Selective delayed gains following motor imagery of complex movements

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A B S T R A C T

There is now compelling evidence that sleep contributes to the motor memory consolidation. More recent studies further showed that a night of sleep or a nap may play a equivalent functional role following motor imagery (MI) practice, hence resulting in similar delayed performance gains. Here we examined whether offline gains following MI of a finger tapping sequence depends on the degree of complexity of the motor sequence, and whether this improvement differentially affects the individual transitions of the motor-sequence pattern being learned. The data revealed greater delayed performance gains in motor skill procedures that were most difficult, with larger sleep-dependent overnight improvement for movements involving bimanual coordination. The analyses of single transitions between sequence elements further showed greatest overnight improvement in speed for the slowest (i.e., most difficult) transitions at the re-test. These findings suggest that sleep-related performance gains for imagined movements depend on motor skill complexity, and that difficult transition movements are most effectively enhanced after a night of sleep.

Key words
Movement imagery • Sleep • Memory consolidation • Motor learning complexity

The motor memory consolidation process refers to the automatic post-encoding processing occurring without awareness allowing the conversion of an initial unstable memory representation into a more robust and effective form (Stickgold and Walker, 2007). Over the last 10 years, a substantial number of studies have supported the role of sleep in the consolidation of the procedural memory (Walker et al., 2003a,b; Robertson et al., 2004; Stickgold and Walker, 2005), and in motor sequence learning. Doyon et al. (2009) showed that the expression of consolidation gains in a sequential finger tapping task benefits from sleep, while that related to the visuomotor adaptation task does not. These data suggest that procedural memory consolidation pro-

cesses depend on the nature of the task demands. Interestingly, Kuriyama, Stickgold, and Walker (2004) demonstrated that following a night of sleep, greater delayed performance gains were observed in motor skill procedures that were most difficult, i.e. involving bimanual coordination. Altogether, these findings provided evidence that when studying the effect of sleep, both the nature and the complexity level of the motor learning should be considered to determine the optimization of training protocols. Referring to the somatotopy of the motor cortex and the cerebellum (Kurth et al., 2000; Beisteiner et al., 2001), Kuriyama et al. (2004) hypothesized that the size of the neural networks controlling movements might vary as a function of the digit numbers used

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in task performance, which may then be mediated by the sleep-dependent synaptic plasticity.

Motor imagery (MI) is a dynamic state during which a movement is internally reactivated within working memory and without any motor output (Decety, 1996; Malouin et al., 2004). There is ample evidence that MI contributes to enhance cognitive and motor performances (Feltz and Landers, 1983; Guillot and Collet, 2008). More recent data further demonstrated that a period of sleep after MI practice resulted in similar motor memory consolidation than following physical practice of the same task, while participants who were not subjected to MI practice did not improve their motor performance (Debarnot et al., 2009a,b; Debarnot et al., 2011). The effect of MI on finger tapping sequence learning has been extensively considered in the literature (Boecker et al., 2002; Rodriguez et al., 2008; Avanzino et al., 2009; Debarnot et al., 2010a). For instance, Avanzino et al. (2009) claimed that MI facilitates the brain network involved in sensorimotor control, particularly acting on those neural structures involved in the motor program, and that this effect is greater in complex movements. Boecker et al. (2002) further reported that the relevant brain areas mediating finger tapping sequence learning are challenged by the processing demands of a specific task when pursued mentally, but these authors did not look at the impact of the sleep consolidation process *per se*. Hence, it has been suggested that MI might contribute to sleep-related delayed gains on performance, on the one hand, and that MI would affect primarily the learning of most complex movements, on the other.

Based on the results mentioned above, the present study aimed to investigate whether offline gains following MI practice of a sequential finger tapping task depends on the degree of complexity of the motor sequence. With reference to the experimental design proposed by Kuriyama et al. (2004), we used an adapted version of the sequential finger tapping task first developed by Karni et al. (1995), by varying two characteristics: (1) limb complexity (i.e., unimanual *vs*. bimanual), and (2) length of the sequence (five-elements *vs*. eight-elements). Motor performance was evaluated before MI training, as well as before and after a night of sleep or a similar daytime interval without intervening sleep. Thus, six groups of participants were distinguished: 5-Night, 5-Day, 8 Uni-Night, 8 Uni-Day, 8 Bi-Night, and 8

Bi-Day. Participants subjected to a night of sleep, but not those assigned to daytime groups, were expected to show delayed performance gains. As increased motor-skill proficiency is associated with improved temporal automaticity between key-press transitions (Miller, 1956; Sakai et al., 2003; Wright et al., 2010), we further expected significant changes in the motor-sequence performance profile after a night of sleep. More specifically, we postulated that the most difficult transition points of the sequence (i.e., the slowest) would be selectively enhanced. To assess this latter possibility, we analyzed differences in transition speeds between each of the separate key-press movements within each sequence, both before and after sleep.

Methods

Participants

A total of 48 healthy volunteers aged between 20 and 35 years (mean age: 27.8 ± 4.2 years; 23 women) took part in this study. All were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). They reported sleeping regularly between 7 and 9 hours per night, and extreme evening- and morning-type individuals, as well as regular nappers and smokers, were excluded. None had any prior history of drug or alcohol abuse, neurological, psychiatric, or sleep disorders, and they were instructed to be drug, alcohol, and caffeine free for 24h prior, and during the experiment. Musicians and professional typists were excluded to avoid participants with previous experience on finger tapping sequence tasks. This study was approved by the Research Ethics Committee of the University of Pisa, and all participants signed an informed consent form. The procedure was explained, and instructions regarding the motor task and questionnaires were given, but no information was provided about the objectives of the study, or the dependent variables of interest.

