Received: 1 July 2024 | Revised: 11 September 2024 | Accepted: 16 September 2024

DOI: 10.1111/jsr.14371

RESEARCH ARTICLE

Overnight changes in performance fatigability and their relationship to modulated deep sleep oscillations via auditory stimulation

Manuel Carro-Domínguez[1] | Stephanie Huwiler[1] | Fabia M. Stich[1] | Rossella Sala[1] | Florent Aziri[1] | Anna Trippel[1] | Caroline Heimhofer[1] | Reto Huber[2,3,4,5] | Sarah Nadine Meissner[1] | Nicole Wenderoth[1,3,6] | Caroline Lustenberger[1,2,3]

[1]Neural Control of Movement Laboratory, Institute of Human Movement Sciences and Sport, Department of Health Sciences and Technology, ETH Zurich, Zurich, Switzerland

[2]Centre of Competence Sleep & Health Zurich, University of Zurich, Zurich, Switzerland

[3]Neuroscience Centre Zurich (ZNZ), University of Zurich, ETH Zurich, Zurich, Switzerland

[4]Child Development Centre, University Children's Hospital, University of Zurich, Zurich, Switzerland

[5]Department of Child and Adolescent Psychiatry and Psychotherapy, Psychiatric Hospital Zurich, University of Zurich, Zurich, Switzerland

[6]Future Health Technologies, Singapore-ETH Center, Campus for Research Excellence and Technological Enterprise (CREATE), Singapore

Correspondence
Caroline Lustenberger, Neural Control of Movement Laboratory, Department of Health Sciences and Technology, ETH Zurich, Zurich 8092, Switzerland.
Email: caroline.lustenberger@hest.ethz.ch

Funding information
Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung, Grant/Award Numbers: 320030_179443, 32003B_207719, PZ00P3_179795; As part of the Hochschulmedizin Zürich Flagship project SleepLoop, ETH Zürich and University Zürich; National Research Foundation, Prime Minister's Office, Singapore under its Campus for Research Excellence and Technological Enterprise (CREATE) program (FHT)

Summary

Deep sleep oscillations are proposed to be central in restoring brain function and to affect different aspects of motor performance such as facilitating the consolidation of motor sequences resulting in faster and more accurate sequence tapping. Yet, whether deep sleep modulates performance fatigability during fatiguing tasks remains unexplored. We investigated overnight changes in tapping speed and resistance against performance fatigability via a finger tapping task. During fast tapping, fatigability manifests as a reduction in speed (or "motor slowing") which affects all tapping tasks, including motor sequences used to study motor memory formation. We further tested whether overnight changes in performance fatigability are influenced by enhancing deep sleep oscillations using auditory stimulation. We found an overnight increase in tapping speed alongside a reduction in performance fatigability and perceived workload. Auditory stimulation led to a global enhancement of slow waves and both slow and fast spindles during the stimulation window and a local increase in slow spindles in motor areas across the night. However, overnight performance improvements were not significantly modulated by auditory stimulation and changes in tapping speed or performance fatigability were not predicted by individual changes in deep sleep oscillations. Our findings demonstrate overnight changes in fatigability

---

Sarah Nadine Meissner, Nicole Wenderoth, and Caroline Lustenberger have contributed equally to this paper and are shared last authors.

but revealed no evidence suggesting that this effect is causally linked to temporary augmentation of slow waves or sleep spindles. Our results are important for future studies using tapping tasks to test the relationship between sleep and motor memory consolidation, as overnight changes in objectively measured and subjectively perceived fatigue likely impact behavioural outcomes.

KEYWORDS
auditory stimulation, fatigue, finger tapping, motor slowing, performance fatigability, sleep, sleep spindles, slow waves

1 | INTRODUCTION

Sleep oscillations during non-rapid eye movement (NREM) sleep are believed to play a pivotal role in the restoration of brain function and in solidifying the retention of learned motor patterns. Yet, while most of the research has traditionally focussed on how sleep enhances motor sequence learning and enables motor memory consolidation, little is known about whether sleep modulates performance fatigability. Fatigability describes the objectively measurable reduction in performance which emerges during prolonged task execution. Subjective fatigue, by contrast, is defined by the individual's perception of how demanding a task feels, including sensations of tiredness, increased effort, and a discrepancy between the effort felt and the actual performance achieved (Kluger et al., 2013). Elevated and sustained fatigue, observed in many neurological disorders, is frequently accompanied by deteriorated sleep (Brass et al., 2010; Kluger et al., 2013; Manjaly et al., 2019) and discrepancies between subjective fatigue and performance fatigability increase with sleep deprivation (Magnuson et al., 2023), but whether NREM sleep oscillations contribute to our resilience to fatigue remains to be investigated.

Performance fatigability has been investigated via different tasks such as fast, repetitive, low-force movements. These movements are typically assessed by measuring the change in tapping time between key presses during a 30 s finger tapping task at maximal speed and evoke fatigability irrespective of whether the participants tap with only one finger, or execute a motor sequence (Bächinger et al., 2019; Rickard et al., 2008). When executed as quickly as possible, a significant slowing of tapping speed occurs throughout the 30 s, which has been referred to as “motor slowing” (Bächinger et al., 2019; Heimhofer et al., 2024). An alternative approach for measuring fatigability is sustained muscle contractions, which are typically assessed by measuring the maximum voluntary contraction torque during a sustained contraction task (Arias et al., 2015; Madrid et al., 2016; Magnuson et al., 2023; Post et al., 2009). In a study comparing acute sleep deprivation with a normal night's sleep, Magnuson et al. observed similar levels of performance fatigability in sustained muscle contractions following both conditions but greater perceived fatigue in the sleep deprivation conditions. While isometric contractions measure a mix of supraspinal and neuromuscular mechanisms, prolonged finger tapping at high speeds have been shown to not significantly affect markers of peripheral or muscular fatigability and instead predominantly test supraspinal mechanisms of fatigability (Arias et al., 2015; Bächinger et al., 2019; Madrid et al., 2016; Rodrigues et al., 2009). One supraspinal mechanism of fatigability is the breakdown in $GABA_A$-inhibitory circuits in motor areas of the cortex involved in finger tapping. This breakdown is not only present in prolonged finger tapping at high speeds but, interestingly, also in motor sequence learning (Bächinger et al., 2019).

Resilience to fatigability could potentially be promoted by two hallmark oscillations of NREM sleep: slow waves and sleep spindles. Slow waves are large-amplitude, low-frequency brain oscillations which are measured using electroencephalography (EEG). They reflect collective synchronisation of excitatory and inhibitory neurons throughout the cortex, contributing to synaptic renormalisation and memory consolidation (Frankland & Bontempi, 2005; Tononi & Cirelli, 2014). Sleep spindles can also be measured using EEG and are thought to result from thalamocortico-cortical activity in the forebrain that favours intracortical plasticity (Fernandez & Lüthi, 2020). Slow spindles emerge in the EEG as 9–12.5 Hz activity primarily in the frontal areas of the cortex whereas fast spindles emerge in the 12.5–16 Hz frequency range in primarily centroparietal areas (Cox et al., 2017). Although various imaging modalities reveal that slow and fast spindles appear in different cortical areas, it is unclear whether slow and fast spindles serve distinct functional roles or whether they reflect different ends of the same functional spectrum (Anderer et al., 2001; Andrade et al., 2011; Manshanden et al., 2002; Schabus et al., 2007; Siclari et al., 2014; Sleep, 2010). In summary, the renormalisation and plasticity of cortical synapses associated with slow wave or spindle activity may contribute to restoring the resilience of cortical neurons in sensorimotor areas affected by performance fatigability from one day to the next.

