Tactile vs Motor Imagery: the Effects on Corticospinal Excitability Assessed with single-pulse TMS

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Abstract

Tactile Imagery (TI) remains a fairly understudied phenomenon despite an increased attention to this topic in recent years. Here we investigated the effects of TI on corticospinal excitability by measuring motor evoked potentials (MEPs) induced by single-pulse transcranial magnetic stimulation (TMS). The effects of TI were compared with those of tactile stimulation (TS) and kinesthetic motor imagery (kMI). Twenty two participants were asked to perform three tasks in random order: imagine finger tapping (kMI); perceive vibration sensations on the middle finger (TS); and mentally reproduce these tactile sensations (TI). We found no statistically significant difference in MEP amplitudes between baseline and TS condition, whereas both TI and kMI facilitated corticospinal excitability. MEP amplitudes during TI were significantly lower compared to MEP amplitudes during kMI condition. This finding confirms the differential effects of TI and kMI on corticospinal excitability, which has practical implications for the development of imagery-based brain-computer interfaces (BCIs), particularly the ones intended to improve neurorehabilitation by evoking plastic changes in sensorimotor circuitry.

Significance Statement

While it is known that tactile imagery (TI) engages the primary somatosensory cortex activation similarly to the real tactile perception, it is still unknown what effect TI has on the primary motor cortex (M1). This study employed transcranial magnetic stimulation (TMS) to examine the excitability of M1 during different modalities of somatosensory imagery. It was found that TI facilitates M1 activity but to a significantly lesser extent compared to kinesthetic motor imagery (kMI). There is evidence for the distinct effects of TI and kMI on M1, suggesting that various imagery strategies lead to differing cortical representations within sensorimotor cortex areas. These findings have practical implications for the development of imagery-based brain-computer interfaces (BCIs) for neurorehabilitation of sensorimotor impairments.

Introduction

Kinesthetic and tactile imagery are subdomains of the mental imagery, a simple but practically significant mental endeavor where actions and perceptions are imagined but not performed overtly. Most of us can effortlessly imagine actions like playing the piano. This kind of motor imagery has both visual and kinesthetic components, that is the movements are not only imagined as being seen but also felt as movements of body parts and muscle contractions. The latter component, which we refer to as kinesthetic motor imagery (kMI) is associated with activation of the same neural structures that participate in the control of overt motor activity (1–3). KI is used in sports as a way to rehearse and improve motor performance (4). Additionally, kMI is utilized as therapy (5) and a neurorehabilitation approach (6).

By contrast to kMI which has been studied for decades, a somewhat different type of somatosensory imagery which we call tactile imagery (TI) received little attention. In TI,

subjects imagine experiencing sensations arising from the skin receptors, such as being touched with a brush or stimulated with a vibrating probe. We assert that distinction between kMI and TI is important because kinesthetic and tactile imagery engage different types of somatosensory modalities (proprioceptive versus cutaneous) as well as incorporating different types of actions (self-initiated movements versus passive application of stimuli). Indeed, kMI involves a mental enactment of kinesthetic sensations resulting from voluntary movements (muscle contraction, joint position, tendons tension, *etc.*) and in some versions the sense of body position (2,7–9) while TI is about perceiving touch in a particular location on the skin surface (10–12). Unsurprisingly, TI specifically activates the primary somatosensory cortex (10,11,13,14), as well as the areas subserving the act of mentally imagery, namely the prefrontal cortex (11) and parietal cortex (15). TI-induced cortical activities can be revealed using electroencephalographic (EEG) recordings, where event related desynchronization (ERD) of the mu rhythm is the most prominent effect (12,16,17).

While EEG recordings are useful to study kMI and TI and numerous applications have emerged in the BCI field (16,18–20), EEG alone does not tell the whole story (21,22) and additional methods that probe neural effects of imagery are useful for both gaining understanding of brain mechanisms and developing practical BCI applications. Here we employed transcranial magnetic stimulation (TMS) to assess changes in corticospinal excitability induced by different types of imagery. Corticospinal excitability, measured using TMS, is known to change during the performance of sensorimotor related tasks such as kMI and action observation (7,23–26), which makes TMS an appropriate tool to study the effects of TI, as well. Previously, kMI and TI induced changes in spinal excitability were assessed using F-wave measurements (27).