Sleep characteristics and MI abilities

All participants were asked to fill out the Pittsburg Sleep Quality Index (PSQI, Buysse et al., 1989) to assess sleep quality and quantity. This test was administered to exclude participants experiencing obvious disturbances during their sleep/wakeful-

ness cycles, and to ascertain their predisposition to benefit from the natural effects of sleep. Subjective measures of alertness and fatigue were also collected using the Stanford Sleepiness Scale (SSS, Hoddes et al., 1972) at the training and re-test sessions. Regarding the individual imagery ability, the Revised version of the Movement Imagery Questionnaire (MIQ-R, Hall and Martin, 1997) was used to measure the individual ability to form kinesthetic and visual mental images. This is an 8-item self-report questionnaire, in which participants rate the vividness of their mental representation using two 7-point scales (1 = very hard to see/feel, and 7 = very easy to see/feel).

Procedure

A computerized version of the sequential finger tapping task developed by Karni et al. (1995) was used to measure motor sequence learning. Participants were randomly assigned into one of the three following experimental conditions: 5-digit unimanual, 8-digit unimanual, or 8-digit bimanual finger sequence (Fig. 1). Each was followed either by a night of sleep or a similar interval during daytime. Hence, to compare the offline effect of different motor complexity sequences with MI practice, there were 6 experimental groups.

All participants were first asked to learn explicitly a predetermined sequence of fingers corresponding to one of the three experimental conditions, until they were able to recall it from memory. During each test session (pre-training, post-training, and re-test), they were requested to tap the sequence as fast and accurately as possible on a computer keyboard during periods lasting 30s, while making as few errors as possible. Performance on each sequence task trial was validated by pushing the space bar of the computer, to record the duration of each motor sequence. All key presses were recorded and averaged over the entire sequence using a home-made MATLAB-written routine. For each participant, this software compared the sequence of key presses produced by the participant to the correct sequence template to be performed, hence allowing the detection of any discordance between the real and expected taps within the given sequence. Each 30s-period was then followed by a rest-period of 20s. The number of correct sequences and the average speed used to perform each sequence constituted the dependent variables of interest.

Pre-training session

The experiment was scheduled to begin at 8:00 pm in the three groups subjected to a night of sleep (5-Night, 8 Uni-Night, and 8 Bi-Night groups), and at

Groups 1, 2: 5-Night, 5-Day
Groups 3, 4: 8Uni-Night, 8Uni-Day
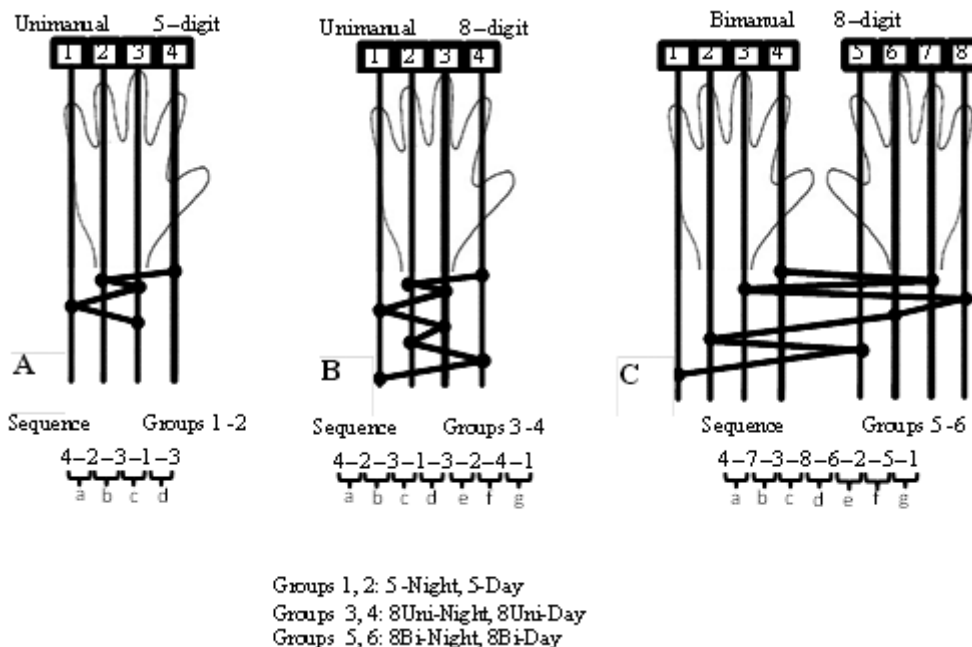Groups 5, 6: 8Bi-Night, 8Bi-Day

Fig. 1. - Schematic representation of the finger sequences.

8:00 am in the three other groups (5-Day, 8 Uni-Day, and 8 Bi-Day groups). After learning the finger tapping sequence, they were given few trials until being able to physically perform five successive correct finger sequences. Participants who needed more than 10 trials were excluded from the study to ensure that the number of trials necessary to achieve five correct sequences did not differ among groups. Following this introductory session, the pre-training session consisted in four practice blocks lasting 30s each. Without any feedback, participants had to repeat the sequence physically as fast and accurately as possible. To start each block, as well as after completing each finger sequence, they were requested to push the space bar of the computer. At the end of the 30s-period, a 20s countdown was automatically initiated on the computer screen before the next 30s-period. During this time lapse, the participants were explicitly asked to have rest, i.e., to avoid mentally or physically perform the finger sequence. Hence, each 30s-period was systematically followed by a 20s rest period, so that the pre-training session lasted three minutes.

