadmehr 2006; Censor et al. 2006); they may reflect the absence of strict constraints and the affordance of subtle, but nevertheless acceptable, differences in task solution as imposed by the training protocols, as well as by the choice of behavioral parameters and data analyses.

Several theoretical accounts may be invoked to explain the reported task-related differences between studies on the necessity of sleep in motor memory consolidation: (1) The VMA task includes a strong perceptual component, which distinguishes it from the FTSL task (e.g., the latter does not involve any visual feedback). Perceptual skill learning has been found to be sleep-independent in a number of conditions including, for example, visual discrimination learning (Karni and Sagi 1993; Karni et al. 1994; Gais et al. 2000; Censor et al. 2006), visuo-motor learning (Maquet et al. 2003), and auditory identification learning (Roth et al. 2005), in which significant delayed gains in performance have also been observed in the awake state. (2) Robertson's Awareness Theory (2004) proposes that sleep contributes to off-line gains only when subjects are aware of the motor skill they have to learn. In the FTSL task, subjects have full explicit knowledge about the nature of the sequence of movements prior to the beginning of training. By contrast, the acquisition of a kinematic visuomotor adaptation task is believed to be independent of explicit/cognitive strategies (Mazzoni and Krakauer 2006). (3) In the current experimental design, subjects in the FTSL groups were trained with their non-dominant, left hand, whereas those in the VMA groups were trained with their dominant, right hand in order to minimize the differences in the amount of training needed to achieve asymptotic performance during training between the two tasks. Thus, there is a theoretical possibility that sleep may interact differentially with the hand used during training. Yet we are unaware of a study that would support this assumption. To the contrary, the results of previous studies suggest that training of either dominant or non-dominant hand may trigger delayed gains in performance (e.g., Balas et al. 2007) (4) There may be a critical difference between the neural substrates engaged in the learning process of the two skills (for reviews see Doyon et al. 2002, 2003). In a recent model, Doyon and colleagues (Doyon and Benali 2005) have proposed that both cortico-striatal (CS) and cortico-cerebellar (CC) systems play a critical role in motor learning, but that plastic changes within these two systems may also depend on task demands (type of motor skill acquired). The model suggests that in the fast learning (within-session) phase, both FTSL and VMA tasks recruit the CS and CC systems. When consolidation has

occurred, however, the neural representation of the task may be represented by one of the two loops; the CS and CC systems being crucial, respectively, for the consolidation of a new motor sequence and a VMA skill. Peigneux et al. (2003) and Fischer et al. (2005) have shown that the basal ganglia are activated during the acquisition of sequence learning, and that the same structures may then be reactivated during sleep. It may thus be the case that sleep may not be necessary to optimize neuronal plasticity associated with consolidation involving the cerebellum.

One should note that the parameters used to assay the change in speed and accuracy in the two tasks were different. For example, the term “accuracy” in the FTSL task refers to the number of sequencing errors (a binary parameter) while “accuracy” in the VMA task reflects deviation from an ideal path to the target (a measure of magnitude). The nature of the performance parameters and their scale of change in the two tasks may therefore result in quantitative and even qualitative differences, masking the differences in learning and memory effects. Because of these concerns, in the current context, the differences between tasks were assayed not in a direct comparison but rather through the differential effect of sleep on the magnitude of the post-training interval dependent gains. For the FTSL task, the effects of sleep were robust (given delayed gains on the order of 10% and more of the absolute end of session performance), while because the post-training changes in performance in the VMA task were quite small (on the order of 3–4% of the absolute end of session performance), the effects of time per-se, as well as of time with sleep, may have been masked.