The effects of these sleep oscillations on central motor control have primarily been researched in terms of motor sequence learning. When evaluating sleep-dependent motor memory consolidation, sleep spindles have been observed to play an important role. Increases in sigma (9–16 Hz) activity, manifesting as the number of spindles (Morin, 2008), clustered spindles (Boutin et al., 2024), and spindle density (Nishida & Walker, 2007), have been documented to rise after sleep in cortical areas involved in motor sequence learning. Although it has been shown that reducing slow waves using auditory stimulation can lead to a reduction in motor performance in a motor sequence learning task (Fattinger et al., 2017), it is unclear whether enhancing slow wave and sigma activity using auditory stimulation can lead to improved motor performance (Baxter et al., 2023; Choi et al., 2019; Choi & Jun, 2022). The success of learning a sequence of finger movements after a sleep period is typically quantified as the improvement in movement speed (e.g. tapping time between key presses) in combination with accuracy measures (e.g. considering only correctly performed sequences) (Lustenberger et al., 2016; Rickard et al., 2008; Walker et al., 2002). As movement speed is susceptible to fatigability, it remains under-investigated to what extent performance metrics used to assess sleep-related motor memory and learning, are confounded by performance fatigability.

Rickard et al. first reported performance fatigability during fast tapping movements as a potential confounding effect when assessing whether improvements in motor sequence learning are due to active sleep learning processes (Rickard et al., 2008). They found that reducing the tapping block from the more common 30 s duration to 10 s (which causes significantly less fatigability) can lead to improvements in the accuracy difference scores before and after sleep. However, overnight improvements were similar to those observed between pre-sleep trials. One would anticipate more pronounced overnight improvements if there existed a sleep-related mechanism for enhancing performance. Here, we investigated differences in performance fatigability during a simple tapping task before and after sleep and whether such differences are specifically linked to sleep oscillations.

Sleep oscillations involved in consolidating learned motor sequences may also affect mechanisms of fatigability. To dissociate motor performance from sequence learning, we investigate whether enhancing slow waves overnight changes motor performance in a motor task without a sequence learning component. We enhanced slow wave activity bouts through auditory stimulation, a neuromodulatory technique that has been used previously (Huwiler et al., 2023; Ngo et al., 2013). Additionally, we report auditory stimulation effects on both slow wave and sigma activity. By analysing how these oscillations correlate with overnight changes in finger tapping performance and overall fatigability, we aim to elucidate the contributory roles of both slow waves and sleep spindles in motor resilience and general motor performance.

2 | METHODS

2.1 | Participants

Twenty-six healthy adult males were recruited for participation in a randomised controlled, double-blind, crossover trial, registered under ClinicalTrials.gov NCT04166916. Of these, eight participants were excluded: seven due to not meeting pre-established inclusion criteria during the screening night, and one due to non-adherence to the experimental protocol (see Figure S2 for a more detailed justification for their exclusion). The final cohort comprised 18 participants, aged between 30.0 and 57.1 years, who were non-smokers and exhibited no cardiovascular, sleep, or significant concurrent health issues. Ethical approval for the study was obtained from the Cantonal Ethics Committee Zurich (KEK ZH, BASEC 2019-01538), and all participants provided written informed consent before commencement, with monetary compensation provided for their involvement. The study was conducted in accordance with the Declaration of Helsinki.

2.2 | Procedure

All participants underwent three experimental nights where one of three auditory stimulation (stim) modalities were applied in a counterbalanced, cross-over design (no stim, low volume stim, high volume stim). The two latter stimulation conditions were used to examine dose dependency effects of auditory stimulation on cardiovascular effects (Alessandrelli et al., 2024; Huwiler et al., 2023). However, the experimental session with low volume stim was excluded from this analysis as our hypotheses were on the effects of auditory stimulation on motor performance, rather than any potential dose-dependency effects. Three days prior to each experimental night, the participants had to adhere to a regular sleep rhythm and compliance was monitored by questionnaires. Each experimental night was preceded by a behavioural task battery in the evening and followed by the same task battery in the morning. These task batteries included a psychomotor vigilance task, an oddball task, a word pair task, a decision-making task, and a finger tapping task. Here, findings from the finger tapping task are reported.

Eighteen healthy male participants conducted the finger tapping block the evenings before (∼8:30 pm) and the mornings (∼9 am) after two nights of sleep (included in the reported analysis) in the sleep lab during which polysomnography with high-density surface EEG was measured. The two nights took place ∼1–2 weeks apart. Each night of sleep consisted of a 7.5 h sleep window where, on one night, we applied an auditory stimulation (stim) condition during the up phase of NREM slow waves and, on the other night, we applied a control (sham) condition without stimulation (Figure 1). More details on the study protocol can be found elsewhere (Alessandrelli et al., 2024; Huwiler et al., 2023).

2.2.1 | Finger tapping block

Participants sat in a comfortable chair with their chin placed in a chin rest to ensure a stable head position for pupil size measurements (not reported here). The chair height was adjusted to accommodate participants. The right forearm rested on the table with the hand placed on a keyboard (K55 RGB PRO, Corsair Gaming Inc., California, United States). Participants were instructed to keep their wrist on the keyboard rest to avoid compensatory movements during the task. They were also instructed to tap as fast as possible with maximum effort throughout the entire trial. Each tapping block comprised six trials, during which participants alternated between index and middle finger taps of their right hand at their maximal voluntary rate for 30 s, followed by 30 s rest (Figure 1). Our methodology departs from classical motor sequence learning approaches by utilising a simple,

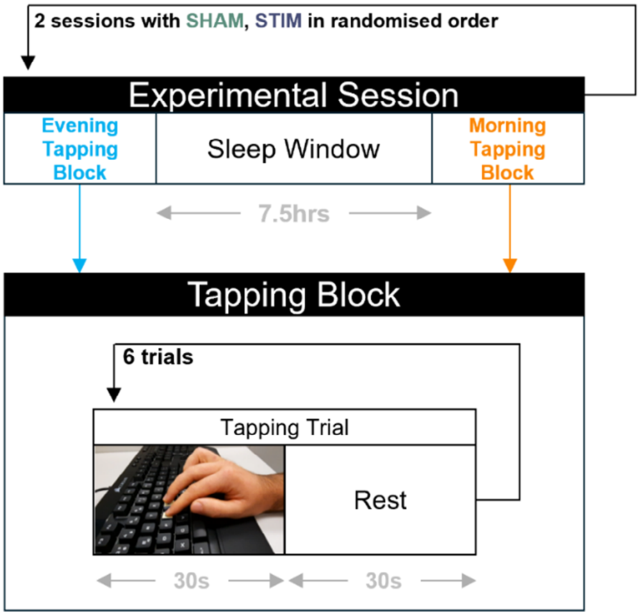

FIGURE 1 Experimental design. Two experimental sessions took place, and the two experimental conditions (sham and stim) were administered in a pseudo-randomised order. For each experimental session, participants conducted a tapping block in the evening prior to the 7.5 h sleep window and in the morning after the sleep window, each comprising six consecutive tapping trials. During each trial, participants alternated tapping between the "G" and "H" buttons using their right index and middle fingers, respectively, with each tapping and rest period lasting 30 s.

repetitive, two-finger tapping task to assess baseline motor performance and fatigue, devoid of any learning or memory components typically associated with motor sequence learning tasks. The onset of the tapping window was indicated by a crosshair on the centre of the screen positioned behind the keyboard. “Pause” was displayed to indicate the beginning of the rest period which included a “Get ready!” display in the last 6 s of the rest period, prompting the participant to expect the subsequent tapping trial to begin. On the first experimental night, participants were accustomed to the task with two trial runs. Presentation v22.0 was used to run the protocol. Eye tracking and EEG were also acquired during the behavioural task but are not reported here. After each block, participants completed the National Aeronautics and Space Administration-Task Load Index (NASA-TLX), a questionnaire assessing the perceived amount of mental and physical resources required to execute the task (Hart & Staveland, 1988). Workload is assessed along six dimensions: mental demand, physical demand, temporal demand, performance, effort, and frustration.

