Corticospinal and spinal adaptations following lower limb motor skill training: A meta-analysis with best evidence synthesis.

*Alex Woodhead[1], Jamie S. North[1], Jessica Hill[1], Colm P. Murphy[2], Dawson J. Kidgell[3], Jamie Tallent[3,4]

[1]Faculty of Sport, Allied Health and Performance Science, St. Mary's University, Twickenham, United Kingdom

[2]Cardiff School of Sport and Health Sciences, Cardiff Metropolitan University, Cardiff, United Kingdom

[3]Department of Physiotherapy, School of Primary and Allied Health Care, Faculty of Medicine, Nursing and Health Science, Monash University, Melbourne, VIC 3199, Australia

[4]School of Sport, Rehabilitation and Exercise Sciences, University of Essex, Wivenhoe Park, Colchester, United Kingdom

***Address for correspondence:**
Alex Woodhead
Faculty of Sport, Allied Health and Performance Sciences
St. Mary's University, Twickenham, UK
Middlesex, TW1 4SX
Email: alex.woodhead@stmarys.ac.uk
ORCID ID: 0000-0001-6163-833X

Author contributions

All authors contributed to the study conception and design (Alex Woodhead, Jamie S. North, Jessica Hill, Colm. P Murphy, Dawson. J Kidgell, Jamie Tallent). Literature search and data extraction was performed by Alex Woodhead and Jamie Tallent. The first draft of the manuscript was written by Alex Woodhead and all authors (Jamie. S North, Jessica Hill, Colm. P Murphy, Dawson. J Kidgell, Jamie Tallent) commented on previous versions of the manuscript. All authors read and improved the final manuscript.

Declaration of interest

The authors declare no conflict of interest, financial or otherwise.

Data availability statement

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Abstract

Motor skill training alters the human nervous system, however lower limb motor tasks have been less researched compared to upper limb tasks. This meta-analysis with best evidence synthesis aimed to determine the cortical and subcortical responses that occur following lower limb motor skill training, and whether these responses are accompanied by improvements in motor performance. Following a literature search that adhered to the PRISMA guidelines, data was extracted and analysed from six studies (*n* = 172) for the meta-analysis, and eleven studies (*n* = 257) were assessed for the best evidence synthesis. Pooled data indicated that lower limb motor skill training increased motor performance, with a standardised mean difference (SMD) of 1.09 being observed. However, lower limb motor skill training had no effect on corticospinal excitability (CSE), H-reflex or M_{MAX} amplitude. The best evidence synthesis found strong evidence for improved motor performance and reduced short-interval cortical inhibition (SICI) following lower limb motor skill training, with conflicting evidence towards the modulation of CSE. Taken together, this review highlights the need for further investigation on how motor skill training performed with the lower limb musculature modulates corticospinal responses. This will also help shed light on whether these neuronal measures are underpinning mechanisms that support an improvement in motor performance.

Keywords: lower limb, motor skill training, corticospinal excitability, motor performance, meta-analysis, best evidence synthesis.

Abbreviations

CI	Confidence interval
CSE	Corticospinal excitability
EEG	Electroencephalogram
EMG	Electromyography
FDI	First dorsal interosseous
fMRI	Functional magnetic resonance imagining
GABA	Gamma aminobutyric acid
H-reflex	Hoffmann reflex
ISI	Interstimulus interval
LTP	Long-term potentiation
M1	Primary motor cortex
MEP	Motor evoked potential
M_{MAX}	Muscle compound action potential
SICI	Short-interval intracortical inhibition
SMD	Standardised mean difference
STP	Short-term potentiation
TA	Tibialis anterior
TMS	Transcranial magnetic stimulation

1 Introduction

Motor skill training alters the human nervous system, (Mooney et al. 2019; Paparella et al. 2020) with adaptations often attributed to structural and functional reorganisation of the primary motor cortex (M1) (Muellbacher et al. 2001; Kleim et al. 1996). Acute responses following motor skill training provides evidence towards a highly modifiable M1, which manifest as an alteration of spinal (Perez et al. 2005; Ung et al. 2005) and supraspinal circuits (Mooney et al. 2019; Pascual-Leone et al. 1995). Defined as the acquisition and refinement of novel movement sequences (Adkins et al. 2006), skill training has both functional and clinical relevance and forms an essential part of neurorehabilitation programmes (Fimland et al. 2010). Following brain trauma or lesions on the brain, fundamental motor skills can be negatively affected, this has an impact on the ability of an individual to perform day-to-day activities (Hatem et al. 2016). Therefore, a primary goal of sporting and clinical practitioners is to support the learning (or re-learning) of motor skills which will, in turn, facilitate an improved level of performance or quality of life (Tallent et al. 2020).

Transcranial magnetic stimulation (TMS) is a non-invasive brain stimulation technique based on the principle of electromagnetic induction, first described by Faraday in 1831, that states a rapidly changing magnetic field induces a concomitant electrical current which in turn activates underlying neural tissue (Terao and Ugawa 2002). This results in the production of multiple descending volleys (i.e. action potentials) that activates corticospinal and intracortical neurones (Berardelli et al. 1990; Edgley et al. 1997; Rossini et al. 2015). Through the integration of electromyography (EMG), the muscle activity generated as a result of magnetic stimulation can be recorded, monitored and used to indicate the corticospinal response (Kobayashi and Pascual-Leone 2003). When a single TMS pulse is applied to the M1, an electrical recording at the targeted muscle contralateral to the site of stimulation is captured, which is referred to as a motor evoked potential (MEP) and provides a measure of corticospinal excitability (CSE) (Abbruzzese and Trompetto 2002). Paired pulse TMS involves the delivery of two consecutive stimuli interspersed with a selected interstimulus interval (ISI), providing researchers with a measure of intracortical inhibition or facilitation (Brownstein et al. 2018). Different ISI are manipulated to investigate the cortical networks facilitated by glutamate and GABA neurotransmitters (Ni and Chen 2011). Specifically, GABA-$_A$ mediated inhibition represents the measure of short-interval intracortical inhibition (SICI), GABA-$_B$ mediated inhibition indicates long-interval intracortical inhibition (LICI) and intracortical facilitation (ICF) is contingent on glutamate mediation (Kujirai et al. 1993). Taken together, TMS is a vital tool used to assess the integrity of the M1 and corticospinal pathway with many applications in the sporting, clinical and research settings (Hallett, 1996; Brownstein et al. 2017; Tallent et al. 2017).

Upper limb motor skill training has been assessed via visuomotor tracking (Tracy et al. 2007), ballistic movements (Lee et al. 2010; Dickins et al. 2015) and sequential tasks (Takeo et al. 2021), with the corticospinal responses assessed across distal and proximal muscles (Poh et al. 2013; Mason et al. 2019; Mooney et al. 2019). Increases in CSE (i.e. peak-to-peak MEP amplitude) and reductions in SICI (i.e. conditioned MEP amplitude calculated as a percentage of the unconditioned MEP) have been reported following just a single session of upper limb motor skill training (Jensen et al. 2005; Leung et al. 2015; Mason et al. 2019), with others reporting the same responses after multiple weeks of training (Jensen et al. 2005; Leung et al. 2017). Manipulation of task demands and feedback have also been shown to shape the corticospinal response, namely in the form of external pacing (Ackereley et al. 2011), progressive increases in task difficulty (Christiansen et al. 2018; Christiansen et al. 2020) and altered feedback frequencies (Smyth et al. 2010). However, non-skill based simple movements without external pacing, such as self-paced single-limb resistance exercises have no effect on CSE after a single session (Leung et al. 2015) with reductions in CSE being observed after four weeks resistance training (Jensen et al. 2005). This shows that skill based complex tasks are more centrally demanding (i.e. movements with a requirement for motor acuity or precision) and provide a clear stimulus for training-induced adaptations along the neuroaxis, compared to those without additional demands.

In addition to concomitant increases in CSE and reductions in SICI, skill acquisition has also been inferred via an improvement in motor performance of the task (Smyth et al. 2010). Visuomotor tracking error has been shown to reduce following four weeks of motor skill training in the elbow flexors (Jensen et al. 2005; Leung et al. 2017); however, a recent meta-analysis has questioned the association between the corticospinal responses that are induced after a period of motor skill training, and the behavioural response specific to the trained task (Berghuis et al. 2017; Hortobágyi et al. 2021). It was reported by Berghuis et al (2017) that the TMS parameters assessed (CSE and SICI) were unrelated to the changes in motor skill acquisition, despite finding an increase in CSE after visuomotor but not ballistic training in young adults, and no change in SICI in either task. Despite the lack of association between corticospinal responses and changes in motor performance, for which several reasons are responsible (Bestmann and Krakauer 2015), it could be suggested that the increased CSE and reduced SICI observed following motor skill training are mediating factors which contribute towards an improvement in motor performance. However, the aforementioned changes in corticospinal responses do result from the training task itself, but are not a prerequisite of skill acquisition. It is important to also note that Berghuis et al (2017) assessed responses in the upper limbs, making it difficult to draw any conclusions regarding lower limb responses.

Compared to the upper limb, the corticospinal responses and associated performance outcomes following lower limb motor skill training has received considerably less empirical investigation. Researchers have investigated the cortical and subcortical responses after balance and ballistic training (Schubert et al. 2008); although assessment of motor performance/behaviour was not recorded. This failure to measure motor performance was also apparent in cross-sectional comparisons of non-trained and well-trained athletes, where improved corticospinal adaptations were evident following long-term training (Saito et al. 2014; Grospetre et al. 2019). Improvement in lower limb motor performance has, however, been reported by Perez et al (2004) who showed that, following a single session of completing a visuomotor tracking task, there was a reduction in motor error alongside an increase in CSE and reduced SICI in the tibialis anterior (TA). However, the relative lack of further motor performance data following lower limb motor skill training makes it difficult to draw firm conclusions as to whether the corticospinal responses induced are related to motor skill acquisition.

The difficulty (or risk) in drawing conclusions on how lower limb muscles respond to motor skill training based on findings from research employing upper limb tasks may be explained using their physiological characteristics. Assessing the strength of corticospinal projections, Brouwer and Ashby (1990) observed a smaller compound muscle action potential (CMAP) in the lower limb, which also required a much stronger stimulus compared to the upper limb. The leg muscles, in particular the quadriceps, are predominantly involved in gross motor control, with a greater proportion of motor units driven by larger motoneurones, with higher activation thresholds (Smith et al. 2017; Kesar et al. 2018). Due to the lower evoked amplitude and stronger stimulus needed, it is conceivable to assume the corticospinal projections from the M1 to spinal motoneurones which innervate the skeletal muscle of the lower limbs may be weaker in comparison to the upper limb. However, Brouwer and Ashby (1990) also reported similar CMAP amplitudes between the TA and first dorsal interosseous (FDI), which are lower and upper limb muscles respectively. This is particularly interesting given the TA is also implicated in human locomotion and linked to the activation of the corticospinal tract during walking (Capaday et al. 1999). Given this similarity in amplitudes, the specific nuances must be taken into consideration when comparing the corticospinal responses between muscles, and simply generalising the upper and lower limb muscles may overlook potential differences within each isolated region of the body.

Lower limb motor skill training and its effect on neuromuscular function requires further empirical investigation to support the mechanisms that have thus far been observed. Therefore, this meta-analysis with best evidence synthesis aims to determine the cortical and subcortical responses that occur following lower limb motor skill training, and whether these responses are accompanied by improvements in motor performance. Enhancing our understanding of the mechanisms underpinning motor skill training in the lower extremities will enable us to provide some much-needed clarity and ascertain where the responses occur along the neuroaxis.

2 Methods

This systematic review and meta-analysis were conducted in line with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Page et al. 2021).

2.1 Eligibility criteria

Studies were included for analysis if they fulfilled the following criteria: (i) recreationally trained or untrained healthy adults (males and females) between the ages of 18 and 45; (ii) motor skill training performed in the lower limb that was restricted to a single session or completed across multiple weeks; (iii) training intervention compared to a control group; (iv) stimulation of the M1 at baseline and post-training to quantify changes in corticospinal responses using single-and paired-pulse TMS indicators, as well as variables assessed through electrical stimulation (H-reflex and M-wave responses) between an experimental and control group; and (v) motor performance of the training task quantified prior to and after the intervention. Studies were considered eligible if at least one of the above variables assessed via either form of neurostimulation were measured.

