Corticospinal and spinal adaptations to motor skill and resistance training: Potential mechanisms and implications for motor rehabilitation and athletic development. \*Jamie Tallent<sup>1</sup>, Alex Woodhead<sup>1</sup>, Ashlyn K Frazer<sup>2</sup>, Jessica Hill<sup>1</sup>, Dawson J Kidgell<sup>2</sup>, Glyn Howatson<sup>3,4</sup> <sup>1</sup>Faculty of Sport, Health and Applied Sciences, St Mary's University, Twickenham, England. <sup>2</sup>Department of Physiotherapy, School of Primary and Allied Health Care, Faculty of Medicine, Nursing and Health Science, Monash University, Melbourne, Australia. <sup>3</sup>Department of Sport, Exercise and Rehabilitation, Northumbria University, Newcastle-upon-Tyne, <sup>4</sup>Water Research Group, Faculty of Natural and Agricultural Sciences, North West University, Potchefstroom, South Africa \*Corresponding Author Address St Mary's University Waldgrave Road Twickenham TW1 4SX **United Kingdom** Tel: +44 20 8240 4000 Fax: +44 20 8240 4255 Email: jamie.tallent@stmarys.ac.uk Word Count: 4051 

#### Abstract

33

34

35

36

37

38

39

40

41

42

43

44

45

46

47

48

49

50

51

52

Optimal strategies for enhancing strength and improving motor skills are vital in athletic performance and clinical rehabilitation. Initial increases in strength and the acquisition of new motor skills have long been attributed to neurological adaptations. However, early increases in strength may be predominantly due to improvements in inter-muscular coordination rather than the force generating capacity of the muscle. Despite the plethora of research investigating neurological adaptations from motor skill or resistance training in isolation, little effort has been made in consolidating this research to compare motor skill and resistance training adaptations. The findings of this review demonstrated that motor skill and resistance training adaptations show similar shortterm mechanisms of adaptations, particularly at a cortical level. Increases in corticospinal excitability and a release in short-interval cortical inhibition occur as a result of the commencement of both resistance and motor skill training. Spinal changes show evidence of task-specific adaptations from the acquired motor skill, with an increase or decrease in spinal reflex excitability, dependant on the motor task. An increase in synaptic efficacy of the reticulospinal projections is likely to be a prominent mechanism for driving strength adaptations at the subcortical level, though more research is needed. Transcranial electric stimulation has been shown to increase corticospinal excitability and augment motor skill adaptations, but limited evidence exists for further enhancing strength adaptations from resistance training. Despite the logistical challenges, future work should compare the longitudinal adaptations between motor skill and resistance training to further optimise exercise programming.

53

54

- **Key Words:** Electromyography, Neuroplasticity, Resistance Training, Transcranial Magnetic
- 55 56

Stimulation.

57

58

59

60

61

63	Abbreviations
64	CNS: Central nervous system
65	H-Reflex: Hoffman reflex
66	LTD: Long-term depression
67	LTP: Long-term potentiation
68	M1: Primary motor cortex
69	MEP: Motor evoked potential
70	MEP <sub>MAX</sub> : Maximum motor evoked potential
71	PNS: Peripheral nerve stimulation
72	rTMS: Repetitive transcranial magnetic stimulation
73	SICI: Short-interval intracortical inhibition
74	STP: Short-term potentiation
75	sEMG: Surface electromyography
76	tACS: Transcranial alternating current stimulation
77	tDCS: Transcranial direct current stimulation
78	tES: Transcranial electric stimulation
79	TMS: Transcranial magnetic stimulation
80	V-wave: Volitional drive
81	
82	
83	
84	Acknowledgments
85	No funding for this work was received from any source.
86	

#### 1. Introduction

The enhancement of muscular strength, defined as the maximal force developed by a muscle performing a specific movement (Enoka, 1988), is a fundamental adaptation associated with an improved quality of life (Hart and Buck 2019; Marcos-Pardo et al. 2019), increased life expectancy (Kraschnewski et al. 2016) and enhanced sporting performance (Otero-Esquina et al. 2017; Joffe and Tallent 2020). Motor skills involve the precise movement of muscles with the intent to perform a specific act, in which the acquisition and long-term retention are essential to the development and maintenance of health across a lifespan (Dayan and Cohen 2011). Motor skill learning is defined as a permanent change in the capability of movement resulting from practice (Schmidt and Lee 1999). Several experimental paradigms have been used to assess the degree of motor skill learning (i.e. visuomotor tracking, isometric force-production), and the continued performance of these tasks across a set period of time is described as motor skill training (Christiansen et al. 2020). Motor skill performance is vital not only for the long-term engagement in physical activity (Wrotniak et al. 2006), but also in achieving sporting success. Interestingly, motor skill and resistance training adaptations are almost solely studied in isolation, despite resistance-based movements requiring the coordination of numerous muscles to maximise force output (Carroll et al. 2001). Understanding the unique neurological responses to motor skill and resistance training allows medical and sporting practitioners to optimise neurological adaptations to their programmes.

The central nervous system (CNS) is a highly adaptive, dynamically changing system in which continuous modifications are driven by afferent input, efferent demands and environmental influences (Pascual-Leone et al. 1999). The capacity for the nervous system to adapt existing and acquire new motor skills is commonly known as neuroplasticity (Gokeler et al. 2019; Kwon et al. 2019; Floyer-Lea and Matthews 2005). Technological advancements in neurophysiology instruments have allowed non-invasive means of experimentally inducing neuroplasticity (Siebner and Rothwell 2003; Sale et al. 2007). Physical activity, specific training interventions and repetitions of simple motor actions are capable of developing use-dependent plasticity. Described as the strengthening of existing and formation of new neural connections within the primary motor cortex (M1) after voluntary motor activity, a selective release of inhibition also facilitates improvements in synaptic efficacy. In turn, GABAergic inhibition as a mechanism responsible for use-dependent plasticity has been found in the intact M1, potentially underlying further principles of neuroplasticity (Ackerley et al. 2011, Bütefisch et al. 2000 Kleim et al. 2004).

Several frameworks have been proposed to explain the neurophysiological processes that underlie motor performance. Short-term potentiation (STP), long-term potentiation (LTP) and long-term depression (LTD) are activity-dependent cellular responses that occur following motor behaviour (Bliss and Collingridge 1993). STP refers to a transient elevation in synaptic transmission that lasts 5 minutes to 3 hours. In turn, the removal of gamma aminobutyric acid-mediated inhibition unmasks latent or dormant synapses of existing pyramidal tract neurons (Ziemann et al. 1998). The LTP results in prolonged increases in the strength of synaptic connections lasting from hours to days and is commonly attributed to structural neuroplasticity after neuronal stimulation (Monfils et al. 2005). Training-induced LTP within neural networks, most notably the M1, has been proposed to occur via the formation of new synapses (i.e., synaptogenesis) and the increase in the size of trained-limb movement representations (Sanes and Donoghue 2000; Kleim et al. 2004). A sustained increase in the strength of synaptic connection over time reaches a level of maximum efficiency, whereby LTD could down regulate specific synapses within existing structures and, in turn, allow for a continued improvement in synaptic transmission (Purves et al. 2001).

Improvements in motor performance are driven by use-dependent mechanisms, with motor skill and resistance training demonstrating considerable short-and long-term neurological adaptations, that occur at different segments of the neuroaxis (Mason et al. 2020; Tallent et al. 2017). The aim of this review was to identify and compare the short-term and long-term corticospinal adaptations to both motor skill and resistance training. It is suggested that there are similarities in corticospinal adaptions associated with both motor skill and resistance training. However, several methodological factors, such as the motor complexity, type of task, and length of the resistance training intervention, will influence how corticospinal adaptations manifest and how they might explain some of the highly-variable findings in the literature. For the purpose of this review, temporal corticospinal and spinal adaptations will be defined as:

- Acute responses following a single training session
- Short-term adaptations from 2 to 30 training sessions
  - Long-term 3+ years training history

## 2. Adaptations To Motor Skill And Resistance Training

A large body of research has examined the plastic nature of the neurological system to motor skill (Christiansen et al. 2017; Holland et al. 2015; Mason et al. 2017) and resistance training (Weier et al.

2012; Tallent et al. 2017; Giboin et al. 2018). However, research has almost exclusively examined adaptations to motor skill or resistance training in isolation (Mason et al. 2020), with little direct comparison (Remple et al. 2001; Jensen et al. 2005; Leung et al. 2017). This section will segmentally identify similarities and differences in corticospinal and spinal adaptations between motor skill and resistance training.

