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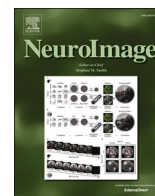
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Low-frequency sounds combined with motor imagery elicits a transient disruption of force performance: A path to neuromotor reprogramming?

Typhanie Dos Anjos^{a,b}, Aymeric Guillot^a, Sebastien Daligault^c, Donna-Maria Chamoun^a, Thomas De Sousa^a, Franck Di Rienzo^{a,*}

^a Université Lyon 1, UCB-Lyon 1, Laboratoire Interuniversitaire de Biologie de la Motricité-UR 7424, F-69622, Villeurbanne Cedex, France

^b Allyane®, 84 quai Joseph Gillet, 69004 Lyon, France

^c Centre de Recherche Multimodal et Pluridisciplinaire en Imagerie du Vivant (CERMEP), Department of Magnetoencephalography, F-69500 Bron, France

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ABSTRACT

The effectiveness of motor imagery (MI) training on sports performance is now well-documented. Recently, it has been proposed that a single session of MI combined with low frequency sound (LFS) might enhance muscle activation. However, the neural mechanisms underlying this effect remain unknown. We set up a test-retest intervention over the course of 2 consecutive days to evaluate the effect of (i) MI training (MI, $n = 20$), (ii) MI combined with LFS (MI + LFS, $n = 20$), and (iii) a control condition (CTRL, $n = 20$) on force torque produced across repeated maximal voluntary contractions of the quadriceps before (PRETEST), after (POSTTEST) and at +12 h (RETENTION) post-intervention. We collected the integrated electromyograms of the quadriceps muscles, as well as brain electrical potentials during each experimental intervention. In the CTRL group, total force torque decreased from PRETEST to RETENTION and from POSTTEST to RETENTION. By contrast, there was an increase between POSTTEST and RETENTION in both MI + LFS and MI groups (both $\eta_p^2 = 0.03$, $p < 0.05$). Regression analyses further revealed a negative relationship between force performance and EEG activity in the MI + LFS group only. The data support a transient interference of LFS on cortical activity underlying the priming effects of MI practice on force performance. Findings are discussed in relation to the potential for motor reprogramming through MI combined with LFS.

1. Introduction

Motor imagery (MI) is the mental simulation of an action without engaging in its physical execution. MI can be generated by a voluntary effort to build a mental representation of an action, although there is also evidence of spontaneous uses of MI by athletes as an emergent mental state during training or competitive events, or musicians who may experience involuntary imagery (Floridou et al., 2022). Meta-analyses demonstrated that MI practice is effective to enhance athletic performance (Simonsmeier et al., 2021), and can be used to improve force produced by maximal voluntary contractions (Paravlic et al., 2018). Pioneering experiments by Cornwall et al. (1991), followed by Yue and Cole (1992), reported force gains > 15 % during isometric

contractions of the quadriceps, and ranging 10–30 % during isometric contractions of distal and proximal muscles of the upper limb. It was recently postulated that the benefits of MI practice interventions on force could be superior when the targeted somatic effectors benefited from a large somatotopic representation on the cortical homunculus (Liu et al., 2023). Yet, the benefits of MI practice interventions on isometric force produced by lower limb muscles are also well-documented, with gains ranging from 11 % for the knee extensors up to 36 % for plantar-flexor muscles (Zijdewind et al., 2003; De Ruiter et al., 2012; Saumur and Perry, 2018).

There is a consensus that the effect of MI practice on force produced during maximal voluntary contractions stem from central adaptations. Meta-analyses emphasized profound similarities in the spatial

Abbreviations: CTRL, control; EEG, Electroencephalographic; EMG, electromyograms; iEMG, integrated electromyograms; MI, Motor imagery; LFS, Low frequency sounds; MVIC, maximal voluntary isometric contractions; SENIAM, Surface electromyography for the non-invasive assessment of muscles; PSD, Power spectrum densities; PSD_{NORM}, Normalized power spectrum densities; MIQ-3, Movement Imagery Questionnaire-3; PSQI, Pittsburgh Sleep Quality Index; iEMG_{RATIO}, ration between agonist and antagonist of integrated electromyograms.

* Corresponding author.

E-mail address: franck.di-rienzo@univ-lyon1.fr (F. Di Rienzo).

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distribution of cortical and subcortical activations patterns during MI and physical practice of the same action (Héту et al., 2013; Hardwick et al., 2018). The neural networks mediating the two tasks are also partially distinct and of reduced magnitude during MI, with lower involvement of the primary motor cortex, parietal cortex, basal ganglia and cerebellum. Noteworthy, the neurofunctional equivalence hypothesis between overt and covert action states is being increasingly questioned, and fundamental research on the *differences* rather than similarities between MI and physical practice of the same task is gaining interest (Hurst and Boe, 2022). Nevertheless, although not strictly identical, functional and effective connectivity patterns suggest parallel patterns of information processing (Gao et al., 2011; Simos et al., 2017). Furthermore, results from transcranial magnetic stimulation experiments indicate that the specificity of corticospinal facilitation during MI accounts for its leveraging effects on force performance through experience-based cortical and spinal plasticity (Grosprêtre et al., 2016; Dos Anjos et al., 2022). MI practice intervention yielded increased cortical output during maximal voluntary contractions, as evidenced by measures of motor evoked potentials (Ranganathan et al., 2004; Yao et al., 2013). At the spinal level, MI elicits a downregulation of pre-synaptic inhibition, facilitating the recruitment and synchronization of motor units in response to efferent supraspinal commands (Grosprêtre et al., 2019). Functional connectivity measures suggest that MI-induced corticomotor plasticity could reduce agonist-antagonist coactivation during maximal isometric force trials (Dos Anjos et al., 2022).

To enhance the effects of MI practice on corticomotor plasticity and improve both motor performance in athletes and functional recovery in patients, current research focuses on the synergistic effects of combining MI practice with exogenous methods of neurostimulation. For instance, anodal transcranial direct current stimulation is known to increase cortical excitability and enhance cortical activation in the primary motor cortex when combined with MI (Xie et al., 2021). These methods remain, however, semi-invasive and require expensive equipment. The human brain is characterized by spontaneous electrical activities that describe functional networks across large populations of neurons. While it is generally accepted that brain oscillations reflect neural communication within these networks, the close relationship between brain oscillations and behavior suggests that targeting specific brain wave frequencies through exogenous forms of stimulation could be a relevant approach to improve cognitive functions (Polanfa et al., 2018). As a result, extensive research sought to delineate brain stimulation techniques susceptible to induce specific frequencies and induce desired brain states. Among them, auditory beat stimulation represents a non-invasive neuromodulation technique that has recently shown promising effects on oscillatory brain activity, particularly by inducing a synchronization of endogenous brain activity with the frequencies of audible stimuli. This brainwave entertainment effect was primarily described based on electroencephalographic (EEG) recordings during passive listening of binaural beats (Ingendoh et al., 2023; Krasnoff and Chevalier, 2023). The presence and magnitude of the brainwave entertainment effect, however, is strongly influenced by the frequency of auditory tones – which varies extensively across experiments. Auditory beat stimulation using binaural beats can elicit a brainwave entertainment effect across a wide 100–900 Hz frequency range (for review, Ingendoh et al., 2023), although several experiments used a carrier tone of 400 Hz (Goodin et al., 2012; Vernon et al., 2014; Solcà et al., 2016). Interestingly, it was also demonstrated that listening to low frequency sounds (LFS) around 250 Hz elicited a decrease in the power of beta oscillations within left parietal brain regions compared to audio listening of higher frequency sounds (Di et al., 2018). Further, an increase in N100 amplitude during audio listening of LFS suggests the involvement of larger neurons populations compared to higher frequencies (Dimitrijevic et al., 2008). Therefore, compared to binaural beats, LFS appears to elicit neural desynchronization. In a unique design, Cameron et al. (2022) demonstrated that LFS increased spontaneous dancing movements among participants who were unaware of the

presence or absence of LFS while listening to music. This suggests that LFS may be used to prompt changes in motor behavior. For instance, the combination between MI and LFS was used in two recent pilot studies to improve neuromuscular activation in patients suffering from arthrogenic muscle inhibition (Colombié and Ladoucette, 2023; Dos Anjos et al., 2023).

