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Sleep dependent consolidation of gross motor sequence learning with motor imagery

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UD: Conceptualization, Data curation, Formal analysis, Methodology, Project administration, Resources, Supervision, Writing Original Draft, Review & editing, Validation

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1. Introduction

Motor imagery practice (MIP), which is the mental rehearsal of an action without overt movement (Jeannerod & Decety, 1995), promotes the online acquisition of motor skills by stimulating the activity and neuroplasticity of the sensorimotor networks (Di Rienzo, et al., 2016). Pioneer studies have established that the memory trace elicited with MIP benefits from offline sleep consolidation processes (Debarnot, Castellani, Valenza, Sebastiani, & Guillot, 2011; Debarnot, Creveaux, Collet, Doyon, & Guillot, 2009; Debarnot, Creveaux, Collet, Gemignani, et al., 2009; Debarnot, Maley, Rossi, & Guillot, 2010; Debarnot, Valenza, et al., 2011). Practically, it has been previously reported delayed performance gains on a sequential finger-tapping task (SFTT) with MIP after a period of sleep but not after a comparable time awake (Debarnot, Creveaux, Collet, Doyon, et al., 2009; Debarnot, et al., 2010). This pattern of findings echoes the extensive literature with the same fine motor paradigm but using physical practice (PP, King, Hoedlmoser, Hirschauer, Dolfen, & Albouy, 2017). Sleep-dependent consolidation of SFTT was shown to rely mainly on the non-rapid eye movement sleep and its specific features (i.e., sleep spindles; for review see King, et al., 2017). Boutin et al. (2018) further reported that sleep spindle oscillations play a crucial role by reactivating and functionally binding cortical and subcortical regions involved during both the acquisition and consolidation of motor skills (e.g. hippocampus, thalamus, motor cortical network). The SFTT does not, however, optimally represent the sequential whole-body movements typically encountered in everyday life or those more specifically involved in sport or functional rehabilitation contexts. The paucity of knowledge on the acquisition and consolidation processes of gross motor sequences precludes any clear-cut conclusion regarding either MIP-dependent or sleep-dependent changes in performance.

It is well accepted that motor sequence learning (MSL) is composed of the simultaneous acquisition of two dimensions, namely the spatial and motor representations, which depend on the requirements of the task (Hikosaka, Nakamura, Sakai, & Nakahara, 2002). The former corresponds to the learning of the sequence of response goals within an allocentric frame of reference (i.e. goal-based learning), while the latter refers to the learning of sequential movement responses per se under an egocentric frame of reference (i.e. movement-based learning, Grafton, Hazeltine, & Ivry, 1998). There is now accumulated evidence showing that consolidation of goal-based representation is sleep-dependent, while the movement-based representation benefits from the simple passage of time to consolidate (Albouy, et al., 2013; Cohen, Pascual-Leone, Press, & Robertson, 2005; Robertson, 2009; Willingham, 1999). Briefly, it has been suggested that two distinct neural mechanisms would be engaged in mediating goal- vs. movement-based consolidation over sleep (i.e. hippocampus) and wakefulness (i.e. motor cortex, Robertson, 2009), respectively. Supporting data for this time- or sleep-dependent effect of consolidation relative to these two dimensions of MSL have been reported mainly using modified versions of SFTT (Albouy, et al., 2013; Pace-Schott & Spencer, 2013), but whether similar consolidation effects might occur after the acquisition of a gross motor sequence remain unknown. This issue is of importance and has been underlined in the recent meta-analysis by Schmid et al. (2020), who failed to find any differences in sleep-dependent benefits when considering several motor tasks features (e.g. fine vs gross, sequential vs adaptive). The authors posit that identifying the sleep-dependency related to task dimensions should become a major current endeavour in the domain of motor learning consolidation (Schmid, et al., 2020). Interestingly, using a whole-body reaching task, Saito et al. (2014) reported that improvements in the postural dynamics (centre of pressure and anticipatory postural

adjustments) correlated strongly with the enhancement of reaching performance with the upper limb during acquisition; however, consolidation effects on the two motor components were not examined.

Up to now, far too little attention has been paid to the goal- and movement-based representations of MSL using MIP, while both dimensions may constitute the content of the mental rehearsal. In fact, MIP has been suggested to rather promote the goal components of SFTT, and movement components in paradigms requiring more egocentric representations, such as, for example, sequential pointing tasks (Debarnot, Castellani, et al., 2011; Debarnot, Creveaux, Collet, Doyon, et al., 2009; Ruffino, et al., 2021). These findings are in line with neuroimaging investigations that examine how the motor map is organised in motor imagery of different hand-related types of action, including SFTT, squeezing and extension-flexion tasks (Pilgramm, et al., 2016; Zabicki, et al., 2017). Specific patterns of activity in the premotor and posterior parietal regions have been shown to modulate with the representational organisation of imagined hand actions, supposed to underpin goal- and movement-based components. The few behavioural studies conducted with MIP using either an SFTT or other motor skill tasks (i.e. arm-pointing or adaptation-tracking tasks) to examine the consolidation effect reported that performance improvement with the former was sleep-dependent (Debarnot, Castellani, & Guillot, 2012; Debarnot, Castellani, et al., 2011; Debarnot, Creveaux, Collet, Doyon, et al., 2009), while the latter benefited from the simple passage of time (Debarnot, Valenza, et al., 2011; Ruffino, et al., 2021). Despite these promising findings, the question of how both MSL dimensions might consolidate after MIP of an ecological whole-body movement has not been investigated.

In an attempt to test whether findings from the sleep consolidation literature using the SFTT may be generalised to sequential gross motor tasks, it has been recently developed

a new sequential whole-body task, the sequential footstep task (SFST), requiring participants to perform sequences of footsteps that are associated with changes in postural dynamics (i.e., displacements of the centre of mass and anticipatory postural adjustments, Freitas, Saimpont, Blache, & Debarnot, 2020). Briefly, participants were required to practice this task mentally or physically during a morning or an evening session and were retested after a night of sleep or an equivalent amount of daytime spent awake. The main results show a performance gain following a night of sleep in the MIP group only, while stabilisation of performance was sleep-independent in the PP groups. Nonetheless, the interpretation of findings regarding the effects of MIP during acquisition and consolidation were limited by the lack of a control group without training, while only goal-based components of the SFST were assessed.