159

160

161

162

163

164

165

166

167

168

169170

171

172

173

174

175

176

154155

156

157

158

Initial increases in strength are manifested as modulations in the nervous system (Sale 1988; Enoka 1997). Large increases in integrated surface electromyography (sEMG) of over 50% have been shown in as little as four weeks (20 training sessions) of resistance training (Yue and Cole 1992). Whilst much of this early work (Carolan and Cafarelli 1992; Behm 1995; Hakkinen et al. 1998) provided evidence of the rapid plastic nature of the nervous system in response to resistance training, there is still a lack of understanding regarding differences or similarities in resistance and motor skill training adaptations. Early work indicated changes in muscle coordination strategies from resistance training (Carolan and Cafarelli 1992; Behm 1995; Hakkinen et al. 1998), with any resultant increase in force expression suggested to be in part due to improved motor skill performance (Sale et al. 1983). Earlier studies (Carolan and Cafarelli 1992; Behm 1995; Hakkinen et al. 1998) used sEMG to identify neurological adaptations to resistance training and, consequently, could not identify specific neurological sites of adaptations on the brain to muscle pathway. Only relatively recently have researchers been able to identify segmental changes in the CNS using techniques such as transcranial magnetic stimulation; TMS (Goodwill et al. 2012; Kidgell and Pearce 2010), peripheral nerve stimulation; PNS (Tallent et al. 2017; Aagaard et al. 2002) and transcranial electric stimulation; tES (Kobayashi et al. 2014; Carroll et al. 2002), that enables the assessment of the segmental adaptations the occur between motor skill and resistance training.

177

178

179

180

181

182183

184

185

186

# 3.1 Short-Term Corticospinal Adaptations (2-30 training sessions)

TMS allows for the assessment between corticospinal excitatory and inhibitory synaptic activity within the corticospinal tract (Hallett 2000). Jensen et al. (2005) originally used TMS to compare corticospinal adaptations to visuomotor skill and resistance training. Following four weeks (12 training sessions) of visuomotor skill training, there was an increase in the maximum motor evoked potential (MEP<sub>MAX</sub>) compared to a decrease following resistance training. Though visuomotor skill-based tasks have continually shown an increase corticospinal excitability from as little as a single session (Kouchtir-Devanne et al. 2012; Tallent et al. 2012; Schmidt et al. 2011; Goodwill et al. 2015), short-term resistance training (9 to 16 training sessions) has shown more inconsistent findings with

studies observing no change (Kidgell and Pearce 2010; Hendy and Kidgell 2013; Beck et al. 2007), an increase (Weier et al. 2012; Kidgell et al. 2010; Goodwill et al. 2012), and a decrease (Christie and Kamen 2014; Jensen et al. 2005; Carroll et al. 2002). Despite these inconsistencies, a recent meta-analysis demonstrated that corticospinal excitability is increased from resistance training when recorded during an active contraction (Siddique et al. 2020), possibly through a release of short-interval intracortical inhibition (SICI). Some of the inconsistencies in the resistance training literature might be a result of the differences in the demands of the resistance training task, the total number of resistance training sessions or the specificity of the assessment task (Brownstein et al. 2018), though assessment during an active muscle contraction appears essential.

196

197

198

199

200

201

202

203

204

205

206

207

208

209

210

211212

213

214

215

216

217

218

219

220

187188

189

190

191

192

193

194

195

Since the work of Jensen et al. (2005), limited literature has directly compared the neuroplastic mechanisms underpinning muscular strength adaptations and compared these to skill training adaptations. Leung et al. (2017) compared metronome-based resistance training, visuomotor skill training and self-paced resistance training. The visuomotor skill training and metronome-based resistance training required greater attention from the participant and, consequently, were considered a more skill-based movement compared to self-paced resistance training. Following four weeks of training (12 training sessions), there was an increase in corticospinal excitability and a release in SICI in the visuomotor skill training and metronome-based group, but not the self-paced resistance training group. In both the metronome and visuomotor skill groups, establishing the correct motor commands with the perceived sensory cues is vital in the early stages of skill learning (Halsband and Lange 2006). As the self-paced resistance training group was not exposed to the same level of feedback and attention to the task, it could be proposed that increased corticospinal excitability and release of SICI is amplified through motor skill acquisition. Interestingly, the cognitive demands of the metronome-based group were not at the detriment to increases in strength which, in the application to designing clinical rehabilitation programmes, is an important finding. Conversely, motor control balance tasks have shown an increase in SICI compared to explosive resistance training (Taube et al. 2020). At first glance, this might appear contradictory, however increases in SICI were only observed during balance perturbation and not at rest, suggesting taskspecific modulation of intra-cortical changes. Finally, from a limited number of studies, inconsistent findings in cervicomedullary excitability changes have been shown from resistance training (Nuzzo et al. 2016; Nuzzo et al. 2017). This, in addition to a high variability between participants in cervicomedullary excitability changes from visuomotor skill training, (Giesebrecht et al. 2012) does not allow for any conclusive site-specific cervicomedullary adaptations to be presented in this review.

The concepts of early and late phases of neuroplasticity have been well established within the context of skill literature (Dayan and Cohen, 2011; Floyer-Lea & Matthews, 2005; Kleim et al. 2004). For example, at first exposure to a novel task there is an improvement in synaptic efficacy mediated through STP mechanisms (Coxon et al. 2014). As motor skill acquisition progresses from early to late stages (i.e. with more training sessions), the mechanisms of neuroplasticity occur at a structural level in the form of synapse formation (i.e. synaptogenesis) and an expansion of M1 movement representations (Kleim et al. 2004). The developmental process of STP and LTP mechanisms allow for continued and sustained improvements in motor performance (Romano et al. 2010). In particular, online and offline adaptations have been proposed to explain the mechanisms of use-dependent plasticity following motor skill training, and more recently applied to resistance training regimes (Mason et al. 2020). Online mechanisms of neuroplasticity refer to corticospinal responses that develop during and immediately after the training session (Reis et al. 2009), with offline adaptations representing changes that occur between sessions (Dayan and Cohen, 2011). Frameworks described within the skill literature, in particular those associated to early and late stages of neuroplasticity, may underpin improvements in strength following resistance training interventions. Mason et al. (2020) observed increases in wrist flexor strength after three sessions of resistance exercise separated by 48 hours rest, with further increases after six sessions across a two-week period. Presession motor evoked potential (MEP) amplitudes were higher from session five onwards compared to the initial three sessions. This indicates an early phase of strength development that is driven by an improved efficacy of synaptic connections and is likely to occur online (Mason et al. 2020). The increases in corticospinal excitability in the later stages of the intervention were attributed to offline mechanisms, with synaptogenesis considered a dominant adaptation reflecting structural changes (Kleim et al. 2004). This evidence demonstrates that the rapid cellular responses following a single session of resistance training develop into structural adaptations across a short-term training period that underpins increases in muscular strength. It therefore appears that early and late stages of neuroplasticity are associated with strength developments and, interestingly, are similar to the frameworks established in the context of skill literature.

248

249

250

251

252253

221222

223

224

225

226

227

228

229

230

231

232233

234

235

236

237

238

239

240

241

242

243

244

245

246

247

# 3.2 Long-Term Corticospinal Adaptations

Due to the logistical demands of conducting longitudinal training programmes, no study has directly assessed corticospinal adaptations from motor skill training or resistance training that has exceeded a couple of months. As a result, conclusions regarding long-term cortical modifications from motor skill or resistance training are drawn from cross-sectional analysis between resistance trained

individuals and highly motor skilled performers. There is a lack of change shown in corticospinal excitability associated with long-term resistance trained individuals (Tallent et al. 2013; Philpott et al. 2015; Fernandez del Olmo et al. 2006), nevertheless there is an increase in cervicomedullaryevoked potentials (Philpott et al. 2015). Clear indications of a long-term increase in M1 representation or excitability occur as a result of complex motor skill training and can be seen in highly-skilled Paralympic congenital amputation athletes when compared to able-bodied controls (Nakagawa et al. 2020). However, in able-bodied, highly-skilled individuals, an increase in cortical movement representations and decrease in corticospinal excitability have been shown. For example, in professional painters (Krings et al. 2000) and an international soccer player (Naito and Hirose 2014), a reduction in movement representation has been suggested, but conversely, musicians (Bangert and Schlaug 2006) and racquet-based athletes (Pearce et al. 2000) have reported an increase. Exact reasons for the differences are unclear, but the range of expertise and assessment task could contribute to the discrepancies in the findings. Naito and Hirose (2014) and Krings et al. (2000) attributed the decrease in movement-related cortical representation to improvements in neural efficiency during the examination task. The increase in neural efficiency is likely a result of the skill becoming more automated (Debarnot et al. 2014) or a reduction in the sensory activity, leading to a reduced energy expenditure (Nakata et al. 2010; Zhang et al. 2019). Once a sustained synaptic strength is reached, LTD probably down regulates specific synapses within existing structures causing an improvement in synaptic efficiency (Purves et al. 2001). It seems logical to suggest that increases in corticospinal excitability or movement-related cortical representation are associated with the earlier stages of skill learning that plateau or reduce without the introduction of a further novel task and new sensory information (Figure 1).