Spurred by these findings, the present study was designed to assess the effect of MI combined with audio listening of LFS on lower limbs force performance. Recent reports of a potential for therapeutic effects of combining LFS with MI practice on walking recovery led to the choice of a lower limb force task (Colombié and Ladoucette, 2023; Dos Anjos et al., 2023). We hypothesized that force would increase after both MI + LFS and MI, compared to a control condition. Recent studies testing the priming effect of MI practice on force performance reported immediate gains after a single-session in the range of 2 – 5 % (Di Rienzo et al., 2015; Dos Anjos et al., 2022). We also measured EEG activity to investigate the neurophysiological correlates of combining MI with LFS on brain oscillations, with the aim to better understand the mechanisms mediating the hypothesized benefits on force. MI is typically associated with a reduction in oscillatory power in both alpha and beta brain rhythms (Pfurtscheller and Lopes da Silva, 1999; McFarland et al., 2000). A greater desynchronization of alpha and beta brain rhythms was expected during MI + LFS compared to MI, since audio listening of LFS is known to elicit a decrease in EEG brain power rhythms (Di et al., 2018). Finally, we examined the relationship between EEG activity and motor performance to elucidate whether neurophysiological process mediating the putative effects of MI + LFS and MI on performance were similar. We hypothesized that EEG changes elicited by MI + LFS would exhibit a stronger predictive relationship with the magnitude of performance improvements.

2. Material and methods

2.1. Participants

We carried out *a priori* power analyses to determine the sample size needed to detect effect sizes corresponding to 5–10 % of explained variation within the context of the two-way interactions involving TEST (PRETEST, POSTTEST, RETENTION) and GROUP (MI, MI + LFS, Control). A sample of 17 participants per group was needed to achieve a statistical power of $p_{1-\beta} = 0.80$ with a 5 % type 1 error rate. As a precaution against the potential loss of data due to participant attrition or technical issues, 3 additional participants were included in each group.

Healthy adult participants ($n = 60$, 36 males, 24 females) aged between 18 and 47 years (mean age = 25.35 ± 5.35 years), were recruited from the local university departments and laboratory environment. Participants had regular practice of physical and/or sporting activities at recreational level (1–3 sessions of ~1 h per week over the last 6 months). None had history of extensive practice of sporting disciplines susceptible to elicit expertise-related differences in neural activations during MI (Olsson et al., 2008; Orlandi et al., 2020; Guillot et al., 2023). Likewise, no participant was a regular practitioner of a sport susceptible to elicit force asymmetries between the right and the left quadriceps (e.g. fencing). Participants reported normal hearing with no neurological impairment or recent health problems. They were assigned to one of the experimental groups, using simple randomization: (i) control group (CTRL, $n = 20$, 7 females), (ii) MI group (MI, $n = 20$, 11 females), and (iii) MI combined with LFS listening (MI + LFS, $n = 20$, 6 females). All participants were right-legged in the CTRL group (20/20), 85 % in the MI group (17/20) and 90 % in the MI + LFS group (18/20). While a clear right leg dominance was present in all groups, leggedness was not considered an exclusion criterion. Indeed, there is no statistical effect of limb dominance on functional performance of the lower limbs, including isokinetic quadriceps force and hamstring/quadriceps force ratios (McGrath et al., 2016). Prior to the experiment, all participants completed the Movement Imagery Questionnaire-3 (MIQ-3; Williams

et al., 2012) and the Pittsburgh Sleep Quality Index (PSQI; Buysse et al., 1989) to assess baseline MI ability and sleep quality, respectively. The study was approved by the institutional ethics committee (2022-A00412-41). All participants provided written informed consent before enrollment, in accordance with the tenets of the Declaration of Helsinki (1964) and its later amendments.

2.2. Experimental design

The independent group design consisted in a test-retest procedure over two consecutive days (Fig. 1). Both the pretest and posttest were scheduled the same day, while the retention test was administered at +12 h. Experiments were carried out in a dimly lit room, in which an isokinetic leg-extensor machine was placed behind a computer. On the first day, the experimental session lasted approximately 90 min, including preparation. The session was dedicated to the warm-up, pretest, experimental intervention and immediate posttest of force performance (see 2.3.1 for further description). The pretest and posttest occurred before and immediately after a force training session, during which participants performed maximal isometric contractions of their knee extensor muscles on an isokinetic leg-extensor machine. The second day was dedicated to the retention test at +12 h, which lasted 20 min. Prior to the pretest, participants completed a warm-up consisting in six incremental voluntary contractions of the right knee extensors from 20 % to 90 % of their maximal voluntary isometric contraction (MVIC), each sustained for 7 s (followed by 7 s of rest). This enabled participants to get familiar with the force paradigm. Testing sessions consisted in performing 6 MVIC of knee extensor muscles with the right lower limb. For each MVIC, separated from the next by a rest period of 7 s, participants were requested to sustain their effort for 7 s (Fig. 1). During isometric knee extensions, a force trial was declared valid if participants maintained the standardized position without any help from the

contralateral lower limb, and with both arms positioned across their chest to prevent compensatory trunk movements. Between the pretest and the posttest, participants were required to close their eyes and focus on the experimental instructions, avoiding body or head movements. Participants in the MI group were instructed to perform 3 blocks of 12 MI trials of a MVIC on the leg extension machine. Participants were instructed to combine visual and kinesthetic MI, according to the following script:

“Imagine yourself pushing against the resistance with all your force. Feel the intense contraction of your quadriceps and leg muscles during the sustained maximal contraction. Focus on the total recruitment of muscle fibers throughout the duration of the effort”.

While no specific instruction to use a first-person imagery perspective was provided, performing kinesthetic MI concomitant to third-person visual perspective is empirically acknowledged as very unfamiliar. By contrast, performing kinesthetic MI combined with first-person visual MI is more congruent. MI frameworks early acknowledged that the different MI modalities can be considered in terms of “distance” with the physical performance of the action (Jeannerod, 1995). Although third-person MI be experienced as a spectator, much like mental images, a kinesthetic representation of an action requires an experience from within, i.e. “as the result of a ‘first person’ process” (Jeannerod, 1995 p. 1419). Since then, a series of experiments confirmed that kinesthetic and first-person visual MI were more embodied modalities than third-person visual MI (Stinear, Byblow, et al., 2006; Guillot et al., 2009; Voisin et al., 2011).