The purpose of the current study was to further test the effect of MIP and PP on the processes of acquisition and consolidation of gross MSL. The SFST offered the opportunity to explore for the first time both goal- and movement-based components of MSL with respect to the type of practice. To do so, we assessed simultaneously the number of correct footsteps (goal-based component) and the displacement of the centre of mass (movement-based component) when the task is performed before and after PP or MIP training (acquisition), and after a night of sleep of an equivalent period of daytime consolidation.

2. Material and Methods

2.1. Participants

Seventy-six healthy students (21.04 ± 2.26 years; 38 women) were recruited in the Department of Sport Science of the University of Lyon to participate in this study. Eligible participants were right-footed with a score greater than -6 on the Waterloo Footedness Questionnaire-Revised (Elias, Bryden, & Bulman-Fleming, 1998), had a visuospatial span > 3

on the computerised version of the Corsi block test (PsyToolkit, Kessels, van Zandvoort, Postma, Kappelle, & de Haan, 2000)), and had an intermediate circadian type (ranged between 31 to 69) as assessed by the Horne-Ostberg Morningness–Eveningness Questionnaire (Horne & Ostberg, 1976). Individuals who regularly participated in an activity involving strong and regular lower limb coordination (dance, rhythmic gymnastics > 2 hours/week); who had locomotor or postural problems, neurological or psychiatric disorders, or lower limb injuries during the three months prior to the test; or who had excessive sleep problems, with a score > 10 on the Pittsburgh Sleep Quality Index (PSQI, Buysse, Reynolds, Monk, Berman, & Kupfer, 1989; Hinz, et al., 2017) were not included. Characteristics of the participants in terms of age, gender, height, Waterloo score, PQSI and chronotype were equivalent between groups (see Supplementary Table 1). Also, participants who performed MIP were comparable regarding their motor imagery ability, with moderate vividness scores at the short version of the Kinesthetic and Visual Imagery Questionnaire (KVIQ-10, Malouin, et al., 2007), and good timing of MI (See Supplementary Table 2). For the duration of the study and for 24 h before they started the experiment, participants were instructed to abstain from caffeine, alcohol and drugs. This study was approved by the Institutional Review Board of the University of Lyon, and all participants signed an informed consent form. Participants were not aware of the hypotheses of the study.

2.2. The sequential footstep task

The SFST involved an instrumented floor mat of 1 m² composed of nine 33 cm² squares. There was a pressure sensor of 5 cm² (Interlink FSR402 short) under the centre of each square, materialised by a red circle/target on the mat (Figure 1). The footstep sequence was composed of eight steps on eight different targets. **At the beginning of each block, participants were positioned upright with the feet on the central square (target 5; see Figure**

1 for target locations). They started the footsteps sequence of with the right foot on target 3, then with the left foot on target 1, and alternated the movements of the right and left foot until completing the following sequence i.e. 3-1-9-8-4-7-6-5. They had to repeat the sequence continuously for several blocks of 30 s. During each block, the pressure of each step on the red target was recorded (PowerLab, ADInstrument, Australia), and the trajectory of the pelvis was tracked using a three-dimensional motion capture system (MiquisX Qaulisys, Sweden). Four reflective markers were placed on the anterior and posterior superior iliac spines, as illustrated in Figure 1. Their displacement was recorded using a 10-camera optoelectronic system (Qualysis, Sweden). The experimenter indicated the start and end of each block with 'TOP' and 'STOP' verbal signals. A digital timer was used to control the duration of the 30 s block (100 Hz, XL-013 anytime®), and the different measures were synchronised by pressing a trigger linking the two types of acquisition software.

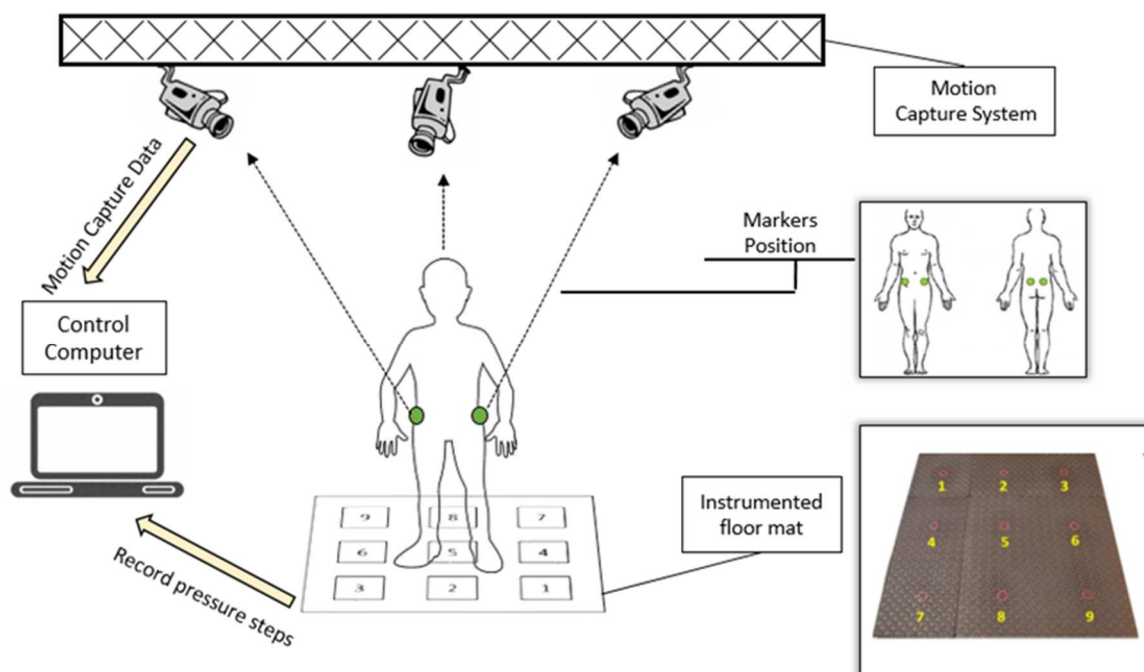


Fig.1. The Sequential Footstep Task (SFST) and experimental setup. The participants were positioned upright on the instrumented mat which was composed by nine 33 cm² squares with pressure sensor of 5 cm² under the center of each square, materialized by a red circle/target on the mat. The participants performed an eight-stepping sequence using