276

277

278

279

280

281

282

283

284

285

286

275

254

255

256

257

258

259

260

261

262

263

264

265

266

267

268

269

270

271

272

273274

# 3.3 Spinal Adaptations

Spinal adaptations to resistance training and, to a lesser extent, motor skill adaptations have been largely assessed through global reflexes such as the Hoffman reflex (H-reflex) and volitional drive (V-wave). The H-reflex is a measure of la afferent monosynaptic reflex (Knikou 2008) that excludes muscle spindle discharge (Zehr 2002). It reflects the motor neuron excitability and the presynaptic inhibition of the la afferents reflex (Aagaard et al. 2002). V-wave is performed during maximal contractions and is a sEMG variant of the H-reflex (Aagaard et al. 2002). Supramaximal stimulation is applied during a maximal contraction. The descending drive from the maximal contraction causes antidromic action potentials that create a pathway for an evoked reflex, termed the V-wave. Consequently, this is a spinal reflex, reflective of volitional drive to M1 (Aagaard et al. 2002).

Discrepancies in spinal changes exist in the resistance training literature. Spinal reflexes, such as the V-wave, have shown evidence of short-term (Aagaard et al. 2002; Gondin et al. 2006; Del Balso and Cafarelli 2007; Fimland et al. 2009a; Fimland et al. 2009b; Ekblom 2010; Vila-Cha et al. 2012; Tallent et al. 2017) and long-term increases (Milner-Brown et al. 1975; Upton and Radford. 1975) from resistance training. There also appear to be task-specific changes in V-wave with concentric and eccentric resistance training showing greatest adaptations in V-waves when recorded during the respective contractions (Tallent et al. 2017). Although there are no studies assessing changes in V-wave with motor skill training, it appears that there is an element of task specificity to the contraction type that may be applicable for enhancing motor skill performance. Unlike changes in V-waves from resistance training that have been shown to increase (standardized mean difference = 1.04), a recent meta-analysis has shown no change in H-reflex following resistance training (Siddique et al. 2020).

Long-term changes in motor skill training have been shown from evoked reflexes. Ballet dancers have been reported to have a reduced H-reflex compared to well-trained controls (Nielsen et al. 1993). Classical ballet requires high volumes of high- and low-intensity landings (Shaw et al. 2020; Wyon et al. 2011). It is proposed that the reduction in H-reflex is from an increase in presynaptic inhibition that supresses the la afferent loop (Perez et al. 2005); this in turn causes a desynchronization of the alpha motor neurons and increases muscle coordination. Consequently, it is logical to suggest that there is a reduction in sensitivity of the la afferents to enhance the aesthetic landing of the jump and improve the motor control of the task. Spinal changes, particularly spinal reflex, seem therefore to adapt to the specific motor task.

Direct comparisons in animal models between motor skill and resistance training adaptations have provided clear adaptive differences. Consistent with previous findings in humans (Nudo et al. 1996; Karni et al. 1995), Remple et al. (2001) reported an increase in movement cortical representation in rats that learnt the motor skill of reaching and breaking pasta strands. This increase in cortical representation occurred whether this was a resistance training-based task with the rats breaking multiple pasta strands or a single pasta strand. The notable differences between the resistance trained and motor skill task occurred at a spinal level with the resistance trained group breaking multiple pasta strands causing greater excitatory synapse expression onto the spinal motor neurons. Glover and Baker (2020) also demonstrated unique spinal changes following unilateral resistance

training in female macaque monkeys. Facilitation of medial longitudinal fasciculus MEPs demonstrated an increase in reticulospinal function through an increase in synaptic efficacy of the reticulospinal projections to the spinal cord. Whilst there are no comparisons to motor skill training, adaptations in reticulospinal function could be a prominent mechanism driving strength adaptations, though more research is needed before definite conclusions are made.

### 4. Innovative Techniques To Augment Motor Skill Training and Resistance Training

Due to the relative ease of application compared to other neurophysiology techniques, the use of non-invasive brain stimulation to enhance motor skill performance and resistance training has received considerable attention in recent years (Cox et al. 2020; Ciechanski et al. 2019; Kim and Wright 2020; Frazer et al. 2019). Non-invasive tES includes all methods of the non-invasive application of electrical currents to the brain used in research and clinical practice (Guleyupoglu et al. 2013). Transcranial direct current stimulation (tDCS) and transcranial alternating current stimulation (tACS) are the most explored methods of tES and, consequently, this section will focus on these methods.

Transcranial direct current stimulation consists of a constant low-intensity current (1 to 2mA) below a threshold required to generate an action potential, however it can alter corticospinal excitability through increasing or decreasing the possibility of an action potential occurring (Nitsche et al. 2008). Consequently, short-term adaptations are likely attributed to membrane polarity and more long-term changes related to synaptic efficiency (Nitsche et al. 2003; Liebetanz et al. 2002). Transcranial direct current stimulation has been shown to augment sport-based motor skills such as golf putting performance (Zhu et al., 2015) and more laboratory-based visuomotor skill training (Antal et al., 2004). Furthermore, tDCS has also been shown to enhance the motor skill training effects in clinical populations such as stroke patients (Lefebvre et al. 2012).

The acute responses of tDCS on maximal strength have been slightly more conflicting (Cogiamanian et al. 2007; Hazime et al. 2017; Vargas et al. 2018; Frazer et al. 2019), however a recent review of literature has shown that anodal tDCS has a small benefit on acute increases in strength (Lattari et al. 2018). Increases in strength were attributed to an elevation in corticospinal excitability and release of intracortical inhibition, in agreement with the short-term resistance training adaptation literature (described previously). Despite this, there is no evidence that supports the notion that

tDCS can augment strength adaptations. For example, Hendy and Kidgell (2013) prescribed three weeks (9 sessions) of resistance training with tDCS or a sham condition. Despite superior cortical plastic responses between the two groups, there were no differences in the strength changes. Similarly, in stroke patients where the resistance training was conducted at a lower intensity, tDCS and resistance training had no superior gains in strength compared to resistance training alone (Beaulieu et al. 2019), though there is evidence that tDCS may improve the retention of motor based tasks in stroke patients (Goodwill et al. 2016). Whilst there is a lack of evidence suggesting a longer-term enhancement in strength using tDCS, rehabilitation programmes require the enhancement in motor skills and force-generating capacity of the muscle (Abbruzzese et al. 2016; Rio et al. 2016). Consquently, any possible improvement in strength or motor skills will speed up recovery and therefore, the use of tDCS could be a worthwhile tool to augment the rehabilitation process.

Compared to tDCS, tACS has been suggested to be a more-targeted approach to brain stimulation as the oscillation can match the natural frequency of certain regions of the brain (Antal and Herrmann 2016). Transcranial alternating current stimulation has also shown an increase in motor performance that is accompanied by an increase in corticospinal excitability and a reduction in intracortical inhibition (Naro et al. 2017; Giustiniani et al. 2019; Wessel et al. 2020). Similar to tDCS, tACS has been shown to improve motor skill performance through intrinsic changes in the micro-circuits of the M1 (Wischnewski et al. 2019). This, accompanied with the lack of negative effect on resistance training reported and possible facilitation, suggest that both tACS and tDCS could be useful tools, particularly in the early stages of skill learning or resistance training. Future research may want to consider stimulation between training sessions rather than during.

Finally, repetitive transcranial magnetic stimulation (rTMS) might also provide an additional tool to augment motor skill or resistance training adaptions. High-frequency rTMS above 1 Hz has been shown to increase corticospinal excitability and low-frequency rTMS below 1 Hz has been shown to decrease corticospinal excitability (Pascual-Leone et al. 1998). More specifically, rTMS has been suggested to cause LTP of GABAergic synaptic strength that can modulate cortical excitability or inhibition (Lenz and Vlachos 2016). Motor performance and strength gains have been shown to suppress (Hortobagyi et al. 2009; Carey et al. 2006) and enhance (Rumpf et al. 2020) motor skill training/learning depending on the between-pulse frequency and the distribution of pulses across a session. rTMS has also been shown to have positive effects in enhancing the rehabilitation process in stroke patients (Fisicaro et al. 2019).

# 5. Implications For Rehabilitation And Athletic Performance

A reduction in strength and neuromuscular coordination are associated with injury (Wilson et al. 2020; Harput et al. 2020; Ward et al. 2015) and disease (Milosevic et al. 2017; Stock et al. 2019), whilst strength is a key quality of athletic performance (Joffe and Tallent 2020). Consequently, the enhancement of strength and neuromuscular coordination through maximising neurological adaptation is vital. In clinical rehabilitation, enhancing recovery from disease or injury is not only important for patients, but greater optimisation of exercise prescription can have positive financial implications and reduce the resource demands on health services. For example, a reduction in inpatient or outpatient rehabilitation time through effective and efficient exercise prescription, can decrease the short-term care duration, long-term costs and secondary complications associated with disease and injury (Morrison et al. 2018). Similarly, reducing the time lost from injury in sport through reducing the rehabilitation time has implications for performance (Tallent et al. 2020), and also reduce the financial costs to the organisation (Marshall et al. 2016).