All experimental conditions took place within a 15 min time window between pretest and posttest force assessments (Fig. 1). Participants in the MI + LFS group performed the same task while concomitantly listening to LFS. During CTRL, participants listened to an audio podcast about lower limbs anatomy for a roughly equivalent amount of time. The

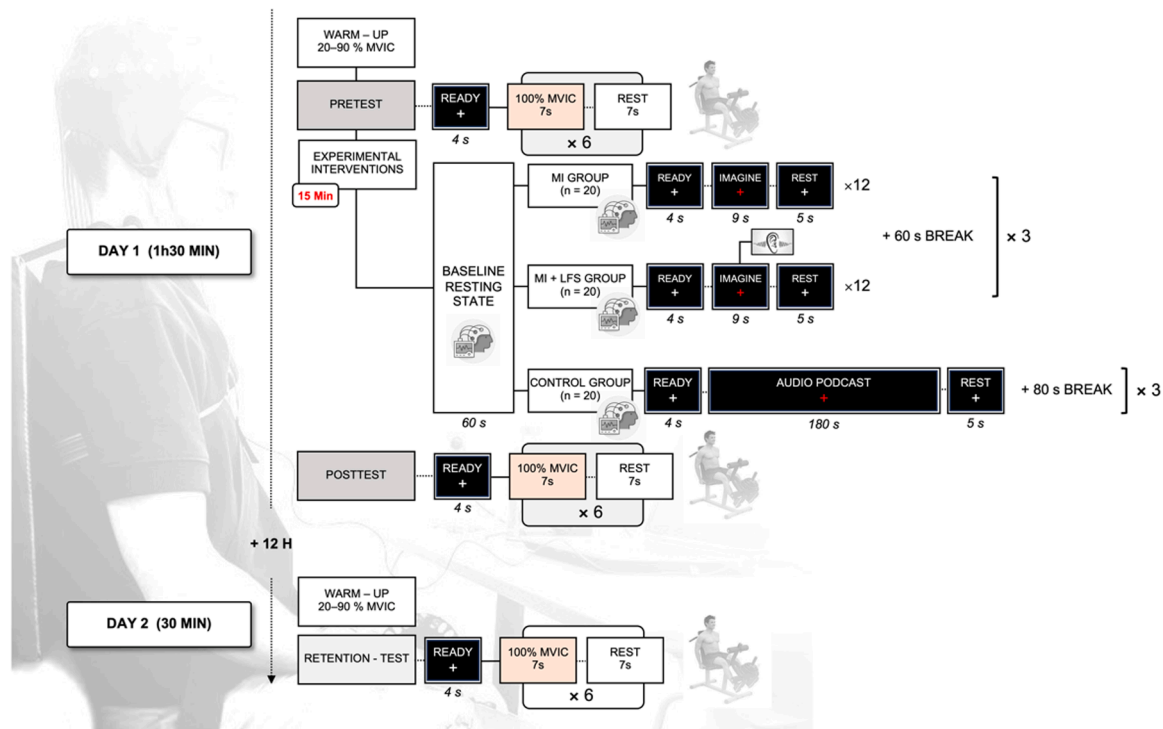


Fig. 1. Flowchart of the experimental design. On the first day, participants underwent a warm-up consisting in incremental isometric contractions of the quadriceps, followed by repeated evaluations of force performance. We implemented a paradigm consisting in repeated maximal voluntary isometric contractions (MVIC) of the quadriceps, i.e. knee extension against a fixed resistance. Participants performed 6 MVIC, each sustained for 7 s. 7 s were allocated between trials to passive recovery. The next day, participants reproduced the same warm-up and completed the same force performance evaluations. Participants sat with their hips and knees flexed at 90°, and were stabilized by straps across the abdomen and pelvis to ensure a standardized trunk position. MI: Motor Imagery. MVIC: Maximal Voluntary Isometric Contractions. LFS: Low Frequency Sounds.

CTRL condition did not involve either motor or auditory beat stimulation. The choice of a no-stimulation control condition compared to a LFS only condition may be surprising. First, the LFS group was deemed facultative to address the primary working hypotheses when building the experimental design. Indeed, we sought to address whether combining MI + LFS may elicit additional gains on MVIC compared to MI performed alone. In other words, we were interested a putative contribution of the (bottom-up) effects of LFS to enhance the (top-down) priming effects of MI practice on force performance, not whether LFS alone could elicit behavioral changes in force performances. While there is a strong scientific rationale supporting MI use to enhance force through experience-based corticomotor plasticity, this is not the case for LFS administered alone. We thus considered control and experimental conditions along a stimulation gradient, ranging from a quasi-absence of stimulation – yet controlling for exposure to auditory stimuli and attention paid to the lower limbs – up to motor simulation combined with LFS. We also considered potential weaknesses of a LFS only condition compared to a control condition without stimulation. A LFS only condition would not strictly control for habituation effects across the repeated force assessments of the design, including fatigue effects between the posttest and the retention test since these could, arguably, be affected to some degree by LFS exposure. Finally, a LFS only condition would not control for the cognitive demand of MI, particularly regarding attention paid to the lower limbs, which is sufficient to influence corticospinal facilitation (Conte et al., 2007).

2.3. Measurements

2.3.1. Force torque elicited by maximal voluntary isometric contractions

Participants sat on the isokinetic leg-extensor machine, with the backrest angle and knee angle set at 90°. Stabilizing straps were placed across the pelvis and chest. Knee extension force was measured using the Tedeo Huntleigh 615 dynamometer (Vishay, Precision Group). The force signal was sampled at 2 kHz using a Powerlab system and synchronized by LabChart Pro V8© (ADInstruments Pty Ltd., Dunedin, New Zealand, 2014). The timing of each MVIC was externally cued using the Presentation® software (Version 18.0, Neurobehavioral Systems, Inc., Berkeley, CA, USA, <http://www.neurobs.com>). After frequency and residual analysis on the raw signals, data were smoothed with a zero-lag 4th order low-pass Butterworth filter with a cut-off frequency of 15 Hz. Torque was calculated a posteriori from the force measured with a calibrated force sensor attached to the chair by multiplying the force signal by the lever arm measured from the knee axis of rotation to the contact point on the tibia. Total force torque was calculated by integrating the slope of the torque with respect to the 7 s of each trial.

2.3.2. Auditory stimuli

Absolute thresholds were acquired through a pre-experimental up and down adaptive staircase auditory test in which participants were required to press a button on a keyboard each time they listened to a tone with the ear lateralized. All audio stimuli were calibrated to be presented at 40 dB through earphones noise cancelling (1MORE USA Inc).

The podcast used in the CTRL group was selected from a medical educational database (NeuroXtrain®), provided general information about lower limb anatomy for 3 min and was displayed three times. LFS ranged 200–400 Hz and were delivered by the patented medical device Alphabox® (Allyane, France). The device did not allow access to psychoacoustic parameters of sound stimuli (e.g. sharpness, fluctuation strength, etc.). LFS displayed by the Alphabox®, however, consisted in a series of single-tone frequencies within the 200–400 Hz range, displayed in a pseudo-randomized order by sequences of 9 s.

2.3.3. Electromyography

During MVIC, surface electromyographic activity (EMG) was recorded from the *vastus lateralis*, *vastus medialis*, *rectus femoris* and

semitendinosus muscles, using pairs of Ag/AgCl electrodes (50 × 48 mm foam electrode solid gel, Asept inmed, France, inter-electrode distance 20 mm center to center). After shaving and cleaning the skin with alcohol, electrodes were positioned according to the recommendations of the “Surface Electromyography for the Non-Invasive Assessment of Muscles” (SENIAM) project (Hermens et al., 2000). Electrode positions were marked with a pen and photographed to ensure reproducible positioning across experimental sessions. As force signals, raw EMG signals were continuously recorded using a Powerlab system and synchronized by LabChart Pro V8© (ADInstruments Pty Ltd., Dunedin, New Zealand, 2014). Raw EMG signals were rectified and smoothed with a 20–500 Hz pass-band filter (Butterworth 4th). For each MVIC, the integrated EMG (iEMG) was calculated with respect to the 7 s of sustained effort, and normalized as a percentage of the maximum value. We also calculated the iEMG_{RATIO} ratio, which is the ratio of the agonist muscles iEMG to the antagonist muscle iEMG, as illustrated by the following formula:

$$iEMG_{RATIO} = \frac{(iEMG_{vastus\ lateralis} + iEMG_{vastus\ medialis} + iEMG_{rectus\ femoris})}{iEMG_{semitendinosus}} / 3$$

2.3.4. Electroencephalography

2.3.4.1. Acquisition. Spontaneous electrical brain activity was recorded using 32 Ag-AgCl sintered electrodes (MLAEC2 Electro-cap system 2, ADInstrument®, Dunedin, New Zealand) in a 10/20 system (FP1, FPZ, FP2, FZ, F3, F4, F7, F8, FT7, FT8, FCZ, FC3, FC4, CZ, C3, C4, CPZ, CP3, CP4, PZ, P3, P4, T3, T4, TP7, TP8, T5, T6, OZ, O1, O2). The ground electrode was located within the cap at the AFZ position. The reference electrodes were external to the cap, positioned on the right internal canthus and the right acromion. The EEG signal was recorded and amplified using a Powerlab system (PL3516, Power Lab 16/35, ADInstrument®, Dunedin, New Zealand) and two amplifier systems (FE238, Octal Bio Amp, ADInstrument®, Dunedin, New Zealand) at 250 Hz with electrode impedance less than 5 kΩ. The raw EEG signal was filtered at 0.5–200 Hz with an additional 50 Hz hardware notch filter to avoid power line contamination.