MI training

To ensure that the improvement in performance during the learning and consolidation processes would not depend upon the individual imagery abilities, we verified that the individuals' MIQ-R test scores did not significantly differ among the six groups. During practice, all participants imagined the finger sequence during 12 blocks of 30s each, which were separated by 20s rest-periods, for a total duration of nine minutes. All participants were required to imagine the motor sequence using a combination of internal visual and kinesthetic imagery, i.e. imagining movement from within one's body and perceiving the sensations of how it feels to perform the action. They rehearsed the finger sequence in a quiet room, without any environmental constraints, that is, without distracting stimuli, to facilitate a focused attention on the formation of the mental images. A validated imagery script was read to the participants to ensure that they followed similar instructions throughout MI sessions (Debarnot et al., 2009a). To prevent actual finger movements during MI, the participants were required to leave their left hand motionless on their right forearm, and were asked to keep their eyes open in order to see the changes in screen background, indicating the 30s training and

20s rest-periods. All participants were requested to imagine performing the finger sequence at a pace that was similar to the duration of the motor performance during the pre-training session. To make sure that they would follow such guidelines, and to be able to record the duration of each MI sequence, they were asked to push the space bar with their right hand at the end of the motor sequence.

Post-training and re-test sessions

Two post-training tests were carried out to determine the immediate effects of MI training on the task performance, as well as the sleep or wake-related effects on motor memory consolidation. The first post-training test was performed immediately at the end of the training session, and was similar to the pre-training test (four 30s periods during which the participants were asked to execute physically the finger sequence as fast and as accurately as possible, interleaved with a 20s rest period). Individual debriefings were further scheduled to investigate adherence to the MI instructions, and to determine whether they encountered difficulty in forming mental images. Simultaneously, participants were asked to auto-evaluate the quality of their mental images using a Likert-type scale (from 1 = inaccurate mental representation to 6 = vivid mental representation). To evaluate the night or daytime effects, a second similar post-training test (re-test) was performed following an 8h (± 1h) night of sleep (the session began 2h after waking up), or after 8h daytime period in the day groups. Between the first and second post-training tests, the participants were asked neither to imagine nor to execute the sequential finger movements.

Data analysis

For each test session (pre-training, post-training, and re-test), we calculated the total number of correct sequences (within the four blocks) and the mean sequence duration. Imagined times were also considered to check whether participants complied with the imagery guidelines, i.e. whether MI was performed in real-time. To do so, we performed three repeated measure analyses of variance (ANOVA$_{RM}$) with GROUP (5-Night, 5-Day or 8 Uni-Night, 8 Uni-Day or 8 Bi-Night, 8 Bi-Day) as between-subjects factor and SESSION (pre-training/MI training) as within-subjects factor (Statistica, StatSoft Inc., USA).

The effect of training and the magnitude of the delayed performance both on the number of correct sequences and the mean sequence duration were expressed in percents. The effect of training was estimated by computing the increase in performance between the pre and post-training tests, while the magnitude of the delayed gain in performance (i.e., after a night or daytime) was estimated by computing the increase in performance, between the post-training test and re-test. An ANOVA$_{RM}$ with GROUP (5-Night, 5-Day, 8 Uni-Night, 8 Uni-Day, 8 Bi-Night, 8 Bi-Day) as between-subjects factor and SESSION ([post-training - pre-training] / [re-test - post-training]) as within-subjects factor was used to examine effects of training and amplitude of the delayed performance. A one-way ANOVA with GROUP (5-Night, 5-Day, 8 Uni-Night, 8 Uni-Day, 8 Bi-Night, 8 Bi-Day) as between-subjects factor was also performed to determine the difference in delayed performance gains following a night of sleep or a similar daytime interval ([re-test - post-training] data). Finally, a one-way ANOVA was performed to compare performance among the three night groups. When necessary, corrected post-hoc comparisons were carried out using a Fisher's LSD test.

In order to investigate the presence of more subtle changes in motor performance, we further analyzed the transition phase between each finger. Practically, we measured differences in transition speeds between each of the separate key press movements within each sequence on the last two blocks of the post-training test, as well as those of the re-test session. We therefore identified, prior to sleep (or daytime), the fastest and slowest transition positions at the post-training session, and then measured changes in speed in each of these transition positions during the re-test. For the statistical analyses, we first checked that all of the data fitted a normal distribution, and that there was not any group difference during the pre-training test performance. Then, a two-way ANOVA with GROUP as between-subjects factors and SESSION (post-training/ re-test) was performed with Fisher's LSD post-hoc comparisons to compare behavioral data in all groups. Group scores on questionnaires were finally compared using ANOVAs. The results are presented as mean (standard deviation [SD]) and a level of $p < 0.05$ was considered critical for assigning statistical significance.