Altogether, the results for the FTSL task replicate findings of previous studies showing that a night of sleep, and even a 90-min post-training nap, promote the expression of delayed gains in performance, while comparable intervals of wakefulness do not promote additional improvements beyond the immediate post-training gains (Korman et al. 2003, 2007; Walker et al. 2002). Findings from the VMA task are also in line with recent observations (Doyon and Benali 2005) that a period of 6–8 h of wakefulness was enough to induce significant performance gains in healthy young adults performing the same adaptation task used here. Donchin et al. (2002) recently found no detrimental effect of sleep deprivation on subsequent off-line performance. The current results are also in agreement with those of Shadmehr and Brashers-Krug (1997) who have reported that the internal model presumably necessary to adapt to dynamic disturbances (via a force-field applied by a robot-like arm) can be consolidated over time per se. Although the latter studies were not specifically designed to address the role of sleep in motor consolidation, these results support the notion that time, rather than sleep, is essential and sufficient to engage the consolidation process in motor adaptation paradigms (but see Huber et al. 2004).

The current results thus show that the expression of consolidation (“off-line”) gains in the FTSL task benefits from sleep, even a short nap, while in the VMA task, simple passage of time is as effective as time in sleep. Our results also suggest that procedural memory consolidation processes may differ, depending on the nature of the task demands; hence revealing that the optimization of training protocols should take this behavioral dissociation into account when considering to study the effect of sleep on motor memory processes.

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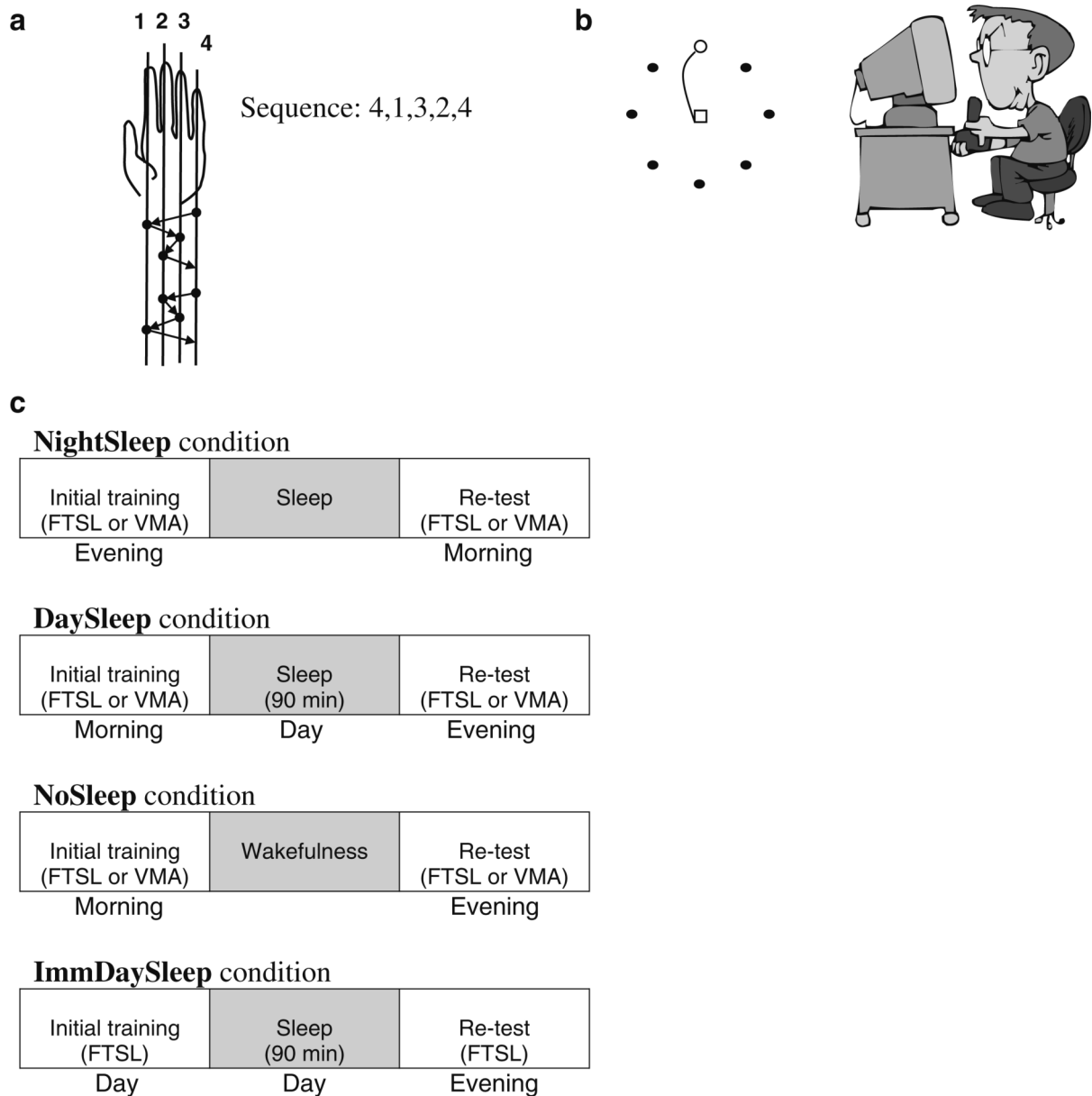