2.2.2 | EEG recording during sleep

A high-density EEG system with 128 electrodes (Geodesic Sensor Net, Magstim EGI, Eugene, USA) was attached prior to the tapping block in the evening and was removed after the tapping block in the morning. All impedances were kept below 40kΩ. After lights out, participants were allowed to sleep for 7.5 h while polysomnography was recorded (BrainProducts GmbH, Gilching, Germany) at a sampling rate of 500 Hz.

2.2.3 | Auditory stimulation

We investigated a stim condition that was selected based on their dynamic effects on the brain and compared it with a no stimulation (sham) condition (Huwiler et al., 2022). Namely, we used 1 Hz rhythmic EEG feedback-controlled (single channel Fpz-A2) auditory stimulation of a 50 ms burst of pink noise with a sound level of 45 dB (stim). Auditory stimuli were delivered through Etymotic insert earphones (Etymotic Research Inc., ER 3C) during NREM sleep. Stimulations were delivered in a windowed 10 s ON (auditory stimulation presented) followed by 10 s OFF (no auditory stimulation presented) design (see Huwiler et al., 2022; Lustenberger et al., 2022 for a detailed description of stimulation algorithms). Only stimulation windows in artefact- and arousal-free NREM2 and NREM3 were included in further analyses.

2.3 | Data analysis

One participant out of 18 was excluded from the finger tapping analysis for not alternating fingers between taps (Figure 2), while another participant out of 18 was excluded from the EEG analysis because of a measurement error during the sham recording (Figures 3a–c and S1a–c). Both of these participants were therefore excluded from the analysis that combined finger tapping and EEG results (Figures 3d–i and S1d–i).

2.3.1 | Behavioural analysis

Tapping speed was calculated as the number of taps per second (Hz) in 5 s bins for each 30 s tapping trial (Figure 2a). To quantify motor slowing, tapping speed was calculated in 2 s bins. A linear (first order) polynomial was fitted to the binned tapping speed data using the MATLAB function *polyfit*. The slope of the linear fit (Hz/s) describes the degree of motor slowing for the given trial. The 2 s bin where the maximum tapping speed took place was defined as the time of maximum performance. If maximum performance was not achieved within the initial 10 s of the trial, indicating a lack of maximal effort from the beginning, the trial was excluded from subsequent analysis (6.12% per participant). Tapping speed and motor slowing values were averaged across trials within a tapping block prior to plotting and statistical analysis.

2.3.2 | EEG analysis

EEG pre-processing was performed using the EEGLAB toolbox (Delorme & Makeig, 2004) in MATLAB (R2019a, MathWorks Inc., Natick, MA). Pre-processing consisted of down-sampling to 200 Hz,

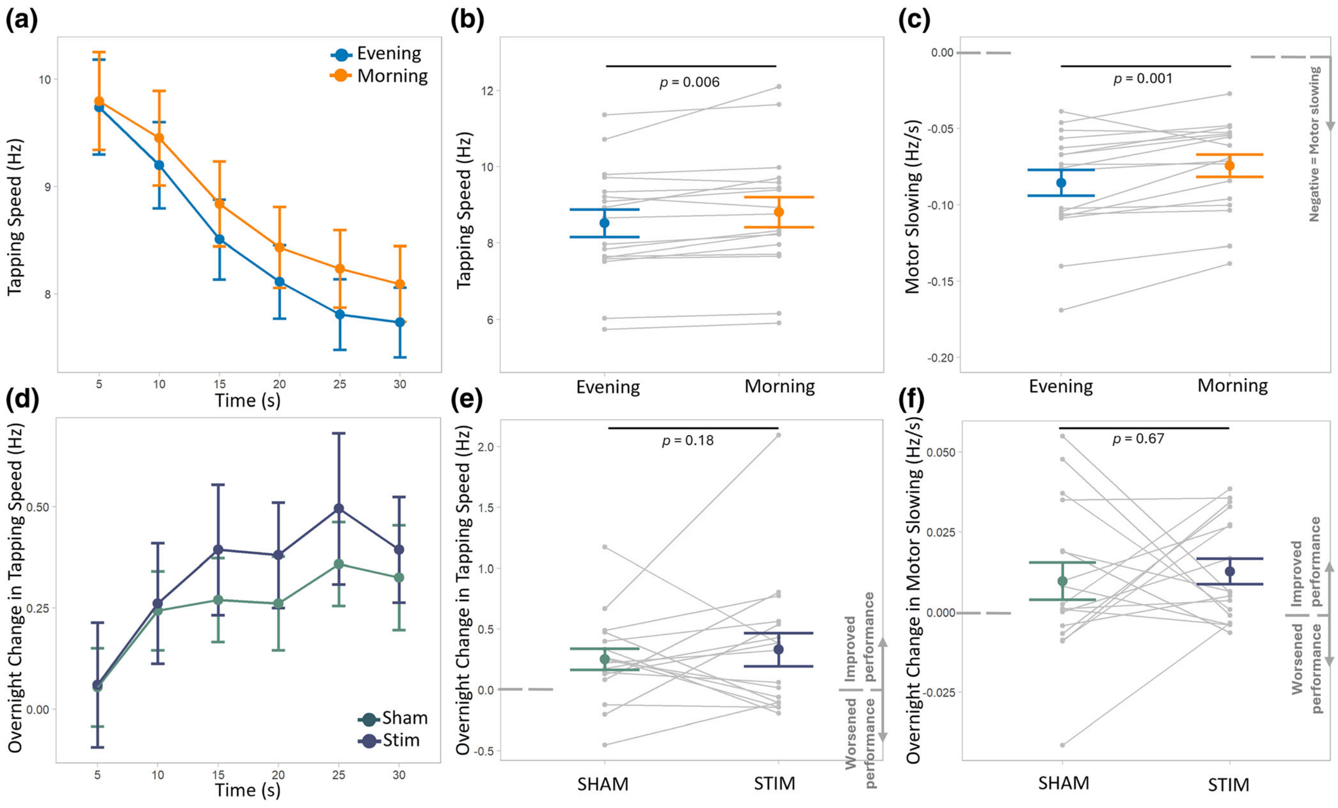

FIGURE 2 Overnight change in motor performance. (a) Time course of tapping speed averaged across participants and in 5 s bins for the evening tapping block (blue) and the morning tapping block (orange). Average speed (b) and slowing (c) in the evening versus the morning. (d) Time course of overnight change in speed averaged across participants and in 5 s bins for the sham condition (green) and the stim condition (blue). Average overnight change in speed (e) and slowing (f) for the sham versus the stim condition. All data are presented as mean ± standard error of the mean of 17 participants. The data of each participant are depicted in grey.