Results

Sleep characteristics and MI abilities

The average PSQI sleep score was 2.0 (± 0.8), thus attesting to the "good quality" of sleep in all participants. As expected, there was no significant difference when comparing the rating of SSS among groups during the pre-training session, $F (5, 4) = 0.6$, $p = 0.7$, as well as between the training and re-test sessions, $F (1, 42) = 0.05$, $p = 0.8$, suggesting that the alertness of subjects from all six groups was identical during the whole experiment. Mean scores of the MIQ-R were 46.5 (± 4.9) in the 5-Day group, 45.6 (± 4.6) in the 5-Night group, 46.7 (± 5.0) in the 8 Uni-Day group, 44.7 (± 5.5) in the 8 Uni-Night group, 43.7 (± 6.5) in the 8 Bi-Day group, and 44.6 (± 3.9) in the 8 Bi-Night group. There was no group difference $F (5, 42) = 0.3$, $p = 0.9$, thus ensuring homogeneity in terms of individual ability to form mental motor images. As expected, visual imagery scores were higher than kinesthetic imagery scores in all groups $F (1, 42) = 56.5$, $p < 0.001$.

Practice-dependent learning

The average number of correct sequences during the pre-training session was 46.5 (± 2.4) in the 5-Night group, 41.1 (± 4.0) in the 5-Day group, 26.7 (± 1.8) in the 8 Uni-Night group, 26.1 (± 2.6) in 8 Uni-Day groups, 22.4 (± 4.0) in the 8 Bi-Night, and 17.1 (± 1.8) in the 8 Bi-Day group (Table I).

The data revealed that all groups improved their performance from the pre-training to the post-training session. In the post-training session, the number of correct sequences increased by 32% (± 4.6) in the 5-Night group, 41% (± 8.8) in the 5-Day group, 32% (± 3.2) in the 8 Uni-Night group, 42% (± 6.8) in the 8 Uni-Day group, 40% (± 8.8) in the 8 Bi-Night group, and 39% (± 8.8) in the 8 Bi-Day group (Fig. 2 and Table II). Interestingly, in the three night groups, the number of correct sequences further increased at the re-test to 51% (± 5.2) in the 5-Night group, 64% (± 7.5) in the 8 Uni-Night group, and 78% (± 9.2) in the 8 Bi-Night group, while lower performance were observed in the three day groups (36% ± 9.2 in the 5-Day group, 28% ± 9.6 in the 8 Uni-Day group and 27% ± 10.4 in the 8 Bi-Day group). Comparing performance gains yielded a significant main effect of GROUP, $F (5, 42) = 2.5$, $p < 0.05$, and SESSION, $F (1, 42) = 7.3$, $p < 0.01$, as

Table I. - Mean (standard deviation) Number of Correct Sequences and Movement Speed.					
	Number of correct sequences			Movement times (s)		
	Pre-training	Post-training	Re-test	Pre-training	Post-training	Re-test
5-Night	46.50 (2.37)	61.38 (2.95)	70.50 (4.95)	1.88 (0.10)	1.43 (0.07)	1.27 (0.08)
5-Day	41.13 (4.04)	57.88 (3.40)	55.88 (3.48)	2.25 (0.23)	1.60 (0.13)	1.64 (0.10)
8 Uni-Night	26.75 (1.87)	35.25 (1.73)	43.88 (2.80)	3.30 (0.25)	2.47 (0.15)	2.08 (0.16)
8 Uni-Day	26.13 (2.63)	37 (4.31)	33.50 (4.42)	3.51 (0.37)	2.67 (0.38)	3.07 (0.39)
8 Bi-Night	22.38 (4.04)	31.38 (5.84)	39.88 (6.26)	4.05 (0.82)	2.94 (0.50)	2.23 (0.49)
8 Bi-Day	17.13 (1.79)	23.75 (2.27)	21.88 (3.07)	5.13 (0.57)	3.75 (0.29)	4.40 (0.55)

well as a significant GROUP X SESSION interaction, F (5, 42) = 7.1, p < 0.001. Post-hoc revealed no group difference when comparing the post-training and the pre-training sessions, p > 0.05 for all comparisons, thus indicating that the effect of MI training were equally efficient for all complexity conditions and induced gains in performance of comparable amplitude. Post-hoc comparisons further revealed that the differences in performance improvement from the pre-training to the re-test session was significant in the night groups, p < 0.05 in the 5-Night group, and p < 0.001 in the 8 Uni and Bi-Night groups, but not in the corresponding Day groups, p > 0.05.