2.3.4.2. Signal processing. The EEG data processing was performed using Brainstorm (Tadel et al., 2011), which is documented and freely available under the GNU general public license (<https://neuroimage.usc.edu/brainstorm> accessed on October 17, 2022). After relative referencing to the average reference electrode, EEG signals were corrected from heart beat and muscle artifacts with a signal space projection algorithm (Uusitalo and Ilmoniemi, 1997). The artifact detection procedure was completed with a visual inspection to identify EEG channels containing artefacts (5.57 % total rejection rate) before applying a band pass filter (0.5–80 Hz) to the raw signals. The EEG signals were then epoched using different active time windows depending on the experimental group: [−1, 9] s time window for the MI and MI + LFS groups relative to the onset of each trial, and [−1, 180] s time window for the CTRL group relative to the onset of the podcast. As a control time window, we used the [−1, 60] s time window corresponding to the baseline resting-state for all groups. Power spectral densities (PSD) were then calculated in the alpha (8–12 Hz) and beta (15–29 Hz) bands using Welch’s method. Finally, the PSDs were normalized according to the following formula:

$$PSD_{NORM} = \frac{(PSD_{(control\ time\ window)} - PSD_{(active\ time\ window)})}{(PSD_{(control\ time\ window)} + PSD_{(active\ time\ window)})}$$

2.3.5. Self-Report ratings

Participants were requested to rate, before and after the first experimental session, their motivation to engage in the experimental session and their fatigue between MVIC sessions, using a 10-point Likert-type scale (1 = “very low”; 10 = “very high”). An additional question,

rated on a 10-point Likert-type scale, asked participants in the MI + LFS group how strongly they agreed with the following statement: "Listening to the LFS was helpful while imagining" (1 = "Totally disagree"; 10 = "Totally agree").

2.4. Statistical analyses

2.4.1. EEG data

We first selected the frequency ranges of interest between alpha (8–12 Hz), beta (15–29 Hz), and gamma (30–59 Hz) oscillations based on their PSD_{NORM} values. We were interested in event-related desynchronization/synchronization patterns, which were tested using one-way ANOVA models. We then determined sensors of interest based on the main GROUP (MI, MI + LFS, CTRL) effect on alpha (8–12 Hz) and beta (15–29 Hz) PSD_{NORM} , which were tested using a one-way ANOVA model on each sensor of the 32-channel EEG grid. To control the false discovery rate during the selection procedure, we implemented permutation ANOVA tests using R (R Core Team, 2014) and the *permuco* package (Frossard and Renaud, 2021). EEG sensors for which the main GROUP effect on PSD_{NORM} exhibited a type 1 error rate < 5 % were selected as sensors of interest. Within this cluster of interest, we used *nlme* (Pinheiro et al., 2014) to run a linear mixed effects analysis with a by-subject random intercept of PSD_{NORM} data. We entered GROUP (MI, MI + LFS, CTRL) and SENSOR as fixed effects, with an interaction term.

2.4.2. Motor performance data

We also analyzed the total force torque and $iEMG_{RATIO}$ data using linear mixed effects analyses. Specifically, we built a series of random-coefficient regression models with by-subject random intercepts. For both total force torque and $iEMG_{RATIO}$, we entered GROUP and TEST (PRETEST, POSTTEST, RETENTION) as fixed effects, with interaction term. We also included TRIAL (numeric regressor, 1–6) to account for fatigability across the successive MVIC of the quadriceps (Zhou, 1996). To quantify whether total force torque and $iEMG_{RATIO}$ variability across groups and tests of the design could be predicted by the EEG activity recorded during the experimental intervention, we also entered the average of alpha and beta PSD_{NORM} recorded from the cluster of sensors of interest as numerical regressors of the model. We analyzed scores obtained from

standardized questionnaires (MIQ-3, PSQI) and Likert-type scales using simple linear regression models testing for the main GROUP effect. For all analyses, the statistical significance threshold was set at a type 1 error rate of 5 %. As effect sizes, we reported partial coefficients of determination (η_p^2) calculated using ad-hoc methods for linear mixed effects models from the *effectsize* package (Ben-Shachar et al., 2020). Main and interaction effects were investigated post-hoc using general linear hypothesis testing of planned contrasts from the *multcomp* package (Hothorn et al., 2008). Holms' sequential Bonferroni corrections were applied to control for false discovery rate (Holm, 1979).

3. Results

3.1. EEG data analysis

Linear mixed effects model analysis was carried out on the total EEG data and revealed a main effect of FREQUENCY on PSD_{NORM} ($\eta_p^2 < 0.01$, $F_{(3, 6994)} = 7.79$, $p < 0.001$). Post-hoc analyses indicated that the alpha and beta frequency ranges exhibited event-related desynchronization patterns compared to gamma oscillations (both $p < 0.001$; Fig. 2A). MI and MI + LFS groups both exhibited reduced alpha and beta PSD_{NORM} (Fig. 2B). P-values obtained from permutation ANOVA test of the main GROUP effect on alpha PSD_{NORM} revealed a {CP3, CPZ, PZ, T4} cluster of sensors of interest (Fig. 3A). For beta PSD_{NORM} , p-values based on the permutation ANOVA test revealed a more widespread {CP3, CPZ, CZ, FZ, FCZ, P3} cluster of sensors of interest (Fig. 3A). Average alpha and beta PSD_{NORM} within the corresponding clusters were positively related in all experimental groups, as shown by simple linear regression [$R^2 = 0.25$, 0.91, 95 % CI (0.50, 1.33), $p < 0.001$; Fig. 3B].

Within the alpha cluster of interest, the linear mixed effects analysis of PSD_{NORM} revealed no GROUP \times SENSOR interaction ($\eta_p^2 = 0.03$, $F_{(6, 165)} = 0.88$, $p = 0.50$). There was also no SENSOR effect ($\eta_p^2 = 0.02$, $F_{(3, 165)} = 0.93$, $p = 0.42$). Alpha PSD_{NORM} were however affected by the main effect of GROUP ($\eta_p^2 = 0.11$, $F_{(2, 56)} = 3.43$, $p = 0.03$). Post-hoc contrast tests revealed that PSD_{NORM} during MI [−0.08, 95 % CI (−0.15, −0.01)] and MI + LFS [−0.07, 95 % CI (−0.14, 0.00)] were reduced compared to CTRL [0.04, 95 % CI (−0.03, 0.11)] (Fig. 3A, both $p < 0.05$). Within the beta cluster of interest, the GROUP \times SENSOR