alternatively the right and left foot to press targets in the following order: 3-1-9-8-4-7-6-5. The numbers in yellow were not visible to the participants. Four reflective markers were placed on the anterior and posterior superior iliac spines to track the trajectory of the pelvis (CoP) during the task. The marker position data were recorded by a 10-camera optoelectronic system (Qualysis, Sweden).

2.3. Experimental procedure

The participants were pseudo-randomly assigned (stratifying by gender) into six groups according to the type of learning method (PP, MIP or no training CTRL) and consolidation (Sleep or Day, Fig. 2). The sleep groups (PP_{sleep}, MIP_{sleep} and CTRL_{sleep}) practised the task in the evening (session 1; 18:00) and performed the retention test the next morning (session 2; 8:00), after a night of sleep. The day groups (PP_{day}, MIP_{day} and CTRL_{day}) practised the task in the morning (session 1; 08:00) and performed the retention test in the evening (session 2; 18:00), after normal daytime activities.

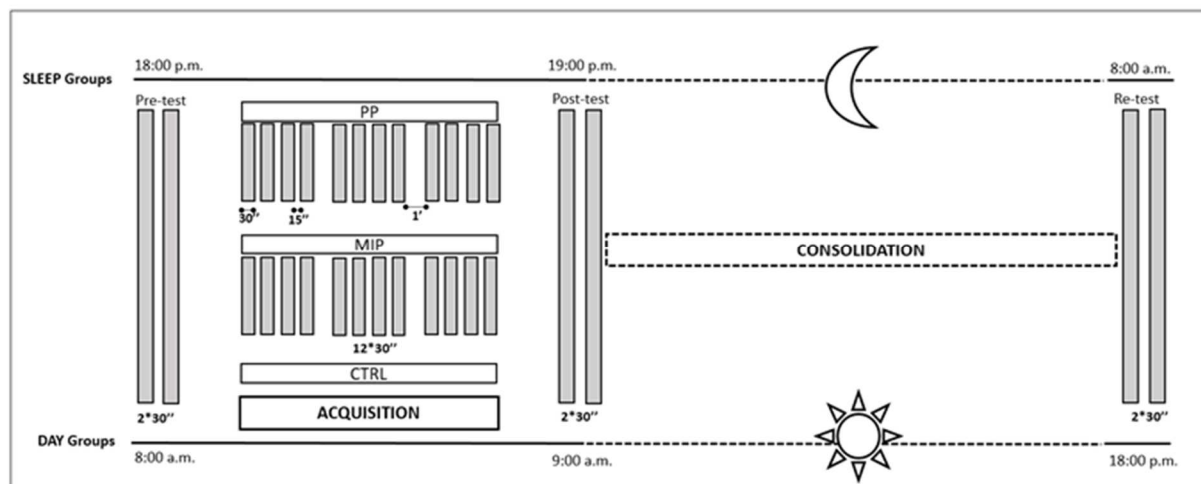


Fig. 2. Timeline of the experimental design. Participants were divided into six groups according to the type of learning methods (PP, MIP or no training CTRL) and consolidation (Sleep or Day). PP_{sleep}, MIP_{sleep} and CTRL_{sleep} performed the task in the evening (session 1; 18:00) and performed the retention test the next morning (session 2; 8:00), after a night of sleep. PP_{day}, MIP_{day} and CTRL_{day} performed the task in the morning (session 1; 08:00) and performed the retention test in the evening (session 2; 18:00), after normal daytime activities. Before (Pre-test) and after (Post-test) training, as well as during the Retention test, participants had to physically repeat the sequence, as fast and accurately as possible, for two blocks of 30s (interspaced with 15s of rest). During the training (acquisition phase), the

participants repeated the sequence physically (PP groups) or mentally (MIP groups) for 12 blocks of 30 s interspaced with 15 s of rest. After the 4th, 9th and 12th block, they had a one-minute break during which they were asked to report their level of fatigue (PP and MIP groups) and the vividness of the imagined movements by using the KVIQ scale (MIP groups only). The CTRL groups read a magazine during a period of time equivalent to that spent by the other groups in physical and mental training.

2.3.1. Session 1

Warm-up and familiarization. The warm-up consisted of moving randomly on the squares of the mat, continuously, in order to stimulate cognitive and motor awakening and familiarized the participants with the environment and device. After 2 min, the experimenter asked the participants if they were ready to start the experiment.

Encoding. After 2 min of warm-up and familiarisation of participants with the environment and the device, the experimenter demonstrated the sequence to be learned. The participants had to perform three consecutive sequences without any error to certify its encoding and to proceed with the pretest.

Pretest. All participants practised the sequence physically as fast and accurately as possible for two blocks of 30 s interspaced with 15 s of rest.

Training.

Training. The participants in the PP groups repeated the sequence physically for 12 blocks of 30 s interspaced with 15 s of rest. After the 4th, 9th and 12th block, they had a one-minute break to avoid fatigue. During these breaks, participants were asked to report their level of general fatigue on a scale ranging from 0 (no fatigue) to 5 (extreme fatigue). The dose of practice and rest was chosen to reach an asymptotic level of performance in the last three blocks of training, as in Freitas et al. (2020). Participants from the MIP groups repeated the

sequence mentally for 12 blocks of 30 s interspaced with 15 s of rest. They were asked to imagine the movements from a first-person perspective using both internal visual and kinaesthetic MI modalities (for details see MIP guideline in Supplementary Information). After the 4th, 9th and 12th block, they also had a one-minute break during which they were asked to report the vividness of the imagined movements by using the KVIQ scale, as well as their level of fatigue using the same scale as for the PP groups. The CTRL groups read a magazine during a period of time equivalent to that spent by the other groups in physical and mental training (i.e. 11 min).