Exclusion criteria included: (i) diseased populations or older adults (mean age > 45 years); (ii) studies that utilised an element of strength training in the skill training task, ballistic movements or motor tasks performed at an intensity > 30% MVC; (iii) no comparison to a control group would exclude studies from the meta-analysis, but were included in the best evidence synthesis; (iv) no post-intervention assessment of neural responses or motor performance; (v) participants that received additional treatments or factors (i.e. supplementation, transcranial direct current stimulation) that may have affected the neurological response; and (vi) non-English publications, non-peer reviewed documents or theses.

2.2 Information sources

An electronic search of the literature was conducted in the following databases from inception until 12th April 2022: PubMed, Sports Discus, Web of Science, PsycINFO, CINAHL and Cochrane Library. To ensure the entire field of literature had been reached, a final search was conducted via Google Scholar by all authors using the relevant key terms. Following these processes, the reference lists of all included studies were screened for additional relevant papers.

2.3 Search strategy

Electronic databases were searched using an extensive list of key terms (i.e. “motor skill training”, “neural plasticity”, “TMS”) and its associated synonyms. The key terms that were applied to each specific database are outlined in Table 1.

2.4 Selection process

All studies identified as a result of the literature search were exported onto a custom-built Microsoft Excel document (Microsoft Excel, Version 16.55). One of the authors (AW) performed the initial search and screened all retrieved articles to remove duplicates and any items that were deemed outside the scope of the meta-analysis. Two authors (AW and JT) then independently screened and reviewed the remaining titles and corresponding abstracts. Full text articles that satisfied the inclusion criteria were read in full, with eligible studies then included within the meta-analysis. Next, these authors met to discuss and agree on any discrepancies in included studies. A full list of included studies within the meta-analysis and best evidence synthesis are shown in Table 2 and Table 3, respectively.

2.5 Data collection process and data items

Data from included studies were extracted from the available text (AW and JT) onto a custom-made Excel document. Information on the study intervention, participant characteristics (age and sex), target muscle from stimulation, sampling method, key measures and results were extracted from all included studies. In addition, the following outcome measures were retrieved: motor performance (specific to the training task), corticospinal excitability (peak-to-peak motor evoked potential (MEP) waveform expressed as raw amplitude, normalised as a percentage of peripheral M-wave amplitude, relative to motor threshold, MEP_{MAX} or arbitrary units extracted from a stimulus-response curve), Hoffmann's reflex (H-reflex (expressed in mV, μV, % M_{MAX} or $\text{H}_{\text{MAX}}/\text{M}_{\text{MAX}}$)) and maximal muscle compound action potential (M_{MAX}; mV, μV), and SICI (quantified as the size of the conditioned paired-pulse MEP expressed relative to the size of the unconditioned MEP). Data were extracted as means and standard deviation at pre-training and post-training time points for each outcome measure in both the experimental and control groups. Where post-intervention means ± standard deviations were not reported within the available text, raw data (means ± standard deviations) was converted from the number of participants (N), standard error, 95% confidence intervals, P values, t values or F values. Where standard deviations were presented across multiple time points, data was pooled into a single value and subsequently used for analysis. For studies that presented results in figures, publicly available software (WebPlotDigitizer, Version 4.5) was used to extrapolate the required data. All extracted data were checked for accuracy independently by two authors (AW and JT). Where agreements could not be reached regarding data extraction from the included studies, two further researchers were consulted (JN and CM).

2.6 Study risk of bias assessment

Two authors (AW and JT) assessed the quality of included studies using a modified version of the Downs and Black checklist (Downs & Black, 1998). Eleven items (4, 8, 9, 13, 15, 17, 19, 22, 23, 24 and 27) were not deemed relevant for this review and subsequently excluded from the quality assessment. Previous systematic reviews and meta-analyses have utilised a similar modified version (Alibazi et al. 2021; Maniar et al. 2016). In addition, the Cochrane Risk of Bias tool was used which categorised the included studies as "high risk", "low risk", or "unclear risk" across six independent criteria: random sequence generation, allocation concealment, blinding of participants and personnel, blinding of outcome assessment, incomplete outcome data, selective reporting, and other sources of bias (Higgins & Green 2011).

2.7 Statistical analysis

Post-training data after lower limb motor skill interventions in the experimental and control groups from included studies were used for the following outcome measures: motor performance, CSE, H-reflex, M_{MAX} and SICI. Meta-analysis was performed using a random effects model to compare the overall pooled effect for each outcome measure. This was deemed appropriate considering the differences in researchers, methods, and interventions between included studies (Borenstein et al. 2010). Standardised mean difference (SMD) with 95% confidence intervals (CIs) were used to measure the intervention effect as the included studies presented data in several different ways. The SMD values of $0.2 \leq 0.49$, $0.5 \leq 0.79$ and ≥ 0.8 indicated small, medium, and large comparative effects, respectively (Cohen, 1988). The results for each outcome measure are reported as SMD, 95% CIs and the associated P value. This approach provides information on both the existence of an effect, as well as the size and direction of the effect following the intervention. Heterogeneity between included studies was assessed using the I^2 statistic, with cut-off points indicating low (25%), moderate (50%) and high (75%) heterogeneity. Statistical analyses were performed in RevMan 5.4 using an alpha level of $P < 0.05$ to determine statistical significance.

Where it was deemed that reported data from included studies were insufficient for meta-analysis (i.e. no comparison to a control condition) and could not be obtained via additional methods (e.g. through email communication with authors), a best evidence synthesis was employed to assess the remaining data. Data was extracted from eleven studies using the following outcome measures: Motor performance (quantified as the within-group difference from pre- to post-training specific to the task), MEP amplitude (peak-to-peak motor evoked potential waveform expressed as raw amplitude, normalised as a percentage of peripheral M-wave amplitude, relative to motor threshold, MEP_{MAX} or arbitrary units extracted from a stimulus-response curve) and SICI (quantified as the size of the conditioned paired-pulse MEP expressed relative to the size of the unconditioned MEP). The level of evidence used to rank the available data was consistent with previous systematic reviews (Alibazi et al. 2021; Maniar et al. 2016) and is defined using the following criteria:

- Strong evidence: two or more studies of high quality and generally consistent findings (≥ 75% of studies showing consistent results).
- Moderate evidence: one high quality study and two or more low quality studies and generally consistent findings (≥ 75% of studies showing consistent results).
- Limited evidence: one low quality study.
- Conflicting evidence: inconsistent findings (< 75% of studies showing consistent results).
- No evidence: no supportive findings.

Studies with a risk of bias score of ≥ 70% and < 70% were considered as high-quality and low- quality studies, respectively (Maniar et al. 2016). Cohen's d effect size and 95% CIs were displayed in forest plots using Prism 9 for Mac (GraphPad Software, Inc, La Jolla, California). Effect sizes were quantified as small (≤ 0.20), moderate (0.50) and large (≥ 0.80) (Cohen 1988).

3 Results

3.1 Study selection

The PRISMA flow chart (Figure 1) outlines the process involved in study identification, screening, and evaluation of the eligibility of included studies. The initial search returned 6,011 articles from all electronic databases, plus a further eight articles identified via additional sources. These were reduced to 5,333 articles after the removal of duplicates. Further screening of titles and abstracts left 143 full-text articles. Searching the reference lists of included studies did not retrieve any additional papers. On the basis of inclusion criteria, 137 articles were removed from the 143. In turn, 11 papers were included in the final sample. Six papers were assessed as part of the meta-analysis, and 11 papers were assessed under the best evidence synthesis.

3.2 Study characteristics

The six studies included in the meta-analysis had recruited a total of 172 participants (84 males & 76 females), with an age range between 22-28 years old. Four studies assessed the effect that motor skill training has on lower limb musculature in the soleus (Giboin et al. 2019; Gruber et al. 2007; Keller et al. 2012; Taube et al. 2007), whereas two studies assessed responses in the TA (Bakker et al. 2021; Perez et al. 2004). The motor training task employed varied between studies, with five examining balance (Bakker et al. 2021; Giboin et al. 2019; Gruber et al. 2007; Keller et al. 2012; Taube et al. 2007) and one utilising a visuomotor tracking task (Perez et al. 2004). The duration of the intervention ranged from a single session- (Bakker et al. 2021), four weeks- (Gruber et al. 2007; Keller et al. 2012; Taube et al. 2007) to six weeks (Giboin et al. 2019) in those employing a balance task. The study employing a visuomotor tracking task examined the corticospinal response before and after a single session (Perez et al. 2004). In addition, two studies included a third experimental group consisting of a ballistic strength training (Gruber et al. 2007) and a cycling training intervention (Bakker et al. 2021), both of which were excluded from the analysis. A detailed summary of all studies included within the meta-analysis is presented in Table 2, with a further summary of the additional included studies for the best evidence synthesis presented in Table 3.

3.3 Quality assessment

A modified version of the Downs and Black checklist was used to assess the quality of included studies (Alibazi et al. 2021; Maniar et al. 2016) (Table 4). This checklist revealed that studies meeting the inclusion criteria ranged between 12 (71%) and 14 (82%) out of a possible 17 points, with a mean score of 13 ± 0.63. The Cochrane risk of bias tool showed that all included studies demonstrated high risk of allocation concealment, blinding of participants and personnel, and blinding of outcome. The risk of bias graph is displayed in Figure 2.

3.4 Motor performance

Changes in motor performance were extracted from six studies that assessed balance parameters or visuomotor tracking error post-training (n = 80) compared to a control (n = 75). The pooled data showed an increase in performance after lower limb motor skill training (SMD 1.09; 95% CI 0.74, 1.43, $P < 0.00001$). There was also low heterogeneity across these studies ($\tau^2 = 0.00$; $\chi^2 = 1.47$; $df = 5$; $P = 0.92$; $I^2 = 0\%$). Figure 3 displays the forest plot showing the effect of lower limb motor skill training on measures of motor performance.

3.5 Corticospinal excitability

Data from two studies were used to assess changes in CSE post-training (n = 22) compared to a control (n = 22). Pooled data indicated that lower limb motor skill training did not alter CSE (SMD 0.56; 95% CI -0.78, 1.90, P = 0.41), with high heterogeneity across these studies ($\tau^2 = 0.73$; $\chi^2 = 4.50$; $df = 1$; $P = 0.03$; $I^2 = 78\%$). Figure 4 displays the forest plot demonstrating the effect of lower limb motor skill training on CSE.

3.6 H-reflex

Post-training data was extracted from four studies (n = 52) that examined the H-reflex response compared to a control (n = 44). Pooled data showed that lower limb motor skill training had no effect on the H-reflex (SMD 0.34; 95% CI -0.44, 1.11, P = 0.39), with high heterogeneity across these studies ($\tau^2 = 0.44$; $\chi^2 = 10.09$; $df = 3$; $P = 0.02$; $I^2 = 70\%$). Figure 5 displays the forest plot showing the effect of lower limb motor skill training on the H-reflex response.

3.7 M_{MAX}

Changes in M_{MAX} were extracted from two studies post-training (n = 28) compared to a control (n = 25). Pooled data demonstrated that lower limb motor skill training had no effect on M_{MAX} amplitude (SMD 0.97; 95% CI -1.07, 3.00, P = 0.35), with high heterogeneity ($\tau^2 = 1.95$; $\chi^2 = 10.53$; $df = 1$; $P = 0.001$; $I^2 = 91\%$). Figure 6 shows the forest plot demonstrating the effect of lower limb motor skill training on M_{MAX} amplitude.

3.8 Best evidence synthesis

Motor performance (single session). Six studies (Bakker et al. 2021; Hirano et al. 2015; Hirano et al. 2018; Kubota et al. 2015; Tatemoto et al. 2019) were assessed, with strong evidence that a single session of lower limb motor skill training improved motor performance. The magnitudes of the intervention effect were moderate to large, with an effect size ranging between 0.71 to 3.00 (Figure 7).

Motor performance (multiple weeks of training). Four studies (Giboin et al. 2019; Giboin et al. 2020; Gruber et al. 2007; Keller et al. 2012) were assessed, with strong evidence that lower limb motor skill training performed across multiple weeks improved motor performance. The magnitudes of the intervention effect were large, with an effect size ranging between 0.90 to 3.07 (Figure 8).

Corticospinal excitability. Five studies (Bakker et al. 2021; Hirano et al. 2015; Hirano et al. 2018; Perez et al. 2004; Tatemoto et al. 2019) examined CSE from either a resting or active leg muscle. There was conflicting evidence for modulating CSE following lower limb motor skill training. The magnitudes of the intervention effect were small to moderate, with an effect size range between -0.15 to 0.59 (Figure 9).