removing line-noise, robust average referencing, and bad channel interpolation using the PREP pipeline (Bigdely-Shamlo et al., 2015). Sleep was visually scored in 20 s epochs and reported previously (Huwiler et al., 2023). The power spectral density in the frequency range of slow wave (1–2 Hz) (Fattinger et al., 2017), slow sigma (9–12.5 Hz), and fast sigma (12.5–16 Hz) (Cox et al., 2017) was used to calculate the activity of each band. The power spectral densities (PSD) in the frequency bands of interest were computed by applying a fast Fourier transform using the MATLAB *pwelch* function. This was performed with a Hanning window duration of 4 s and 50% overlap (Huwiler et al., 2022). Windowed stimulation effects in sigma and slow wave activity induced by stimulation condition were defined as the difference in activity during the 10 s of stimulation (ON period) when compared with the subsequent 10 s (OFF period). In addition, overall stimulation effects of NREM in sigma and slow wave activity were determined by averaging the activity during NREM2 and NREM3 stages together. We then focussed on a cluster of electrodes covering sensorimotor areas affected during performance fatigability (Bächinger et al., 2019; Heimhofer et al., 2024). This includes the C3 electrode and its six surrounding electrodes (C3 cluster).

2.4 | Statistical analysis

Statistical analyses of behavioural data were conducted in R (v 3.6.3; R Core Team, Vienna, Austria). Using the R packages lme4 (Bates et al., 2015) and lmertest (Kuznetsova et al., 2017), we computed linear mixed-effects models with an overnight change in tapping speed and an overnight change in motor slowing as outcome variables, with fixed factors set to time bins within trial or to stimulation condition. Random factors were set to time bins within trial and participant. We derived t-values using the Satterwhaite method of the package lmerTest (Kuznetsova et al., 2017). For the NASA-TLX analysis, both the average score across dimensions and the score for the physical demand dimensions were set as outcome measures, with fixed factors set to time of day and stimulation condition, and with random factors set to participant.

Cluster-based permutation t-tests implemented in FieldTrip (Oostenveld et al., 2011) were performed to assess overall stimulation effects of NREM (Figure 3a–c) and windowed stimulation effects (ON–OFF periods, Figure S1a–c) in slow wave and sigma activity, while controlling for multiple comparisons across electrodes. The minimum distance between electrodes was set to 4 cm (average 6.2

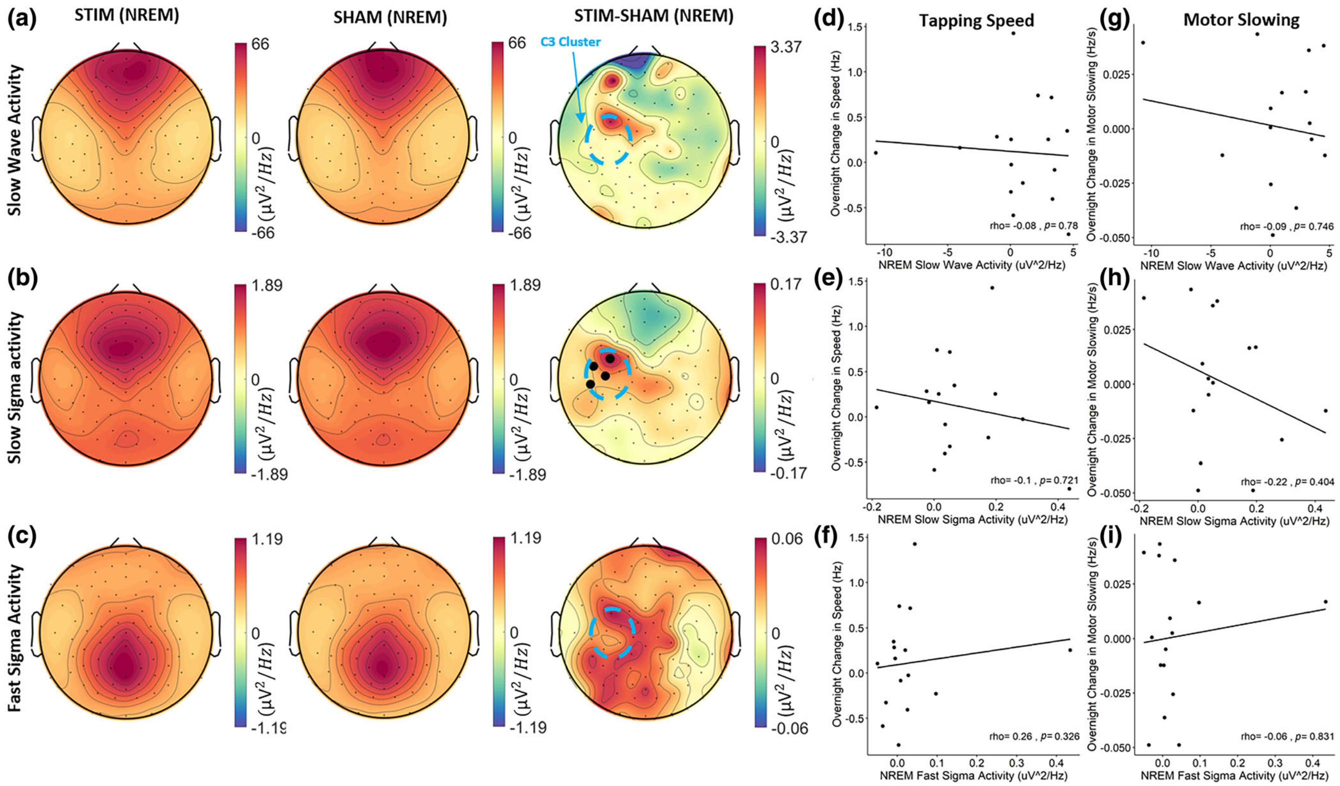

FIGURE 3 NREM slow wave and sigma activity across stimulation conditions and its link to motor performance. (a–c) Topographical distribution of the NREM activity for slow wave (a: 1–2 Hz), slow sigma (b: 9–12.5 Hz), and fast sigma (c: 12.5–16 Hz). The left topoplot shows the stim condition, the middle topoplot shows the sham condition, and the right topoplot is their difference with the electrodes around C3 highlighted in blue. For the right panel only, highlighted dots indicate significant differences ($p < 0.05$) in the windowed stimulation effects between stim and sham. Values of p were calculated applying linear-mixed effects models with condition entered as the fixed factor and participant as the random factor compared with the sham condition. p-values for each topoplot in the right panel have been corrected for multiple comparisons by applying cluster-based correction. (d–i) Spearman correlations between the overnight change in tapping speed (d–f) and motor slowing (g–i) versus the average activity in the C3 cluster of electrodes for slow wave (d, g), slow sigma (e, h), and fast sigma (f, i). The black dots represent each individual participant. $N = 17$ participants for a–c and $N = 16$ for d–i.

neighbours per channel) and the condition labels were randomly shuffled 1000 times with maximum cluster-level statistics being retained for each permutation.

Since motor performance and slow wave activity as well as fast and slow sigma activity values significantly deviated from normal distribution (revealed by Shapiro–Wilk tests $p < 0.05$), we correlated motor performance and activity in the three frequency bands across participants using Spearman rho correlation coefficients implemented in R using the R base function *cor.test* (Figures 3d–f and S1d–f). Values of p <0.05 were considered significant. Plots were generated using the R package ggplot2 (Wickham, 2016) and MATLAB. Where applicable, tapping speed or motor slowing values, and NASA-TLX scores reported in the main body of text are in the format mean ± standard error of the mean.