Fig. 1. Motor skill learning paradigms and protocols. **(a)** Finger tapping sequence learning task (FTSL) **(b)** Visuomotor adaptation learning task (VMA) **(c)** Experimental design. Subjects in the **NightSleep** condition were trained in the evening on either the FTSL or the VMA task, and re-tested 12 h post-training (12 h PT) after a night of sleep. In the **NoSleep** condition, subjects were trained on either the FTSL or the VMA task in the morning and re-tested at 12 h PT. In the **DaySleep** condition, subjects were trained on either the FTSL or the VMA task in the morning. At noon, subjects afforded a 90-min nap and were re-tested at 12 h PT. In the **ImmDaySleep** condition, subjects were trained on the FTSL task at noon and afforded a 90-min nap immediately after the training period. They were then re-tested at 8 h PT

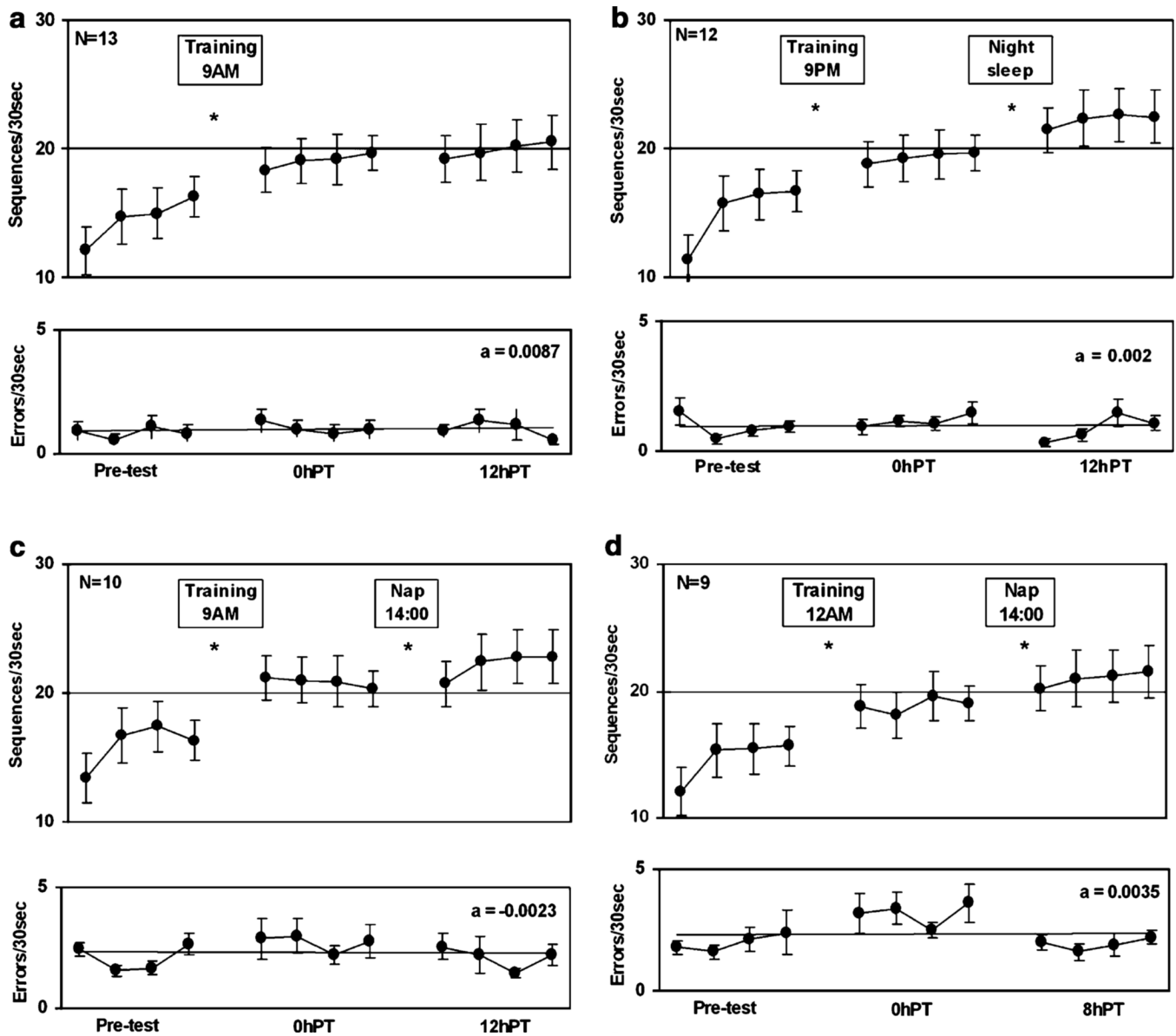


Fig. 2. FTSL task performance changes (mean group speed and accuracy) during the first 12 or 8 h after a single training session. **NoSleep** group (a) participants stayed awake after training at 09:00 AM, performance of the trained sequence was re-tested at 09:00 PM; no napping was afforded. **NightSleep** group (b) after training at 09:00 PM subjects had a normal night sleep, performance of the trained sequence was re-tested at 09:00 AM. **DaySleep** group (c) after training at 09:00 AM, subjects were allowed a 90 min day-time afternoon nap and the performance of the trained sequence was re-tested at 09:00 PM. **ImmDaySleep** group (d) after training at 12:00 PM subjects had 90 min day-time afternoon sleep. Performance of the trained sequence was re-tested at 09:00 PM. Baseline (Pre-test), immediate post-training (0 h PT), 8 or 12 h (8 or 12 h PT) scores for speed (*upper panels*) and accuracy (*lower panels*) are shown. Bars S.E.M., * $p < 0.05$. A slope of the regression line fitted to the accuracy data points