Short interval intracortical inhibition. Three studies (Bakker et al. 2021; Perez et al. 2004; Tatemoto et al. 2019) assessed SICI following lower limb motor skill training. There was strong evidence showing a reduction in SICI, suggesting that the intrinsic intracortical circuitry is altered as a result of motor skill training performed in the lower limb. The magnitudes of the intervention effect were small to large, with effect sizes ranging from 0.13 to 2.59 (Figure 10).

4 Discussion

The aim of this meta-analysis with best evidence synthesis was to determine the cortical and subcortical responses following lower limb motor skill training, and to assess the effect on motor performance. Overall, there was a large effect towards an improved performance (SMD, 1.09), showing that both visuomotor and balance interventions resulted in successful motor skill acquisition. This meta-analysis also found that lower limb motor skill training did not affect CSE, H-reflex or the M_{MAX} response, suggesting that mechanisms underpinning an improvement in task performance are not supported by changes along the corticospinal pathway, spinal cord or maximal muscle membrane excitability. The best evidence synthesis assessed corticospinal responses, finding strong evidence towards an improved motor performance and reduced SICI, but conflicting evidence for the modulation of CSE.

4.1 Motor performance

Motor performance following lower limb motor skill training was assessed in six studies, with five studies investigating balance performance (Bakker et al. 2021; Giboin et al. 2019; Gruber et al. 2007; Keller et al. 2012, Taube et al. 2007) and one study utilising visuomotor tracking (Perez et al. 2004). The pooled estimate revealed a large increase (SMD, 1.09) in motor performance, with improved behavioural outcomes specific to the trained task often observed after a single session of visuomotor ankle dorsi/plantar flexion movements (Perez et al. 2004) and skilful cycling (Tatemoto et al. 2019), as well as short-term interventions (Christiansen et al. 2020; Jensen et al. 2005; Leung et al. 2017). Similarly, a meta-analysis by Berghuis and colleagues demonstrated improved motor performance following visuomotor and ballistic training in the upper limb muscles of young adults (Berghuis et al. 2017). However, the present study excluded ballistic interventions from the analyses, due to the involvement of strength in the task, and instead examined only visuomotor and balance assessments. Continuing this notion of improved behavioural outcomes, the best evidence synthesis found strong evidence towards an improvement in motor performance after balance tasks performed over a 4-6-week duration (Giboin et al. 2019; Gruber et al. 2007; Keller et al. 2012; Taube et al. 2007) and visuomotor tracking movements during a single session (Perez et al. 2004). Much of the previously published literature has been conducted in the upper limb and has shown clear evidence for improved motor-performance and by-proxy an improvement in motor skill acquisition. The results of the current meta-analysis and best evidence synthesis indicate that, despite reported physiological differences between upper and lower limbs (see Brouwer and Ashby 1990) and their typical differential involvement in fine and gross motor tasks respectively, improved motor performance following a motor skill training intervention is not confined to the upper limbs alone and extends the body of evidence to the lower limbs.

4.2 Corticospinal excitability

The present meta-analysis pooled data from two studies which utilised a visuomotor tracking (Perez et al. 2004) and balance task (Bakker et al. 2021), respectively, finding that lower limb motor skill training did not have an effect on CSE (SMD, 0.56). The best evidence synthesis, which is able to assess within-group differences, found conflicting evidence towards the modulation of CSE following motor skill training in the lower extremities.

Collectively, four of the studies included within the best evidence synthesis utilised a visuomotor tracking paradigm as the training task, with a further study assessing balance performance, and both of which measured the associated corticospinal responses in the immediate time period post-exercise. Two of these studies reported an increase in CSE (Hirano et al. 2018; Perez et al. 2004), whilst the remaining three studies found no differences in CSE after the training intervention (Bakker et al. 2021; Hirano et al. 2015; Tatemoto et al. 2019). These contrasting results are surprising, as a large body of evidence has reported transient elevations in CSE following motor training (Jensen et al. 2005; Leung et al. 2015; Mason et al. 2019; Perez et al. 2004). Early research from Jensen et al. (2005) found an increased CSE after the first session and a decrease at the cessation of training. Specifically, tasks involving a greater degree of external feedback have demonstrated a consistent facilitation in CSE, with visuomotor skill training and metronome-paced movements increasing CSE to a larger extent than self-paced movements (Leung et al. 2015). Based on these findings, it appears the demands, novelty, complexity, application of visual feedback and degree of somatosensory feedback implicated within the task are likely key contributing factors which lead to greater modulations of the corticospinal pathway. However, it is important to highlight that the aforementioned studies assessed the corticospinal responses in the upper limbs, as opposed to the lower limbs.

Despite the lack of difference in CSE reported within the present meta-analysis, of the five studies included within the best evidence synthesis, two found an increase in CSE (Hirano et al. 2018; Perez et al. 2004). This disparity in CSE could be attributed to the methodology during the stimulation protocol, in which background muscle activation has been shown to influence TMS measures of CSE (Hand et al. 2020; Zoghi et al. 2003). Due to the inclusion of studies assessing the responses in either a resting or active muscle, this may account for the differences observed following lower limb motor skill training. Further, there is little information on how the lower limb muscles respond after the performance of skilled movements, with the majority of researchers choosing to select the wrist, upper limb digits or elbow flexors as a more appropriate medium to assess the corticospinal response (e.g. Dickins et al. 2015; Poh et al. 2013). The increase in CSE reported by two included studies suggests that tasks in which the visual and motor systems are sufficiently challenged, the corticospinal responses may, to some degree, follow the same trend as those reported in the literature which have employed upper limb tasks (Jensen et al. 2005; Leung et al. 2015; Mason et al. 2019). This is an important finding given the differences in physiological characteristics between the upper and lower limbs. Corticospinal neurons which project from the M1, onto spinal motoneurones and subsequently innervate lower limb musculature may be weaker compared to the upper limbs (Brouwer and Ashby 1990). Therefore, despite a lower projection strength, the present study presents an initial basis to suggest the corticospinal responses may be, in part, modulated following lower limb motor skill training. However, this should be interpreted with caution due to the lack of difference found within the meta-analysis and conflicting support following the outcomes of the best evidence synthesis. The inclusion of only two studies meeting the eligibility criteria demonstrates that to resolve the lack of consensus regarding the corticospinal responses of the lower limbs, that further studies are required which will allow for more substantive conclusions to be drawn.

4.3 H-reflex

This meta-analysis pooled the statistical effects from four studies assessing the H-reflex response, demonstrating no difference (SMD, 0.34) after lower limb motor skill training. However, the intervention utilised across each of these four studies were all balance tasks, performed across 4-6 weeks with 2-4 sessions per week. Balance training typically involves the use of a slackline or the requirement to complete a range of postural stabilisation tasks, which has normally resulted in a reduced H-reflex response and has been consistently observed in individual studies (e.g. Gruber et al. 2007; Taube et al. 2007). This reduction in H-reflex following balance training is attributed to a series of neurophysiological processes, which begins via a suppression of Ia afferent transmission that in turn inhibits reflex mediation joint oscillations and subsequently allows for an improved balance performance (Trimble and Koceja 1994). It is surprising, therefore, that the present meta-analysis did not detect the same trend in H-reflex response that has been observed in discrete studies. Some of the included papers measured the H-reflex responses across a number of different conditions; for example, Keller et al. (2012) used four separate surfaces (stance, cushion, Posturomed, slackline). To circumvent this potential issue, the extracted data were pooled across these conditions to determine through a holistic approach whether lower limb motor skill training modulates the H-reflex. It is possible that our method may have contributed to the disparate results between the present meta-analysis and those consistently reported by individual studies. There are several different methods that can be used to assess the H-reflex response, which include the calculation of the raw amplitude, H/M_{MAX} or H_{MAX}/M_{MAX}. In turn, the H-reflex can be evoked at different parts of the recruitment curve, as well as potentially with respect to the M-wave recruitment curve. Given the nuances in H-reflex assessment, it is possible that different methodologies employed across studies may have contributed to the disparate outcomes observed. Of note, each included study assessed the H-reflex response across short-term training durations (i.e. 4-6 weeks) with pre-post measurements taken. As observed with other neurophysiological variables, it is possible that transient changes in H-reflex amplitude may occur on an acute basis immediately after a single training session but, in the context of the present study, be missed due to inclusion of longer training studies and lack of data on acute responses.

4.4 M_{MAX}

The M-wave has been used extensively to provide quantitative information regarding changes in maximal muscle membrane excitability after fatiguing contractions, muscle damage protocols and strength training interventions (e.g. Goodall et al. 2018; Place et al. 2010; Skarabot et al. 2021). However, its utility in response to motor skill training is limited and has not been investigated. The present meta-analysis pooled the estimate obtained from two studies, finding no change in M_{MAX} (SMD, 0.97) following lower limb motor practice and, more specifically, balance assessments (Giboin et al. 2019; Keller et al. 2012). Often within studies that utilise neurostimulation techniques, either in the form of TMS of electrophysiological reflex methods, assessing the M-wave response is typically used as a normalisation strategy to account for methodological and physiological issues (Rodriguez-Falces and Place 2017). However, in the context of fatiguing contractions there is mixed evidence regarding the trend of M_{MAX} (Neyroud et al. 2013; Pageaux et al. 2013). Due to the relative intensity of motor skill tasks, particularly visuomotor and balance assessments, it is not surprising that M_{MAX} remained unchanged following motor skill training.

4.5 Short interval intracortical inhibition

Paired-pulse TMS can be used to assess the degree of intracortical inhibition within the nervous system, which is synaptic in origin and mediated by GABAergic neurons acting via $GABA_A$ receptors (Di Lazzaro et al. 2000; Siddique et al. 2020; Ziemann et al. 1996). There is good evidence to show that the modulation of SICI is implicated in selective hand muscle activation (Stinear and Byblow 2003), and although this is prevalent in the upper limbs, it indicates that intracortical inhibition is implicit for motor performance (Ziemann et al. 2001). Previous literature has reported a reduction in SICI after learning a simple and complex motor task in young adults (Garry et al. 2004; Liepert et al. 1998; Perez et al. 2004). Of particular importance to the present review, Perez et al (2004) found a single session of visuomotor ankle dorsi/plantar flexion movements modified local intracortical networks (i.e. decreased SICI). Consistent with this, further support has found a reduced SICI within the lower extremities following low-intensity pedalling (Yamaguchi et al. 2012) and acute aerobic exercise (Yamazaki et al. 2019), with more recent evidence concluding that the GABAergic interneuronal circuits of the hand and leg representations are similar (Mrachacz-Kersting et al. 2021). The present best evidence synthesis revealed strong evidence that SICI is reduced after lower limb motor skill training, which builds on the findings of Berghuis et al. (2017) who observed that upper limb visuomotor training had no effect on SICI in young adults but the opposite in older adults. Due to the nature of the task, visuomotor movements require greater precision to accurately follow the intended direction (Zoghi et al. 2003). It is surprising that young adults did not have the same inhibitory response, and questions whether the removal of inhibition after motor practice is an important substrate for motor learning and M1 plasticity (Rantalainen et al. 2013). In light of the idea that the inhibitory networks are similar between the upper and lower extremities (Mrachacz-Kersting et al. 2021), the majority of literature to date has examined the effect of upper limb motor skill training on intracortical inhibition, which in turn is limiting the understanding of how the lower extremity musculature, given its role in gross motor function, interacts with GABAergic inhibitory networks.

4.6 Further considerations and limitations

Although beyond the scope of this paper, the low number of studies that satisfied eligibility criteria lends itself to a suggestion of potential publication bias. Whilst we can only comment tentatively upon this, it is perhaps somewhat surprising that there are not more studies which report no significant main effects. Publication bias is a well-recognised issue in science (DeVito and Goldacre 2018) with a tendency to favour publication of studies reporting significant over null effects (Fanelli, 2013; Schmucker et al. 2014). Whether it is a case of journal editors being less inclined to publish null findings, or researchers not submitting such work for publication given the perception that it will be less well received, the (unintended) consequence is that the ability to accurately represent the body of evidence in a given area is impaired (Driessen et al. 2015). We therefore encourage replication studies of those published works that have been included in our review, and collectively highlight the importance of null effect studies being published.