3 | RESULTS

The tapping speed significantly decreased over the 30 s tapping period for both the morning and the evening session (Figure 2a, t(67) = 3.35, $p < 0.01$). The average speed over the 30 s was higher in the morning compared with the evening (Figure 2B, t(16) = 3.15, $p < 0.01$). Also, the motor slowing during the 30 s trial was significantly reduced in the morning (Figure 2c, t(67.12) = 3.35, $p < 0.01$). To investigate whether this overnight improvement in motor performance was influenced by NREM sleep, we compared the overnight change in tapping speed and motor slowing between the auditory stimulation night and the sham night. Both after the stim night and the sham night overnight improvements were observed by means of faster speed and less slowing observed in the morning compared with the evening (Figure 2d–f). Even though overnight changes in motor performance were descriptively greater after the stim night than after the sham night, the auditory stimulation condition did not significantly influence overnight changes in tapping speed (Figure 2e, t(186) = 1.35, $p = 0.18$), and motor slowing (Figure 2f, t(32) = 0.43, $p = 0.67$).

Furthermore, the participant's perceived task workload was assessed using the overall NASA-TLX workload, calculated as the average of the six dimensions, where higher scores indicate higher perceived workload. Participants reported lower scores in the morning

(38.75 ± 2.61) relative to the evening (44.07 ± 2.66), as indicated by a significant effect observed for the time of day ($F(1,54) = 13.19$, $p < 0.001$). However, there was no significant effect observed for stimulation condition ($F(1,54) = 0.0002$, $p = 0.99$). As our finger tapping task is designed to assess performance fatigability, the participant's response to physical demand may be the NASA-TLX dimension that best reflects their perception of fatigue. Lower physical demand scores were reported in the morning (56.03 ± 4.70) when compared with the evening (63.91 ± 4.11), as indicated by a significant effect for the time of day ($F(1,54) = 5.28$, $p < 0.03$) but not the stimulation condition ($F(1,54) = 1.40$, $p = 0.24$).

We first profiled the topography of the windowed stimulation effects in slow wave and sigma activity, defined as the difference in activity during the 10 s of stimulation (ON period) when compared with the subsequent 10 s (OFF period). As shown in previous studies, auditory stimulation significantly and globally enhanced the difference between the ON and the OFF period in slow wave, slow sigma, and fast sigma activity during times of auditory stimulation when compared with sham (Figure S1a–c right panel). As reported previously by Huwiler et al., our auditory stimulation protocol enhanced the windowed stimulation effect in slow wave activity, particularly over frontal areas, during times of stimulation when compared with sham (Figure S1a right panel) (Huwiler et al., 2023). Interestingly, slow sigma power was particularly enhanced in frontocentral areas whereas the enhancement in fast sigma power was most pronounced in parietal areas (Figure S1b,c right panel). When comparing the stim night with the sham night, the difference in windowed stimulation effects in neither slow wave, slow sigma, nor fast sigma over the C3 cluster was associated with neither an increased overnight improvement in finger tapping speed ($|\text{rho}| < =0.47$, $p > =0.068$, Figure S1d–f) nor reduced motor slowing ($|\text{rho}| < =0.31$, $p > =0.25$, Figure S1g–i). Noticeably, there was the tendency that a smaller windowed stimulation effect in slow sigma activity in the C3 cluster during auditory stimulation versus sham was associated with stronger overnight improvement in speed ($\text{rho} = -0.47$, $p = 0.068$, Figure S1e) but not with reduced slowing ($\text{rho} =0.06$, $p = 0.822$, Figure S1f).

Next, we investigated whether auditory stimulation modulated slow wave (1–2 Hz), slow sigma (9–12.5 Hz), and fast sigma (12.5–16 Hz) activity (in $\mu V^2/Hz$) during the entire NREM sleep and whether individual differences in NREM sleep characteristics could account for the overnight improvement in motor performance. The overall stimulation effect on slow wave and fast sigma activity during all averaged NREM sleep epochs were not significantly different between conditions (Figure 3a,c right panel). Interestingly, NREM slow sigma activity in electrodes proximal to the left primary motor cortex exhibited higher levels during the stim night, despite our auditory stimulation protocol primarily targeting the slow oscillations of a frontal electrode. As motor slowing has been associated with a release of inhibition in sensorimotor areas (Bächinger et al., 2019), we tested whether NREM activity in C3 and its surrounding electrodes (C3 cluster) could influence overnight changes in motor performance. When comparing the stim night with the sham night, the difference in NREM activity in neither slow wave, slow sigma, nor fast sigma over the C3 cluster was associated with overnight improvement in finger tapping speed ($|\text{rho}| < =0.26$, $p > =0.33$, Figure 3d–f) or reduced motor slowing ($|\text{rho}| < =0.22$, $p > =0.40$, Figure 3g–i).

4 | DISCUSSION

In the present study, we investigated overnight changes in tapping speed and resistance against performance fatigability via a finger tapping task and whether these changes are functionally influenced by enhanced NREM sleep oscillations using auditory stimulation. We found an overnight increase in average tapping speed, less motor slowing, and lower perceived workload (Figure 2b,c). However, modulating cortical NREM oscillations via auditory stimulation did not lead to significantly greater speed or resistance against fatigability when compared with sham.

Optimal performance and skill learning have been shown to vary with time since awakening, diurnal variations, and sleep, but little is known about changes in motor fatigability (Della-Maggiore, 2005; Facer-Childs & Brandstaetter, 2015; Walker et al., 2003). Magnuson et al. recently found that acute sleep deprivation led to greater perceived fatigue when performing an isometric force production task without significantly affecting performance fatigability measures compared with a normal night's sleep (Magnuson et al., 2023). This study highlights critical discrepancies between perceived fatigue and performance fatigability after sleep deprivation. However, in isometric tasks, fatigability measures are heavily influenced by neuromuscular mechanisms. Fast repetitive tasks, by contrast, are primarily affected by supraspinal fatigability mechanisms. Our findings indicate that the physical demand of the tapping task was perceived to be lower in the morning than in the evening but also that there was less objectively measured motor fatigability, i.e. less motor slowing. Even though we investigated two-finger tapping in the present study, motor slowing has been equally demonstrated for sequence tapping (Bächinger et al., 2019). As such, our result is also relevant for studies that have reported sleep-related improvements in motor memory consolidation in 30 s sequence tapping tasks (Nishida & Walker, 2007; Walker et al., 2002). Tapping a motor sequence for 30 s is among the most frequently used tasks to describe and investigate sleep-related motor memory consolidation and performance is usually quantified by indices that consider tapping speed and often also accuracy. However, our findings indicate that overnight changes in this task might, at least partly, have been driven by a reduction in motor slowing, reflecting changes in motor fatigability rather than motor learning. This aligns with a previous study where it was reported that a 10 s sequence tapping task, which induces significantly less fatigability than one lasting 30 s, led to markedly reduced off-line gains compared with 30 s tapping, further questioning the direct association of improved overnight task performance with motor learning (Rickard et al., 2008).

In many daily activities, such as typing on a keyboard, playing musical instruments, and rehabilitation, enhancing the timing and accuracy of our movements can be as crucial as improving speed. To better understand how sleep influences our ability to learn these motor sequences, it is important to also use performance measures and tasks that account for timing and accuracy while controlling for the effects of speed. For instance, Antony et al. explored sleep-related motor skill enhancements through a sequence tapping task devoid of maximal tapping speed, employing a performance score focussed on timing and accuracy (Antony et al., 2012). The authors reported post-sleep improvements correlating with increased slow wave sleep duration when comparing pre- and post-nap scores, suggesting improved motor sequence learning with marginal tapping speed confounds (Antony et al., 2012). In summary, designing finger tapping tasks to have marginal fatigability or that are not dependent on tapping at maximum speed may provide further evidence of the sleep-related mechanisms involved in motor learning.