Posttest. After a one-minute break at the end of the training, participants repeated the sequence physically as fast and accurately as possible for two blocks of 30 s interspaced with 15 s of rest.

2.3.2. Session 2

After daytime or night-time consolidation, all participants warmed up for 2 min (i.e. continuous movements on the mat) and then performed the retention test, which consisted in physically performing the same sequence as fast and accurately as possible for two blocks of 30 s interspaced with 15 s of rest.

2.4. Complementary measures

Alertness. At the beginning of each session, the participants evaluated their level of awareness and vigilance by rating themselves from 1 (awake) to 8 (sleepy) on the Stanford Sleepiness Scale (Maclean et al., 1992). We further computed the awakening period between time bed out using self-reported data (as no actigraphy data were recorded for the day groups) and the start time of the experimental session.

Sleep. In sessions 1 (all groups) and 2 (sleep groups only), the participants reported their hours of sleep and rated the quality of their sleep from 1 (very bad) to 5 (very good). Furthermore, the amount of sleep obtained by participants in the night groups was controlled with wrist actigraphy (wGT3X-BT, Pensacola, USA). The sleep parameters were extracted and processed with Actilife 6 software (ActiGraph, Pensacola, FL, US).

2.5. Data analysis

Goal- and Movement-based performance. To assess goal-based performance, we averaged the number of correct steps over the two blocks of each test (i.e. Pretest, Posttest and Retention test). To assess movement-based performance, the barycentre of the four pelvis-marker (centre of pelvis, CoP) trajectories was computed and assimilated to the body centre of mass (Gard et al., 2004; Mapelli et al., 2014). Then, the distance travelled by the CoP was calculated by correct sequence and averaged over the two blocks of each test (i.e. Pretest, Posttest and Retention test).

Motor imagery during training. To assess MI vividness during MIP of the SFST, we calculated the average visual and kinaesthetic scores from the three self-reported vividness scores.

2.6. Statistical analysis

For each variable, the normality of the data was verified by the Shapiro-Wilk test. If the data were normally distributed, parametric tests were performed; otherwise, non-parametric tests were used. The statistical significance threshold was set at $P = 0.05$ and eta squared (η^2) effect sizes were reported for significant results. Post-hoc tests with Bonferroni correction for multiple comparisons were performed when appropriate. Statistical analysis was performed with the STATISTICA software (version 7.1, StatSoft Inc., Tulsa, OK, USA).

Goal- and Movement-based Performance. The mean numbers of correct steps and the displacement of the CoP were analysed using repeated-measures ANOVAs with *GROUP* (PP_{day}, MIP_{day}, CTRL_{day}, PP_{sleep}, MIP_{sleep} and CTRL_{sleep}) as the between-subjects factor and *TEST* (Pretest, Posttest, Retention test) as the within-subjects factor. We performed a one-tailed analysis on test effect and test*group interaction for these variables.

Physical Training. To verify the achievement of the performance asymptote, we analysed the evolution of the number of physical steps during the 12 training blocks by comparing the last five blocks of the training. A repeated-measures ANOVA with *GROUP* (PP_{day} and PP_{sleep}) as the between-subjects factor and *BLOCK* (block 8, 9, 10, 11 and 12) as the within-subjects factor on the number of steps was performed on these numbers.

Motor imagery during training. To compare the vividness scores for the SFST, we performed an ANOVA with *GROUP* (MIP_{day} and MIP_{sleep}) as the between-subjects factor and *MODALITY* (visual and kinaesthetic) as the within-subjects factor.

Fatigue. The level of fatigue was compared between groups, for each time of measure, with Kruskal-Wallis tests. Also, it was compared between measurement times, for each group, with Friedman ANOVAs. Subsequent Wilcoxon tests were performed for paired comparisons.

Alertness and Sleep. The Stanford Sleepiness Scale scores were compared between groups, for each session, with Kruskal-Wallis tests. Self-reported sleep times and time between bed out and tests were analysed with a one-way ANOVA with *GROUP* (PP_{day}, MIP_{day}, CTRL_{day}, PP_{sleep}, MIP_{sleep} and CTRL_{sleep}) as the between-subjects factor. Actigraphy and self-reported quality of night data from the sleep groups were analysed with Kruskal-Wallis tests.

2.7. Sample size and SFST reliability

We ensured adequate statistical power in the present design with *a-priori* sample size calculation, using t G*Power (G*Power 3.1.7, Faul, Erdfelder, Buchner, & Lang, 2009). Based on the medium effect size ($\eta^2 = 0.39$) of the group x test interaction found in our previous study (Freitas et al., 2020) for goal-based data (i.e. number of correct steps), a cohort of 72 individuals would have been required for the present study, with statistical power set at 80% and significance at 5%. By considering a risk of subject/data loss of around 5%, we increased this number to 76, thus leading 12 participants by group. This sample size was similar to that from prior studies using comparable gross motor paradigms. For instance, using riding an inverse steering bicycle paradigm or a juggling task, Hoedlmoser et al. (2015) and Morita et al. (2016) recruited 12 and 9 participants per group respectively.

The reliability of the results was tested using a Pearson correlation, which showed that performance in the SFST (i.e. number of correct steps) was highly correlated with previous acquired data from Freitas et al. (2020). This strong correlation ($r: 0.95 [0.71-0.99]$) suggests that the reliability of the SFST is excellent.