Of 143 studies, 42 were excluded based on the lack of motor performance data. Despite evidence that TMS measures and motor skill acquisition is not correlated in the upper limbs (Berghuis et al. 2017), further research should assess the degree of skill acquisition and corticospinal responses to determine whether the two are related in the lower limb muscles, as currently there is little evidence to inform this conclusion beyond the upper limbs. Future studies should also apply a multi-focal approach combining techniques including functional magnetic resonance imagining (fMRI), electroencephalogram (EEG), TMS and electrical nerve stimulation to increase the overall quality of research design and provide new information outside of the current body of literature. By understanding the mechanisms following lower limb motor skill training, it will enable targeted and effective prescription guidelines that can be easily translated into clinical practice.

All included papers within the meta-analysis and best evidence synthesis stimulated either the soleus or TA. This is most likely attributed to their physiological distinctions from other lower limb muscles, whereby the TA has been shown to demonstrate strong corticospinal projections which are similar to some upper limb muscles (Brouwer and Ashby 1990). It is clear the TA has important functionality in the control of foot trajectory during the gait cycle and is known to be affected through foot drop in patients with cortical and spinal cord injuries (Thompson et al. 2018). However, the role of the quadriceps in gross motor control is not to be understated and, in turn, requires more investigation around the corticospinal responses. This is also related to the small number of studies employing lower limb tasks, which is further reflected in the discussions of Berghuis et al (2017) who did not return any lower limb studies despite not placing any restrictions on body region. A more comprehensive understanding on how the lower limb responds to motor skill training is needed, and this is clear from six studies returning from the literature search. To circumvent the low number, the best evidence synthesis presented alongside the meta-analysis accounts for within-groups differences and includes studies that may have previously been excluded based on no comparison to a control group. Although this provides a wider picture about the corticospinal responses following lower limb motor skill training, further empirical support is required to develop this area in line with the upper limb literature. It is also important to recognise that behavioural improvements and corticospinal responses may diverge at different stages of the motor learning process. For example, Dupont-Hadwen et al (2019) investigated the profile of SICI dynamics before and in response to a thumb abduction task. Disinhibition in the M1, via a release of SICI, was observed during the movement preparation phase with no overall changes observed during the motor task. At the early stages of training there was a correlation between behavioural improvements and increases in late pre-movement SICI, whereas later stage training-induced behavioural improvements were correlated to early changes in SICI. This indicates that as individuals prepare to move, and during the execution of the movement itself, there is a changing profile of inhibitory dynamics that acts to coordinate the muscle activity and perform the intended motor action (Dupont-Hadwen et al. 2019). Taken together, future work should consider the different shifts in corticospinal responses during each phase of motor learning when aiming to provide pooled effects.

4.7 Conclusions

This is the first meta-analysis and best evidence synthesis to provide quantitative information regarding lower limb motor skill training. The results of the meta-analysis revealed positive improvements in motor performance, but had no effect on CSE, H-reflex and M_{MAX}. The best evidence synthesis found strong evidence for improved motor performance and reduced SICI following lower limb motor skill training, with conflicting evidence towards the modulation of CSE. Taken together, this review highlights the need for further investigation on how motor skill training performed with the lower limb musculature modulates corticospinal responses. This will also help shed light on whether these neuronal measures are underpinning mechanisms that support an improvement in motor performance.

References

1. Ackerley, S., Stinear, C., & Byblow, W. (2011). Promoting use-dependent plasticity with externally-paced training. *Clinical Neurophysiology*, *122*(12), 2462-2468. https://doi.org/10.1016/j.clinph.2011.05.011

2. Adkins, D., Boychuk, J., Remple, M., & Kleim, J. (2006). Motor training induces experience-specific patterns of plasticity across motor cortex and spinal cord. *Journal of Applied Physiology*, *101*(6), 1776-1782. https://doi.org/10.1152/japplphysiol.00515.2006

3. Alibazi, R., Pearce, A., Rostami, M., Frazer, A., Brownstein, C., & Kidgell, D. (2020). Determining the Intracortical Responses After a Single Session of Aerobic Exercise in Young Healthy Individuals: A Systematic Review and Best Evidence Synthesis. *Journal of Strength and Conditioning Research*, *35*(2), 562-575. https://doi.org/10.1519/jsc.0000000000003884

4. Bakker, L., Nandi, T., Lamoth, C., & Hortobágyi, T. (2021). Task specificity and neural adaptations after balance learning in young adults. *Human Movement Science*, *78*, 102833. https://doi.org/10.1016/j.humov.2021.102833

5. Berardelli, A., Inghilleri, M., Cruccu, G., & Manfredi, M. (1990). Descending volley after electrical and magnetic transcranial stimulation in man. *Neuroscience Letters*, *112*(1), 54–58. https://doi.org/10.1016/0304-3940(90)90321-y

6. Berghuis, K., Semmler, J., Opie, G., Post, A., & Hortobágyi, T. (2017). Age-related changes in corticospinal excitability and intracortical inhibition after upper extremity motor learning: a systematic review and meta-analysis. *Neurobiology of Aging*, *55*, 61-71. https://doi.org/10.1016/j.neurobiolaging.2017.03.024

7. Bestmann, S., & Krakauer, J. (2015). The uses and interpretations of the motor-evoked potential for understanding behaviour. *Experimental Brain Research*, *233*(3), 679-689. doi: 10.1007/s00221-014-4183-7

8. Borenstein, M., Hedges, L., Higgins, J., & Rothstein, H. (2010). A basic introduction to fixed-effect and random-effects models for meta-analysis. *Research Synthesis Methods*, *1*(2), 97-111. https://doi.org/10.1002/jrsm.12

9. Brouwer, B., & Ashby, P. (1990). Corticospinal projections to upper and lower limb spinal motoneurons in man. *Electroencephalography And Clinical Neurophysiology*, *76*(6), 509-519. https://doi.org/10.1016/0013-4694(90)90002-2

10. Brownstein, C., Ansdell, P., Škarabot, J., Howatson, G., Goodall, S., & Thomas, K. (2018). An optimal protocol for measurement of corticospinal excitability, short intracortical inhibition and intracortical facilitation in the rectus femoris. *Journal Of The Neurological Sciences*, *394,* 45-56. doi: 10.1016/j.jns.2018.09.001

11. Brownstein, C., Dent, J., Parker, P., Hicks, K., Howatson, G., Goodall, S., & Thomas, K. (2017). Etiology and Recovery of Neuromuscular Fatigue following Competitive Soccer Match-Play. *Frontiers In Physiology*, *8*. doi: 10.3389/fphys.2017.00831

12. Capaday, C., Lavoie, B. A., Barbeau, H., Schneider, C., & Bonnard, M. (1999). Studies on the corticospinal control of human walking. I. Responses to focal transcranial magnetic stimulation of the motor cortex. *Journal of Neurophysiology*, *81*(1), 129–139. https://doi.org/10.1152/jn.1999.81.1.129

13. Christiansen, L., Larsen, M., Madsen, M., Grey, M., Nielsen, J., & Lundbye-Jensen, J. (2020). Long-term motor skill training with individually adjusted progressive difficulty enhances learning and promotes corticospinal plasticity. *Scientific Reports*, *10*(1). https://doi.org/10.1038/s41598-020-72139-8

14. Christiansen, L., Madsen, M., Bojsen-Møller, E., Thomas, R., Nielsen, J., & Lundbye-Jensen, J. (2018). Progressive practice promotes motor learning and repeated transient increases in corticospinal excitability across multiple days. *Brain Stimulation*, *11*(2), 346-357. https://doi.org/10.1016/j.brs.2017.11.005

15. Cohen, J. (1998). *Statistical power analysis for the behavioural sciences*. *New York Lawrence Erlbaum Associates.*

16. DeVito, N., & Goldacre, B. (2018). Catalogue of bias: publication bias. *BMJ Evidence-Based Medicine*, *24*(2), 53-54. doi: 10.1136/bmjebm-2018-111107

17. Di Lazzaro, V., Oliviero, A., Meglio, M., Cioni, B., Tamburrini, G., Tonali, P., & Rothwell, J. (2000). Direct demonstration of the effect of lorazepam on the excitability of the human motor cortex. *Clinical Neurophysiology*, *111*(5), 794-799. doi: 10.1016/s1388-2457(99)00314-4

18. Dickins, D., Sale, M., & Kamke, M. (2015). Intermanual transfer and bilateral cortical plasticity is maintained in older adults after skilled motor training with simple and complex tasks. *Frontiers In Aging Neuroscience*, *7*. https://doi.org/10.3389/fnagi.2015.00073

19. Downs, S., & Black, N. (1998). The feasibility of creating a checklist for the assessment of the methodological quality both of randomised and non-randomised studies of health care interventions. *Journal of Epidemiology &Amp; Community Health*, *52*(6), 377-384. https://doi.org/10.1136/jech.52.6.377

20. Driessen, E., Hollon, S., Bockting, C., Cuijpers, P., & Turner, E. (2015). Does Publication Bias Inflate the Apparent Efficacy of Psychological Treatment for Major Depressive Disorder? A Systematic Review and Meta-Analysis of US National Institutes of Health-Funded Trials. *PLOS ONE*, *10*(9), e0137864. doi: 10.1371/journal.pone.0137864

21. Dupont-Hadwen, J., Bestmann, S., & Stagg, C. J. (2019). Motor training modulates intracortical inhibitory dynamics in motor cortex during movement preparation. *Brain Stimulation*, *12*(2), 300–308. https://doi.org/10.1016/j.brs.2018.11.002

22. Edgley, S. (1997). Comparison of activation of corticospinal neurons and spinal motor neurons by magnetic and electrical transcranial stimulation in the lumbosacral cord of the anaesthetized monkey. *Brain*, *120*(5), 839–853.

23. Fanelli, D. (2013). Positive results receive more citations, but only in some disciplines. *Scientometrics*, *94*(2), 701-709. doi: 10.1007/s11192-012-0757-y

24. Fimland, M., Helgerud, J., Gruber, M., Leivseth, G., & Hoff, J. (2010). Enhanced neural drive after maximal strength training in multiple sclerosis patients. *European Journal of Applied Physiology*, *110*(2), 435-443. https://doi.org/10.1007/s00421-010-1519-2

25. Garry, M., Kamen, G., & Nordstrom, M. (2004). Hemispheric Differences in the Relationship Between Corticomotor Excitability Changes Following a Fine-Motor Task and Motor Learning. *Journal Of Neurophysiology*, *91*(4), 1570-1578. doi: 10.1152/jn.00595.2003

26. Giboin, L., Loewe, K., Hassa, T., Kramer, A., Dettmers, C., & Spiteri, S. et al. (2019). Cortical, subcortical and spinal neural correlates of slackline training-induced balance performance improvements. *Neuroimage*, *202*, 116061. https://doi.org/10.1016/j.neuroimage.2019.116061

27. Giboin, L., Tokuno, C., Kramer, A., Henry, M., & Gruber, M. (2020). Motor learning induces time-dependent plasticity that is observable at the spinal cord level. *The Journal of Physiology*, *598*(10), 1943-1963. https://doi.org/10.1113/jp278890

28. Goodall, S., Howatson, G., & Thomas, K. (2017). Modulation of specific inhibitory networks in fatigued locomotor muscles of healthy males. *Experimental Brain Research*, *236*(2), 463-473. doi: 10.1007/s00221-017-5142-x

29. Goodall, S., Howatson, G., Romer, L., & Ross, E. (2014). Transcranial magnetic stimulation in sport science: A commentary. *European Journal Of Sport Science*, *14*(S1), S332-S340. doi: 10.1080/17461391.2012.704079

30. Grosprêtre, S., Bouguetoch, A., & Martin, A. (2019). Cortical and spinal excitabilities are differently balanced in power athletes. *European Journal of Sport Science*, *20*(3), 415-425. https://doi.org/10.1080/17461391.2019.1633414

31. Gruber, M., Taube, W., Gollhofer, A., Beck, S., Amtage, F., & Schubert, M. (2007). Training-Specific Adaptations of H- and Stretch Reflexes in Human Soleus Muscle. *Journal Of Motor Behavior*, *39*(1), 68-78. https://doi.org/10.3200/jmbr.39.1.68-78

32. Hallett, M. (1996). Transcranial magnetic stimulation: A useful tool for clinical neurophysiology. *Annals Of Neurology*, *40*(3), 344-345. doi: 10.1002/ana.410400303

33. Hand, B., Opie, G., Sidhu, S., & Semmler, J. (2020). TMS coil orientation and muscle activation influence lower limb intracortical excitability. *Brain Research*, *1746*, 147027. doi: 10.1016/j.brainres.2020.147027