In the present study, we applied vibrotactile stimuli to the participants' fingertips (i.e. tactile stimulation, TS) or asked the same people to imagine these sensations (TI) or imagine performing finger taps (kMI). During the performance of these tasks, TMS was applied to the contralateral motor cortex, which resulted in motor-evoked potentials (MEPs) in the forearm and hand muscles. We found that the MEP differed depending on the stimulation/imagery conditions. Namely, MEPs were stronger during kMI than during TI, which suggests that although both types of imagery belong to the somatosensory domain, their effects on corticospinal excitability are quite specific, particularly in the way the projections from the motor cortex to the spinal cord are affected.

Methods

Participants

Twenty two healthy right-handed volunteers (4 females and 18 males, age=24.5±3.3 years.; mean±standard deviation) participated in the study. The participants had 6–9 hr of sleep prior to the TMS procedure, no alcohol or medication 24 hr before the procedure, and no coffee intake in the preceding 2 hr. All subjects were screened for contraindications to TMS (28). Experimental protocol was approved by the Institutional Review Board of the

Skolkovo Institute of Science and Technology and followed by the Declaration of Helsinki. All participants gave their informed consent to get involved in the study.

Experimental Design

Participants sat comfortably in an armchair with their eyes open. They were instructed to keep their hands relaxed. Throughout the experiment, we monitored the EMG activity and asked participants to relax their hands if any muscle contraction was detected. We avoided TMS application during the periods of increased EMG activity. During the experimental conditions, participants were asked to fix their gaze on the fixation cross shown on the television screen (Samsung 46″ TV, South Korea) that was placed at a distance of 2.5 m in front of the participant. Firstly, *m. flexor digitorum superficialis* (FDS) hotspot was found. Next, a resting motor threshold (RMT) was determined with the Nexstim built-in threshold determination system. TMS pulses were delivered over the FDS hotspot at 110% RMT intensity.

An experimental session comprised three experimental conditions: tactile stimulation (TS), tactile imagery (TI) and kinaesthetic motor imagery (kMI). Each condition consisted of up to 40 trials lasting about 5–8 seconds with interstimulus intervals lasting for 3 s. During each trial, from 1 to 3 TMS pulses were applied at random times. Eighty TMS pulses were applied for each experimental condition in total (Fig. 1A).

Figure 1. Experimental design. **A.** Schematics of task sequence. Baseline resting state MEP measurements were made before and after the main experimental conditions (TS, kMI and TI) performed in separate runs (recordings). TS, kMI and TI runs were randomly intermixed for each subject. Active 5-8 s trials of each run were followed by resting state 3 s trials. The total number of MEPs for each condition in active trials was n=80. **B.** Placement of EMG electrodes and vibratory motors on the forearm and hand.

During the TS task, participants were asked to pay attention to the skin sensations arising from the vibration applied to the base of the middle finger. The participants were instructed to fix their gaze on the fixation cross and not to look at the hand.

During the TI task, participants were asked to mentally reproduce the sensations experienced during the vibrotactile stimulation (12,17). Before the TI trials, participants were also acquainted with the tactile sensations produced by stimulation with a brush of the proximal parts of index, middle, ring and little fingers and distal part of the palm. We instructed the participants that they had to imagine tactile sensation as emerging from these skin locations.

During the kMI task, participants were instructed to mentally generate the kinesthetic sensations associated with performing finger movements. The finger movements consisted of flexions and extensions at the metacarpophalangeal joint − an action referred to as finger tapping. We chose this specific type of movement based on our previous results, where participants learned it with ease and comfortably performed it repetitively (21,22). Prior to the kMI run, participants were first trained to execute these finger movements correctly, ensuring they achieved the full range of motion and demonstrated appropriate speed. They performed the movements at various speeds and executed isometric contractions, as well. The participants were instructed to memorize the kinesthetic sensations associated with various aspects and phases of the movement, including muscle contraction, tendon tension, and joint position. The imagined finger movements were to be performed sequentially in a random order (22). The duration and complexity of TI and kMI training before the corresponding TMS sessions were approximately equal.