398

399400

401

402

403

404

405

406

407

408

409

410

411

412

413

414415

416

417

385

386

387

388

389

390

391

392

393

394

395

396

397

Following injury, both clinical (Hansen et al. 2019) and athletic rehabilitation programmes (Maestroni et al. 2020) are focused on restoring strength and motor skills (Hardwick et al. 2017; Gokeler et al. 2019; Hansen et al. 2019). Within rehabilitation and athletic-performance training programmes, understanding neurological motor skill and strength adaptations is vital in prescribing the most efficient and targeted exercise programme. In clinical neurological conditions such as stoke that require a dynamic interplay between numerous descending neurological processes (Xu et al. 2017), exercise programmes should target inefficiencies in the brain to muscle pathway that will enhance recovery. Whilst similarities in neurological adaptations appear between strength and motor skill training, a comprehensive motor skill and strength programme should be prescribed to maximise adaptations. Figure 2 is a continuum of higher- to lower-force gym-based exercises of the lower limb with the suggested contribution of motor skill efficiency to maximal force output. We propose that, to maximise corticospinal and spinal adaptations, practitioners need to consider the prescription of movements across a continuum of simple movements with high-force outputs, to low-force outputs with highly coordinated movements. It has to be noted that complex highly coordinated movements can still produce high-force outputs. For example, highly-trained weightlifters produce large amounts of force in a highly coordinated movement (Olympic lifting). However, these often require years of practice over 1000's of resistance training sessions. Understanding the complexity of the task, novelty of movement, and force associated with the movement will assist practitioners in the optimisation of programmes. Finally, where rapid increases

in motor skill learning or enhancements in strength are needed, the use of tDCS might facilitate this process (see section 4). The short-term plastic responses from strength and motor skill training appear mainly cortically derived (see section 3), with tDCS facilitating resistance training and motor skill adaptations such as increased corticospinal excitability (Lattari et al. 2018; Vaseghi et al. 2015).

### 6. Conclusion

Both resistance training and motor skill training elicit rapid and longitudinal plastic changes, as summarised in figure 3. At a cortical level, motor skill and resistance training seem to have similar neuroplastic adaptations with a release of intracortical inhibition and an increase in corticospinal excitability. The magnitude of change could be associated with the novelty of the afferent feedback and the uniqueness of the movement or task. Differences at a spinal level appear to be slightly more distinctive with reflexes showing long-term adaptions specific to the task demands. The combination of high-intensity resistance training with simple movements and complex un-resisted movements may target strength or motor skill neurological adaptations. With no negative effects reported, the use of tES may facilitate motor skill learning and resistance training adaptations, though the optimal application (before, during or after training) is still to be determined. Future research should directly compare longitudinal resistance and motor skill training programmes.

447	References
44/	References

448	Aagaard P, Simonsen EB, Andersen JL, Magnusson P, Dyhre-Poulsen P (2002) Neural adaptation to
449	resistance training: changes in evoked V-wave and H-reflex responses. J Appl Physiol
450	92:2309-2318. https://doi:10.1152/japplphysiol.01185.2001
451	Abbruzzese G, Marchese R, Avanzino L, Pelosin E (2016) Rehabilitation for Parkinson's disease:
452	Current outlook and future challenges. Parkinsonism Relat Disord 22 Suppl 1:S60-64.
453	https://doi:10.1016/j.parkreldis.2015.09.005
454	Ackerley SJ, Stinear CM, Byblow WD (2011) Promoting use-dependent plasticity with externally-
455	paced training. Clin Neurophysiol 122:2462-2468. https://doi:10.1016/j.clinph.2011.05.011
456	Antal A, Herrmann CS (2016) Transcranial Alternating Current and Random Noise Stimulation:
457	Possible Mechanisms. Neural Plast 2016:3616807. https://doi:10.1155/2016/3616807
458	Bangert M, Schlaug G (2006) Specialization of the specialized in features of external human brain
459	morphology. Eur J Neurosci 24:1832-1834. https://doi:10.1111/j.1460-9568.2006.05031.x
460	Beaulieu LD, Blanchette AK, Mercier C, Bernard-Larocque V, Milot MH (2019) Efficacy, safety, and
461	tolerability of bilateral transcranial direct current stimulation combined to a resistance
462	training program in chronic stroke survivors: A double-blind, randomized, placebo-controlled
463	pilot study. Restor Neurol Neurosci 37:333-346. https://doi:10.3233/RNN-190908
464	Beck S, Taube W, Gruber M, Amtage F, Gollhofer A, Schubert M (2007) Task-specific changes in
465	motor evoked potentials of lower limb muscles after different training interventions. Brain
466	Res 1179:51-60 https://doi:10.1016/j.brainres.2007.08.048
467	Behm DG (1995) Neuromuscular implications and applications of resistance training. J Strength Cond
468	Res 9:264-274.
469	Bliss TV, Collingridge GL (1993) A synaptic model of memory: long-term potentiation in the
470	hippocampus. Nature 361:31-39. https://doi:10.1038/361031a0
471	Brownstein CG, Ansdell P, Škarabot J, Frazer A, Kidgell D, Howatson G, Goodall S, Thomas K (2018)
472	Motor cortical and corticospinal function differ during an isometric squat compared with
473	isometric knee extension. Exp Physiol 103:1251-1263. https://doi.org/10.1113/EP086982
474	Bütefisch C, Davis B, Wise S, Sawaki L, Kopyley L, Classen J, Cohen L (2000) Mechanisms of use-
475	dependent plasticity in the human motor cortex. Proceedings of the National Academcy of
476	Sciences 97(7):3661-3665. doi: 10.1073/pnas.97.7.3661
477	Carey JR, Fregni F, Pascual-Leone A (2006) rTMS combined with motor learning training in healthy
478	subjects. Restor Neurol Neurosci 24:191-199.
479	Carolan B, Cafarelli E (1992) Adaptations in coactivation after isometric resistance training. J Appl
480	Physiol 73 (3):911-917

481	Carroll TJ, Riek S, Carson RG (2001) Neural adaptations to resistance training: implications for
482	movement control. Sports Med 31:829-840 http://doi:10.2165/00007256-200131120-00001
483	Carroll TJ, Riek S, Carson RG (2002) The sites of neural adaptation induced by resistance training in
484	humans. The Journal of Physiology 544:641-652. doi:10.1113/jphysiol.2002.024463
485	Christiansen L, Larsen MN, Grey MJ, Nielsen JB, Lundbye-Jensen J (2017) Long-term progressive
486	motor skill training enhances corticospinal excitability for the ipsilateral hemisphere and
487	motor performance of the untrained hand. Eur J Neurosci 45:1490-1500.
488	doi:10.1111/ejn.13409
489	Christiansen L, Larsen MN, Madsen MJ, Grey MJ, Nielsen JB, Lundbye-Jensen J (2020) Long-term
490	motor skill training with individually adjusted progressive difficulty enhances learning and
491	promotes corticospinal plasticity. Scientific Reports 10 (1):15588. doi:10.1038/s41598-020-
492	72139-8
493	Christie A, Kamen G (2014) Cortical inhibition is reduced following short-term training in young and
494	older adults. Age (Dordr) 36:749-758. https://doi:10.1007/s11357-013-9577-0
495	Ciechanski P, Kirton A, Wilson B, Williams CC, Anderson SJ, Cheng A, Lopushinsky S, Hecker KG (2019)
496	Electroencephalography correlates of transcranial direct-current stimulation enhanced
497	surgical skill learning: A replication and extension study. Brain Res 1725:146445.
498	https://doi:10.1016/j.brainres.2019.146445
499	Cogiamanian F, Marceglia S, Ardolino G, Barbieri S, Priori A (2007) Improved isometric force
500	endurance after transcranial direct current stimulation over the human motor cortical areas.
501	Eur J Neurosci 26:242-249. https://doi:10.1111/j.1460-9568.2007.05633.x
502	Cox ML, Deng ZD, Palmer H, Watts A, Beynel L, Young JR, Lisanby SH, Migaly J, Appelbaum LG (2020)
503	Utilizing transcranial direct current stimulation to enhance laparoscopic technical skills
503 504	Utilizing transcranial direct current stimulation to enhance laparoscopic technical skills training: A randomized controlled trial. Brain Stimul 13:863-872.
504	training: A randomized controlled trial. Brain Stimul 13:863-872.
504 505	training: A randomized controlled trial. Brain Stimul 13:863-872. doi:10.1016/j.brs.2020.03.009
504 505 506	training: A randomized controlled trial. Brain Stimul 13:863-872. doi:10.1016/j.brs.2020.03.009  Coxon J, Peat N, Byblow W (2014) Primary motor cortex disinhibition during motor skill learning. J
<ul><li>504</li><li>505</li><li>506</li><li>507</li></ul>	training: A randomized controlled trial. Brain Stimul 13:863-872. doi:10.1016/j.brs.2020.03.009  Coxon J, Peat N, Byblow W (2014) Primary motor cortex disinhibition during motor skill learning. J ournal of Neurophysiology 112(1):156-164. doi: 10.1152/jn.00893.2013
<ul><li>504</li><li>505</li><li>506</li><li>507</li><li>508</li></ul>	training: A randomized controlled trial. Brain Stimul 13:863-872. doi:10.1016/j.brs.2020.03.009  Coxon J, Peat N, Byblow W (2014) Primary motor cortex disinhibition during motor skill learning. J ournal of Neurophysiology 112(1):156-164. doi: 10.1152/jn.00893.2013  Debarnot U, Sperduti M, Di Rienzo F, Guillot A (2014) Experts bodies, experts minds: How physical
504 505 506 507 508 509	training: A randomized controlled trial. Brain Stimul 13:863-872. doi:10.1016/j.brs.2020.03.009  Coxon J, Peat N, Byblow W (2014) Primary motor cortex disinhibition during motor skill learning. J ournal of Neurophysiology 112(1):156-164. doi: 10.1152/jn.00893.2013  Debarnot U, Sperduti M, Di Rienzo F, Guillot A (2014) Experts bodies, experts minds: How physical and mental training shape the brain. Front Hum Neurosci 8:280.