34. Hatem, S., Saussez, G., della Faille, M., Prist, V., Zhang, X., Dispa, D., & Bleyenheuft, Y. (2016). Rehabilitation of Motor Function after Stroke: A Multiple Systematic Review Focused on Techniques to Stimulate Upper Extremity Recovery. *Frontiers In Human Neuroscience*, *10*. https://doi.org/10.3389/fnhum.2016.00442

35. Heise, K.-F., Zimerman, M., Hoppe, J., Gerloff, C., Wegscheider, K., & Hummel, F. C. (2013). The Aging Motor System as a model for plastic changes of GABA-mediated intracortical inhibition and their behavioral relevance. *Journal of Neuroscience*, *33*(21), 9039–9049. https://doi.org/10.1523/jneurosci.4094-12.2013

36. Higgins, J., Green, S. (2011). Cochrane handbook for systematic reviews of interventions. The Cochrane Collaboration. Available from www.cochrane-handbook.org

37. Hirano, M., Kubota, S., Koizume, Y., & Funase, K. (2018). Acquisition of motor memory determines the interindividual variability of learning-induced plasticity in the primary motor cortex. *Journal of Applied Physiology*, *125*(4), 990-998. https://doi.org/10.1152/japplphysiol.00470.2018

38. Hirano, M., Kubota, S., Tanabe, S., Koizume, Y., & Funase, K. (2015). Interactions Among Learning Stage, Retention, and Primary Motor Cortex Excitability in Motor Skill Learning. *Brain Stimulation*, *8*(6), 1195-1204. https://doi.org/10.1016/j.brs.2015.07.025

39. Hortobágyi, T., Granacher, U., Fernandez-del-Olmo, M., Howatson, G., Manca, A., & Deriu, F. et al. (2021). Functional relevance of resistance training-induced neuroplasticity in health and

disease. *Neuroscience & Biobehavioral Reviews*, *122,* 79-91. https://doi.org/10.1016/j.neubiorev.2020.12.019

40. Hummel, F. C., Steven, B., Hoppe, J., Heise, K., Thomalla, G., Cohen, L. G., & Gerloff, C. (2009). Deficient intracortical inhibition (SICI) during movement preparation after chronic stroke. *Neurology, 72*(20), 1766–1772. https://doi.org/10.1212/wnl.0b013e3181a609c5

41. Jensen, J., Marstrand, P., & Nielsen, J. (2005). Motor skill training and strength training are associated with different plastic changes in the central nervous system. *Journal of Applied Physiology*, *99*(4), 1558-1568. https://doi.org/10.1152/japplphysiol.01408.2004

42. Keller, M., Pfusterschmied, J., Buchecker, M., Müller, E., & Taube, W. (2012). Improved postural control after slackline training is accompanied by reduced H-reflexes. *Scandinavian Journal of Medicine & Science In Sport*, *22*(4), 471-477. https://doi.org/10.1111/j.1600-0838.2010.01268.x

43. Kesar, T., Stinear, J., & Wolf, S. (2018). The use of transcranial magnetic stimulation to evaluate cortical excitability of lower limb musculature: Challenges and opportunities. *Restorative Neurology and Neuroscience, 36*(3), 333-348. https://doi.org/10.3233/rnn-170801

44. Kidgell, D., Bonanno, D., Frazer, A., Howatson, G., & Pearce, A. (2017). Corticospinal responses following strength training: a systematic review and meta-analysis. *European Journal Of Neuroscience, 46*(11), 2648-2661. doi: 10.1111/ejn.13710

45. Kleim, J., Lussnig, E., Schwarz, E., Comery, T., & Greenough, W. (1996). Synaptogenesis and FOS Expression in the Motor Cortex of the Adult Rat after Motor Skill Learning. *The Journal of Neuroscience, 16*(14), 4529-4535. https://doi.org/10.1523/jneurosci.16-14-04529.1996

46. Kobayashi, M., & Pascual-Leone, A. (2003). Transcranial magnetic stimulation in neurology. *The Lancet Neurology*, *2*(3), 145-156. doi: 10.1016/s1474-4422(03)00321-1

47. Kubota, S., Hirano, M., Koizume, Y., Tanabe, S., & Funase, K. (2015). Changes in the Spinal Neural Circuits are Dependent on the Movement Speed of the Visuomotor Task. *Frontiers In Human Neuroscience, 9*. https://doi.org/10.3389/fnhum.2015.00667

48. Kujirai, T., Caramia, M., Rothwell, J., Day, B., Thompson, P., & Ferbert, A. et al. (1993). Corticocortical inhibition in human motor cortex. *The Journal Of Physiology, 471*(1), 501-519. doi: 10.1113/jphysiol.1993.sp019912

49. Lee, M., Hinder, M., Gandevia, S., & Carroll, T. (2010). The ipsilateral motor cortex contributes to cross-limb transfer of performance gains after ballistic motor practice. *The Journal of Physiology*, *588*(1), 201-212. https://doi.org/10.1113/jphysiol.2009.183855

50. Leung, M., Rantalainen, T., Teo, W., & Kidgell, D. (2015). Motor cortex excitability is not differentially modulated following skill and strength training. *Neuroscience*, *305*, 99-108. https://doi.org/10.1016/j.neuroscience.2015.08.007

51. Leung, M., Rantalainen, T., Teo, W., & Kidgell, D. (2017). The corticospinal responses of metronome-paced, but not self-paced strength training are similar to motor skill training. *European Journal of Applied Physiology*, *117*(12), 2479-2492. https://doi.org/10.1007/s00421-017-3736-4

52. Liepert, J., Classen, J., Cohen, L., & Hallett, M. (1998). Task-dependent changes of intracortical inhibition. *Experimental Brain Research*, *118*(3), 421-426. doi: 10.1007/s002210050296

53. Maniar, N., Shield, A., Williams, M., Timmins, R., & Opar, D. (2016). Hamstring strength and flexibility after hamstring strain injury: a systematic review and meta-analysis. *British Journal of Sports Medicine*, *50*(15), 909-920. https://doi.org/10.1136/bjsports-2015-095311

54. Mason, J., Frazer, A., Jaberzadeh, S., Ahtiainen, J., Avela, J., & Rantalainen, T. et al. (2019). Determining the Corticospinal Responses to Single Bouts of Skill and Strength Training. *Journal of Strength and Conditioning Research*, *33*(9), 2299-2307. https://doi.org/10.1519/jsc.0000000000003266

55. Mooney, R., Cirillo, J., & Byblow, W. (2019). Neurophysiological mechanisms underlying motor skill learning in young and older adults. *Experimental Brain Research*, *237*(9), 2331-2344. https://doi.org/10.1007/s00221-019-05599-8

56. Mrachacz-Kersting, N., Stevenson, A., & Ziemann, U. (2021). Short-interval intracortical inhibition and facilitation targeting upper and lower limb muscles. *Scientific Reports*, *11*(1). doi: 10.1038/s41598-021-01348-6

57. Muellbacher, W., Ziemann, U., Boroojerdi, B., Cohen, L., & Hallett, M. (2001). Role of the human motor cortex in rapid motor learning. *Experimental Brain Research*, *136*(4), 431-438. https://doi.org/10.1007/s002210000614

58. Neyroud, D., Rüttimann, J., Mannion, A., Millet, G., Maffiuletti, N., Kayser, B., & Place, N. (2013). Comparison of neuromuscular adjustments associated with sustained isometric contractions of four different muscle groups. *Journal Of Applied Physiology*, *114*(10), 1426-1434. doi: 10.1152/japplphysiol.01539.2012

59. NI, Z., & Chen, R. (2011). Excitatory and Inhibitory Effects of Transcranial Magnetic Stimulation. *Biocybernetics And Biomedical Engineering*, *31*(2), 93-105. doi: 10.1016/s0208-5216(11)70014-6

60. Page, M., McKenzie, J., Bossuyt, P., Boutron, I., Hoffmann, T., & Mulrow, C. et al. (2021). The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. *BMJ*, 372, n71. https://doi.org/10.1136/bmj.n71

61. Pageaux, B., Marcora, S., & Lepers, R. (2013). Prolonged Mental Exertion Does Not Alter Neuromuscular Function of the Knee Extensors. *Medicine &Amp; Science In Sports &Amp; Exercise*, *45*(12), 2254-2264. doi: 10.1249/mss.0b013e31829b504a

62. Paparella, G., Rocchi, L., Bologna, M., Berardelli, A., & Rothwell, J. (2020). Differential effects of motor skill acquisition on the primary motor and sensory cortices in healthy humans. *The Journal of Physiology*, *598*(18), 4031-4045. https://doi.org/10.1113/jp279966

63. Pascual-Leone, A., Nguyet, D., Cohen, L., Brasil-Neto, J., Cammarota, A., & Hallett, M. (1995). Modulation of muscle responses evoked by transcranial magnetic stimulation during the acquisition of new fine motor skills. *Journal of Neurophysiology*, *74*(3), 1037-1045. https://doi.org/10.1152/jn.1995.74.3.1037

64. Perez, M., Lungholt, B., & Nielsen, J. (2005). Presynaptic control of group Ia afferents in relation to acquisition of a visuo-motor skill in healthy humans. *The Journal of Physiology*, *568*(1), 343-354. https://doi.org/10.1113/jphysiol.2005.089904

65. Perez, M., Lungholt, B., Nyborg, K., & Nielsen, J. (2004). Motor skill training induces changes in the excitability of the leg cortical area in healthy humans. *Experimental Brain Research*, *159*(2), 197-205. https://doi.org/10.1007/s00221-004-1947-5

66. Place, N., Yamada, T., Bruton, J., & Westerblad, H. (2010). Muscle fatigue: from observations in humans to underlying mechanisms studied in intact single muscle fibres. *European Journal of Applied Physiology*, *110*(1), 1-15. doi: 10.1007/s00421-010-1480-0

67. Poh, E., Riek, S., & Carroll, T. (2012). Ipsilateral corticospinal responses to ballistic training are similar for various intensities and timings of TMS. *Acta Physiologica*, *207*(2), 385-396. https://doi.org/10.1111/apha.12032

68. Rantalainen, T., Weier, A., Leung, M., Brandner, C., Spittle, M., & Kidgell, D. (2013). Short-interval intracortical inhibition is not affected by varying visual feedback in an isometric task in biceps brachii muscle. *Frontiers In Human Neuroscience*, *7*. doi: 10.3389/fnhum.2013.00068

69. Rodriguez-Falces, J., & Place, N. (2017). Determinants, analysis and interpretation of the muscle compound action potential (M wave) in humans: implications for the study of muscle fatigue. *European Journal of Applied Physiology*, *118*(3), 501-521. doi: 10.1007/s00421-017-3788-5

70. Rossini, P. M., Burke, D., Chen, R., Cohen, L. G., Daskalakis, Z., Di Iorio, R., Di Lazzaro, V., Ferreri, F., Fitzgerald, P. B., George, M. S., Hallett, M., Lefaucheur, J. P., Langguth, B., Matsumoto, H., Miniussi, C., Nitsche, M. A., Pascual-Leone, A., Paulus, W., Rossi, S., … Ziemann, U. (2015). 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. *Clinical Neurophysiology*, *126*(6), 1071–1107. https://doi.org/10.1016/j.clinph.2015.02.001

71. Saito, S., Obata, H., Endoh, T., Kuno-Mizumura, M., & Nakazawa, K. (2014). Corticospinal Excitability of the Ankle Extensor Muscles Is Enhanced in Ballet Dancers. *Medical Problems of Performing Artists*, *29*(3), 144-149. https://doi.org/10.21091/mppa.2014.3030

72. Schmucker, C., Schell, L., Portalupi, S., Oeller, P., Cabrera, L., & Bassler, D. et al. (2014). Extent of Non-Publication in Cohorts of Studies Approved by Research Ethics Committees or Included in Trial Registries. *Plos ONE*, *9*(12), e114023. doi: 10.1371/journal.pone.0114023

73. Schubert, M., Beck, S., Taube, W., Amtage, F., Faist, M., & Gruber, M. (2008). Balance training and ballistic strength training are associated with task-specific corticospinal adaptations. *European Journal of Neuroscience*, *27*(8), 2007-2018. https://doi.org/10.1111/j.1460-9568.2008.06186.x

74. Siddique, U., Rahman, S., Frazer, A., Pearce, A., Howatson, G., & Kidgell, D. (2020). Determining the Sites of Neural Adaptations to Resistance Training: A Systematic Review and Meta-analysis. *Sports Medicine*, *50*(6), 1107-1128. doi: 10.1007/s40279-020-01258-z