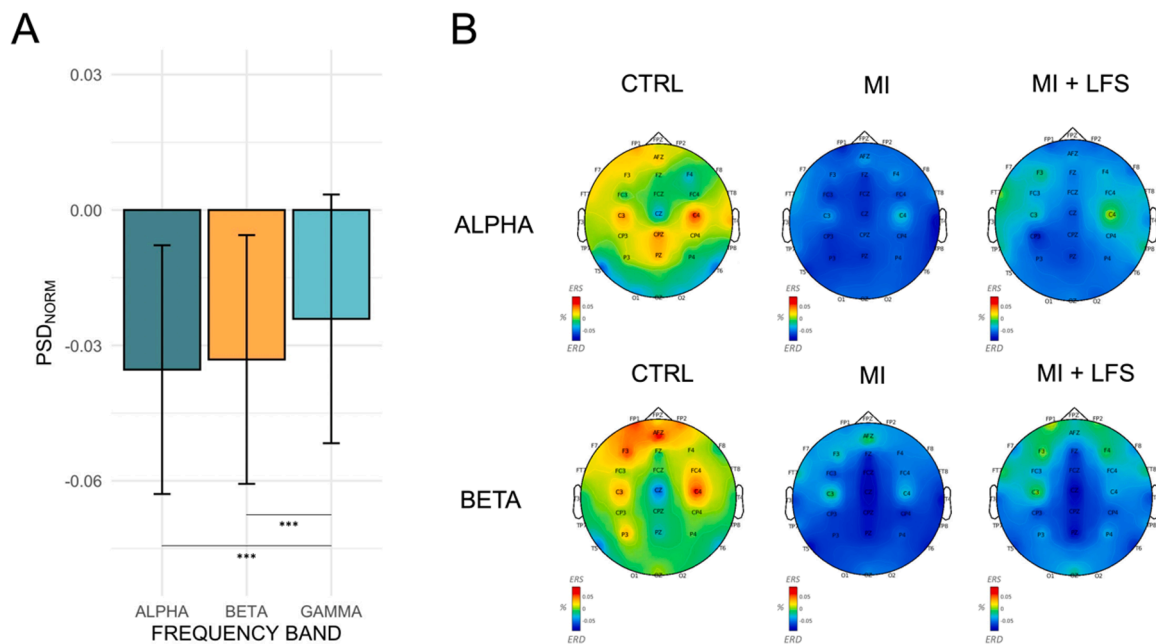


Fig. 2. EEG power spectrum density normalized against the baseline (PSD_{NORM}). A. Barplot depicting the main effect of FREQUENCY [Alpha (8–12 Hz), Beta (15–29 Hz), Gamma (30–59 Hz)] on PSD_{NORM} across groups. B. Spatial distribution of PSD_{NORM} in the sensors-space for alpha and beta brain oscillations across groups. CTRL: Control. MI: Motor imagery. MI + LFS: Motor imagery + low frequency sounds. ERD/S: Event-related desynchronization/synchronization. *** $p < 0.001$.

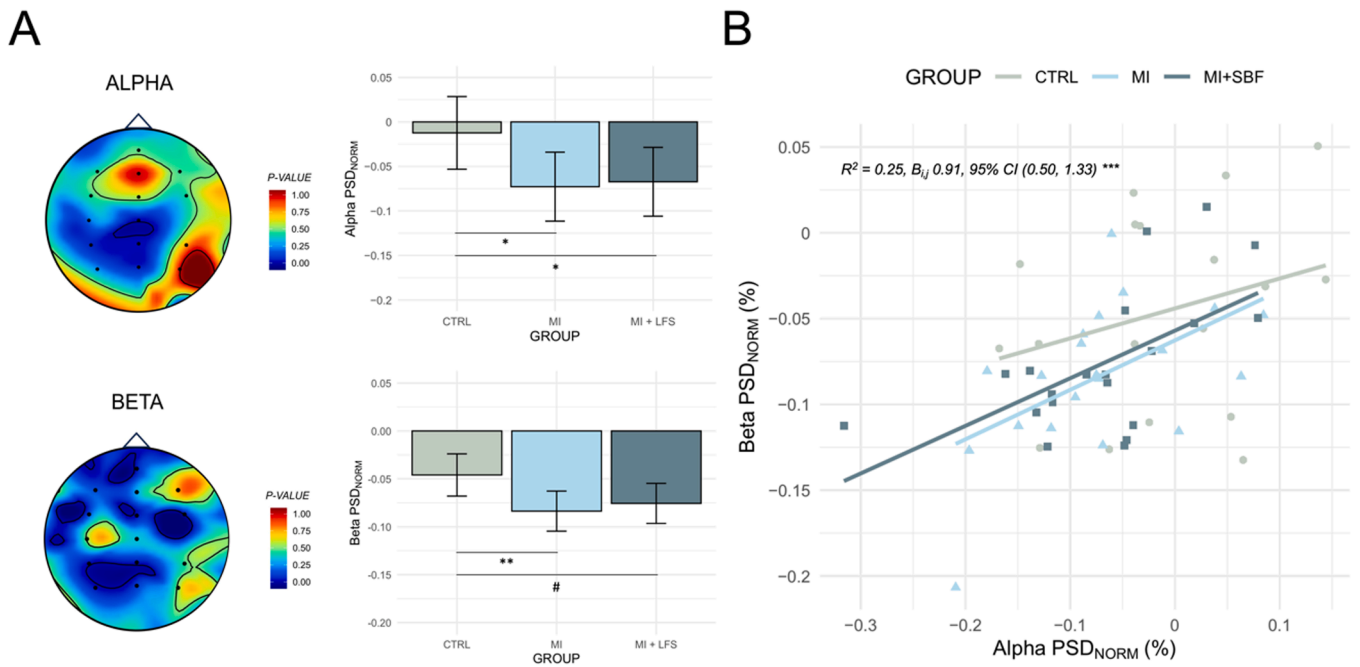


Fig. 3. Overview of the EEG power analysis in the sensors-space. A. (left) Topographical distribution of the p-values revealed by permutation ANOVA tests in the alpha (8–12 Hz) and beta (15–29 Hz) frequency domains. Sensors with a p-value < 0.05 were selected as sensors of interest. A. (right) Barplot of the main effect of GROUP on power spectrum density normalized against the baseline (PSD_{NORM}), for alpha and beta oscillations. B. Scatterplot with regression slopes depicting the relationship between alpha and beta PSD_{NORM} within the cluster of sensors of interest. MI + LFS: Motor imagery combined with low frequency sounds. MI: Motor imagery. CTRL: Control. # $p < 0.10$. * $p < 0.05$. ** $p < 0.01$.

interaction did not affect PSD_{NORM} ($\eta_p^2 = 0.02$, $F_{(10, 270)} = 0.44$, $p = 0.92$). However, there was a main effect for GROUP ($\eta_p^2 = 0.11$, $F_{(2, 55)} = 3.24$, $p = 0.04$) and SENSOR ($\eta_p^2 = 0.31$, $F_{(5, 270)} = 24.33$, $p < 0.001$). Post-hoc contrasts revealed that beta PSD_{NORM} recorded during CTRL [−0.05, 95%CI (−0.06, −0.02)] were higher than those recorded during

MI [−0.08, 95 % CI (−0.10, −0.06)] (Fig. 3A, $p = 0.01$). The difference between CTRL and MI + LFS [−0.07, 95 % CI (−0.10, −0.05)] fell short from the statistical significance threshold ($p = 0.06$). There was no difference between MI and MI + LFS ($p > 0.05$). Beta PSD_{NORM} recorded in P3 [−0.03, 95 % CI (−0.04, 0.01)] was superior to those recorded for