513	Del Balso C, Cafarelli E (2007) Adaptations in the activation of human skeletal muscle induced by
514	short-term isometric resistance training. J Appl Physiol 103:402-411.
515	https://doi:00477.200610.1152/japplphysiol.00477.2006
516	Ekblom MM (2010) Improvements in dynamic plantar flexor strength after resistance training are
517	associated with increased voluntary activation and V-to-M ratio. J Appl Physiol 109 (1):19-
518	26. https://doi:10.1152/japplphysiol.01307.2009japplphysiol.01307.2009
519	Enoka RM (1988). Muscle strength and its development. New perspectives. Sports Medicine 6:146-
520	168.
521	Enoka RM (1997) Neural strategies in the control of muscle force. Muscle Nerve Suppl 5:S66-69
522	Fernandez del Olmo M, Reimunde P, Viana O, Acero R, Cudeiro J (2006) Chronic neural adaptation
523	induced by long-term resistance training in humans. Eur J Appl Physiol 96:722-728.
524	https://doi:10.1007/s00421-006-0153-5
525	Fimland M, Helgerud J, Gruber M, Leivseth G, Hoff J (2009a) Functional maximal strength training
526	induces neural transfer to single-joint tasks. Eur J Appl Physiol 107:21-29.
527	https://doi:10.1007/s00421-009-1096-4
528	Fimland MS, Helgerud J, Solstad GM, Iversen VM, Leivseth G, Hoff J (2009b) Neural adaptations
529	underlying cross-education after unilateral strength training. Eur J Appl Physiol 107:723-730.
530	https://doi:10.1007/s00421-009-1190-7
531	Fisicaro F, Lanza G, Grasso AA, Pennisi G, Bella R, Paulus W, Pennisi M (2019) Repetitive transcranial
532	magnetic stimulation in stroke rehabilitation: review of the current evidence and pitfalls.
533	Ther Adv Neurol Disord 12:1756286419878317. doi:10.1177/1756286419878317
534	Floyer-Lea A, Matthews PM (2005) Distinguishable brain activation networks for short- and long-
535	term motor skill learning. J Neurophysiol 94 (1):512-518. https://doi:10.1152/jn.00717.2004
536	Frazer AK, Howatson G, Ahtiainen JP, Avela J, Rantalainen T, Kidgell DJ (2019) Priming the Motor
537	Cortex With Anodal Transcranial Direct Current Stimulation Affects the Acute Inhibitory
538	Corticospinal Responses to Strength Training. J Strength Cond Res 33:307-317.
539	https://doi:10.1519/JSC.000000000002959
540	Giesebrecht S, van Duinen, H, Todd, G, Gandevia, SC Taylor, JL (2012) Training in a ballistic task but
541	not a visuomotor task increases responses to stimulation of human corticospinal axons. J
542	neurophysiol 107:2485-2492. https://doi.org/10.1152/jn.01117.2010
543	Giboin LS, Weiss B, Thomas F, Gruber M (2018) Neuroplasticity following short-term strength
544	training occurs at supraspinal level and is specific for the trained task. Acta Physiol (Oxf)
545	222:e12998. https://doi:10.1111/apha.12998

546	Giustiniani A, Tarantino V, Bonaventura RE, Smirni D, Turriziani P, Oliveri M (2019) Effects of low-
547	gamma tACS on primary motor cortex in implicit motor learning. Behav Brain Res
548	376:112170. https://doi:10.1016/j.bbr.2019.112170
549	Glover IS, Baker SN (2020) Cortical, corticospinal and reticulospinal contributions to strength
550	training. J Neurosci. 40:5820-5832 https://doi:10.1523/JNEUROSCI.1923-19.2020
551	Gokeler A, Neuhaus D, Benjaminse A, Grooms DR, Baumeister J (2019) Principles of Motor Learning
552	to Support Neuroplasticity After ACL Injury: Implications for Optimizing Performance and
553	Reducing Risk of Second ACL Injury. Sports Med 49:853-865. https://doi:10.1007/s40279-
554	019-01058-0
555	Gondin J, Duclay J, Martin A (2006) Soleus- and gastrocnemii-evoked V-wave responses increase
556	after neuromuscular electrical stimulation training. J Neurophysiol 95:3328-3335.
557	https://doi:01002.200510.1152/jn.01002.2005
558	Goodwill AM, Daly RM, Kidgell DJ (2015) The effects of anodal-tDCS on cross-limb transfer in older
559	adults. Clin Neurophysiol 126:2189-2197. https://doi:10.1016/j.clinph.2015.01.006
560	Goodwill AM, Pearce AJ, Kidgell DJ (2012) Corticomotor plasticity following unilateral strength
561	training. Muscle Nerve 46:384-393. https://doi:10.1002/mus.23316
562	Goodwill AM, Teo WP, Morgan P, Daly RM, Kidgell DJ (2016) Bihemispheric-tDCS and upper limb
563	rehabilitation improves retention of motor function in chronic stroke: a pilot study. Front.
564	Hum. Neurosci 10:258. http://doi:10.3233/RNN-190908
565	Guleyupoglu B, Schestatsky P, Edwards D, Fregni F, Bikson M (2013) Classification of methods in
566	transcranial electrical stimulation (tES) and evolving strategy from historical approaches to
567	contemporary innovations. J Neurosci Methods 219:297-311.
568	https://doi:10.1016/j.jneumeth.2013.07.016
569	Hakkinen K, Kallinen M, Izquierdo M, Jokelainen K, Lassila H, Malkia E, Kraemer WJ, Newton RU, Alen
570	M (1998) Changes in agonist-antagonist EMG, muscle CSA, and force during strength training
571	in middle-aged and older people. J Appl Physiol 84:1341-1349.
572	https://doi:10.1152/jappl.1998.84.4.1341
573	Hallett M (2000) Transcranial magnetic stimulation and the human brain. Nature 406:147-150.
574	http://doi:10.1109/EMBC.2014.6943638
575	Halsband U, Lange RK (2006) Motor learning in man: a review of functional and clinical studies. J
576	Physiol Paris 99:414-424. https://doi:10.1016/j.jphysparis.2006.03.007
577	Hansen D, Abreu A, Doherty P, Voller H (2019) Dynamic strength training intensity in cardiovascular
578	rehabilitation: is it time to reconsider clinical practice? A systematic review. Eur J Prev
579	Cardiol 26:1483-1492. https://doi:10.1177/2047487319847003

580	Hardwick RM, Rajan VA, Bastian AJ, Krakauer JW, Celnik PA (2017) Motor Learning in Stroke: Trained
581	Patients Are Not Equal to Untrained Patients With Less Impairment. Neurorehabil Neural
582	Repair 31:178-189. https://doi:10.1177/1545968316675432
583	Harput G, Tunay VB, Ithurburn MP (2020) Quadriceps and Hamstring Strength Symmetry After
584	Anterior Cruciate Ligament Reconstruction: A Prospective Study. J Sport Rehabil:1-8.
585	https://doi:10.1123/jsr.2019-0271
586	Hart PD, Buck DJ (2019) The effect of resistance training on health-related quality of life in older
587	adults: Systematic review and meta-analysis. Health Promot Perspect 9:1-12.
588	https://doi:10.15171/hpp.2019.01
589	Hazime FA, da Cunha RA, Soliaman RR, Romancini ACB, Pochini AC, Ejnisman B, Baptista AF (2017)
590	Anodal Transcranial Direct Current Stimulation (Tdcs) Increases Isometric Strength of
591	Shoulder Rotators Muscles in Handball Players. Int J Sports Phys Ther 12:402-407
592	Hendy AM, Kidgell DJ (2013) Anodal tDCS applied during strength training enhances motor cortical
593	plasticity. Med Sci Sports Exerc 45:1721-1729. https://doi:10.1249/MSS.0b013e31828d2923
594	Holland L, Murphy B, Passmore S, Yielder P (2015) Time course of corticospinal excitability changes
595	following a novel motor training task. Neurosci Lett 591:81-85.
596	https://doi:10.1016/j.neulet.2015.02.022
597	Hortobagyi T, Richardson SP, Lomarev M, Shamim E, Meunier S, Russman H, Dang N, Hallett M
598	(2009) Chronic low-frequency rTMS of primary motor cortex diminishes exercise training-
599	induced gains in maximal voluntary force in humans. J Appl Physiol 106:403-411.
600	https://doi:10.1152/japplphysiol.90701.2008
601	Jensen JL, Marstrand PCD, Nielsen JB (2005) Motor skill training and strength training are associated
602	with different plastic changes in the central nervous system. J Appl Physiol 99:1558-1568.
603	https://doi:10.1152/japplphysiol.01408.2004
604	Joffe SA, Tallent J (2020) Neuromuscular predictors of competition performance in advanced
605	international female weightlifters: a cross-sectional and longitudinal analysis. J Sports Sci
606	38:985-993. https://doi:10.1080/02640414.2020.1737396
607	Karni A, Meyer G, Jezzard P, Adams MM, Turner R, Ungerleider LG (1995) Functional MRI evidence
608	for adult motor cortex plasticity during motor skill learning. Nature 377:155-158.
608 609	for adult motor cortex plasticity during motor skill learning. Nature 377:155-158. https://doi:10.1038/377155a0