3. Results

3.1. Goal-based performance

The repeated-measures ANOVA on the numbers of correct steps revealed a *GROUP*TEST* interaction ($F_{(10, 140)} = 10.08$; $p < .001$; $\eta^2 = 0.42$). At pretest, they were not significantly different between groups. The number of correct steps significantly increased from pretest to posttest in CTRL_{day} ($p < 0.01$), MIP_{day} ($p = 0.05$), MIP_{sleep} ($p < 0.001$), PP_{day} ($p < 0.001$) and PP_{sleep} ($p < 0.001$) but not in CTRL_{sleep} ($p = 0.32$). At posttest, they were significantly greater in both PP groups than in all other groups ($p < 0.001$), with no difference between them ($p >$

0.05 for all comparison). The mean numbers of correct steps significantly increased from posttest to retention test in MIP_{sleep} ($p < 0.01$), while they remained stable for all other groups ($p = 1.00$). At retention test, PP_{sleep} performed significantly better than MIP_{sleep} ($p < 0.05$), MIP_{day}, CTRL_{sleep} ($p < 0.001$) and CTRL_{day} ($p < 0.01$), and PP_{day} performed significantly better than MIP_{day} ($p < 0.01$), CTRL_{sleep} ($p = 0.01$) and CTRL_{day} ($p < 0.05$). No other significant differences were observed (see Figure 2 and Supplementary Table 3).

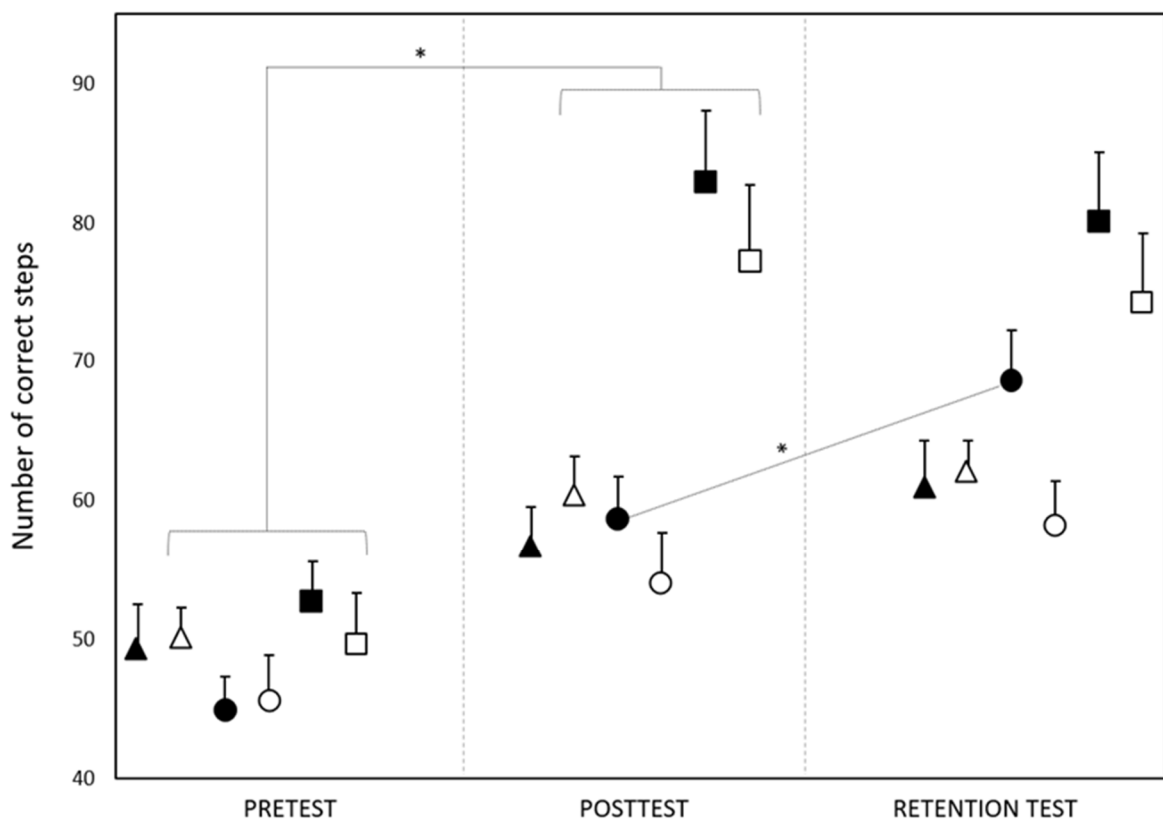


Fig.2. Goal-Based performance. Mean numbers of correct steps for all groups and tests. Data are mean \pm standard error. \square CTRL_{sleep/day} \triangle MIP_{sleep/day} \bullet PP_{sleep/day}. * Excepted the CTRL_{sleep}, all groups increased their number of correct steps during the acquisition phase (pretest to posttest). During the consolidation (posttest to retention), only the MIP_{sleep} group increased the number of correct steps. See supplementary Table 3 for complete data and statistics.

The analysis of the number of correct steps during physical training showed a *BLOCK* effect ($F_{(4,96)} = 4.95$; $p < 0.01$; $\eta^2 = 0.17$), no *GROUP* effect ($F_{(2, 24)} = 0.39$; $p = 0.54$) and no *GROUP*BLOCK* interaction ($F_{(4,96)} = 1.67$; $p = 0.16$). For both PP groups, the asymptotic

performance was reached at block 9, with no difference between each block from 9 to 12 (72.6 ± 17.3 ; 73 ± 14.6 ; 74.7 ± 14.7 ; 75.1 ± 15.6 respectively with all comparison $p > 0.05$).

3.2. Movement-based performance

The repeated-measures ANOVA on the mean distance travelled by the CoP revealed a *GROUP*TEST* interaction ($F_{(10, 116)} = 4.51$; $p < 0.001$; $\eta^2 = 0.28$). At pretest, the distance travelled by the CoP did not significantly differ between the groups. The mean distance travelled by the CoP significantly decreased from pretest to posttest in MIP_{day} ($p < 0.001$), MIP_{sleep} ($p < 0.001$), PP_{day} ($p < 0.001$) and PP_{sleep} ($p < 0.001$) but not in CTRL_{day} ($p = 0.48$) or CTRL_{sleep} ($p = 0.50$). At posttest, the PP groups performed significantly better than all other groups ($p < 0.05$ for all comparison). The mean distance travelled by the CoP between posttest and retention test significantly decreased only for MIP_{sleep} ($p = 0.03$) and remained stable for all other groups ($p = 1.00$). At retention test, PP_{sleep} performed significantly better than MIP_{sleep} ($p < 0.05$), MIP_{day} ($p < 0.01$), CTRL_{sleep} ($p < 0.001$) and CTRL_{day} ($p < 0.05$), and PP_{day} performed significantly better than MIP_{day} ($p < 0.01$) and CTRL_{sleep} ($p < 0.001$). No other significant differences were observed (see Figure 3 and Supplementary Table 4).