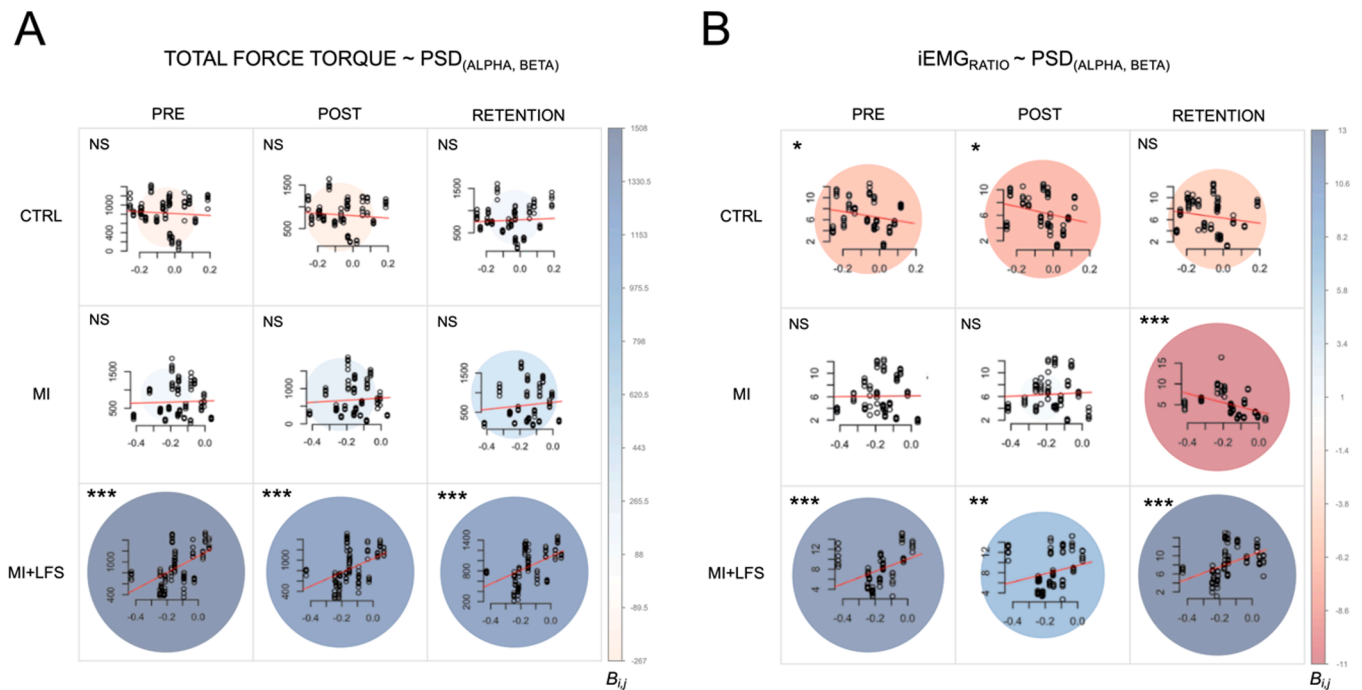


Fig. 4. Correlation matrix (corrected p-values). A. Relationship between total force torque and normalized power spectrum densities across groups and tests of the design. B. Relationship between iEMG_{RATIO} and normalized power spectrum densities across groups and tests of the design. The color and bubble indicate the strength and direction of the regression coefficients. PSD_(ALPHA, BETA): Normalized power spectrum densities across alpha and beta frequency domains. CTRL: Control. MI + LFS: Motor Imagery combined with Low Frequency Sounds. MI: Motor Imagery. * $p < 0.05$. ** $p < 0.01$. NS: Not statistically significant.

all sensors of the cluster (all $p < 0.001$). Also, PSD_{NORM} in CP3 [-0.07, 95 % CI (-0.08, -0.05)] was lower than that recorded in CZ [-0.09, 95 % CI (-0.07, -0.10)] ($p < 0.001$).

3.2. Motor performance analysis

Due to the positive correlation between alpha and beta PSD_{NORM} (Fig. 3B), PSD_{NORM} included the average of alpha and beta PSD_{NORM} . The total force torque was affected by the $GROUP \times TEST \times PSD_{NORM}$ interaction ($\eta_p^2 = 0.04$, $F_{(4, 961)} = 6.54$, $p < 0.001$). Post-hoc comparisons revealed a positive association between the average alpha and beta PSD_{NORM} and the total force torque in the MI + LFS group during the PRETEST [1508.23, 95 % CI (10.44, 19.72), $p < 0.001$], POSTTEST [1330.22, 95 % CI (873.68, 1785.76), $p < 0.001$] and RETENTION [1330.14, 95 % CI (872.19, 1783.09), $p < 0.001$]. There was no association, however, between the average alpha and beta PSD_{NORM} and the total force torque in the MI and CTRL groups (all $p > 0.05$, Fig. 4A). The $GROUP \times TEST \times PSD_{NORM}$ interaction also affected the $iEMGRATIO$ ($\eta_p^2 = 0.07$, $F_{(4, 767)} = 11.38$, $p < 0.001$). As shown in Fig. 4B, there was a positive association between the average alpha and beta PSD_{NORM} and the $iEMGRATIO$ in the MI + LFS group during the PRETEST [12.37, 95 % CI (6.41, 18.33), $p < 0.001$], POSTTEST [8.17, 95 % CI (1.70, 14.64), $p < 0.01$] and RETENTION [13.38, 95 % CI (8.19, 18.57), $p < 0.001$]. In contrast, the MI group exhibited a negative relationship between average alpha and beta PSD_{NORM} and the $iEMGRATIO$ [-10.93, 95 % CI (-15.61, -6.24), $p < 0.001$], similarly to the CTRL group during the PRETEST [-6.54, 95 % CI (1.05, 12.03), $p < 0.05$] and POSTTEST [-6.30, 95 % CI (0.81, 11.79), $p < 0.05$, Fig. 4B].

Total force torque and $iEMGRATIO$ were both affected by the $GROUP \times TEST$ interaction ($\eta_p^2 = 0.03$, $F_{(4, 961)} = 7.67$, $p < 0.001$; $\eta_p^2 = 0.01$, $F_{(4, 767)} = 2.71$, $p = 0.02$, respectively). Importantly, pairwise contrasts revealed no between-groups difference during the PRETEST, for both variables (all $p > 0.10$). Post-hoc contrasts revealed a total force torque decrease from the PRETEST to the POSTTEST in the MI + LFS group [-52.29 N.m.s, 95 % CI (29.18, 75.39)], which was greater than the corresponding difference in the MI group [+11.03 N.m.s, 95 % CI (-12.49, 35.00)], ($p < 0.01$, Fig. 5A). The difference with the CTRL group [10.38 N.m.s, 95 % CI (-16.7, 37.46)] fell short from the statistical significance threshold ($p = 0.09$). Also, the increase in total force torque from the PRETEST to the RETENTION was greater in the MI group [38.67 N.m.s, 95 % CI (14.37, 62.97)] than in the MI + LFS [-24.76 N.m.s, 95 % CI (-48.37, -1.14)] and CTRL [-66.48 N.m.s, 95 % CI (-93.56, -39.39)]

groups (both $p < 0.01$). Noteworthy, the POSTTEST to RETENTION increase in total force torque in the MI + LFS [27.53 N.m.s, 95 % CI (3.91, 51.14)] and MI [27.64 N.m.s, 95 % CI (4.02, 51.26)] groups was superior to the difference observed in the CTRL [-56.10 N.m.s, 95 % CI (-83.18, -29.01)] group (both $p < 0.001$). Post-hoc contrasts for $iEMGRATIO$ revealed a decrease from the POSTTEST to the RETENTION in the MI group [-9.91 %, 95 % CI (-13.98, -5.84)], which was superior to the corresponding difference in the MI + LFS [3.35 %, 95 % CI (-0.7, 7.43)] and CTRL [-1.26 %, 95 % CI (-3.39, 5.91)] groups (both $p < 0.05$; Fig. 5B). All other post-hoc contrasts were not statistically significant ($p > 0.05$). Total force torque was finally affected the main effect of TRIAL ($\eta_p^2 = 0.02$, $F_{(1, 961)} = 6.54$, $p < 0.001$), indicative of a reduction [-6.74 N.m.s, 95 % CI (-9.92, -3.56)] in total force torque per MVIC trial. TRIAL, however, did not influence $iEMGRATIO$ ($p = 0.37$).