The order of TS, TI and kMI conditions was randomized for each subject . The start of each trial was initiated by verbal audio cues, with the word "imagine" instructing the imagery conditions (kMI and TI) and the word "feel/perceive" instructing the TS condition. The end of each trial was indicated by a beep sound, occurring between 5 to 8 s after the trial started. The experimenter vocally specified imagery type (kMI or TI) before the start of the run.

In addition to the stimulation and imagery conditions, two baseline resting state runs were recorded, in the beginning and at the end of the experimental session, with 80 TMS pulses applied in each of these runs. During the baseline recordings, the participants fixed their gaze at the fixation cross, relaxed and avoided performing movements.

EMG

Surface EMG recordings were conducted using bipolar probes from the right *m. flexor digitorum superficialis* (FDS), *m. first dorsal interosseous* (FDI) and *m. abductor digiti minimi* (ADM) muscles. The active electrode was placed over the muscle belly, the reference electrode over the tendons distally, and the ground one was located on the wrist of the

opposite (left) hand (Fig. 1B). EMG data were sampled at 3 kHz using the built-in Nexstim EMG system (Nexstim Ltd., Helsinki, Finland).

TMS

Single-pulse, biphasic TMS was applied to the left primary motor cortex (M1) using a cooling co-planar figure-of-eight induction coil (d=70 mm; Nextim Ltd., Finland) connected to an eXimia magnetic stimulator (Nexstim Ltd., Finland, version 3.2.2). An eXimia NBS navigation system (Nexstim Ltd., Finland) was used for MRI-guided navigation. The optimal coil position and stimulation site to induce MEPs in the FDS muscle (FDS-hotspot) were estimated as the position in which MEPs recorded from the FDS had maximal amplitude for suprathreshold stimulation intensity. The resting motor threshold (RMT) was determined as the minimal stimulation intensity (% of the maximum stimulation output) needed to elicit peak-to-peak MEP amplitudes from the FDS muscle above 50 μV in 50% of cases (29,30). In all experimental conditions, stimulation intensity was 110% of RMT. During all interventions, coil orientation and stimulation parameters were fixed and controlled using Nexstim software. Coil tracker accuracy measurements were in the ranges of ±2 mm (3D rms error) and ±2°.

Vibrotactile stimulation

For TS, we used a custom designed vibrotactile stimulator based on Arduino UNO (Arduino, Italy) synced with stimulus presentation software. A flat vibratory motor (d=6 mm; max speed of 12.000 rpm) was placed on the middle finger of the right hand. Variable-frequency stimulation patterns were used: stimulation was delivered as 100-ms pulses with vibratory frequency selected in the range 3.000-12.000 rpm, with the inter-pulse intervals varying in the range 200-400 ms. This random stimulation pattern was used to reduce tactile habituation and residual tactile sensations (12,17).

Data Analysis

To analyze the data, we first split the EMG records into the epochs with the timing of -0.5 to 0.1 s relative to the occurrence of the TMS pulse. These epochs were then baseline corrected by subtracting the mean of -0.5 to 0 seconds temporal window.

Next, we calculated the peak-to-peak EMG amplitude for each MEP epoch by taking the difference between the maximum and minimum values within the 10 to 50 ms temporal window since the stimuli onset. We then calculated the median MEP peak-to-peak amplitude for each participant in each condition (baselines, kMI, TI, TS).

To account for inter-individual variability, we percent normalized the peak-to-peak amplitudes at the median of the baseline before experimental conditions using the formula:

$$\frac{amplitude_{condition} - amplitude_{baseline}}{amplitude_{baseline}} \cdot 100\%$$

It is important to note that these percent changes of peak-to-peak amplitudes were centered around zero, with positive values indicating an increase and negative values indicating a decrease in MEP amplitudes (Fig. 2). For pairwise comparisons of the resulting normalized median peak-to-peak amplitudes across participants, we employed the Wilcoxon

signed rank test for paired samples. To assess the across-participants correlations between MEP amplitudes in different conditions, we used Spearman's rank correlation coefficient.