612	Kidgell DJ, Stokes MA, Castricum TJ, Pearce AJ (2010) Neurophysiological Responses After Short-
613	Term Strength Training of the Biceps Brachii Muscle. J Strength Cond Res 24:3123-3132.
614	http://doi:10.1519/JSC.0b013e3181f56794
615	Kim T, Wright DL (2020) Transcranial Direct Current Stimulation of Supplementary Motor Region
616	Impacts the Effectiveness of Interleaved and Repetitive Practice Schedules for Retention of
617	Motor Skills. Neuroscience 435:58-72. https://doi:10.1016/j.neuroscience.2020.03.043
618	Kleim JA, Hogg TM, VandenBerg PM, Cooper NR, Bruneau R, Remple M (2004) Cortical
619	synaptogenesis and motor map reorganization occur during late, but not early, phase of
620	motor skill learning. J Neurosci 24:628-633. https://doi:10.1523/JNEUROSCI.3440-03.2004
621	Knikou M (2008) The H-reflex as a probe: pathways and pitfalls. J Neurosci Methods 171:1-12.
622	https://doi:10.1016/j.jneumeth.2008.02.012S0165-0270(08)00119-2
623	Kobayashi S, Matsuyama Y, Shinomiya K, Kawabata S, Ando M, Kanchiku T, Saito T, Takahashi M, Ito
624	Z, Muramoto A, Fujiwara Y, Kida K, Yamada K, Wada K, Yamamoto N, Satomi K, Tani T (2014)
625	A new alarm point of transcranial electrical stimulation motor evoked potentials for
626	intraoperative spinal cord monitoring: a prospective multicenter study from the Spinal Cord
627	Monitoring Working Group of the Japanese Society for Spine Surgery and Related Research.
628	J Neurosurg Spine 20:102-107. https://doi:10.3171/2013.10.SPINE12944
629	Kouchtir-Devanne N, Capaday C, Cassim F, Derambure P, Devanne H (2012) Task-dependent changes
630	of motor cortical network excitability during precision grip compared to isolated finger
631	contraction. J Neurophysiol 107:1522-1529. https://doi:10.1152/jn.00786.2011
632	Kraschnewski JL, Sciamanna CN, Poger JM, Rovniak LS, Lehman EB, Cooper AB, Ballentine NH, Ciccolo
633	JT (2016) Is strength training associated with mortality benefits? A 15year cohort study of US
634	older adults. Prev Med 87:121-127. https://doi:10.1016/j.ypmed.2016.02.038
635	Krings T, Topper R, Foltys H, Erberich S, Sparing R, Willmes K, Thron A (2000) Cortical activation
636	patterns during complex motor tasks in piano players and control subjects. A functional
637	magnetic resonance imaging study. Neurosci Lett 278:189-193. https://doi:10.1016/s0304-
638	3940(99)00930-1
639	Kwon Y, Shin JY, Son SM (2019) Deficit of Motor Skill Acquisition on the Upper Limb Ipsilesional to
640	the Injured Hemisphere in Individuals with Stroke. Med Sci Monit 25:5062-5067.
641	https://doi:10.12659/MSM.916484
642	Lattari E, Oliveira BRR, Monteiro Junior RS, Marques Neto SR, Oliveira AJ, Maranhao Neto GA,
643	Machado S, Budde H (2018) Acute effects of single dose transcranial direct current
644	stimulation on muscle strength: A systematic review and meta-analysis. PLoS One
645	13:e0209513. https://doi:10.1371/journal.pone.0209513

646	Lefebvre S, Laloux P, Peeters A, Desfontaines P, Jamart J, Vandermeeren Y (2012) Dual-tDCS
647	Enhances Online Motor Skill Learning and Long-Term Retention in Chronic Stroke Patients.
648	Front Hum Neurosci 6:343. https://doi:10.3389/fnhum.2012.00343
649	Lenz M, Vlachos A (2016) Releasing the Cortical Brake by Non-Invasive Electromagnetic Stimulation?
650	rTMS Induces LTD of GABAergic Neurotransmission. Front Neural Circuits 10:96.
651	https://doi:10.3389/fncir.2016.00096
652	Leung M, Rantalainen T, Teo WP, Kidgell D (2017) The corticospinal responses of metronome-paced,
653	but not self-paced strength training are similar to motor skill training. Eur J Appl Physiol
654	117:2479-2492. https://doi:10.1007/s00421-017-3736-4
655	Liebetanz D, Nitsche MA, Tergau F, Paulus W (2002) Pharmacological approach to the mechanisms
656	of transcranial DC-stimulation-induced after-effects of human motor cortex excitability.
657	Brain 125:2238-2247. https://doi:10.1093/brain/awf238
658	Maestroni L, Read P, Bishop C, Turner A (2020) Strength and Power Training in Rehabilitation:
659	Underpinning Principles and Practical Strategies to Return Athletes to High Performance.
660	Sports Med 50 (2):239-252. https://doi:10.1007/s40279-019-01195-6
661	Marcos-Pardo PJ, Orquin-Castrillon FJ, Gea-Garcia GM, Menayo-Antunez R, Gonzalez-Galvez N, Vale
662	RGS, Martinez-Rodriguez A (2019) Effects of a moderate-to-high intensity resistance circuit
663	training on fat mass, functional capacity, muscular strength, and quality of life in elderly: A
664	randomized controlled trial. Sci Rep 9 (1):7830. doi:10.1038/s41598-019-44329-6
665	Marshall DA, Lopatina E, Lacny S, Emery CA (2016) Economic impact study: neuromuscular training
666	reduces the burden of injuries and costs compared to standard warm-up in youth soccer. Br
667	J Sports Med 50 (22):1388-1393. doi:10.1136/bjsports-2015-095666
668	Mason J, Frazer A, Horvath DM, Pearce AJ, Avela J, Howatson G, Kidgell D (2017) Adaptations in
669	corticospinal excitability and inhibition are not spatially confined to the agonist muscle
670	following strength training. Eur J Appl Physiol 117:1359-1371. https://doi:10.1007/s00421-
671	017-3624-y
672	Mason J, Frazer AK, Avela J, Pearce AJ, Howatson G, Kidgell DJ (2020) Tracking the corticospinal
673	responses to strength training. Eur J Appl Physiol 120:783-798. doi:10.1007/s00421-020-
674	04316-6
675	Milner-Brown HS, Stein RB, Lee RG (1975) Synchronization of human motor units: possible roles of
676	exercise and supraspinal reflexes. Electroencephalogr Clin Neurophysiol 38:245-254.
677	http://doi:10.1016/0013-4694(75)90245-x
678	Milosevic M, Yokoyama H, Grangeon M, Masani K, Popovic MR, Nakazawa K, Gagnon DH (2017)
679	Muscle synergies reveal impaired trunk muscle coordination strategies in individuals with