3.3. Standardized questionnaires and self-reports

At the group level, the MIQ-3 global score indicated that the movement was “easy to see” and “easy to feel” during MI. The MIQ-3 scores were not affected by the GROUP effect ($\eta_p^2 = 0.03$, $F_{(2, 35)} = 0.98$, $p = 0.39$), but the linear mixed effects analysis performed revealed a main effect of DIMENSION ($\eta_p^2 = 0.06$, $F_{(2,70)} = 5.68$, $p < 0.001$), as shown by Table 1. Participants reported a higher ability to imagine based on the visual (internal and external) dimension than the kinesthetic dimension (both $p < 0.05$). The PSQI scores, which revealed that participants had good sleep quality, were unaffected by GROUP ($\eta_p^2 = 0.05$, $F_{(2, 18)} = 0.47$, $p = 0.63$).

Linear mixed effects analysis on motivation and perceived fatigue yielded no GROUP effect ($\eta_p^2 = 0.02$, $F_{(2,55)} = 0.50$, $p = 0.61$; $\eta_p^2 = 0.02$,

Table 1

Scores of standardized questionnaires across groups. Average scores are presented with 95 % confidence intervals. CTRL: Control. MI: Motor imagery. MI + LFS: Motor imagery combined with low frequency sounds. MIQ-3: Movement Imagery Questionnaire-3, PSQI: Pittsburgh Sleep Quality Index.

Scores	CTRL	MI	MI + LFS
MIQ-3 global	5.92 [5.38, 6.45]	5.53 [5.01, 6.03]	5.99 [5.53, 6.44]
External	6.25 [5.55, 6.94]	5.89 [5.23, 6.56]	6.18 [5.59, 6.78]
Internal	6.00 [5.30, 6.69]	5.92 [5.25, 6.58]	5.88 [5.29, 6.48]
Kinesthetic	5.50 [4.80, 6.19]	4.77 [4.10, 5.44]	5.90 [5.30, 6.49]
PSQI	6.12 [3.54, 8.71]	6.36 [4.15, 8.57]	5.00 [2.89, 7.11]

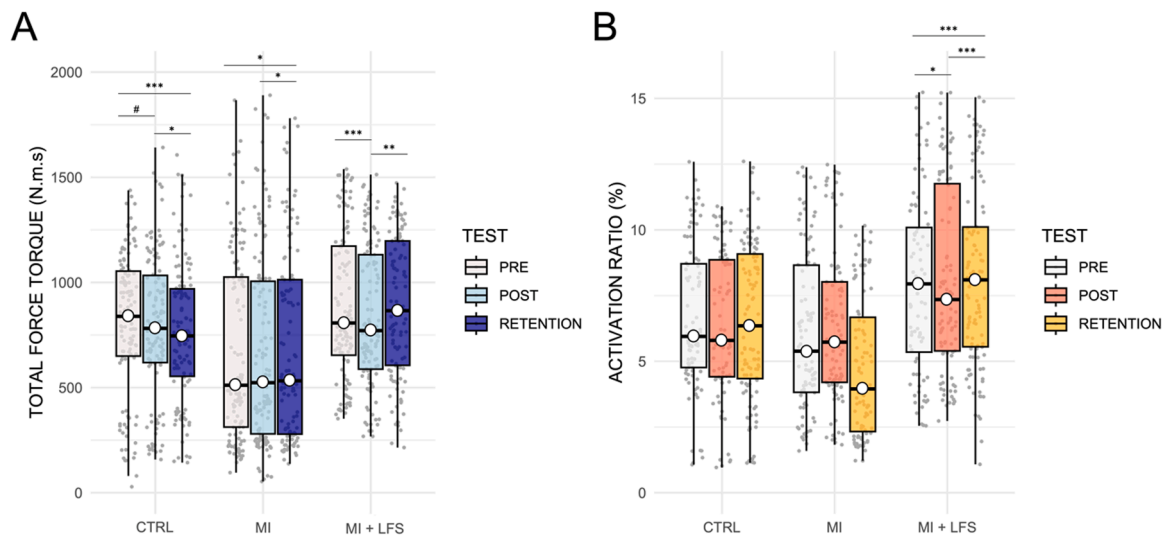


Fig. 5. Boxplot depicting the $GROUP \times TEST$ interaction effect on the dependent variables quantifying force performance. A. Total force torque across groups and test of the design. B. Activation ratio across groups and test of the design. CTRL: Control. MI: Motor imagery. MI + LFS: Motor imagery combined with low frequency sounds. # $p < 0.10$. * $p < 0.05$. ** $p < 0.01$. *** $p < 0.001$.

$F_{(2,55)} = 1.33, p = 0.27$, respectively). Conversely, Likert ratings of perceived difficulty were influenced by the TEST effect ($\eta_p^2 = 0.63, F_{(1,55)} = 93.73, p < 0.01$). Participants reported higher levels of perceived fatigue during the POSTTEST strength training session than during the PRETEST session ($p < 0.01$). Finally, the usefulness of the sounds for imagery after MI + LFS was 5.32 ± 2.69 on a 10-point Likert scale, corresponding to “Neither agree nor disagree”.

4. Discussion

The present study was designed to evaluate whether combining MI with LFS could facilitate the short-term effects of MI practice on force produced by maximal voluntary isometric contractions of the quadriceps. While past experiments provided evidence for the priming effects of MI practice on muscle activation (Di Rienzo et al., 2015; Dos Anjos et al., 2022), we postulated that LFS could enhance the short-term effects of MI practice on force through increased corticomotor activation. We first observed a decrease in motor performance across the repeated measures of the design in the control group, whereas the MI group improved its force performance from the pretest to the retention test at +12 h. Surprisingly, the MI + LFS group exhibited an immediate decrease in force production after the experimental intervention, followed by a return to the pretest baseline during the retention test at +12 h. EEG data revealed a greater desynchronization of alpha and beta oscillations in the MI + LFS and MI groups compared to the control group. Noteworthy, the relationship between force performances and EEG desynchronization elicited by the intervention was negative in the MI + LFS group but positive in the MI group.

The analysis of force performance confirmed the effectiveness of MI to improve force produced by MVICs (Yue and Cole, 1992; Ranganathan et al., 2004; Liu et al., 2023). Indeed, only the MI group outperformed the control group from the pretest to the retention test. The 5.67 % of force improvement observed in the present study is in line with earlier reports of MI practice benefits at the single session level (Di Rienzo et al., 2015; Dos Anjos et al., 2022). Considering that the task involved the right lower limb, the benefits of MI practice on force were possibly facilitated by a left hemisphere dominance of brain activations. Indeed, a left hemispheric dominance has been proposed for MI in relation to hemispheric specialization during motor planning processes (Sabaté et al., 2004; Stinear, Fleming, et al., 2006). Hemispheric lateralization during MI was further assumed to account for lateralized force gains after MI training combined with action observation in a bilateral lower limb force task (Scott et al., 2018). Here, force gains were not found immediately after the experimental intervention, but during the retention test performed at +12 h. Fatigability elicited by the force paradigm, attested from the decrease in total force torque across the successive MVIC, possibly delayed the priming effects of MI practice on force. The present design did not involve embedded MI within rest periods of a resistance training session, but a test-retest evaluation. Our study also administered a force task with the lower limbs, whereas past experiments focused the upper limbs (Di Rienzo et al., 2015; Dos Anjos et al., 2022). Fatigability elicited by maximal voluntary contractions is typically greater for repetitive maximal isometric contractions with the lower limb compared to the upper limbs (Vernillo et al., 2018). The pattern of change in force performance observed in the MI + LFS group did not confirm our primary working hypothesis. Indeed, we observed an immediate decrease in performance in the MI + LFS group. Nonetheless, while the control group exhibited a decrease in force performance across all repeated measures of the design, force in the MI + LFS group decreased from the pretest to the posttest before returning to baseline during the retention test. A parallel pattern of change across repeated measures was found for agonist/activation ratios indexed from EMG recordings. The distinct pattern of changes in motor performance between the MI + LFS and control groups cannot be accounted for by motivation or perceived exertion, since those psychological factors were controlled and identical between groups. Rather, the return to baseline

force levels during the retention test in the MI + LFS group suggests a transient inference of LFS concomitant to MI practice on force production processes. We may first have underestimated the cognitive demand involved by MI + LFS, since added cognitive demand has the potential to interfere with a concurrent motor performance (for a review, see Leone et al., 2017). However, this postulate is inconsistent with the fact that MI + LFS interventions were previously shown to have beneficial effects on muscle activation (Colombié and Ladoucette, 2023; Dos Anjos et al., 2023). Possibly, longer familiarization period with LFS prior to the MI + LFS intervention, and the presentation of auditory stimuli calibrated at less than 40 dB could have facilitated participants' engagement in MI.