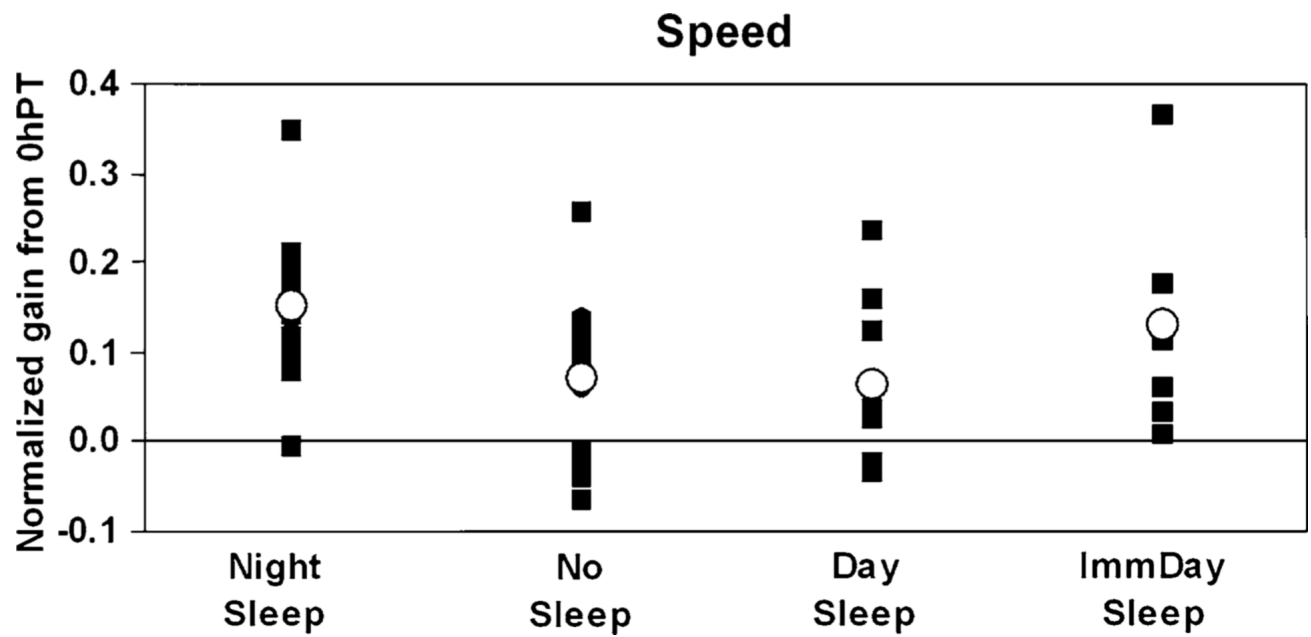


Fig. 3. Individual normalized gains in performance speed for the FTSL task. The difference in each participant's average performance 8 or 12 h post-training from his/her own average 0 h PT performance speed, normalized to the 0 h PT performance. *Black squares* individual normalized gains, *white circles* means of normalized gains. Data for participants in the four groups, **NoSleep**, **NightSleep**, **DaySleep** and **ImmDaySleep** is shown