75. Škarabot, J., Balshaw, T., Maeo, S., Massey, G., Lanza, M., Maden-Wilkinson, T., & Folland, J. (2021). Neural adaptations to long-term resistance training: evidence for the confounding effect of muscle size on the interpretation of surface electromyography. *Journal of Applied Physiology*, *131*(2), 702-715. doi: 10.1152/japplphysiol.00094.2021

76. Smith, M., Stinear, J., Alan Barber, P., & Stinear, C. (2017). Effects of non-target leg activation, TMS coil orientation, and limb dominance on lower limb motor cortex excitability. *Brain Research*, *1655*, 10-16. https://doi.org/10.1016/j.brainres.2016.11.004

77. Smyth, C., Summers, J., & Garry, M. (2010). Differences in motor learning success are associated with differences in M1 excitability. *Human Movement Science*, *29*(5), 618-630. https://doi.org/10.1016/j.humov.2010.02.006

78. Stinear, C., & Byblow, W. (2003). Role of Intracortical Inhibition in Selective Hand Muscle Activation. *Journal of Neurophysiology*, *89*(4), 2014-2020. doi: 10.1152/jn.00925.2002

79. Takeo, Y., Hara, M., Shirakawa, Y., Ikeda, T., & Sugata, H. (2021). Sequential motor learning transfers from real to virtual environment. *Journal of Neuroengineering and Rehabilitation*, *18*(1). https://doi.org/10.1186/s12984-021-00903-6

80. Tallent, J., Goodall, S., Gibbon, K., Hortobágyi, T., & Howatson, G. (2017). Enhanced Corticospinal Excitability and Volitional Drive in Response to Shortening and Lengthening Strength Training and Changes Following Detraining. *Frontiers In Physiology*, *8*. doi: 10.3389/fphys.2017.00057

81. Tallent, J., Woodhead, A., Frazer, A., Hill, J., Kidgell, D., & Howatson, G. (2021). Corticospinal and spinal adaptations to motor skill and resistance training: Potential mechanisms and implications for motor rehabilitation and athletic development. *European Journal of Applied Physiology*, *121*(3), 707-719. https://doi.org/10.1007/s00421-020-04584-2

82. Tatemoto, T., Tanaka, S., Maeda, K., Tanabe, S., Kondo, K., & Yamaguchi, T. (2019). Skillful Cycling Training Induces Cortical Plasticity in the Lower Extremity Motor Cortex Area in Healthy Persons. *Frontiers In Neuroscience*, *13*. https://doi.org/10.3389/fnins.2019.00927

83. Taube, W., Gruber, M., Beck, S., Faist, M., Gollhofer, A., & Schubert, M. (2007). Cortical and spinal adaptations induced by balance training: correlation between stance stability and corticospinal activation. *Acta Physiologica*, *189*, 347-358. https://doi.org/10.1111/j.1748-1716.2007.01665.x

84. Terao, Y., & Ugawa, Y. (2002). Basic mechanisms of TMS. *Journal of Clinical Neurophysiology*, *19*(4), 322–343. https://doi.org/10.1097/00004691-200208000-00006

85. Thompson, A., Cote, R., Sniffen, J., & Brangaccio, J. (2018). Operant conditioning of the tibialis anterior motor evoked potential in people with and without chronic incomplete spinal cord injury. *Journal of Neurophysiology*, *120*(6), 2745-2760. doi: 10.1152/jn.00362.2018

86. Tracy, B. (2007). Visuomotor contribution to force variability in the plantarflexor and dorsiflexor muscles. *Human Movement Science*, *26*(6), 796-807. https://doi.org/10.1016/j.humov.2007.07.001

87. Trimble, M., & Koceja, D. (1994). Modulation of the Triceps Surae H-Reflex with Training. *International Journal of Neuroscience*, *76*(3-4), 293-303. doi: 10.3109/00207459408986011

88. Ung, R., Imbeault, M., Ethier, C., Brizzi, L., & Capaday, C. (2005). On the Potential Role of the Corticospinal Tract in the Control and Progressive Adaptation of the Soleus H-Reflex During Backward Walking. *Journal of Neurophysiology, 94*(2), 1133-1142. https://doi.org/10.1152/jn.00181.2005

89. Yamaguchi, T., Fujiwara, T., Liu, W., & Liu, M. (2012). Effects of pedaling exercise on the intracortical inhibition of cortical leg area. *Experimental Brain Research*, *218*(3), 401-406. doi: 10.1007/s00221-012-3026-7

90. Yamazaki, Y., Sato, D., Yamashiro, K., Nakano, S., Onishi, H., & Maruyama, A. (2019). Acute Low-Intensity Aerobic Exercise Modulates Intracortical Inhibitory and Excitatory Circuits in an Exercised and a Non-exercised Muscle in the Primary Motor Cortex. *Frontiers In Physiology*, *10*. doi: 10.3389/fphys.2019.01361

91. Ziemann, U., Lönnecker, S., Steinhoff, B., & Paulus, W. (1996). The effect of lorazepam on the motor cortical excitability in man. *Experimental Brain Research*, *109*(1). doi: 10.1007/bf00228633

92. Ziemann, U., Muellbacher, W., Hallett, M., & Cohen, L. (2001). Modulation of practice-dependent plasticity in human motor cortex. *Brain*, *124*(6), 1171-1181. doi: 10.1093/brain/124.6.1171

93. Zoghi, M., Pearce, S., & Nordstrom, M. (2003). Differential Modulation of Intracortical Inhibition in Human Motor Cortex during Selective Activation of an Intrinsic Hand Muscle. *The Journal of Physiology*, *550*(3), 933-946. doi: 10.1113/jphysiol.2003.042606

Table 1. Search terms.

Table 2. Study characteristics for included studies within the meta-analysis.

Table 3. Study characteristics for included studies within the best evidence synthesis.

Figure 1. The process of identifying, screening, and assessing the included studies according to the PRISMA 2020 guidelines.

Figure 2. Risk of bias: review authors' judgements about each risk of bias item presented as a) percentages across all included studies and b) Risk of bias summary for each included study.

Figure 3. Forest plots showing the a) pooled effect of lower limb motor skill training on measures of motor performance (six studies, 155 participants), b) effect sizes following a single session and c) multiple weeks of lower limb motor skill training. Std, Standardised mean difference; IV, inverse variance; Random, random effect model; CI, confidence interval; df, degrees of freedom; I^2, inconsistency statistic. Statistical significance set at $P < 0.05$. Effect size, Cohen's *d*; 95% CI, confidence intervals.

Figure 4. Forest plots showing the a) pooled effect of lower limb motor skill training on corticospinal excitability (two studies, 44 participants), and b) effect sizes for corticospinal excitability following lower limb motor skill training. Std, Standardised mean difference; IV, inverse variance; Random, random effect model; CI, confidence interval; df, degrees of freedom; I^2, inconsistency statistic. Statistical significance set at $P < 0.05$. *indicates a single session of motor skill training. Effect size, Cohen's *d*; 95% CI, confidence intervals.

Figure 5. Forest plots showing the effect of lower limb motor skill training on the H-reflex response (four studies, 96 participants). Std, Standardised mean difference; IV, inverse variance; Random, random effect model; CI, confidence interval; df, degrees of freedom; I^2, inconsistency statistic. Statistical significance set at $P < 0.05$.

Figure 6. Forest plots showing the effect of lower limb motor skill training on M_{MAX} amplitude (two studies, 53 participants). Std, Standardised mean difference; IV, inverse variance; Random, random effect model; CI, confidence interval; df, degrees of freedom; I^2, inconsistency statistic. Statistical significance set at $P < 0.05$. *Keller et al. (40) had a lower M_{MAX} at baseline in the experimental compared to control group.

Figure 7. Forest plot showing effect sizes for short-interval intracortical inhibition following lower limb motor skill training. *indicates a single session of motor skill training. Effect size, Cohen's *d*; 95% CI, confidence intervals.

Table 1. Search terms.

Term	**Search strategy**
OR	1. “motor learning” OR “motor skill learning” OR “motor training” OR “motor skill training” OR “motor skill acquisition” OR “motor performance” OR “motor behaviour” OR “motor memory consolidation” OR “lower limb” OR “lower extremities” OR “lower body” OR “leg” OR “single session” OR “multiple sessions” OR “training programme” OR “task learning” OR “sequential learning” OR “balance task” OR “task-specific improvement” OR “visuomotor task” OR “force tracking task”
WITH	2. "neural adaptations” OR “neuronal plasticity” OR “corticospinal plasticity”
OR	3. “transcranial magnetic stimulation” OR “TMS” OR “TMS measures” OR “TMS parameters” OR “motor cortex” OR “corticospinal excitability” OR “motor evoked potential” OR “corticospinal inhibition” OR “silent period” OR “voluntary activation” OR “SICI” OR “short-interval intracortical inhibition” OR “intracortical inhibition” OR “H-reflex” OR “V-wave” OR “F-wave”.

Table 2. Study characteristics for included studies within the meta-analysis.

Study	Intervention	Participant characteristics	Target muscle	Key DV	Key measures	Results	*D&B*
Giboin et al. (2019)	12 sessions over 6 weeks, slackline training 2 x per week	44 untrained healthy young adults. Trained (*n* = 22, 22 ± 2 years, 8M & 14F). Control (*n* = 22, 25 ± 4 years, 12M & 10F)	Soleus	Spinal excitability, balance performance	H-reflex (% M_{MAX}), Number of steps	↓ H-reflex, ↑ Number of steps	12/17
Gruber et al. (2007)	16 sessions over 4 weeks, postural stabilisation tasks of the right leg, 4 x per week	20 untrained healthy young adults. SMT (*n* = 11, 26 ± 5 years, 7M & 4F). Control (*n* = 9, 26 ± 3 years, 5M & 4F)	Soleus	H-reflex, balance performance	H_{MAX}/M_{MAX} Ratio, Cumulative sway path	↓ H_{MAX}/M_{MAX} Ratio, ↓ Cumulative sway path	13/17
Keller et al. (2012)	10 sessions over 4 weeks, 90 min slackline training, 2-3 x per week	24 healthy young adults. Trained (*n* = 12, 6M & 6F). Control (*n* = 12, 6M & 6F)	Soleus	Spinal excitability, balance performance	H_{MAX}/M_{MAX} Ratio, Sway path	↑ H_{MAX}/M_{MAX} Ratio, ↓ Sway path	13/17
Taube et al. (2007)	16 sessions over 4 weeks, postural stabilisation tasks of the right leg, 4 x per week	23 healthy young adults. SMT (*n* = 13, 25 ± 3 years, 8M & 5F). Control (*n* = 10, 27 ± 5 years, 6M & 4F)	Soleus	Spinal excitability, balance performance	H_{MAX}/M_{MAX} Ratio, Cumulative sway path	↓ H_{MAX}/M_{MAX} Ratio, ↓ Cumulative sway path	14/17
Perez et al. (2004)	Single session (32-minutes) of visuomotor training, ankle dorsi-and plantarflexions.	25 healthy young adults (28 ± 7 years, 14M & 11F). Motor skill (*n* = 10), non-skill (*n* = 10) and passive training (*n* = 10).	TA	Corticospinal excitability, SICI, tracking error	MEP amplitude (% of M_{MAX}), Conditioned MEP (% of control MEP), Tracking error	↑ MEP amplitude, ↓ SICI, ↓ Visuomotor tracking error	13/17

Bakker et al. (2021)	Single session (30-minutes) of balance skill training.	36 healthy young adults. BT (*n* = 12, 20.67 ± 1.07 years, 6M & 6F). NC (*n* = 12, 21.58 ± 2.50 years, 6M & 6F).	TA	Corticospinal excitability, SICI, balance performance	MEP amplitude (mV), SICI (% of MEP sitting), balance board – time in balance (%).	↔ MEP amplitude, ↔ SICI, ↑ time to balance.	13/17

BT, balance training; *D&B*, Downs and Black Quality Assessment; F, female; H_{MAX}, maximum H-reflex; M, male; M_{MAX}, maximum M-wave; mV, millivolts; NC, no-intervention control group; SICI, short-interval intracortical inhibition; SMT, sensorimotor training; TA, tibialis anterior. ↑ increase, ↓ decrease, ↔ no change. *Keller et al. (34) shows an increase H-reflex response after pooled across multiple conditions.

Table 3. Study characteristics for included studies within the best evidence synthesis.