A similar pattern of results was observed when comparing mean movement times. The mean movement times of correct sequences during the pre-training session was 1.9 (± 0.1) in the 5-Night group, 2.2 (± 0.2) in the 5-Day group, 3.3 (± 0.2) in the 8 Uni-Night group, 3.5 (± 0.4) in 8 Uni-Day groups, 4.0 (± 0.8) in the 8 Bi-Night, and 5.1 (± 0.6) in the 8 Bi-Day group. The data revealed that all groups reduced the time to complete the sequence from the pre-training to the post-training session (Tables I and II). During the re-test, the velocity further decreased to 12% (± 2.0) in the 5-Night group, 15% (± 4.0) in the 8 Uni-Night group, and 24% (± 8.5) in the Bi-Night group,
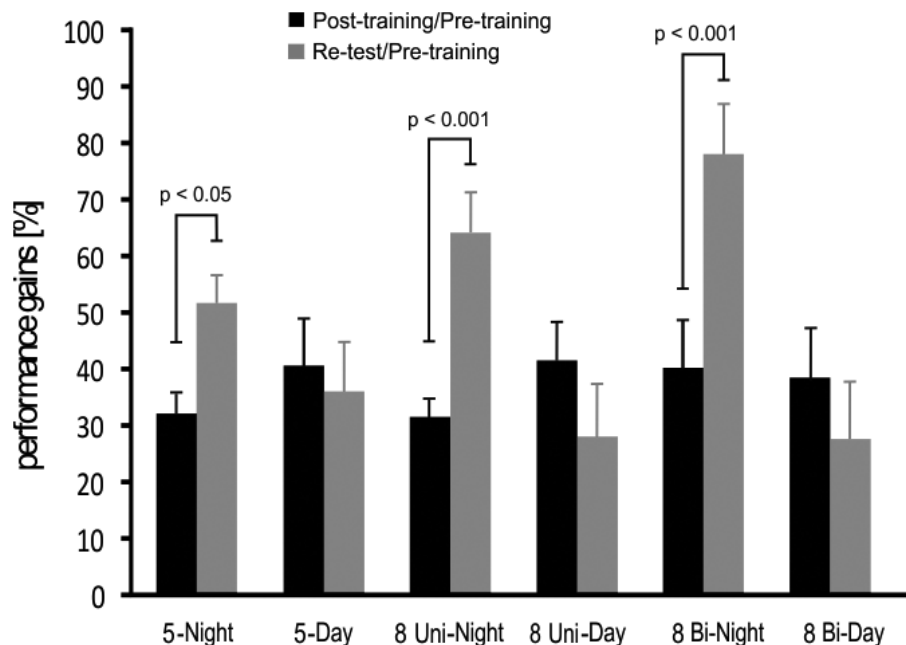

Fig. 2. - Performance gains. The increase in the total number of sequences between the post-training and re-test sessions is expressed in percent with respect to data gathered in the pre-training session.

Table II. - Mean (standard deviation) Percentage of Correct Sequences and Movement Times.					
	Number of correct sequences (%)			Movement times (%)		
	[Post - Pre-training]	[Re-test - Pre-training]	[Re-test - Post-training]	[Post - Pre-training]	[Re-test - Pre-training]	[Re-test - Post-training]
5-Night	32 (4.6)	51 (5.2)	19 (3.0)	23 (2.2)	32 (2.3)	11 (2.0)
5-Day	41 (8.8)	36 (9.2)	-5 (-2.4)	27 (3.2)	25 (3.5)	-3 (2.0)
8 Uni-Night	32 (3.3)	64 (7.5)	32 (6.5)	24 (2.7)	36 (3.0)	15 (4.0)
8 Uni-Day	42 (6.8)	28 (9.6)	-14 (-8.7)	25 (3.2)	20 (5.0)	-7 (3.6)
8 Bi-Night	40 (8.8)	78 (9.2)	38 (2.4)	26 (9.2)	45 (15.9)	24 (8.5)
8 Bi-Day	39 (8.8)	28 (10.4)	-11 (-9.3)	25 (3.0)	15 (2.6)	-15 (6.6)

whereas the three day groups took more time to complete the sequence (- 3.4% ± 2.0 in the 5-Day group, -7% ± 3.6 in the 8 Uni-Day group, and 15% ± 6.6 in the 8 Bi-Day group). The ANOVA$_{RM}$ yielded a main effect of GROUP, F (5, 42) = 4.7, p < 0.001, and a main effect of SESSION, F (1, 42) = 7, p < 0.01, as well as a significant GROUP x SESSION interaction, F (5, 42) = 11.6, p = 0.001. Post-hoc revealed no group difference when comparing the decrease of the velocity from the pre-training to the post-training session, p > 0.05 for all comparisons, indicating that all groups performed the sequential finger faster following MI training. Moreover, post-hoc comparisons revealed that the difference between the night and Day groups reached significance, p < 0.01 in the 5-Night group, p < 0.001 both in the 8 Uni and 8 Bi-Night groups, but not in the day groups, p > 0.05 for the 5 and 8 Uni-Day groups, while the 8 Bi-day group showed a significant increase in the velocity p < 0.01.

Sleep-dependent learning

The performance between the post-training and the re-test sessions increased by 20 % (± 3.0) in the 5-Night group, 32% (± 6.5) in the 8 Uni-Night group, and 38% (± 2.4) in the Bi-Night group (Fig. 3). In contrast, the day groups showed a slight tendency to make more errors during the re-test session (-5% ± 2.4 in the 5-Day group, -13% ± 8.7 in the 8 Uni-Day group and -11% ± 9.3 in the 8 Bi-Day group). The one-way ANOVA revealed that the group difference reached significance, F (5, 42) = 4.2, p < 0.01. Fisher LSD post-hoc analyses further revealed that the change from post-training to re-test was significantly higher in the three night groups than in the three day groups, p ≤ 0.05. Similarly, when comparing the difference in mean movement times between the post-training and the

re-test, the one way ANOVA yielded a main effect of GROUP, F (5, 42) = 7.6, p < 0.0001. Fisher's LSD post-hoc analyses revealed that the night groups performed sequential finger movement significantly faster during the re-test compared to day groups, p < 0.01 for all comparison, while there was no difference in performance gains between night groups, p > 0.05. While these findings suggest that a night of sleep following MI training improved the performance in comparison with a simple passage of day-time, additional analyses revealed that the strongest performance gains were obtained for the most complex configuration of the sequential movement (i.e., the 8 Bi-Night group). Although no difference was found when comparing the number of correct sequences among the three night groups, F (2, 21) = 1.86, p = 0.18, data revealed a significant GROUP effect when comparing movement times, F (2, 21) = 8.3, p < 0.01. Post-hoc comparisons showed that the 8 Bi-Night group outperformed the 5-Night group, p < 0.01, and further tended to outperform the 8 Uni-Night group, p = 0.07.