Figure 2. Individual median MEPs (measured relative to the median MEP at rest) for each of 19 participants for the kMI, TI and TS conditions. Color of each square represents the percent change from the reference. Data are shown for 3 muscles: FDS, FDI and ADM.

Additionally, we used a one-sample Wilcoxon test to determine whether the normalized median peak-to-peak amplitudes were different from zero. This test helped us determine if there were significant changes in amplitude compared to the baseline.

We excluded three participants who exhibited a significant decrease in MEP amplitudes during kMI compared to the initial baseline MEP level. This exclusion was necessary to ensure the validity of our analysis.

Results

General changes in MEP amplitudes

Using Wilcoxon signed rank test for paired samples, we compared the baseline-normalized MEP amplitudes during kMI, TI and TS condition for each muscle (Fig. 3A, Fig. 3B). We found a statistically significant increase in MEP amplitude for the FDS muscle during kMI as compared to the TI and TS conditions ($W_{kMI-TI} = 31$, $p_{kMI-TI} = 0.0082$; $W_{kMI-TS} = 2$, $p_{MI-TS} < 0.0001$). MEP amplitudes for the FDS muscle were statistically significantly greater during kMI than during TS ($W = 25$, $p = 0.0033$). We noticed a similar tendency for the MEP amplitudes being greater during kMI than during TS in the other two recorded muscles (FDI, ADM), with several statistically significant effects. Namely, the FDI response was stronger during kMI and TI than during TS ($W_{kMI-TI} = 44$, $p_{kMI-TI} = 0.0401$; $W_{kMI-TS} = 29$, $p_{kMI-TS} = 0.0062$), and the ADM muscle response was stronger during kMI than

during TI ($W = 35$, $p = 0.014$). Using a one-sample Wilcoxon test, we compared normalized MEP amplitudes during kMI, TI, TS and the final baseline with zero. Normalized MEP amplitudes during kMI, TI and baseline after were statistically significantly greater from zero for each muscle, including FDS ($W_{kMI} = 0$, $p_{kMI} < 0.0001$; $W_{TI} = 32$, $p_{TI} = 0.0095$; $W_{baseline\ after} = 30$, $p_{baseline\ after} = 0.0071$), FDI ($W_{kMI} = 7$, $p_{kMI} < 0.0001$; $W_{TI} = 29$, $p_{TI} = 0.0062$; $W_{baseline\ after} = 24$, $p_{baseline\ after} = 0.0028$), ADM ($W_{kMI} = 3$, $p_{kMI} < 0.0001$; $W_{TI} = 31$, $p_{TI} = 0.0082$; $W_{baseline\ after} = 43$, $p_{baseline\ after} = 0.0361$). Additionally, we found a statistically significant correlation between MEP amplitudes during the kMI and TI conditions for the FDS and FDI muscles (Spearman's correlation coefficient, $r_{S,\ FDS} = 0.71$, $p_{FDS} = 0.0006$; $r_{S,\ FDI} = 0.65$, $p_{FDS} = 0.0025$).

Figure 3. An analysis of MEPs for different conditions. **A.** Normalized median peak-to-peak amplitudes for each condition. Data are shown for 3 muscles, Wilcoxon signed rank test for pairwise comparisons between

conditions among kMI, TI and TS conditions was used. Statistically significant differences are marked. **B.** Extracted motor evoked potentials of one of the participants, FDS muscle.

During the preparation for the TS session, we also asked participants about the intensity and distribution of vibrational sensations. According to the participants, the sensations of vibration were not localized to the stimulated finger but were also felt in the proximal parts of index, middle, ring and little fingers and in the distal part of the palm - the parts of the hand that were also engaged in the kMI task and located in proximity of the FDS muscle hotspot.

Baseline before and after the experimental session.