Study	**Intervention**	**Participant characteristics**	**Muscle**	**Key DV**	**Key measures**	**Results**	***D&B***
Giboin et al. (2020)	Two sessions separated by 24 h (experimental and retention)	18 untrained healthy young adults (*n* = 18, 27 ± 8 years, 8M & 10F)	Soleus	Balance performance	Tilt-board performance (s)	↑ Time spent on tilt-board.	13/17
Hirano et al. (2018)	Single session of visuomotor tracking ankle dorsi-plantar flexions	28 healthy right-footed young adults (*n* = 28, 23 ± 1.2 years, 23M & 5F)	TA	Corticospinal excitability, M_{MAX}, visuomotor performance	I-O curves of MEP amplitude, M_{MAX} amplitude (mV), visuomotor error	↑ I-O curve, ↓ M_{MAX} amplitude, ↓ visuomotor error	12/17
Kubota et al. (2015)	Single session of visuomotor tracking ankle dorsi-plantar flexions	8 healthy young adults (*n* = 8; 22.37 ± 1.59 years, 6M & 5F)	Soleus	M_{MAX}, visuomotor performance	M_{MAX} amplitude (mV), motor error	↑ M_{MAX} amplitude, ↓ motor error	12/17
Hirano et al. (2015)	Two sessions on consecutive days (visuomotor tracking on day 1).	20 young adults. SMT (*n* = 20, 22.5 ± 2.5 years, 16M & 4F)	TA	Corticospinal excitability, M_{MAX}, visuomotor performance	I-O slope, M_{MAX} amplitude (mV), visuomotor performance (au)	↔ I-O slope, ↓ M_{MAX} amplitude, ↓ visuomotor error	12/17
Tatemoto et al. (2019)	Single session of skilful cycling training on a recumbent ergometer.	11 healthy young adults (*n* = 11, 25.4 ± 2.5 years, 8M & 3F).	TA	Corticospinal excitability, SICI, tracking error	MEP amplitude (mV), SICI (ratio), tracking error (au)	↔ CSE, ↓ SICI, ↓ tracking error	13/17

CSE, corticospinal excitability; Downs and Black Quality Assessment; F, female; I-O, input-output; M, male; M_{MAX}, maximal M-wave, SICI, short-interval intracortical inhibition; TA, tibialis anterior. ↑ increase, ↓ decrease, ↔ no change.

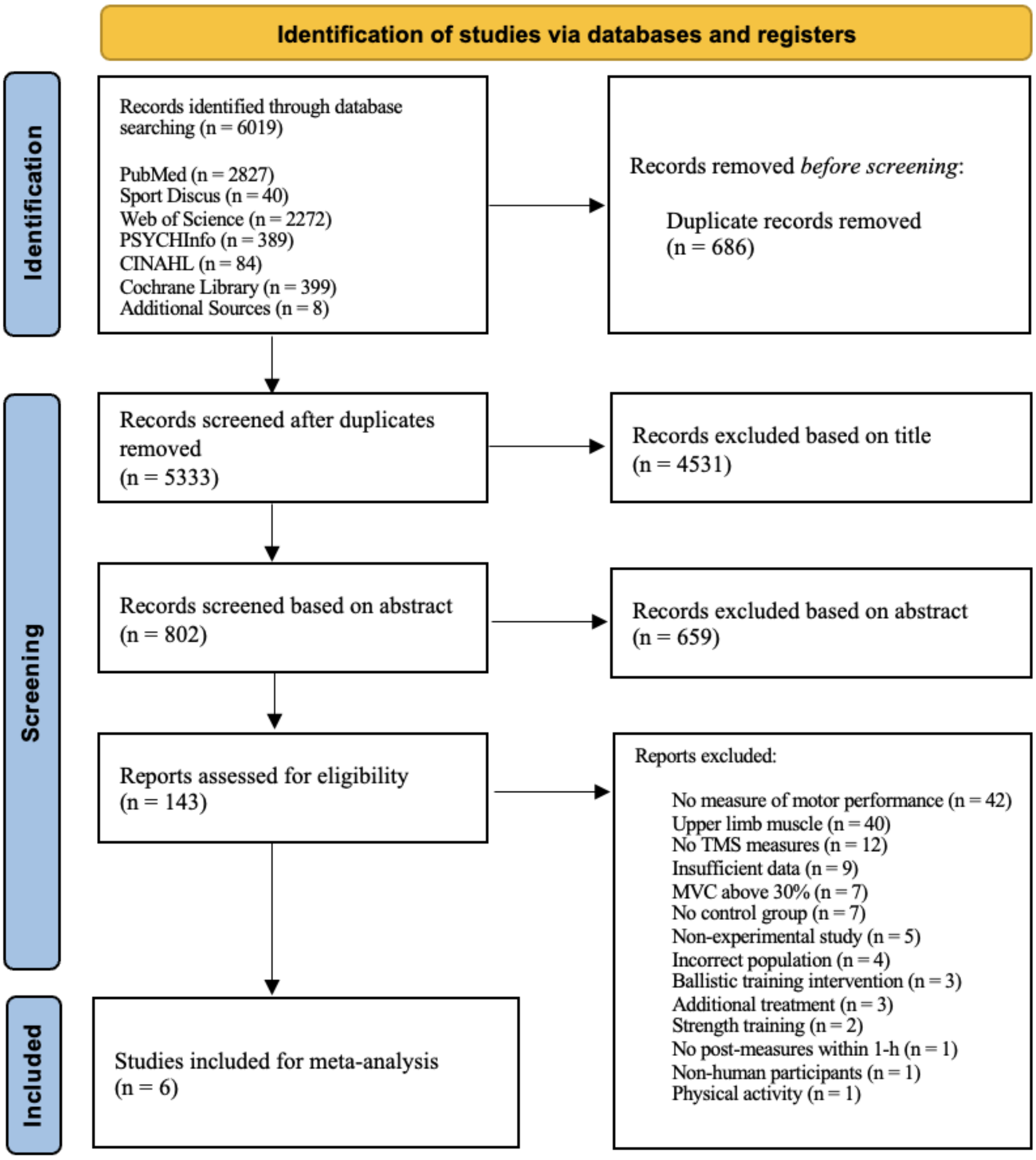
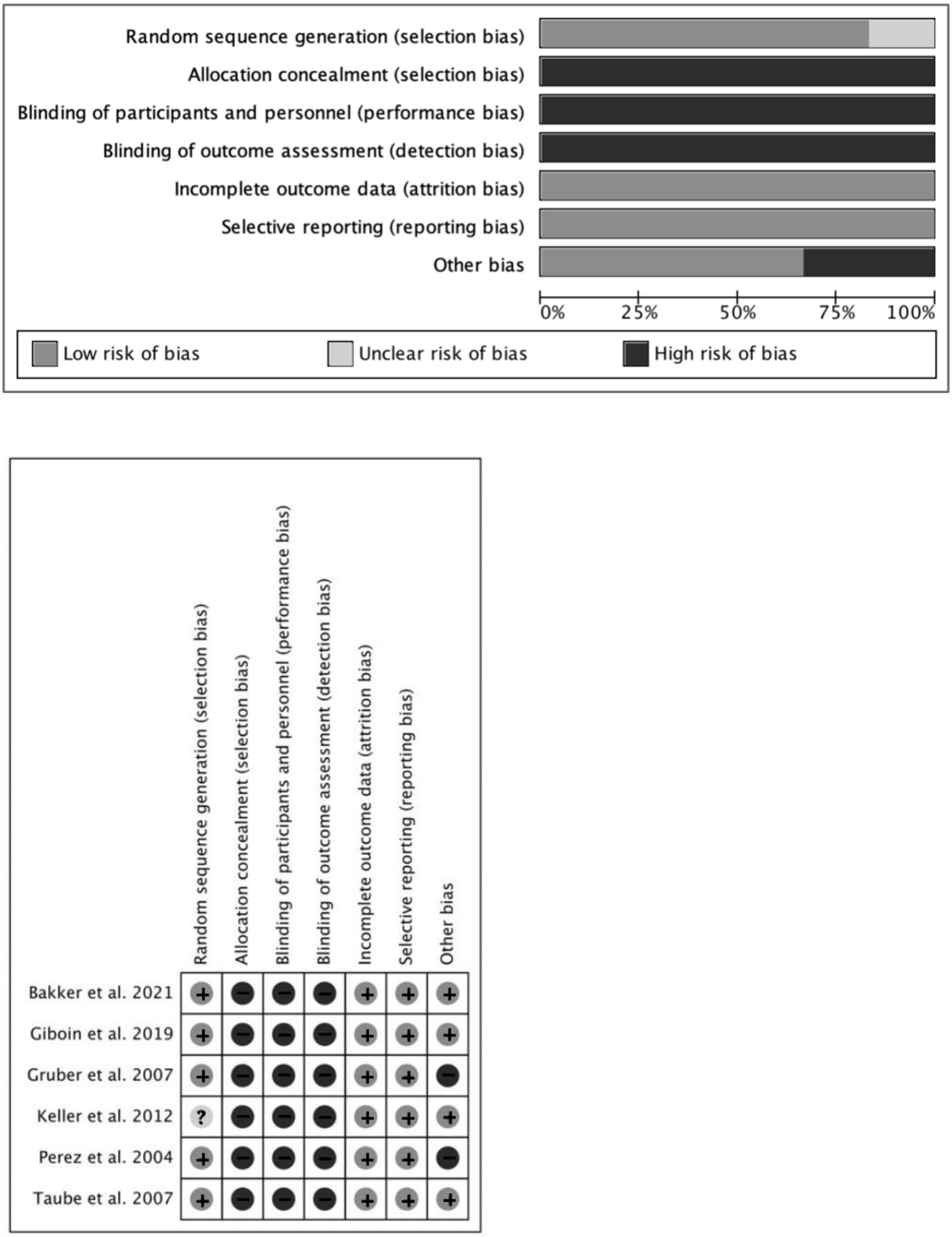


Fig. 1 The process of identifying, screening, and assessing the included studies according to the PRISMA 2020 guidelines



	Random sequence generation (selection bias)	Allocation concealment (selection bias)	Blinding of participants and personnel (performance bias)	Blinding of outcome assessment (detection bias)	Incomplete outcome data (attrition bias)	Selective reporting (reporting bias)	Other bias
Bakker et al. 2021	+	−	−	−	+	+	+
Giboin et al. 2019	+	−	−	−	+	+	+
Gruber et al. 2007	+	−	−	−	+	+	−
Keller et al. 2012	?	−	−	−	+	+	+
Perez et al. 2004	+	−	−	−	+	+	−
Taube et al. 2007	+	−	−	−	+	+	+

Fig. 2 Risk of bias: review authors' judgements about each risk of bias item presented as a) percentages across all included studies and b) Risk of bias summary for each included study