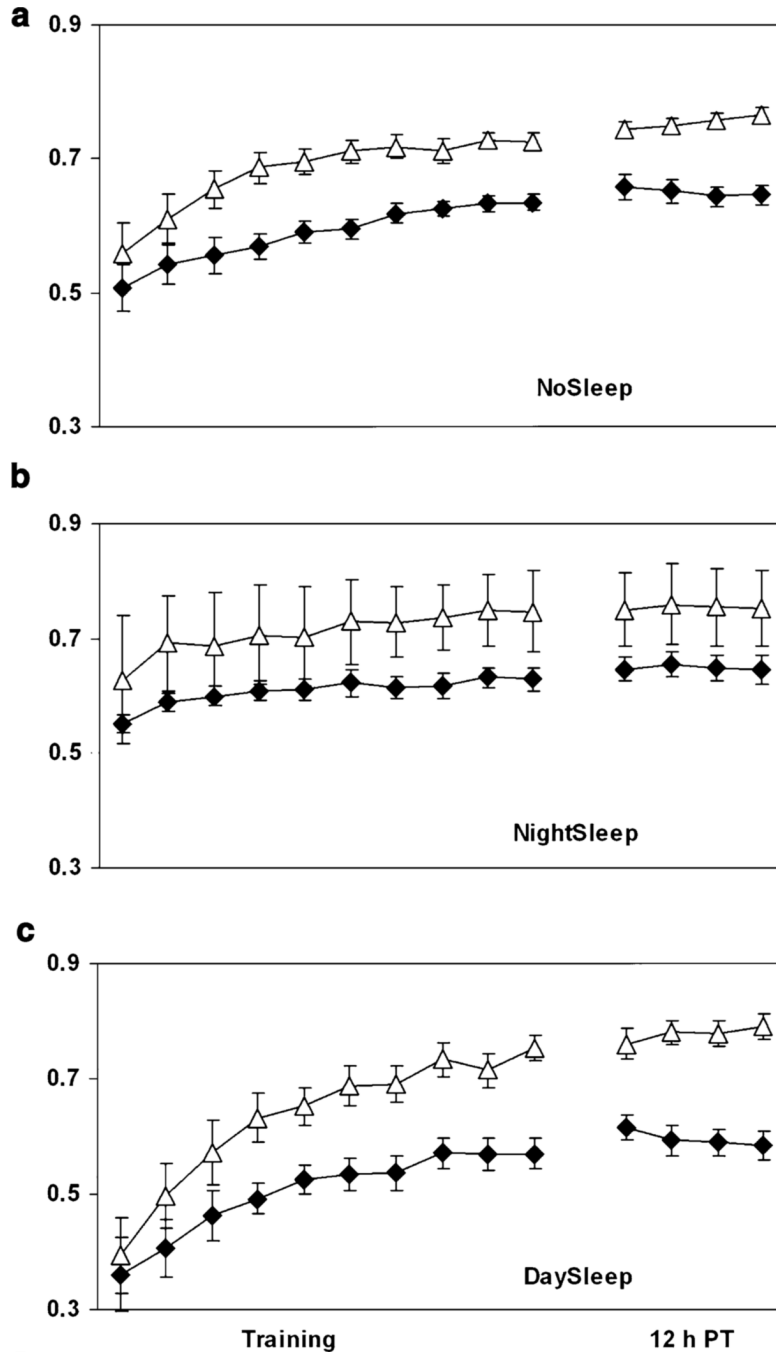


Fig. 4. VMA task performance changes (*white triangles* mean group accuracy, *black rhombs* mean group speed) during the first 12 h after a single training session. Each data point refers to the group mean performance in successive blocks, each block representing mean performance on 64 trials. The delayed improvements are not apparent from the graphs because the scale of the overall improvement in performance starting from the baseline is relatively large, thus, the minor delayed post-training improvements of 3–4% are hardly distinguishable. **NoSleep** group (a) after training at 09:00 AM, performance of the trained sequence was re-tested at 09:00 PM; no napping was afforded. **NightSleep** group (b) after training at 09:00 PM subjects had a normal night sleep, performance of the trained sequence was re-tested at 09:00 AM.

DaySleep group (c) after training at 09:00 AM, subjects were allowed a 90 min day-time afternoon nap and the performance of the trained sequence was re-tested at 09:00 PM. *Bars* SEM