We found a statistically significant difference between median baseline MEP amplitudes before and after the experimental session for the FDS ($W = 30$, $p = 0.0071$) and FDI ($W = 36$, $p = 0.016$) muscles (Fig. 4). To avoid the influence of this posteffect, we used MEP amplitudes during the initial baseline measurement for percent normalization of kMI, TI, TS conditions. The data for the final baseline were normalized the same way.

Figure 4. Median peak-to-peak amplitudes of motor evoked potentials (MEPs) during the initial and last baselines for each muscle (*m. flexor digitorum superficialis*, FDS; *m. first dorsal interosseous*, FDI; *m. abductor digiti minimi*, ADM). Data for each participant are shown as dots. Wilcoxon signed rank test was used for pairwise comparisons where the amplitudes were compared during the initial and final baseline. Statistically significant differences are marked.

Discussion

In this study, we complemented the previous findings, where changes in EEG rhythms were found during TI (12,16,17), with the demonstration that TI effects on the TMS-evoked responses in the forearm and hand muscles were different from those of kMI and TS.

Consistent with the previous reports (7,23,24,31), we detected a statistically significant increase in MEP amplitudes during kMI. Accordingly, in the present study, the

kMI condition served as a useful control for the evaluation of the participants ability to imagine body sensations.

The lowest MEP amplitude was observed for the TS condition, as was evident from the responses of the FDS and FDI muscles (Fig. 2, Fig. 3). The strongest effect for the FDS and FDI muscles corresponds to the location of vibratory sensations, which participants reported were concentrated in the index, middle, and ring fingers, i.e., the fingers moved by these very muscles. Although MEPs were lower during the TS condition as compared to the imagery conditions, no decrease was found compared to the baseline, which indicates that the best description of the contribution of TS is "no effect". However, TS parameters could be adjusted to inhibit MEPs. Thus, in the experiments of Tokimura et al. (32) peripheral nerve stimulation weakend MEP when TMS pulse and nerve stimulation were timed to nearly coincide within the motor cortex. This circuit called short-latency afferent inhibition (SAI) resides within the sensorimotor cortex. Additionally, in an experimental paradigm that was similar to ours, Oda et al. (33) showed that TS of the right middle fingertip suppressed MEPs in the right FDI. The authors explained this finding in terms of muscle-specific surround inhibition, or sensorimotor gating, where cortical areas representing non-stimulated skin are inhibited to enhance the processing of the peripheral input. Furthermore, Kojima et al. (34) showed that TS can modulate corticospinal excitability and that its effects also depend on stimulation patterns. Finally, Tanaka et al. (35) reported the findings similar to our present results: TS applied to the first and second digits did not have an effect on the MEP amplitude in the FDI and ADM. It seems reasonable to suggest that TMS timing with respect to TS onset and its latency are important for MEP change to occur. If this timing is not optimized TS does not affect the MEP. The absence of the inhibition effect in our study is attributed to the stimulation patterns employed (100 ms vibrations with short random interstimulus interval, during 5-8 s trial), which result in an extended duration of contact between the subjects' skin and the vibrational motor. This prolonged contact duration subsequently reduces the chance of achieving a short time window after the cessation of stimulation during which SAI can affect MEPs. This likely accounts for the lack of a decrease in corticospinal excitability during TS in our work.

Our comparison of the effects of kMI and TI revealed that kMI significantly increased corticospinal excitability, while TI had only a slight effect. This observation, in which different imagery strategies affect corticospinal excitability to varying degrees, aligns with previous findings that indicated kMI was more effective in enhancing spinal excitability, as measured by F-wave characteristics (27). The modest yet statistically significant increase in MEPs during TI in our study could be linked to the attentional focus on imagery directed towards the hand, as supported by previous findings indicating that shifts in attention towards hand position can influence MEPs (36).

We found a strong across-subject correlation between the MEP amplitudes during kMI and TI. We suggest that this finding may be related to the imagery content used in the task. Given that actual vibration affects not only skin receptors but also muscle spindle afferents (37,38), the imagined sensations may also become intermixed, even though participants were instructed to base their mental images on the sensations felt on their skin. This could also depend on variations in imagery skills among participants, as some of them might tend to somewhat rely on kinesthetic imagery during the TI task.