Transition speed

Data provided evidence of overnight changes in performance. As suggested by Kuriyama et al. (2004), we further analyzed differences in transition speeds (slow *vs*. fast) to see whether there were more subtle, qualitative performance changes. We identified the fastest and slowest transition positions at post-training (i.e., during the last two blocks) and measured changes in speed at each of these same transitions positions during the re-test following the night of sleep. The ANOVA revealed a main effect of GROUP, F (5, 42) = 15.7, p < 0.001, as well as a main effect of TRANSITION, F (1, 42) = 52.2, p < 0.001 and a significant GROUP x TRANSITION interaction, F (5,

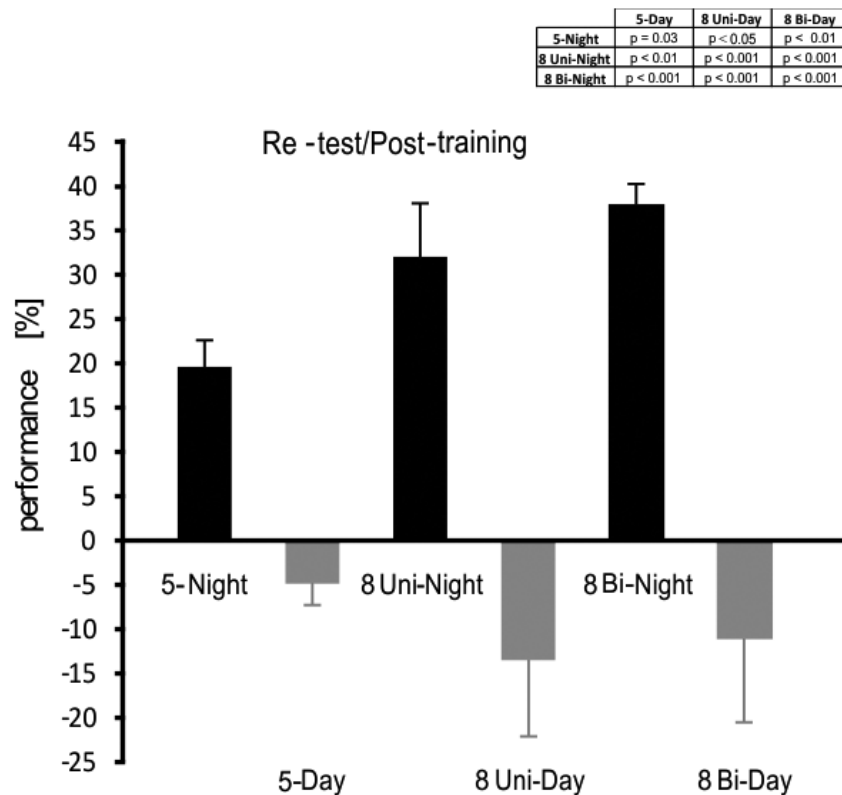|	5-Day	8 Uni-Day	8 Bi-Day
5-Night	p = 0.03	p < 0.05	p < 0.01
8 Uni-Night	p < 0.01	p < 0.001	p < 0.001
8 Bi-Night	p < 0.001	p < 0.001	p < 0.001

Fig. 3. - Delayed performance gains. The amplitude of the delayed gain in performance estimated as the difference between the total number of sequences in the re-test and post-training sessions – in all groups and expressed in percent; only the Night groups showed an increased in performance at the re-test. Error bars indicate one SD.

42) = 8.5, p < 0.001. Interestingly, there was a clear dissociation in overnight improvement between the slowest and fastest transition positions, with greater improvement for the slowest (i.e., most difficult) transition (Fig. 4). Post-hoc analyses revealed that these performance gains in the transition phases differed when comparing the data from the 8 Bi-Night group (i.e., the group subjected to the most complex sequence of movement, and benefiting from sleep) with those of the 5-Day and 5-Night groups, p < 0.001, and p < 0.001, respectively, 8 Uni-Day and 8 Uni-Night groups, p < 0.001, and p < 0.002, respectively, and 8 Bi-Day group, p < 0.001.

Assessment of imagery use

We first compared the mean of imagined sequence times with those of the corresponding actual times recorded during the pre-training for each task configuration. The ANOVA$_{RM}$ revealed no difference for the 5-Day and 5-Night groups, F (1, 14) = 1.9, p = 0.2, as well as for the 8 Bi-Day and Bi-Night