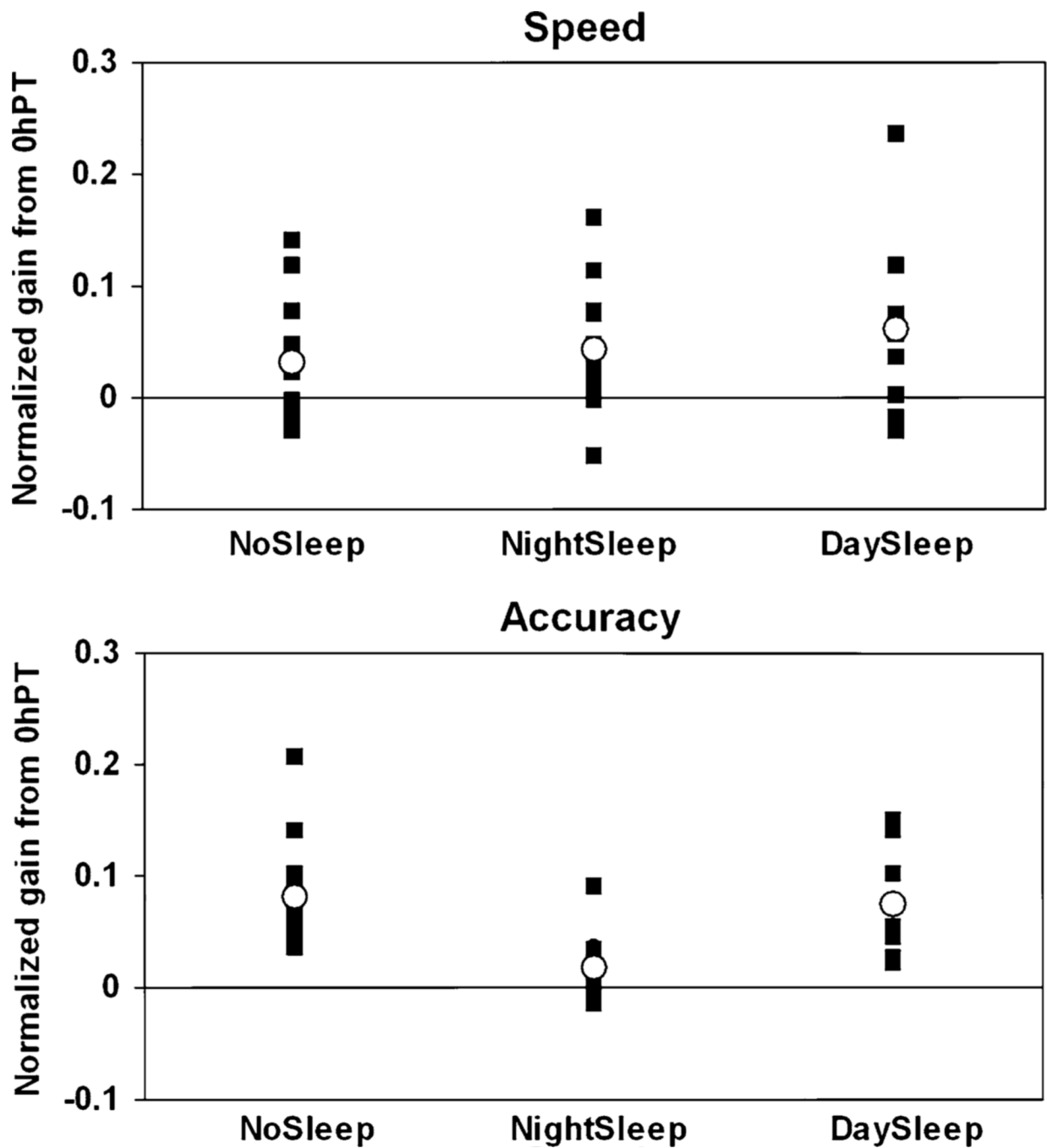


Fig. 5. Individual normalized gains in performance speed and accuracy for the VMA task. The difference in each participant's average performance at 0 and 12 post-training from his/her own average 0 h PT performance, normalized to the 0 h PT performance. *Circles* means of normalized gains, *squares* individual normalized gains. Data for participants in the three groups, **NoSleep**, **NightSleep** and **DaySleep** is shown

Table 1

Results of the group \times gains interaction analyses on performance at 0 h PT versus 8 h or 12 h PT for the four groups tested using the FTSL task

	0 h PT versus 8 h or 12 h PT re-test		
	NightSleep	DaySleep	ImmDaySleep
NoSleep	$p = 0.005$ $F_{(1,23)} = 9.735$	$p = 0.547$	$p = 0.093$ $F_{(1,23)} = 3.122$
NightSleep	\times	$p = 0.032$ $F_{(1,14)} = 5.303$	$p = 0.234$