680	thoracic spinal cord injury. J Electromyogr Kinesiol 36:40-48.
681	https://doi:10.1016/j.jelekin.2017.06.007
682	Monfils MH, Plautz EJ, Kleim JA (2005) In search of the motor engram: motor map plasticity as a
683	mechanism for encoding motor experience. Neuroscientist 11:471-483.
684	https://doi:10.1177/1073858405278015
685	Morrison SA, Lorenz D, Eskay CP, Forrest GF, Basso DM (2018) Longitudinal Recovery and Reduced
686	Costs After 120 Sessions of Locomotor Training for Motor Incomplete Spinal Cord Injury.
687	Arch Phys Med Rehabil 99:555-562. https://doi:10.1016/j.apmr.2017.10.003
688	Naito E, Hirose S (2014) Efficient foot motor control by Neymar's brain. Front Hum Neurosci 8:594.
689	https://doi:10.3389/fnhum.2014.00594
690	Nakagawa K, Takemi M, Nakanishi T, Sasaki A, Nakazawa K (2020) Cortical reorganization of lower-
691	limb motor representations in an elite archery athlete with congenital amputation of both
692	arms. Neuroimage Clin 25:102-144. https://doi:10.1016/j.nicl.2019.102144
693	Nakata H, Yoshie M, Miura A, Kudo K (2010) Characteristics of the athletes' brain: evidence from
694	neurophysiology and neuroimaging. Brain Res Rev 62:197-211.
695	https://doi:10.1016/j.brainresrev.2009.11.006
696	Naro A, Bramanti A, Leo A, Manuli A, Sciarrone F, Russo M, Bramanti P, Calabro RS (2017) Effects of
697	cerebellar transcranial alternating current stimulation on motor cortex excitability and
698	motor function. Brain Struct Funct 222:2891-2906. https://doi:10.1007/s00429-016-1355-1
699	Nielsen J, Crone C, Hultborn H (1993) H-reflexes are smaller in dancers from The Royal Danish Ballet
700	than in well-trained athletes. Eur J Appl Physiol 66:116-121. https://doi:10.1007/bf01427051
701	Nitsche MA, Cohen LG, Wassermann EM, Priori A, Lang N, Antal A, Paulus W, Hummel F, Boggio PS,
702	Fregni F, Pascual-Leone A (2008) Transcranial direct current stimulation: State of the art
703	2008. Brain Stimul 1:206-223. https://doi:10.1016/j.brs.2008.06.004
704	Nitsche MA, Schauenburg A, Lang N, Liebetanz D, Exner C, Paulus W, Tergau F (2003) Facilitation of
705	implicit motor learning by weak transcranial direct current stimulation of the primary motor
706	cortex in the human. J Cogn Neurosci 15 :619-626.
707	https://doi:10.1162/089892903321662994
708	Nudo RJ, Milliken GW, Jenkins WM, Merzenich MM (1996) Use-dependent alterations of movement
709	representations in primary motor cortex of adult squirrel monkeys. J Neurosci 16:785-807.
710	http://doi:10.1523/JNEUROSCI.16-02-00785.1996
711	Nuzzo JL, Barry BK, Gandevia SC, Taylor JL (2016) Acute Strength Training Increases Responses to
712	Stimulation of Corticospinal Axons. Med Sci in Sport and Exer 48:139-150.
713	http://doi:10.1249/mss.000000000000733

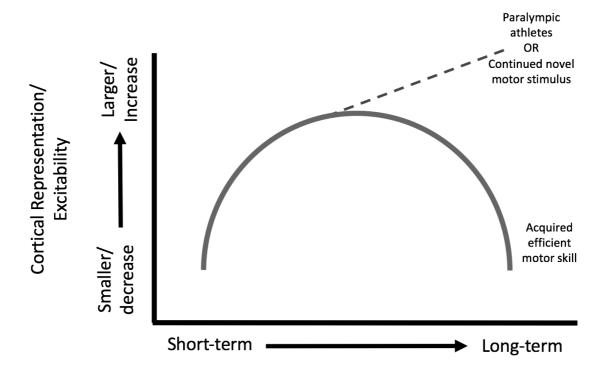
- 714 Nuzzo, JL, Barry BK, Jones MD, Gandevia SC, Taylor JL (2017) Effects of Four Weeks of Strength Training on the Corticomotoneuronal Pathway. Med Sci in Sport and Exer 49:2286-2296. 715 716 http://10.1249/mss.0000000000001367 717 Otero-Esquina C, de Hoyo Lora M, Gonzalo-Skok O, Dominguez-Cobo S, Sanchez H (2017) Is strength-718 training frequency a key factor to develop performance adaptations in young elite soccer 719 players? Eur J Sport Sci 17:1241-1251. https://doi:10.1080/17461391.2017.1378372 720 Pascual-Leone A, Tarazona F, Keenan J, Tormos JM, Hamilton R, Catala MD (1999) Transcranial 721 magnetic stimulation and neuroplasticity. Neuropsychologia 37:207-217. 722 https://doi:10.1016/s0028-3932(98)00095-5 Pascual-Leone A, Tormos JM, Keenan J, Tarazona F, Canete C, Catala MD (1998) Study and 723 modulation of human cortical excitability with transcranial magnetic stimulation. J Clin 724 725 Neurophysiol 15:333-343. https://doi:10.1097/00004691-199807000-00005 Pearce AJ, Thickbroom GW, Byrnes ML, Mastaglia FL (2000) Functional reorganisation of the 726 727 corticomotor projection to the hand in skilled racquet players. Exp Brain Res 130 (2):238-243. https://doi:10.1007/s002219900236 728 Perez MA, Lungholt BK, Nielsen JB (2005) Presynaptic control of group la afferents in relation to 729 730 acquisition of a visuo-motor skill in healthy humans. J Physiol 568:343-354. 731 https://doi:10.1113/jphysiol.2005.089904 732 Philpott DT, Pearcey GE, Forman D, Power KE, Button DC (2015) Chronic resistance training 733 enhances the spinal excitability of the biceps brachii in the non-dominant arm at moderate contraction intensities. Neurosci Lett 585:12-16. https://doi:10.1016/j.neulet.2014.11.009 734 735 Purves D, Augustine G, Fitzpatrick D, Hall W, LaMantia A, White L (2001) Neuroscience. Sinauer 736 Associates, Inc., Sunderland, Massachusetts. 737 Raeder C, Wiewelhove T, Westphal-Martinez MP, Fernandez-Fernandez J, de Paula Simola RA, 738 Kellmann M, Meyer T, Pfeiffer M, Ferrauti A (2016) Neuromuscular Fatigue and Physiological Responses After Five Dynamic Squat Exercise Protocols. J Strength Cond Res 30:953-965. 739 740 https://doi:10.1519/JSC.000000000001181 Remple MS, Bruneau RM, VandenBerg PM, Goertzen C, Kleim JA (2001) Sensitivity of cortical 741 742 movement representations to motor experience: evidence that skill learning but not strength training induces cortical reorganization. Behav Brain Res 123:133-141. 743
- Rio E, Kidgell D, Moseley GL, Gaida J, Docking S, Purdam C, Cook J (2016) Tendon neuroplastic training: changing the way we think about tendon rehabilitation: a narrative review. Br J Sports Med 50:209-215. https://doi:10.1136/bjsports-2015-095215

doi:http://dx.doi.org/10.1016/S0166-4328(01)00199-1

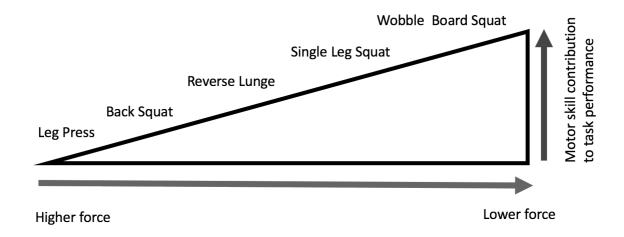
748	Reis J, Schambra H, Cohen L, Buch E, Fritsch B, Zarahn E, Celnik PA, Krakauer JW (2009) Noninvasive
749	cortical stimulation enhances motor skill acquisition over multiple days through an effect on
750	consolidation. Proc Natl Acad Sci 106:1590-1595. doi: 10.1073/pnas.0805413106
751	Romano JC, Howard Jr JH, Howard DV (2010) One-year retention of general and sequence-specific
752	skills in a probabilistic, serial reaction time task. Memory 18(4):427-441
753	Rumpf JJ, May L, Fricke C, Classen J, Hartwigsen G (2020) Interleaving Motor Sequence Training With
754	High-Frequency Repetitive Transcranial Magnetic Stimulation Facilitates Consolidation.
755	Cereb Cortex 30:1030-1039. https://doi:10.1093/cercor/bhz145
756	Sale DG (1988) Neural adaptation to resistance training. Med Sci in Sport and Exer 20:S135-S145
757	Sale DG, MacDougall JD, Upton AR, McComas AJ (1983) Effect of strength training upon motoneuron
758	excitability in man. Med Sci in Sport and Exer 15:57-62
759	Sale MV, Ridding MC, Nordstrom MA (2007) Factors influencing the magnitude and reproducibility of
760	corticomotor excitability changes induced by paired associative stimulation. Exp Brain Res
761	181:615-626. https://doi:10.1007/s00221-007-0960-x
762	Sanes JN, Donoghue JP (2000) Plasticity and primary motor cortex. Annu Rev Neurosci 23:393-415.
763	https://doi:10.1146/annurev.neuro.23.1.393
764	Schmidt MW, Hinder MR, Summers JJ, Garry MI (2011) Long-lasting contralateral motor cortex
765	excitability is increased by unilateral hand movement that triggers electrical stimulation of
766	opposite homologous muscles. Neurorehabil Neural Repair 25:521-530.
767	https://doi:10.1177/1545968310397202
768	Schmidt RA, Lee TD (1999) The learning process. In: Schmidt RA, Lee TD (eds) Motorcontrol and
769	learning: A behavioral emphasis. Human Kinetics, Champaign, IL, pp 357–383
770	Shaw JW, Springham M, Brown DD, Mattiussi AM, Pedlar CR, Tallent J (2020) The Validity of the
771	Session Rating of Perceived Exertion Method for Measuring Internal Training Load in
772	Professional Classical Ballet Dancers. Front Physiol 11:480.
773	https://doi:10.3389/fphys.2020.00480
774	Siddique U, Rahman S, Frazer AK, Pearce AJ, Howatson G, Kidgell DJ (2020) Determining the Sites of
775	
775	Neural Adaptations to Resistance Training: A Systematic Review and Meta-analysis. Sports
776	Neural Adaptations to Resistance Training: A Systematic Review and Meta-analysis. Sports Med 50:1107-1128. https://doi:10.1007/s40279-020-01258-z
776	Med 50:1107-1128. https://doi:10.1007/s40279-020-01258-z
776 777	Med 50:1107-1128. https://doi:10.1007/s40279-020-01258-z Siebner HR, Rothwell J (2003) Transcranial magnetic stimulation: new insights into representational