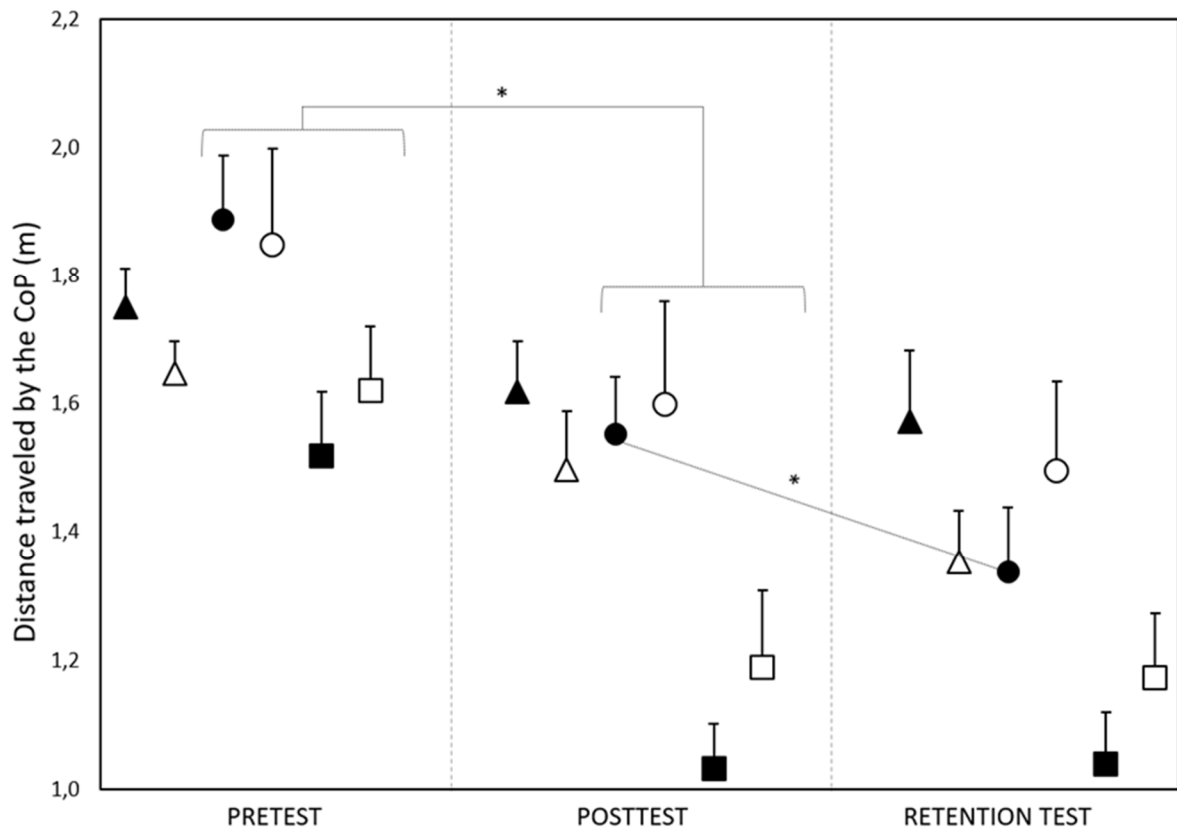


Fig.3. Movement-Based performance. Mean distance traveled by the CoP for all groups and tests. Data are mean \pm standard error. \blacksquare CTRL_{sleep/day} \square MIP_{sleep/day} \triangle PP_{sleep/day}. # During the consolidation phase, only the MIP_{sleep} group decreased the distance traveled by the CoP. See supplementary Table 4 for complete data and statistics.

3.3. Motor imagery during training

The analysis of the mean vividness scores for the SFST revealed a *GROUP* effect ($F_{(1, 48)} = 5.63$; $p = 0.02$; $\eta^2 = 0.10$) and a *MODALITY* effect ($F_{(1, 48)} = 24.44$; $p < 0.001$; $\eta^2 = 0.33$). The MIP_{day} group had greater mean vividness scores than the MIP_{sleep} group, and the visual scores were higher than the kinaesthetic scores (MIP_{day} visual: 3.56 ± 0.84 ; MIP_{day} kinaesthetic: 2.76 ± 0.86 ; MIP_{sleep} visual: 3.31 ± 0.63 ; MIP_{sleep} kinaesthetic: 1.99 ± 0.75).

3.4. Fatigue

The analysis of the level of fatigue revealed no *GROUP* effect for Time 1 ($H_{(3,51)} = 6.72$; $p = 0.08$), Time 2 ($H_{(3,51)} = 4.74$; $p = 0.19$) and Time 3 ($H_{(3,51)} = 2.74$; $p = 0.43$), showing that the training groups had similar levels of fatigue. Furthermore, there was a *TIME* effect for the PP_{sleep} ($\chi^2_{(2,13)} = 6.46$; $p = 0.04$), PP_{day} ($\chi^2_{(2,13)} = 6.25$; $p = 0.04$) and MIP_{day} groups ($\chi^2_{(2,13)} = 6.30$; $p = 0.04$; see supplementary Table 7), but not for the MIP_{sleep} group ($\chi^2_{(2,13)} = 4.53$; $p = 0.10$). The level of fatigue significantly increased between Time 1 and Time 3 for the PP_{sleep} ($p < 0.05$) and MIP_{day} groups ($p < 0.05$), between Time 2 and Time 3 for the PP_{day} group ($p < 0.05$) and stayed stable between all times for the MIP_{sleep} group. Note that, in average, the levels of fatigue remained low ($< 2/5$) for all groups and measurement times, suggesting that the task was not too tiring for the participants.