Finally, we observed a statistically significant difference between the baseline MEPs recorded in the beginning of the experiment and at its end (Fig. 4). It is well known that kMI training results in a sustained increase in motor cortex excitability (36), which could have been the case in our study, as well. We found a statistically significant difference only for the FDS and FDI, and those were the muscles mostly involved in the imagery tasks.

Despite the clear evidence provided by the results of the current study that different types of somatosensory imagery lead to distinct changes in corticospinal excitability, as measured by single-pulse TMS applied over the M1, it is important to acknowledge several limitations in our research.

First and foremost, the vibration stimulation utilized in this work has certain drawbacks. Given that vibration activates not only tactile but also proprioceptive inputs, it is challenging to entirely separate the impact of one perceptual subtype from the other, potentially leading to partially intermixed effects during imagery performance. To mitigate this disadvantage, different stimulation methods, including brush stimulation, von Frey filaments, and pressure-based tactile stimulators, should be employed.

Secondly, in our research, we assessed corticospinal excitability by measuring MEPs resulting from the application of a TMS coil to the M1. To draw stronger conclusions regarding the influence of tactile imagery on changes in corticospinal excitability, additional measures at both the cortical level (e.g., TMS-induced evoked potentials, TEPs; paired-pulse TMS) and the spinal level (e.g., cervical magnetic stimulation, H-reflex, F-wave) would enhance the results.

Lastly, for imagery research, additional psychometric measures could be conducted to estimate general imagery ability in different domains (e.g., visual, motor, tactile) using specialized scales.

Overall, our study has demonstrated that single-pulse TMS over the M1 is specific enough to dissociate the effects of TI and kMI on corticospinal excitability. This finding paves the way for a more in-depth understanding of the mechanisms of mental imagery, especially in the context of sensorimotor integration and imagery-based BCI applications, where kMI and TI are expected to exert different effects on the activity of sensorimotor circuits.

Data Availability

The datasets used and/or analyzed during the current study available from the corresponding author on reasonable request.

Competing interests

Authors report no conflict of interest.

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Author contributions

MM contributed to data collection, analysis and writing the manuscript. AN contributed to data collection and writing the manuscript. LY and NS contributed to the experiment planning, data collection and writing the manuscript. LY, ML and AK supervised the project. All authors contributed to editing and finalization of the manuscript.

References

1. Gerardin E, Sirigu A, Lehéricy S, Poline JB, Gaymard B, Marsault C, et al. Partially overlapping neural networks for real and imagined hand movements. Cereb Cortex N Y N 1991. 2000 Nov;10(11):1093–104.
2. Guillot A, Collet C, Nguyen VA, Malouin F, Richards C, Doyon J. Brain activity during visual versus kinesthetic imagery: an fMRI study. Hum Brain Mapp. 2009 Jul;30(7):2157–72.
3. Kilintari M, Narayana S, Babajani-Feremi A, Rezaie R, Papanicolaou AC. Brain activation profiles during kinesthetic and visual imagery: An fMRI study. Brain Res. 2016 Sep 1;1646:249–61.
4. Ridderinkhof KR, Brass M. How Kinesthetic Motor Imagery works: a predictive-processing theory of visualization in sports and motor expertise. J Physiol Paris. 2015;109(1–3):53–63.
5. Dickstein R, Deutsch JE. Motor imagery in physical therapist practice. Phys Ther. 2007 Jul;87(7):942–53.
6. García Carrasco D, Aboitiz Cantalapiedra J. Effectiveness of motor imagery or mental practice in functional recovery after stroke: a systematic review. Neurol Barc Spain. 2016;31(1):43–52.
7. Stinear CM, Byblow WD, Steyvers M, Levin O, Swinnen SP. Kinesthetic, but not visual, motor imagery modulates corticomotor excitability. Exp Brain Res. 2006 Jan;168(1–2):157–64.
8. Toussaint L, Blandin Y. Behavioral evidence for motor imagery ability on position sense improvement following motor imagery practice. Mov Sport Sci - Sci Mot. 2013;(82):63–8.
9. Yang YJ, Jeon EJ, Kim JS, Chung CK. Characterization of kinesthetic motor imagery compared with visual motor imageries. Sci Rep. 2021 Feb 12;11(1):3751.
10. Yoo SS, Freeman DK, McCarthy JJ, Jolesz FA. Neural substrates of tactile imagery: a functional MRI study. Neuroreport. 2003 Mar 24;14(4):581–5.
11. Schmidt TT, Ostwald D, Blankenburg F. Imaging tactile imagery: Changes in brain connectivity support perceptual grounding of mental images in primary sensory cortices. NeuroImage. 2014 Sep 1;98:216–24.
12. Yakovlev L, Syrov N, Miroshnikov A, Lebedev M, Kaplan A. Event-Related Desynchronization induced by Tactile Imagery: an EEG Study. eNeuro [Internet]. 2023 May 1 [cited 2023 Jun 2]; Available from: https://www.eneuro.org/content/early/2023/05/30/ENEURO.0455-22.2023
13. Schmidt TT, Blankenburg F. The Somatotopy of Mental Tactile Imagery. Front Hum Neurosci [Internet]. 2019 [cited 2023 May 19];13. Available from: https://www.frontiersin.org/articles/10.3389/fnhum.2019.00010
14. Bashford L, Rosenthal I, Kellis S, Pejsa K, Kramer D, Lee B, et al. The Neurophysiological Representation of Imagined Somatosensory Percepts in Human Cortex. J Neurosci Off J Soc Neurosci. 2021 Mar 10;41(10):2177–85.