DaySleep	\times	\times	$p = 0.295$

Results for the **NoSleep**, **NightSleep**, **DaySleep** and **ImmDaySleep** are reported

Table 2

Sleep parameters of the post-training night and day sleep for both tasks

	VMA task, NightSleep, mean (SD)	VMA task, DaySleep, mean (SD)	FTSL task, NightSleep, mean (SD)	FTSL task, DaySleep, mean (SD)
Sleep latency (min)	11.1 (8.3)	5.72 (3.04)	9.5 (7.6)	3.54 (2.43)
Total sleep time (min)	440.1 (51)	80.09 (6.06)	447.6 (25.8)	81.39 (5.48)
Sleep efficiency (%)	94.3 (5.1)	95.86 (4.93)	93.9 (2.7)	97.1 (1.26)
Stage 1 (min)	22.7 (10.3)	7.5 (4.47)	24.7 (11.4)	6.16 (3.52)
Stage 2 (min)	272 (41.9)	48.39 (13.24)	281 (28.8)	56.09 (15.00)
Stage 3-4 (min)	40.2 (27.4)	23.08 (22.07)	36.8 (25.7)	16.13 (13.11)
REM sleep (min)	105.2 (15.8)	21.08 (10.56)	105.1 (22.6)	21.62 (12.51)

Mean (SD) of EEG sleep parameters are shown