groups, F (1, 14) = 0.9, p = 0.3, while both 8 Uni-Day and 8 Uni-Night groups slightly overestimated actual times during MI, F (1, 14) = 5.9, p = 0.03. Taken together, and despite the small increase in MI speed in the latter groups, the data provided evidence that the participants overall complied with MI guidelines. There was no group difference when comparing the individual ratings in the evaluation of the MI vividness during practice, F *(5, 42)* = 0.5, p = 0.7. Mean scores were 4.1 (± 1) in the 5-Day group, 4.4 (± 0.5) in the 5-Night group, 4.6 (± 0.5) in the 8 Uni-Day group, 4.2 (± 0.7) in the 8 Uni-Night group, 4.4 (± 0.5) in the 8 Bi-Day group, and 4.2 (± 0.7) in the 8 Bi-Night group. Furthermore, during the debriefing following MI, all participants reported that they used the imagery type outlined in the scripts. They combined internal visual and kinesthetic imagery without switching to external visual imagery. None reported changing the imagery script to suit individual needs, and all rehearsed the motor sequence as requested. Accordingly, they were able
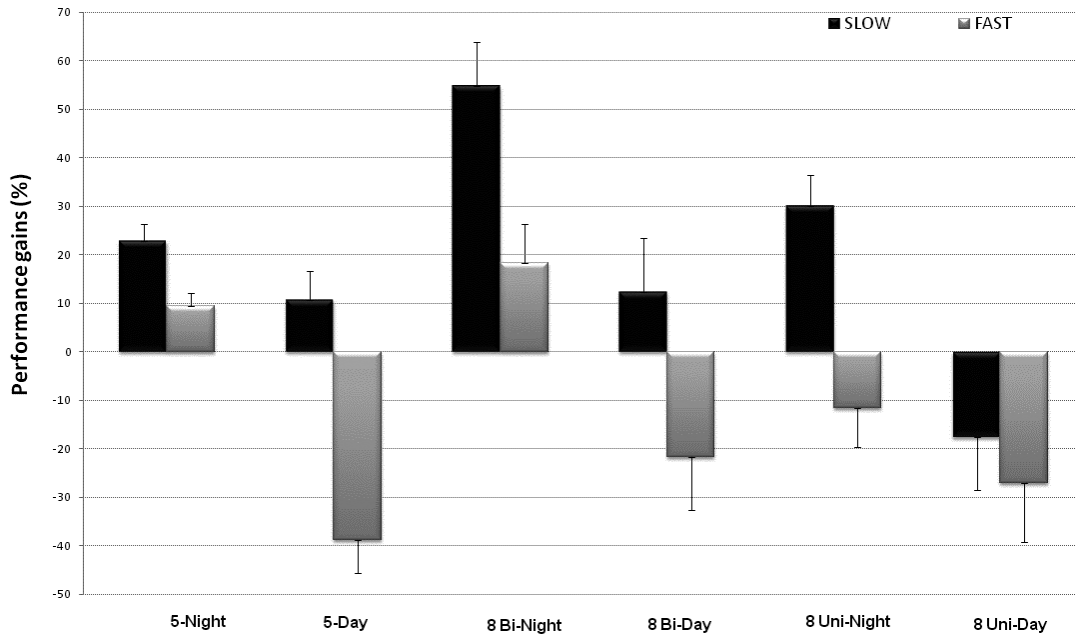
Fig. 4. - Improvement in transition speed occurring at the slowest and fastest transition positions.

to report the movement with an explicit knowledge of each key that they had to press. All participants further reported that they did not imagine nor execute finger movements between the first and second post-training tests.

Discussion

This study aimed to investigate whether sleep-dependent gains following MI of a finger tapping sequence were related to the degree of motor-skill complexity in the same way as sleep-dependent gains following physical practice are related to complexity. The main results showed that sleep-related performance gains for imagined movements were dependent on motor skill complexity, and that difficult transition movements were most effectively enhanced after a night of sleep. Practically, the data confirm the benefit from a night of sleep following MI as compared to a similar daytime interval.

As expected, a first level of analysis revealed similar sleep-related effects following MI practice regardless of the movement complexity, hence supporting recent data (Debarnot et al., 2009a,b; Debarnot et

al., 2010b). Specifically, the participants subjected to a night of sleep significantly increased the number of correct sequences as well as movement speed during the re-test. In contrast, the simple passage of time was not sufficient to provide additional benefits in day groups, where participants stabilized their performance. This latter result confirms the influence of sleep in the offline motor memory consolidation following MI, and further supports that the wake state *per se* is not sufficient to promote significant memory improvement. Interestingly, data also revealed greater delayed performance gains in motor skill procedures that were most difficult, with larger sleep-dependent overnight improvement for movements involving bimanual coordination. In other words, the most complex movement to be imagined was the most effective in promoting the sleep-related performance gains. In a simple practice condition, it has been shown that subjects engage shallow cognitive processes of movement information (Shea and Morgan, 1979), which can be restricted to working memory. Conversely, in the case of more complex motor tasks, participants need to rely upon more effortful working-memory processes in order to reinforce the memory trace in the long term

memory system. It is now well-known that MI is a cognitively challenging practice which allows to simulate the movement internally by requiring the working memory capacity (Malouin et al., 2004), which has been recently shown to benefit from post-training sleep (Kuriyama et al., 2008). Altogether, we postulate that both the implication of the working memory relating to the degree of task complexity and the effect of sleep in the motor memory consolidation might explain the greater delayed gains observed after MI of bimanual movements.