15. Chivukula S, Zhang CY, Aflalo T, Jafari M, Pejsa K, Pouratian N, et al. Neural encoding of actual and imagined touch within human posterior parietal cortex. eLife. 2021 Mar 1;10:e61646.

16. Yao L, Jiang N, Mrachacz-Kersting N, Zhu X, Farina D, Wang Y. Performance Variation of a Somatosensory BCI pBased on Imagined Sensation: LarAgeP oulation Study. IEEE Trans Neural Syst Rehabil Eng. 2022;30:2486–93.

17. Morozova M, Yakovlev L, Syrov N, Perevoznyuk G, Lebedev M, Kaplan A. Tactile Imagery Affects Cortical Responses to Vibrotactile Stimulation of the Fingertip [Internet]. bioRxiv; 2023 [cited 2023 Jul 18]. p. 2023.06.02.543456. Available from: https://www.biorxiv.org/content/10.1101/2023.06.02.543456v1

18. Khan MA, Das R, Iversen HK, Puthusserypady S. Review on motor imagery based BCI systems for upper limb post-stroke neurorehabilitation: From designing to application. Comput Biol Med. 2020 Aug 1;123:103843.

19. Yao L, Sheng X, Zhang D, Jiang N, Farina D, Zhu X. A BCI System Based on Somatosensory Attentional Orientation. IEEE Trans Neural Syst Rehabil Eng. 2017 Jan;25(1):81–90.

20. Yao L, Chen ML, Sheng X, Mrachacz-Kersting N, Zhu X, Farina D, et al. A Multi-Class Tactile Brain–Computer Interface Based on Stimulus-Induced Oscillatory Dynamics. IEEE Trans Neural Syst Rehabil Eng. 2018 Jan;26(1):3–10.

21. Kaplan A, Vasilyev A, Liburkina S, Yakovlev L. Poor BCI Performers Still Could Benefit from Motor Imagery Training. In: Schmorrow DD, Fidopiastis CM, editors. Foundations of Augmented Cognition: Neuroergonomics and Operational Neuroscience [Internet]. Cham: Springer International Publishing; 2016 [cited 2023 Jul 18]. p. 46–56. (Lecture Notes in Computer Science; vol. 9743). Available from: http://link.springer.com/10.1007/978-3-319-39955-3_5

22. Vasilyev A, Liburkina S, Yakovlev L, Perepelkina O, Kaplan A. Assessing motor imagery in brain-computer interface training: Psychological and neurophysiological correlates. Neuropsychologia. 2017 Mar;97:56–65.