MI and MI + LFS yielded distinct patterns of power spectrum densities changes in brain oscillations compared to the control group. These patterns were characterized by a decrease in alpha and beta power (Fig. 2), referred to as event-related desynchronization (ERD). ERD in response to MI practice is well-documented in the scientific literature (Pfurtscheller and Lopes da Silva, 1999; McFarland et al., 2000; Pfurtscheller, 2001; Neuper et al., 2006). We identified, using permutation testing, an electrode cluster of interest sensitive to the main effect of the intervention, which exhibited alpha and beta ERD. This cluster encompassed central and parietal EEG sensors, in both MI and MI + LFS. This observation is consistent with the reduction in the power of rhythmic brain activity localized over the contralateral sensorimotor cortex during MI practice, suggesting the recruitment of these structure during motor simulation (Neuper et al., 2006; Cheyne, 2013; Zabielska-Mendyk et al., 2018). Interestingly, ERD amplitudes within the electrode cluster of interest, considered as an index of cortical activation, were comparable between MI and MI + LFS. By contrast, changes in force performance observed between MI and MI + LFS suggest distinct modulatory effect on corticomotor processes.

Increased cortical activation is not the only factor underlying the facilitatory effects of MI practice on force performances, which also involves spinal mechanisms (Grosprêtre et al., 2016). Although we did not investigate spinal processes, the different profiles of relationship between force performance/electromyographic activity and the desynchronization of sensorimotor rhythms elicited during experimental interventions indicate a selective influence of MI and MI + LFS on corticomotor processes driving force performance. EEG alpha and beta power desynchronization exhibited a negative relationship with the total force torque and agonist/antagonist EMG activation ratios in the MI + LFS group only. Since the MI + LFS intervention elicited an ERD of alpha and beta EEG oscillations, such association suggests that brain activation elicited by MI + LFS negatively predicted the force output. This is in line with the assumption of a transient perturbation of cortical drive to motor units under this experimental condition. By contrast, the MI group demonstrated during the retention test at +12 h positive association between ERD of sensorimotor rhythms elicited during MI practice and agonist/antagonist ratio of the integrated electromyograms during force trials. Since the MI group was the only group to exhibit improvements in force performance from the pretest to the retention test, this finding confirms the potential short-term reduction of agonist/antagonist coactivation through MI practice, a well-established neural adaptation during the early stages of resistance training (Zijdewind et al., 2003; Dos Anjos et al., 2022). Admittedly, the absence of LFS only condition precludes firm conclusions regarding the neural mechanisms underlying the perturbation of force gains through MI. Such condition would also be helpful to ensure that LFS elicits the expected ERD in the alpha/beta range. As supplementary material, we provided an additional EEG sensors-space analysis of the effect of LFS delivered alone on the spatial distribution of alpha and beta power, which was obtained from pilot recordings in 28 healthy participants as part of another experiment conducted in our laboratory (see Supplementary Material 1). LFS elicited an event-related desynchronization of alpha oscillations, but did not elicit a beta event-related desynchronization. The alpha desynchronization was generated from occipital regions of the EEG sensors-space, but did not involve central regions, bilaterally. This

corroborates the assumption of interfering effects of LFS with event-related desynchronization patterns during MI.

Overall, the distinct patterns of covariance between EEG and EMG activity in the MI and MI + LFS groups suggests that both interventions leveraged distinct neurophysiological processes. The combination of LFS with MI training unexpectedly disrupted motor performance in the short term, akin to transient deprogramming effects that preceded a return to baseline levels at +12 h. Possibly, audio listening of LFS interfered with the lateralization of activations during MI, hence reducing left hemisphere involvement and cortical gain over motor units of the contralateral lower limb. While this argues against any recommendation to use MI + LFS to enhance force performance in healthy populations in the short term, a recent experiment provided evidence of improved functional recovery in postoperative anterior cruciate ligament injury patients, largely mediated by increased muscle activation after a single MI + LFS session (Dos Anjos et al., 2023). In this retrospective study, the authors assumed that the intervention elicited *neuromotor reprogramming* through a temporary neutralization of inhibitory mechanisms likely to alter corticomotor excitability. In the present study with healthy participants, changes in cortical activity induced by MI + LFS did not improve performance compared to MI alone. This suggests that while the neurophysiological processes engaged during MI + LFS may not be suitable to facilitate or optimize performance in healthy individuals, such type of intervention could be relevant in populations with dysfunctional corticomotor processes that hamper voluntary activation of motor units, e.g. in patients with arthrogenic muscle inhibition (Rice and McNair, 2010; Lepley and Lepley, 2021). MI + LFS might elicit a transient perturbation of compromised corticomotor networks organization that could facilitate experience-based plasticity in response to a concomitant physical or mental training intervention.

Whether MI + LFS could complement rehabilitation programs by addressing the compensatory neural mechanisms that may not be adequately targeted by existing intervention strategies remains unresolved (Grooms et al., 2023). The combination of MI with audio listening of LFS could be a promising strategy due to the transient interference on corticomotor processes driving neuromuscular activation. The scope of the present research must be expanded by research in patient populations to examine whether it could foster long-term neurophysiological adaptations prompting enhanced functional recovery when embedded within conventional rehabilitation protocols.

5. Conclusion

This study contributes to the growing body of research exploring the synergistic effects of MI with exogenous stimulation to improve motor performance. Our results highlight that the combination of LFS with MI interfered with the short-term effects of MI practice on maximal isometric force, possibly through the transient disruption of the cortical gain over motor units, as evidenced by the relationships between EEG activity changes and muscle recruitment strategies under this specific experimental condition. The relationships between behavioral and brain potential responses following MI + LFS, compared to MI alone and the control condition, confirmed that auditory stimuli combined with MI training has the potential to alter motor excitability and influence muscle activation (Dos Anjos et al., 2023). Although present findings indicate that MI + LFS may not be relevant in individuals without motor control deficits, they bear practical significance in clinical rehabilitation settings where the use of MI + LFS could be a valuable tool to address specific muscle deficits and promote neuroplasticity. Further investigations are warranted to assess the long-term efficacy of this innovative approach. Ultimately, this research opens avenues for interventions targeting neural compensation deficits in muscle strength after injury, such as arthrogenic muscle inhibition, for which current therapeutic interventions offer limited efficacy (Sonnerly-Cottet et al., 2019).

CRedit authorship contribution statement

Typhanie Dos Anjos: Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **Aymeric Guillot:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Sebastien Daligault:** Software, Formal analysis, Data curation. **Donna-Maria Chamoun:** Resources, Investigation. **Thomas De Sousa:** Software, Formal analysis. **Franck Di Rienzo:** Writing – review & editing, Validation, Supervision, Software, Methodology, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this article.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.neuroimage.2024.120746](https://doi.org/10.1016/j.neuroimage.2024.120746).

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