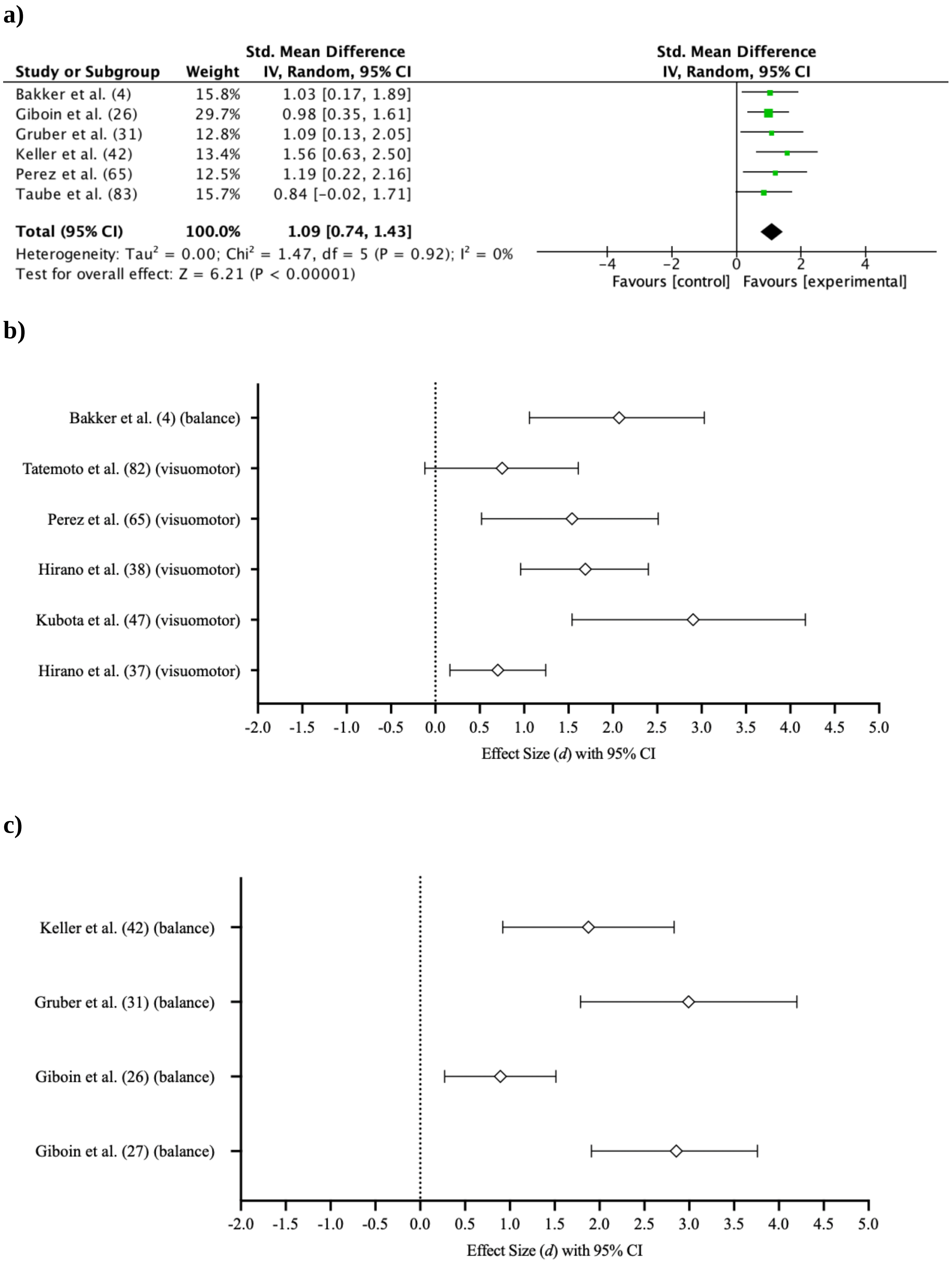


Fig. 3 Forest plots showing the a) pooled effect of lower limb motor skill training on measures of motor performance (six studies, 155 participants), b) effect sizes following a single session and c) multiple weeks of lower limb motor skill training. Std, Standardised mean difference; IV, inverse variance; Random, random effect

model; CI, confidence interval; df, degrees of freedom; I^2, inconsistency statistic. Statistical significance set at $P < 0.05$. Effect size, Cohen's *d*; 95% CI, confidence intervals

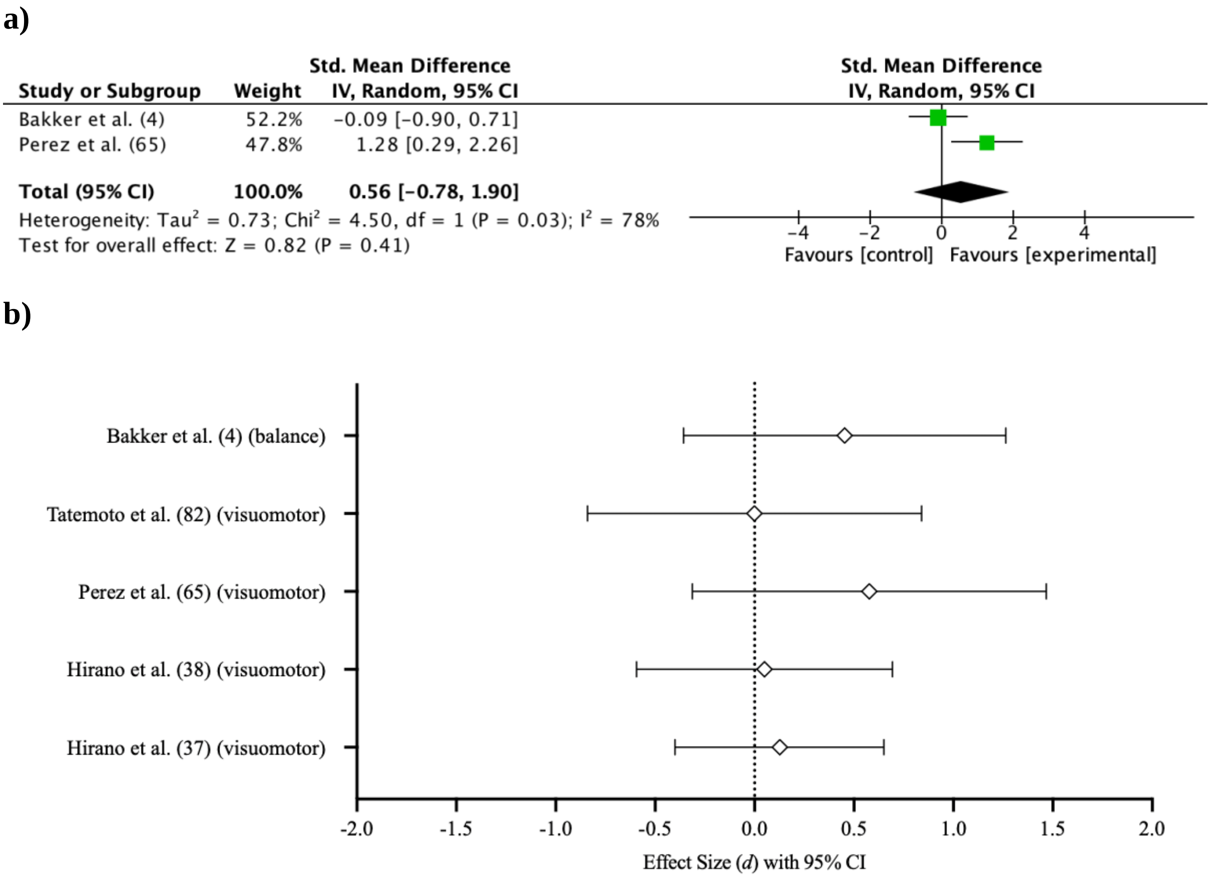
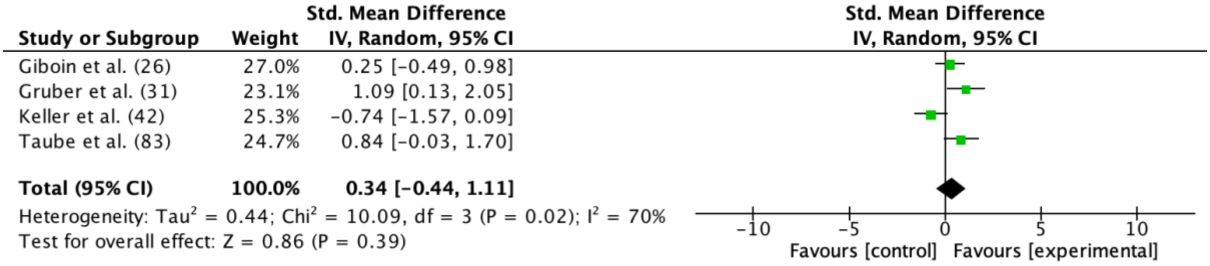


Fig. 4 Forest plots showing the a) pooled effect of lower limb motor skill training on corticospinal excitability (two studies, 44 participants), and b) effect sizes for corticospinal excitability following lower limb motor skill training. Std, Standardised mean difference; IV, inverse variance; Random, random effect model; CI, confidence interval; df, degrees of freedom; I^2, inconsistency statistic. Statistical significance set at $P < 0.05$. Effect size, Cohen's *d*; 95% CI, confidence intervals

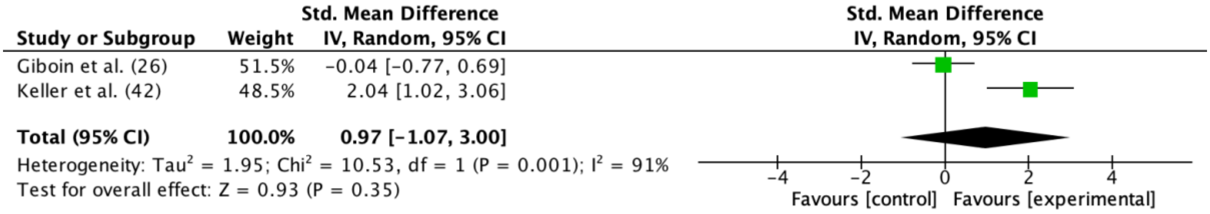


Study or Subgroup	Weight	Std. Mean Difference IV, Random, 95% CI
Giboin et al. (26)	27.0%	0.25 [−0.49, 0.98]
Gruber et al. (31)	23.1%	1.09 [0.13, 2.05]
Keller et al. (42)	25.3%	−0.74 [−1.57, 0.09]
Taube et al. (83)	24.7%	0.84 [−0.03, 1.70]
Total (95% CI)	**100.0%**	**0.34 [−0.44, 1.11]**

Heterogeneity: $Tau^2 = 0.44$; $Chi^2 = 10.09$, $df = 3$ ($P = 0.02$); $I^2 = 70\%$

Test for overall effect: $Z = 0.86$ ($P = 0.39$)

Fig. 5 Forest plots showing the effect of lower limb motor skill training on the H-reflex response (four studies, 96 participants). Std, Standardised mean difference; IV, inverse variance; Random, random effect model; CI, confidence interval; df, degrees of freedom; I^2, inconsistency statistic. Statistical significance set at $P < 0.05$



Study or Subgroup	Weight	Std. Mean Difference IV, Random, 95% CI
Giboin et al. (26)	51.5%	−0.04 [−0.77, 0.69]
Keller et al. (42)	48.5%	2.04 [1.02, 3.06]
Total (95% CI)	**100.0%**	**0.97 [−1.07, 3.00]**

Heterogeneity: $Tau^2 = 1.95$; $Chi^2 = 10.53$, df = 1 (P = 0.001); $I^2 = 91\%$

Test for overall effect: Z = 0.93 (P = 0.35)

Fig. 6 Forest plots showing the effect of lower limb motor skill training on M_{MAX} amplitude (two studies, 53 participants). Std, Standardised mean difference; IV, inverse variance; Random, random effect model; CI, confidence interval; df, degrees of freedom; I^2, inconsistency statistic. Statistical significance set at $P < 0.05$. *Keller et al. (42) had a lower M_{MAX} at baseline in the experimental compared to control group

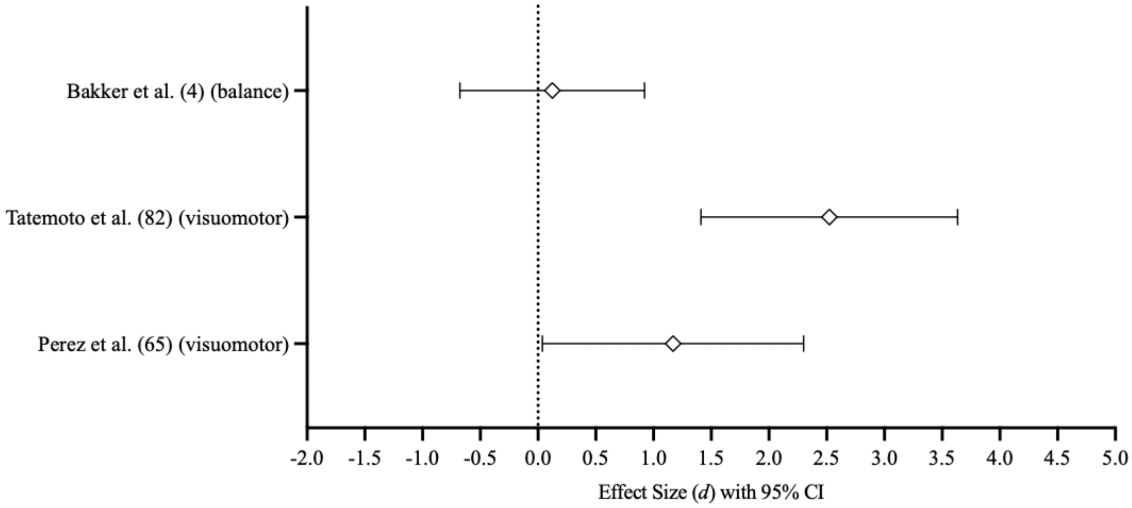


Fig. 7 Forest plot showing effect sizes for short-interval intracortical inhibition following lower limb motor skill training. Effect size, Cohen's *d*; 95% CI, confidence intervals