Alertness and sleep

The analysis of the Stanford Sleepiness Scale ratings revealed no *GROUP* effect, showing that the six groups were in the same state of alertness during the two experimental sessions. The analysis of the subjective sleep data showed a *GROUP* effect ($F_{(5, 70)} = 5.87$; $p < 0.001$; $\eta^2 = 0.29$). The $CTRL_{\text{sleep}}$ group reported sleeping longer than the $CTRL_{\text{day}}$, MIP_{day} , PP_{day} and PP_{sleep} groups before the first session. Nevertheless, all groups reported a similar quality of night before the first session ($F_{(5,70)} = 0.88$; $p = 0.50$). **The analysis of the time between bed out and tests showed no *GROUP* effect ($F_{(4, 46)} = 1.05$; $p = 0.39$).** Finally, actigraphy data were not significantly different between the sleep groups (see Supplementary Table 5).

4. Discussion

We designed the present study to investigate the sleep-related effects of MIP and PP on memory consolidation of a newly learned sequence of gross movements. To address this

issue, we used an SFST, enabling us to disentangle the respective contributions of the goal-based (number of steps) and movement-based (CoP displacement) components of motor learning and consolidation. In line with our previous study (Freitas, et al., 2020), we found that both types of practice improved performance in the two motor components of the SFST during the acquisition session. The main findings revealed sleep-dependent gains in performance after MIP, while no further changes in performance were found after the consolidation that followed PP. Furthermore, data revealed that both the number of sequential steps and kinematic performance changed conjointly during consolidation, regardless of the type of practice.

Our finding that both MIP and PP elicited gains in the number of sequential steps performed and reduced the CoP displacement during acquisition – with, however, an advantage for PP – are consistent with results in the literature showing the efficacy of the mental rehearsal of actions (Di Rienzo, et al., 2016). Importantly, our groups that had no training in the task showed either no performance enhancement at posttest (CTRL_{sleep}) or else enhancement only of the number of steps performed (CTRL_{day}). The most likely explanation supporting the advantage in performance gain in the PP groups lies in the fact that MIP is characterised by a lack of the somatosensory afferent inputs that are available during PP. Briefly, the execution of a movement depends on sensory information as feedback to refine the accuracy of the movement: actual and predicted movement consequences can be compared, which, in turn, improves motor prediction (Hardwick, Caspers, Eickhoff, & Swinnen, 2018). This feedback is missing during MIP, which can only rely on internal forward models that mimic the causal flow of the physical process by predicting the future sensorimotor state that the movement is likely to generate (Gentili, Han, Schweighofer, & Papaxanthis, 2010; Kilteni, Andersson, Houborg, & Ehrsson, 2018). Such

prediction remains less accurate than in PP, which explains the superiority of PP in motor skill acquisition (Mulder, Zijlstra, Zijlstra, & Hochstenbach, 2004; Ruffino, et al., 2021). Interestingly, recent investigations have reported the existence of micro-online and -offline performance improvements during the acquisition of new motor skills, the former related to immediate gains during the practice blocks, the latter corresponding to rapid gains between practice blocks (i.e. during a short rest, Buch, Claudino, Quentin, Bönstrup, & Cohen, 2021). The authors found that performance improvement during the acquisition session largely accounted for micro-offline gains in which binding mechanisms may operate (through hippocampal and neocortical replay) in associating abstract knowledge regarding the action structure of the skill sequence (goal-based) and the kinematics of the elementary movements (movement-based)(Bönstrup, et al., 2019; Jacobacci, et al., 2020). Therefore, it is possible that the lack of sensorimotor feedback during MIP may not only limit the potential of motor improvement online but also hamper the binding process during offline rest blocks. In the same vein, Liu et al. (2019) report that micro-offline processes during acquisition promote the reorganisation of the learned sequence and suggest that semantic knowledge about the task requirements might be sufficient to elicit replay of keypress sequences of the practice (Liu, et al., 2019). This finding provides further support to explain why our CTRL_{day} group improved only the number of correct sequential steps but not the kinematics of the movements without training between the pretest and posttest. However, some caution should be exercised in interpreting our data, given recent reports on micro-gains in performance during skill acquisition that have been collected using PP of SFTT, which preclude general conclusions on the effect of MIP and PP during gross MSL.

In keeping with the study by Freitas et al. (2020), similar stabilisation of performance was seen in the PP groups regardless of the nature of consolidation. Replicating this

stabilisation effect of consolidation after PP supports the view that traditional sleep-related improvement in **explicit fine** SFTT does not necessarily generalise to explicit gross MSL. Indeed, the scarce studies conducted in the field of gross motor consolidation have reported mixed results, showing that the first night of sleep improved sequential whole-body performance but stabilised gross adaptation skills (Bothe, et al., 2020; Genzel, et al., 2012; Malangré & Blischke, 2016). Interestingly, two studies have reported that an additional retention test implemented after a second period of consolidation (8 h after the first retention test) showed supplementary positive changes in gross motor performance (Bothe, et al., 2020; Malangré, Leinen, & Blischke, 2014). Therefore, it seems reasonable to suggest that performance gains in gross motor sequential tasks practised physically might not depend on the following night of sleep but rather may require a brief reactivation of the memory (**i.e. motor skill activation at a later time point; Genzel, et al., 2020**) followed by an **up-dated** reconsolidation process. This speculation is reinforced by investigations that have used follow-up sessions after the initial acquisition of motor skills, which rather re-activated the memory trace, leading to the refinement and reshaping of the learned movement skills (Herszage, Sharon, & Censor, 2021; Walker, Brakefield, Hobson, & Stickgold, 2003; Wymbs, Bastian, & Celnik, 2016).