The primary non-invasive approach to investigate sleep's functional role in cognition and physiology is modulating sleep oscillations using auditory stimulation (Jaramillo et al., 2024; Ngo et al., 2013; Tononi et al., 2010). We first tested whether our auditory stimulation condition successfully modulated slow wave and sigma activity. When compared with sham, auditory stimulation globally increased slow wave activity during the stimulation window versus the 10 s window after (Figure 2e,f, Figure S1a). However, whole-night slow wave activity was not significantly enhanced during auditory stimulation compared with sham (Figure 3a). This may explain why overnight improvements in motor performance were not significantly enhanced with auditory stimulation compared with sham (Figure 2e,f). Moreover, the degree to which auditory stimulation individually modulated whole-night and windowed slow-wave activity did not correlate with motor performance improvements (Figure 3d,g, Figure S1d,g). This further emphasises that changes in tapping speed and performance fatigability may not be related to NREM sleep oscillations. Auditory stimulation studies typically report a redistribution in slow wave activity (windowed effect) rather than an enhancement across the whole night (whole-night effect). This redistribution was sufficient to lead to improved declarative memory consolidation (Ngo et al., 2013; Papalambros et al., 2017, 2019), cardiac function (Huwiler et al., 2023), and immune supportive function (Besedovsky et al., 2017). In another auditory stimulation study using electrodes near motor areas instead, the efficiency in executing motor movements decreased (more specifically sequence tapping variability increased) when slow waves near those motor areas were suppressed for the whole night (Fattinger et al., 2017). Therefore, stimulation protocols that significantly increase the amount of slow waves at sensorimotor and premotor areas across the entire night may modulate the cortical networks driving motor performance or the resilience to performance fatigability.

For sleep-related performance changes in motor memory consolidation, sigma activity, for example, enhanced by transcranial alternating current stimulation (Lustenberger et al., 2016) or olfactory stimulation (Laventure et al., 2016), has been observed to play an important role. This is despite mixed results from other studies investigating the effects of enhancing slow waves and spindles using auditory stimulation in motor sequence learning tasks (Baxter et al., 2023; Choi et al., 2019; Choi & Jun, 2022). Here, we investigated whether sigma activity could be involved in the observed overnight changes in tapping speed and performance fatigability. During times of stimulation (i.e., during stimulation windows compared with the 10s windows after stimulation), slow and fast sigma activity was increased when compared with sham. Such an increase in slow sigma was most prominent in frontal areas, where slow sigma activity is most endogenous. This pattern is similar to the topography of the slow wave enhancement we observed. Increases in fast sigma activity were most prominent in centroparietal areas, where natural fast sigma activity is most pronounced (Fernandez & Lüthi, 2020). These results suggest that auditory stimulation amplifies slow wave and sigma activity particularly in areas where they are most endogenous, at least when directly comparing time windows of stimulation with directly following windows without stimulation. However, previous studies have successfully used auditory stimulation to alter slow wave activity in regions where slow waves are less endogenous (Fattinger et al., 2017; Krugliakova et al., 2020). Despite targeting frontal regions, we found increased slow sigma activity across the night during auditory stimulation when compared with sham in a cluster of electrodes covering sensorimotor areas affected during performance fatigability (Bächinger et al., 2019; Heimhofer et al., 2024). This supports the use of auditory stimulation to increase sigma activity in regions affected by motor slowing. However, the degree to which auditory stimulation increased slow sigma activity in this cluster of electrodes across the night as well as during time windows of stimulation did not significantly correlate with motor performance improvements (Figure 3e,h, Figure S1e,h).

To summarise, motor performance components devoid of learning components and reflecting pure motor output (tapping speed and performance fatigability) are improved after a night of sleep. However, these overnight improvements are not explained by changes in NREM sleep oscillations (slow wave and sleep spindles). Thus, our study revealed no evidence that NREM sleep is causally involved in overnight changes in these components of motor performance. Concretely, auditory stimulation led to a global increase in slow wave and sigma activity during time windows of auditory stimulation, as well as a local increase in whole-night slow sigma activity in motor areas, but these changes in NREM oscillations were not correlated with either overnight changes in performance fatigability or tapping speed. However, other sleep factors that were not the focus of this study (e.g. REM sleep) cannot be excluded as potential influencers of these performance changes. Additionally, we cannot exclude the contribution of circadian and time-since-sleep effects to overnight motor performance improvement as we did not conduct the post-sleep tapping block at the same time of day as the pre-sleep tapping block.

Our findings shed light on how maximal tapping performance is sustained for longer and how the task is perceived to be less fatiguing after a night's sleep. In addition, they encourage future avenues in motor sequence learning to account for performance fatigability confounds, especially when investigating sleep-related effects. Understanding how sleep influences dynamic changes in fatigability can help to distinguish between sleep-induced motor learning and sleep-induced restoration of motor performance.

AUTHOR CONTRIBUTIONS

Manuel Carro-Domínguez: Conceptualization; software; investigation; formal analysis; project administration; writing – original draft; methodology; data curation; validation; visualization; writing – review and editing. **Stephanie Huwiler:** Conceptualization; software; investigation; formal analysis; project administration; methodology; data curation; writing – review and editing. **Fabia M. Stich:** Writing – review and editing; investigation. **Rossella Sala:** Writing – review and editing; investigation. **Florent Aziri:** Writing – review and editing; investigation. **Anna Trippel:** Writing – review and editing; investigation. **Caroline Heimhofer:** Writing – review and editing; methodology. **Reto Huber:** Writing – review and editing; project administration; conceptualization. **Sarah Nadine Meissner:** Writing – review and editing; writing – original draft; resources; project administration; funding acquisition; methodology; supervision; conceptualization. **Nicole Wenderoth:** Writing – review and editing; writing – original draft; resources; funding acquisition; project administration; methodology; supervision; conceptualization. **Caroline Lustenberger:** Writing – review and editing; writing – original draft; resources; funding acquisition; project administration; methodology; supervision; conceptualization.

ACKNOWLEDGEMENTS

All authors thank their trainees, collaborators, and mentors for the inspiring exchanges on the thematic of this article. The authors would like to express their gratefulness to all participants of the study. SleepLoop consortium members provided uncountable discussions and feedback. We are grateful to the Alumni Association of ETH Zurich for their support in participant recruitment for this study. Open access funding provided by Eidgenossische Technische Hochschule Zurich.

FUNDING INFORMATION

The corresponding author Caroline Lustenberger is supported by the Swiss National Science Foundation (PZ00P3_179795) and this work was conducted as part of the Hochschulmedizin Zürich Flagship project SleepLoop, ETH Zürich and University Zürich. Manuel Carro-Domínguez was supported by the Swiss National Science Foundation Grant 32003B_207719 and Nicole Wenderoth by the National Research Foundation, Prime Minister's Office, Singapore under its Campus for Research Excellence and Technological Enterprise (CREATE) programme (FHT). Reto Huber is supported by the Swiss National Science Foundation (320030_179443).

CONFLICT OF INTEREST STATEMENT

The authors have declared no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in ETH Zurich Research Collection, https://doi.org/10.3929/ethz-b-000698644.