23. Fadiga L, Buccino G, Craighero L, Fogassi L, Gallese V, Pavesi G. Corticospinal excitability is specifically modulated by motor imagery: A magnetic stimulation study. Neuropsychologia. 1998 Nov;37(2):147–58.

24. Hashimoto R, Rothwell JC. Dynamic changes in corticospinal excitability during motor imagery. Exp Brain Res. 1999 Mar;125(1):75–81.

25. Cengiz B, Vurallı D, Zinnuroğlu M, Bayer G, Golmohammadzadeh H, Günendi Z, et al. Analysis of mirror neuron system activation during action observation alone and action observation with motor imagery tasks. Exp Brain Res. 2018 Feb;236(2):497–503.

26. Wright DJ, Wood G, Eaves DL, Bruton AM, Frank C, Franklin ZC. Corticospinal excitability is facilitated by combined action observation and motor imagery of a basketball free throw. Psychol Sport Exerc. 2018 Nov 1;39:114–21.

27. Bunno Y. Imagery strategy affects spinal motor neuron excitability: using kinesthetic and somatosensory imagery. Neuroreport. 2019 May 1;30(7):463–7.

28. Rossi S, Hallett M, Rossini PM, Pascual-Leone A. Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. Clin Neurophysiol. 2009 Dec 1;120(12):2008–39.

29. Rossini PM, Barker AT, Berardelli A, Caramia MD, Caruso G, Cracco RQ, et al. Non-invasive electrical and magnetic stimulation of the brain, spinal cord and roots: basic principles and procedures for routine clinical application. Report of an IFCN committee. Electroencephalogr Clin Neurophysiol. 1994 Aug;91(2):79–92.

30. Rossini PM, Burke D, Chen R, Cohen LG, Daskalakis Z, Di Iorio R, et al. Non-invasive electrical and magnetic stimulation of the brain, spinal cord, roots and peripheral nerves:

Basic principles and procedures for routine clinical and research application. An updated report from an I.F.C.N. Committee. Clin Neurophysiol Off J Int Fed Clin Neurophysiol. 2015 Jun;126(6):1071–107.

31. Kasai T, Kawai S, Kawanishi M, Yahagi S. Evidence for facilitation of motor evoked potentials (MEPs) induced by motor imagery. Brain Res. 1997 Jan 2;744(1):147–50.

32. Tokimura H, Di Lazzaro V, Tokimura Y, Oliviero A, Profice P, Insola A, et al. Short latency inhibition of human hand motor cortex by somatosensory input from the hand. J Physiol. 2000 Mar 1;523(Pt 2):503–13.

33. Oda H, Tsujinaka R, Fukuda S, Sawaguchi Y, Hiraoka K. Tactile Perception of Right Middle Fingertip Suppresses Excitability of Motor Cortex Supplying Right First Dorsal Interosseous Muscle. Neuroscience. 2022 Jul 1;494:82–93.

34. Kojima S, Miyaguchi S, Sasaki R, Tsuiki S, Saito K, Inukai Y, et al. The effects of mechanical tactile stimulation on corticospinal excitability and motor function depend on pin protrusion patterns. Sci Rep. 2019 Nov 13;9(1):16677.

35. Tanaka M, Kubota S, Onmyoji Y, Hirano M, Uehara K, Morishita T, et al. Effect of tactile stimulation on primary motor cortex excitability during action observation combined with motor imagery. Neurosci Lett. 2015 Jul 23;600:1–5.

36. Leung MCM, Spittle M, Kidgell DJ. Corticospinal Excitability Following Short-Term Motor Imagery Training of a Strength Task. J Imag Res Sport Phys Act. 2013 Jun 25;8(1):35–44.

37. Roll JP, Vedel JP. Kinaesthetic role of muscle afferents in man, studied by tendon vibration and microneurography. Exp Brain Res. 1982;47(2):177–90.

38. Cordo P, Gurfinkel VS, Bevan L, Kerr GK. Proprioceptive consequences of tendon vibration during movement. J Neurophysiol. 1995 Oct;74(4):1675–88.