The main finding of this study is the sleep-dependent enhancement of performance following MIP; the simple passage of time was not sufficient to provide additional benefits. This finding is in accordance with recent studies reporting sleep-dependent consolidation of the cognitive strategies rather than the motor sequences required to execute them (Conte, Cerasuolo, Giganti, & Ficca, 2020; van den Berg, et al., 2019). For instance, van den Berg et al. (2019) used a modified version of the Tower of Hanoi, enabling researchers to distinguish intertwined dimensions of procedural memory, notably the explicit cognitive strategy used

to solve the problem and the implicit simple movements required to achieve the task (van den Berg, et al., 2019). Results showed peculiar benefits in the cognitive strategy dimension following a night of sleep but not after an equivalent waking period, while no changes in performance following a period of consolidation were observed for the series of movements executed to apply the strategy. These results are in accordance with previous studies reporting sleep-dependent consolidation after procedural tasks that require a high level of cognitive functioning or a new (but complex) cognitive strategy for achieving one's goal (Conte, et al., 2020; Fogel, Ray, Binnie, & Owen, 2015; Kuriyama, Mishima, Suzuki, Aritake, & Uchiyama, 2008; Smith, Nixon, & Nader, 2004). Mental rehearsal of movements drives multiple cognitive processes in which conscious elaboration (e.g. selection and assembly of action elements stored in the working memory) and motor (simulation toward a goal and inhibition) processes are implicated, and which therefore involve executive resources to a much greater extent than PP (Glover, Bibby, & Tuomi, 2020; O'Shea & Moran, 2017). We may suggest here that, compared to PP, MIP of the SFST might have generated costly and challenging high-order cognitive processes, which may preferentially benefit from sleep consolidation.

Importantly, our findings do not reveal any dissociation in goal- and movement-based components, which either improved (MIP_{sleep}) or stabilised (PP and MIP_{day} groups) conjointly after consolidation. Using an arm-pointing task emphasising movement-based components rather than goal-based ones, Ruffino et al. (2021) have also reported different effects of consolidation following MIP and PP, with daytime enhancement for the former and stabilisation for the latter, without sleep-related effects being observed following either modality of practice (Ruffino, et al., 2021). Here, our footstep paradigm required both goal-based (sequential movements and targets to be reached with the lower-limbs) and

movement-based (displacement of the CoP) components, and similar changes in the two components occurred regardless of the nature of consolidation (night vs waking) or the practice modality (MIP vs PP). Therefore, and contrary to experimental manipulations of the SFTT that 'isolate' motor components (Albouy, et al., 2015; Albouy, et al., 2013; Cohen, et al., 2005), we may hypothesise that both goal- and movement-based representations of sequential gross motor tasks might be necessarily involved together, without being distinguished, at least behaviourally. This latter assumption is supported by reports showing that positive changes in postural control (movement-based component) by repetitive motor training led to goal-based performance improvements in a whole-body reaching task (Saito, et al., 2014).

Limitations of this study should be considered when interpreting the present results. First, sleep assessments were captured by means of actigraphy and subjective outputs in the sleep groups, while only the latter was assessed in the day groups (i.e. before the acquisition session). Most studies reported that actigraphy is a valid and reliable measure as compared to polysomnography in healthy sleepers, notably in measuring the total sleep time and sleep efficiency with high sensitivity (> 90%), but yields consistently lower sleep latency compared to polysomnography (Kaplan, Talbot, Gruber, & Harvey, 2012; Lehrer, et al., 2022). It has been observed that actigraphy outputs become less robust when sleep is more disturbed (e.g., insomnia, Matthews, et al., 2018) which is unlikely in our sample of subjects who reported PSQI scores below the cutoff for poor sleep quality (< 7, Pilz, Keller, Lenssen, & Roenneberg, 2018). Here, and besides the typical short sleep latency assessment using actigraphy, sleep efficiency and total sleep time were relatively lower than the normative values in healthy young population reported in the metaanalysis by Boulos et al. (2019) (86.56 % and 389.2 min here vs 89 % vs 410.6 min in Boulos et al.), though our data

remained within the envelope of sleep normality. In line with recent findings from the sleep assessment literature, our subjective sleep-reports yielded higher estimates of total sleep time compared to actigraphy outputs (Lehrer, et al., 2022). Taking together, we believe that the quantitative actigraphy outputs in adjunction to subjective assessments of sleep (e.g. time in bed) and self-report to address the qualitative dimensions of sleep (e.g. subjective sleep quality), provided a reliable control of effective sleep in our samples of subjects (table 5). Nonetheless, sleep-diary combined with actigraphy assessment with sleep log at least 5 nights before the experiment should have been performed to discriminate potential recent sleep-deprived subject (Aili, Åström-Paulsson, Stoetzer, Svartengren, & Hillert, 2017). In the same vein, quantitative assessment of alertness using a psychomotor vigilance task to measure sustained attention rather than subjective evaluation only (SSS) would have better objectivate the state of vigilance of the participants right before motor skill practice. Future studies on sleep and cognitive or motor performance should consider both subjective and quantitative measurements as the former alone might not match with performance on tasks requiring sustained attention and timely responses (Zhou, et al., 2012). Finally, sleep consolidation period (14h including sleep) was longer than the daytime condition (10h), hence it may not be totally excluded that extended period of consolidation promoted an extra opportunity to reinforce the memory trace regardless of sleep. Despite this, however, the Ctrl_{sleep} did not elicit performance improvement while been exposed to similar extended period of consolidation as the MIP_{sleep} group.

5. Conclusions

To conclude, the present results provide strong evidence that MIP and PP of a whole-body sequential motor task elicit different acquisition and consolidation processes. The most striking finding is that consolidation of a gross motor sequential task after MIP is sleep-

dependent, although after PP it is not. Based on several studies demonstrating that MSL of finger tasks with MIP elicits sleep-dependent consolidation (Debarnot, Castellani, et al., 2011; Debarnot, Creveaux, Collet, Doyon, et al., 2009; Debarnot, et al., 2010), we suggest that the cognitive dimension, rather than MSL components, is likely to drive the consolidation process during sleep. Practically, our findings suggest that MIP of sequential gross motor movements, such as fine motor movements, seems to be more valuable with a period of sleep following the practice to yield the benefits of offline motor consolidation.

6. References

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