ORCID

Manuel Carro-Domínguez https://orcid.org/0000-0003-2644-8594
Stephanie Huwiler https://orcid.org/0000-0001-8894-4871
Fabia M. Stich https://orcid.org/0000-0001-9692-845X
Florent Aziri https://orcid.org/0009-0003-9770-8864
Anna Trippel https://orcid.org/0000-0003-2104-083X
Caroline Heimhofer https://orcid.org/0009-0006-9591-8202
Reto Huber https://orcid.org/0000-0002-1400-9466
Sarah Nadine Meissner https://orcid.org/0000-0002-5957-7897
Nicole Wenderoth https://orcid.org/0000-0002-3246-9386
Caroline Lustenberger https://orcid.org/0000-0001-6243-8831

REFERENCES

Alessandrelli, G., Huwiler, S., Bernardi, G., Carro-Dominguez, M., Stich, F., Sala, R., Aziri, F., Trippel, A., Markendorf, S., Niederseer, D., Bohm, P., Cerveri, P., Siclari, F., Huber, R., Wenderoth, N., Schmied, C., & Lustenberger, C. (2024). Cardiovascular responses to natural and auditory evoked slow waves predict post-sleep cardiac function. *BioRxiv*, https://doi.org/10.1101/2024.05.03.592377

Anderer, P., Klösch, G., Gruber, G., Trenker, E., Pascual-Marqui, R. D., Zeitlhofer, J., Barbanoj, M. J., Rappelsberger, P., & Saletu, B. (2001). Low-resolution brain electromagnetic tomography revealed simultaneously active frontal and parietal sleep spindle sources in the human cortex. *Neuroscience*, *103*(3), 581–592.

Andrade, K. C., Spoormaker, V. I., Dresler, M., Wehrle, R., Holsboer, F., Sämann, P. G., & Czisch, M. (2011). Sleep spindles and hippocampal functional connectivity in human NREM sleep. *Journal of Neuroscience*, *31*(28), 10331–10339.

Antony, J. W., Gobel, E. W., O'hare, J. K., Reber, P. J., & Paller, K. A. (2012). Cued memory reactivation during sleep influences skill learning. *Nature Neuroscience*, *15*(8), 1114–1116.

Arias, P., Robles-Garc\'\ia, V., Corral-Bergantiños, Y., Madrid, A., Espinosa, N., Valls-Solé, J., Grieve, K. L., Oliviero, A., & Cudeiro, J. (2015). Central fatigue induced by short-lasting finger tapping and isometric tasks: A study of silent periods evoked at spinal and supraspinal levels. *Neuroscience*, *305*, 316–327.

Bächinger, M., Lehner, R., Thomas, F., Hanimann, S., Balsters, J., & Wenderoth, N. (2019). Human motor fatigability as evoked by repetitive movements results from a gradual breakdown of surround inhibition. *eLife*, *8*, 1–30. https://doi.org/10.7554/eLife.46750

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using the lme4. *Journal of Statistical Software*, *67*(1), 1–48.

Baxter, B. S., Mylonas, D., Kwok, K. S., Talbot, C. E., Patel, R., Zhu, L., Vangel, M., Stickgold, R., & Manoach, D. S. (2023). The effects of closed-loop auditory stimulation on sleep oscillatory dynamics in relation to motor procedural memory consolidation. *Sleep*, *46*(10), 1–14.

Besedovsky, L., Ngo, H.-V. V., Dimitrov, S., Gassenmaier, C., Lehmann, R., & Born, J. (2017). Auditory closed-loop stimulation of EEG slow oscillations strengthens sleep and signs of its immune-supportive function. *Nature Communications*, *8*(1), 1984.

Bigdely-Shamlo, N., Mullen, T., Kothe, C., Su, K.-M., & Robbins, K. A. (2015). The PREP pipeline: Standardized preprocessing for large-scale EEG analysis. *Frontiers in Neuroinformatics*, *9*, 16.

Boutin, A., Gabitov, E., Pinsard, B., Boré, A., Carrier, J., & Doyon, J. (2024). Temporal cluster-based organization of sleep spindles underlies motor memory consolidation. *Proceedings of the Royal Society B*, *291*(2014) 20231408.

Brass, S. D., Duquette, P., Proulx-Therrien, J., & Auerbach, S. (2010). Sleep disorders in patients with multiple sclerosis. *Sleep Medicine Reviews*, *14*(2), 121–129.

Choi, J., & Jun, S. C. (2022). Spindle-targeted acoustic stimulation may stabilize an ongoing nap. *Journal of Sleep Research*, *31*(6), e13583.

Choi, J., Won, K., & Jun, S. C. (2019). Acoustic stimulation following sleep spindle activity may enhance procedural memory consolidation during a nap. *IEEE Access*, *7*, 56297–56307.

Cox, R., Schapiro, A. C., Manoach, D. S., & Stickgold, R. (2017). Individual differences in frequency and topography of slow and fast sleep spindles. *Frontiers in Human Neuroscience*, *11*, 433.

Della-Maggiore, V. (2005). Motor memory consolidation, night and day. *Journal of Neuroscience*, *25*(40), 9067–9068.

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*(1), 9–21.

Facer-Childs, E., & Brandstaetter, R. (2015). The impact of circadian phenotype and time since awakening on diurnal performance in athletes. *Current Biology*, *25*(4), 518–522.

Fattinger, S., De Beukelaar, T. T., Ruddy, K. L., Volk, C., Heyse, N. C., Herbst, J. A., Hahnloser, R. H. R., Wenderoth, N., & Huber, R. (2017). Deep sleep maintains learning efficiency of the human brain. *Nature Communications*, *8*(May), 1–13. https://doi.org/10.1038/ncomms15405

Fernandez, L. M. J., & Lüthi, A. (2020). Sleep spindles: Mechanisms and functions. *Physiological Reviews*, *100*(2), 805–868. https://doi.org/10.1152/physrev.00042.2018

Frankland, P. W., & Bontempi, B. (2005). The organization of recent and remote memories. *Nature Reviews Neuroscience*, *6*(2), 119–130.

Hart, S. G., & Staveland, L. E. (1988). Development of NASA-TLX (task load index): Results of empirical and theoretical research. In *Advances in psychology* (Vol. 52, pp. 139–183). Elsevier.

Heimhofer, C., Bächinger, M., Lehner, R., Frässle, S., Balsters, J. H., & Wenderoth, N. (2024). Dynamic causal modelling highlights the importance of decreased self-inhibition of the sensorimotor cortex in motor fatigability. *Brain structure & function*. https://doi.org/10.1007/s00429-024-02840-1

Huwiler, S., Carro Dominguez, M., Huwyler, S., Kiener, L., Stich, F. M., Sala, R., Aziri, F., Trippel, A., Schmied, C., Huber, R., Wenderoth, N., & Lustenberger, C. (2022). Effects of auditory sleep modulation approaches on brain oscillatory and cardiovascular dynamics. *Sleep*, *45*(9), 1–18.

Huwiler, S., Carro-Domínguez, M., Stich, F. M., Sala, R., Aziri, F., Trippel, A., Ryf, T., Markendorf, S., Niederseer, D., Bohm, P., Stoll, G., Laubscher, L., Thevan, J., Spengler, C. M., Gawinecka, J., Osto, E., Huber, R., Wenderoth, N., Schmied, C., & Lustenberger, C. (2023). Auditory stimulation of sleep slow waves enhances left ventricular function in humans. *European Heart Journal*, *44*(40), 4288–4291.