781	Tallent J, de Weymarn C, Ahmun R, Jones TW (2020) The impact of all-rounders and team injury
782	status on match and series success in international cricket. J Sports Sci 29:1-4.
783	https://doi:10.1080/02640414.2020.1798721
784	Tallent J, Goodall S, Gibbon KC, Hortobagyi T, Howatson G (2017) Enhanced Corticospinal Excitability
785	and Volitional Drive in Response to Shortening and Lengthening Strength Training and
786	Changes Following Detraining. Front Physiol 8:57. https://doi:10.3389/fphys.2017.00057
787	Tallent J, Goodall S, Hortobágyi T, St Clair Gibson A, French DN, Howatson G (2012) Repeatability of
788	Corticospinal and Spinal Measures during Lengthening and Shortening Contractions in the
789	Human Tibialis Anterior Muscle. PLoS ONE 7:e35930 http://doi:
790	10.1371/journal.pone.0035930.
791	Tallent J, Goodall S, Hortobagyi T, St Clair Gibson A, Howatson G (2013) Corticospinal responses of
792	resistance-trained and un-trained males during dynamic muscle contractions. J Electromyogr
793	Kinesiol 23:1075-1081 https://doi:10.1016/j.jelekin.2013.04.014S1050-6411(13)00111-9
794	Taube W, Gollhofer A, Lauber B (2020) Training-, muscle- and task-specific up- and downregulation
795	of cortical inhibitory processes. Eur J Neurosci 51:1428-1440. https://doi:10.1111/ejn.14538
796	Upton ARM, Radford PF (1975) Motoneurone excitability in elite sprinters. , vol 1A. International Ser
797	Biomech, Baltimore, MD: University Park.
798	Vargas VZ, Baptista AF, Pereira GOC, Pochini AC, Ejnisman B, Santos MB, Joao SMA, Hazime FA
799	(2018) Modulation of Isometric Quadriceps Strength in Soccer Players With Transcranial
800	Direct Current Stimulation: A Crossover Study. J Strength Cond Res 32:1336-1341.
801	https://doi:10.1519/JSC.00000000001985
802	Vaseghi B, Zoghi M, Jaberzadeh S (2015) The effects of anodal-tDCS on corticospinal excitability
803	enhancement and its after-effects: conventional vs. unihemispheric concurrent dual-site
804	stimulation. Front Hum Neurosci 9:533. https://doi:10.3389/fnhum.2015.00533
805	Vila-Cha C, Falla D, Correia MV, Farina D (2012) Changes in H reflex and V wave following short-term
806	endurance and strength training. J Appl Physiol 112:54-63.
807	https://doi:10.1152/japplphysiol.00802.2011japplphysiol.00802.2011
808	Ward S, Pearce AJ, Pietrosimone B, Bennell K, Clark R, Bryant AL (2015) Neuromuscular deficits after
809	peripheral joint injury: a neurophysiological hypothesis. Muscle Nerve 51:327-332.
810	https://doi:10.1002/mus.24463
811	Weier AT, Pearce AJ, Kidgell DJ (2012) Strength training reduces intracortical inhibition. Acta
812	Physiologica 206:109-119. https://doi:10.1111/j.1748-1716.2012.02454.x
812 813	Physiologica 206:109-119. https://doi:10.1111/j.1748-1716.2012.02454.x Wessel MJ, Draaisma LR, de Boer AFW, Park CH, Maceira-Elvira P, Durand-Ruel M, Koch PJ, Morishita

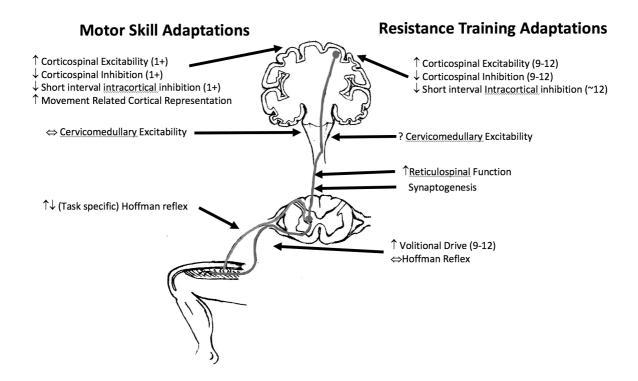
815	range applied during the acquisition of a novel motor skill. Sci Rep 10:11217.
816	https://doi:10.1038/s41598-020-68028-9
817	Wilson KW, Popchak A, Li RT, Kane G, Lin A (2020) Return to sport testing at 6 months after
818	arthroscopic shoulder stabilization reveals residual strength and functional deficits. J
819	Shoulder Elbow Surg 29:S107-S114. https://doi:10.1016/j.jse.2020.04.035
820	Wischnewski M, Schutter D, Nitsche MA (2019) Effects of beta-tACS on corticospinal excitability: A
821	meta-analysis. Brain Stimul 12:1381-1389. https://doi:10.1016/j.brs.2019.07.023
822	Wrotniak BH, Epstein LH, Dorn JM, Jones KE, Kondilis VA (2006) The relationship between motor
823	proficiency and physical activity in children. Pediatrics 118:e1758-1765.
824	https://doi:10.1542/peds.2006-0742
825	Wyon MA, Twitchett E, Angioi M, Clarke F, Metsios G, Koutedakis Y (2011) Time motion and video
826	analysis of classical ballet and contemporary dance performance. Int J Sports Med 32:851-
827	855. https://doi:10.1055/s-0031-1279718
828	Xu J, Ejaz N, Hertler B, Branscheidt M, Widmer M, Faria AV, Harran MD, Cortes JC, Kim N, Celnik PA,
829	Kitago T, Luft AR, Krakauer JW, Diedrichsen J (2017) Separable systems for recovery of finger
830	strength and control after stroke. J Neurophysiol 118:1151-1163. doi:10.1152/jn.00123.2017
831	Yue G, Cole KJ (1992) Strength increases from the motor program: comparison of training with
832	maximal voluntary and imagined muscle contractions. J Neurophysiol 67:1114-1123
833	https//doi:10.1152/jn.1992.67.5.1114
834	Zehr P (2002) Considerations for use of the Hoffmann reflex in exercise studies. Eur J Appl Physiol
835	86:455-468. https://doi:10.1007/s00421-002-0577-5
836	Zhang L, Qiu F, Zhu H, Xiang M, Zhou L (2019) Neural Efficiency and Acquired Motor Skills: An fMRI
837	Study of Expert Athletes. Front Psychol 10:2752. https://doi:10.3389/fpsyg.2019.02752
838	Ziemann U, Hallett M, Cohen LG (1998) Mechanisms of deafferentation-induced plasticity in human
839	motor cortex. J Neurosci 18:7000-7007 https//doi:10.1523/JNEUROSCI.18-17-07000.1998
840	
841	
842	
843	
844	
845	



**Figure 1.** Longitudinal changes in cortical representation/excitability from motor skill training. Corticospinal excitability increases and then decreases as the motor skill is acquired. Continued increases in corticospinal excitability with a novel motor stimulus or in highly-skilled Paralympic congenital amputation athletes when compared to able-bodied controls (adapted from Nakagawa et al. 2020).



**Figure 2.** Continuum of higher- to lower-force gym-based exercises of the lower limb with the proposed contribution of motor skill efficiency to maximal force output.



**Figure 3.** Proposed corticospinal and spinal adaptations to motor skill and strength training, with the number of sessions needed for the adaptation in brackets based on the findings from the literature. With the relatively limited number of studies investigating the time-course adaptations to resistance training, caution should be applied when interpreting the minimal number of sessions required to elicit these adaptations.