An alternative explanation might come from the cerebral plasticity of the neural networks mediating the motor memory consolidation during sleep (Kuriyama et al., 2004). It has been reported that the patterns of brain activity observed during actual practice reappear during subsequent sleep (Maquet et al., 2000; Stickgold and Walker, 2007). As the neural networks activated during simple and bimanual complex movements are not totally overlapping (Jancke et al., 2000; Wannier et al., 2002; Nair et al., 2003), and based on the somatotopy of the motor cortex, it has been postulated that the size of the networks involved in controlling movements vary as a function of the number of digits used in actual task performance (Kurth et al., 2000; Beisteiner et al., 2001). Complex bimanual movements therefore engage a more extensive cortical, subcortical, and cerebellar system compared to that of the 5-digit unimanual task, which could then be reactivated by the sleep-dependent synaptic plasticity (Kuriyama et al., 2004). Consistently, Boecker et al. (2002) reported, by varying the sequence structure of imagined finger movements, task-related activity changes in parietal, premotor and cerebellar structures, thus reflecting their role in mediating sequence control. They observed that the left lateral premotor cortex, right superior parietal areas and right cerebellar vermis yielded a clear gradual increase in regional activity with increasing complexity. Moreover, Rossink and Zijdewing (2010) recently demonstrated that the corticospinal excitability was modulated during MI practice of a simple and complex finger tapping task, and that the increase of task-complexity resulted in a significantly higher corticospinal excitability. Therefore, and based on the present pattern of behavioral measures, we postulate that MI of complex sequences of movements could result in greater neural activations than MI of simple actions, and

that the same pattern of activations is replayed during subsequent sleep to improve the motor memory consolidation. Conversely, the extensive networks underlying complex behaviors would provide more opportunities for the newly acquired trace to be consolidated via a replay mechanism during sleep. Such working hypothesis still awaits experimental investigation, and would reinforce the functional equivalence principle between MI and motor performance (Holmes and Collins, 2001). The latter assumption is also in line with the great amount of research looking for clearer associations between sleep-dependent changes in the neuronal representation and behavior-output measures of memory consolidation (Doyon et al., 2009; Debas et al., 2010; Orban et al., 2010). Interestingly, our results also showed that a night of sleep differentially affects the transitions speeds of a finger tapping motor-sequence. As shown for actual practice (Kuriyama et al., 2004; Wright et al., 2010), analyses of single transitions between sequence elements revealed the greatest overnight improvement in speed for the transitions that were slowest (i.e., most difficult) at the re-test. Memory representations can greatly differ in the strength of the underlying associations. Although discussed in earlier reviews (Cipolli, 1995; Diekelmann et al., 2009), the dependence of sleep-associated memory consolidation on the strength of acquired associations has not been systematically tested. So far, the notion that sleep enhances weak associations in memory to stronger associations has been explained through the chunking phenomenon (Kuriyama et al., 2004; Wright et al., 2010). Practically, a stereotyped temporal pattern or rhythm would emerge as we learn to perform a motor sequence because the sequence is reorganized during learning as serial chunks of movements in both sequence-specific and subject-specific manners (Sakai et al., 2003, 2004; Stocker and Hoffmann, 2004). The motor sequence within a chunk can then be carried out automatically, which reduces the cognitive demand needed to control the performance of the entire sequence. As postulated by Kuriyama et al. (2004) for actual practice, our results show that sleep dependent learning process might allow greater degree of motor-program automatization after MI practice, resulting not only in faster transitions within the sequence, but in more uniform transitions as well. Although the chunk phenomenon has been extensively studied for physi-

cal sequence learning, little is known about its effect when the sequential motor learning is performed with MI. There is no doubt that investigating in greater details the contribution of the chunk strategy during mental practice of a sequential motor task will be of particular interest in future studies.

As with all research, this study has some limitations that should be considered before drawing general conclusions. Based on our previous studies, we already showed that physical and MI of a sequential finger tapping task resulted in similar offline performance gains following a night of sleep (Debarnot et al., 2009a), while participants being not subjected to one of this types of practice showed a stabilization of their motor performance after a night of sleep (Debarnot et al., 2009b). Based on these findings and as the primary aim of this study was to examine the specific sleep-related effect following MI practice of complex movements, we did not test a control sample of participants without intervening MI practice. Practically, one can therefore not totally exclude that the effect of the consolidation delays could be partially related to the few physical practice trials of the testing sessions. This latter effect is however unlikely to be viable as recent data still reinforced the particular role of sleep following observation learning as compared to a control group without practice (Trempe et al., 2011). The same conclusions about sleep-dependent gains in performance for MI practice have been recently drawn for movement observation (Zhang et al., 2011). These authors showed that performing an observation task immediately after little physical practice resulted in behavioral improvement following a 24h offline consolidation process including a night of sleep. In contrast, performing the observation task the day after physical practice did not result in any performance enhancement. Finally, although the study design does not allow to completely exclude a role for circadian influence (e.g. as the day and night groups started at different hours), this is unlikely based on previous studies (e.g. Walker et al., 2002, 2003).

To summarize, present data confirm and expand the benefit of a night of sleep for the motor memory consolidation following MI practice (Debarnot et al., 2009a,b; Debarnot et al., 2010b). In particular, we demonstrated the critical role of sleep for the consolidation of complex imagined movements,

hence reinforcing the principle of functional equivalence between MI and physical practice of the same task. Such specific sleep gains for complex motor skill have also been observed for slower transitions within the motor sequence, which were improved in a greater extent, suggesting that the sleep-dependent learning process involves the unification of smaller memory units into one single memory element. These results may have strong theoretical and practical applications in motor learning and (neuro)rehabilitation processes, in which performing MI is cost effective and easily feasible (de Vries and Mulder, 2007; Munzert et al., 2009). Therefore, mental practice could be incorporated during the classical course of physical therapy, and most especially before a period of sleep, to benefit from the offline motor consolidation during the recovery process.

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