Jaramillo, V., Hebron, H., Wong, S., Atzori, G., Bartsch, U., Dijk, D.-J., & Violante, I. R. (2024). Closed-loop auditory stimulation targeting alpha and theta oscillations during REM sleep induces phase-dependent power and frequency changes. *Sleep*. https://doi.org/10.1093/sleep/zsae193

Kluger, B. M., Krupp, L. B., & Enoka, R. M. (2013). Fatigue and fatigability in neurologic illnesses: Proposal for a unified taxonomy. *Neurology*, *80*(4), 409–416.

Krugliakova, E., Volk, C., Jaramillo, V., Sousouri, G., & Huber, R. (2020). Changes in cross-frequency coupling following closed-loop auditory stimulation in non-rapid eye movement sleep. *Scientific Reports*, *10*(1), 1–12. https://doi.org/10.1038/s41598-020-67392-w

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). {lmerTest} Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, *82*(13), 1–26. https://doi.org/10.18637/jss.v082.i13

Laventure, S., Fogel, S., Lungu, O., Albouy, G., Sévigny-Dupont, P., Vien, C., Sayour, C., Carrier, J., Benali, H., & Doyon, J. (2016). NREM2 and sleep spindles are instrumental to the consolidation of motor sequence memories. *PLoS Biology*, *14*(3), e1002429.

Lustenberger, C., Boyle, M. R., Alagapan, S., Mellin, J. M., Vaughn, B. V., & Fröhlich, F. (2016). Feedback-controlled transcranial alternating current stimulation reveals a functional role of sleep spindles in motor memory consolidation. *Current Biology*, *26*(16), 2127–2136.

Lustenberger, C., Ferster, M. L., Huwiler, S., Brogli, L., Werth, E., Huber, R., & Karlen, W. (2022). Auditory deep sleep stimulation in older adults at home: A randomized crossover trial. *Communications Medicine*, *2*(1), 1–16.

Madrid, A., Valls-Solé, J., Oliviero, A., Cudeiro, J., & Arias, P. (2016). Differential responses of spinal motoneurons to fatigue induced by short-lasting repetitive and isometric tasks. *Neuroscience*, *339*, 655–666.

Magnuson, J. R., Kang, H. J., Debenham, M. I. B., McNeil, C. J., & Dalton, B. H. (2023). Effects of sleep deprivation on perceived and performance fatigability in females: An exploratory study. *European Journal of Sport Science*, *23*(9), 1922–1931.

Manjaly, Z.-M., Harrison, N. A., Critchley, H. D., Do, C. T., Stefanics, G., Wenderoth, N., Lutterotti, A., Müller, A., & Stephan, K. E. (2019). Pathophysiological and cognitive mechanisms of fatigue in multiple sclerosis. *Journal of Neurology, Neurosurgery & Psychiatry*, *90*(6), 642–651.

Manshanden, I., De Munck, J. C., Simon, N. R., & da Silva, F. H. L. (2002). Source localization of MEG sleep spindles and the relation to sources of alpha band rhythms. *Clinical Neurophysiology*, *113*(12), 1937–1947.

Morin, A., Doyon, J., Dostie, V., Barakat, M., Hadj Tahar A., Korman M., Benali H., Karni A., Ungerleider, L.-G., Carrier, J. (2008). Motor sequence learning increases sleep spindles and fast frequencies in post-training sleep. *Sleep*, *31*(8), 1149–1156.

Ngo, H.-V. V., Martinetz, T., Born, J., & Mölle, M. (2013). Auditory closed-loop stimulation of the sleep slow oscillation enhances memory. *Neuron*, *78*(3), 545–553.

Nishida, M., & Walker, M. P. (2007). Daytime naps, motor memory consolidation and regionally specific sleep spindles. *PLoS One*, *2*(4), e341.

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, *2011*, 1–9.

Papalambros, N. A., Santostasi, G., Malkani, R. G., Braun, R., Weintraub, S., Paller, K. A., & Zee, P. C. (2017). Acoustic enhancement of sleep slow oscillations and concomitant memory improvement in older adults. *Frontiers in Human Neuroscience*, *11*, 247563.

Papalambros, N. A., Weintraub, S., Chen, T., Grimaldi, D., Santostasi, G., Paller, K. A., Zee, P. C., & Malkani, R. G. (2019). Acoustic enhancement of sleep slow oscillations in mild cognitive impairment. *Annals of Clinical and Translational Neurology*, *6*(7), 1191–1201.

Post, M., Steens, A., Renken, R., Maurits, N. M., & Zijdewind, I. (2009). Voluntary activation and cortical activity during a sustained maximal contraction: An fMRI study. *Human Brain Mapping*, *30*(3), 1014–1027.

Rickard, T. C., Cai, D. J., Rieth, C. A., Jones, J., & Ard, M. C. (2008). Sleep does not enhance motor sequence learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *34*(4), 834–842.

Rodrigues, J. P., Mastaglia, F. L., & Thickbroom, G. W. (2009). Rapid slowing of maximal finger movement rate: Fatigue of central motor control? *Experimental Brain Research*, *196*, 557–563.

Schabus, M., Dang-Vu, T. T., Albouy, G., Balteau, E., Boly, M., Carrier, J., Darsaud, A., Degueldre, C., Desseilles, M., Gais, S., Phillips, C., Rauchs, G., Schnakers, C., Sterpenich, V., Vandewalle, G., Luxen, A., & Maquet, P. (2007). Hemodynamic cerebral correlates of sleep spindles during human non-rapid eye movement sleep. *Proceedings of the National Academy of Sciences*, *104*(32), 13164–13169.

Siclari, F., Bernardi, G., Riedner, B. A., LaRocque, J. J., Benca, R. M., & Tononi, G. (2014). Two distinct synchronization processes in the transition to sleep: A high-density electroencephalographic study. *Sleep*, *37*(10), 1621–1637.

Sleep, A. G. D. H. (2010). Magnetoencephalography demonstrates multiple. *Journal of Neurophysiology*, *104*, 179–188.

Tononi, G., & Cirelli, C. (2014). Sleep and the Price of plasticity: From synaptic and cellular homeostasis to memory consolidation and integration. *Neuron*, *81*(1), 12–34. https://doi.org/10.1016/j.neuron.2013.12.025

Tononi, G., Riedner, B. A., Hulse, B. K., Ferrarelli, F., & Sarasso, S. (2010). Enhancing sleep slow waves with natural stimuli. *Medicamundi*, *54*(2), 73–79.

Walker, M. P., Brakefield, T., Morgan, A., Hobson, J. A., & Stickgold, R. (2002). Practice with sleep makes perfect: Sleep-dependent motor skill learning. *Neuron*, *35*(1), 205–211.

Walker, M. P., Brakefield, T., Seidman, J., Morgan, A., Hobson, J. A., & Stickgold, R. (2003). Sleep and the time course of motor skill learning. *Learning & Memory*, *10*(4), 275–284.

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag. https://ggplot2.tidyverse.org

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Carro-Domínguez, M., Huwiler, S., Stich, F. M., Sala, R., Aziri, F., Trippel, A., Heimhofer, C., Huber, R., Meissner, S. N., Wenderoth, N., & Lustenberger, C. (2025). Overnight changes in performance fatigability and their relationship to modulated deep sleep oscillations via auditory stimulation. *Journal of Sleep Research*, *34*(3), e14371. https://doi.org/10.1111/jsr.14371