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- 1 Corticospinal and spinal adaptations to motor skill and resistance training: Potential mechanisms
- 2 and implications for motor rehabilitation and athletic development.
- 3
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33 Abstract

34 Optimal strategies for enhancing strength and improving motor skills are vital in athletic 35 performance and clinical rehabilitation. Initial increases in strength and the acquisition of new motor 36 skills have long been attributed to neurological adaptations. However, early increases in strength 37 may be predominantly due to improvements in inter-muscular coordination rather than the force 38 generating capacity of the muscle. Despite the plethora of research investigating neurological 39 adaptations from motor skill or resistance training in isolation, little effort has been made in 40 consolidating this research to compare motor skill and resistance training adaptations. The findings 41 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 42 43 and a release in short-interval cortical inhibition occur as a result of the commencement of both 44 resistance and motor skill training. Spinal changes show evidence of task-specific adaptations from 45 the acquired motor skill, with an increase or decrease in spinal reflex excitability, dependant on the 46 motor task. An increase in synaptic efficacy of the reticulospinal projections is likely to be a 47 prominent mechanism for driving strength adaptations at the subcortical level, though more 48 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 49 50 strength adaptations from resistance training. Despite the logistical challenges, future work should 51 compare the longitudinal adaptations between motor skill and resistance training to further 52 optimise exercise programming.

53

54 Key Words: Electromyography, Neuroplasticity, Resistance Training, Transcranial Magnetic
 55 Stimulation.

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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_{MAX}: 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
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- 83
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86

88 **1. Introduction**

89 The enhancement of muscular strength, defined as the maximal force developed by a muscle 90 performing a specific movement (Enoka, 1988), is a fundamental adaptation associated with an 91 improved quality of life (Hart and Buck 2019; Marcos-Pardo et al. 2019), increased life expectancy 92 (Kraschnewski et al. 2016) and enhanced sporting performance (Otero-Esquina et al. 2017; Joffe and 93 Tallent 2020). Motor skills involve the precise movement of muscles with the intent to perform a 94 specific act, in which the acquisition and long-term retention are essential to the development and 95 maintenance of health across a lifespan (Dayan and Cohen 2011). Motor skill learning is defined as a 96 permanent change in the capability of movement resulting from practice (Schmidt and Lee 1999). 97 Several experimental paradigms have been used to assess the degree of motor skill learning (i.e. 98 visuomotor tracking, isometric force-production), and the continued performance of these tasks 99 across a set period of time is described as motor skill training (Christiansen et al. 2020). Motor skill 100 performance is vital not only for the long-term engagement in physical activity (Wrotniak et al. 101 2006), but also in achieving sporting success. Interestingly, motor skill and resistance training 102 adaptations are almost solely studied in isolation, despite resistance-based movements requiring the 103 coordination of numerous muscles to maximise force output (Carroll et al. 2001). Understanding the 104 unique neurological responses to motor skill and resistance training allows medical and sporting 105 practitioners to optimise neurological adaptations to their programmes.

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107 The central nervous system (CNS) is a highly adaptive, dynamically changing system in which 108 continuous modifications are driven by afferent input, efferent demands and environmental 109 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. 110 111 2019; Floyer-Lea and Matthews 2005). Technological advancements in neurophysiology instruments 112 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 113 114 motor actions are capable of developing use-dependent plasticity. Described as the strengthening of 115 existing and formation of new neural connections within the primary motor cortex (M1) after 116 voluntary motor activity, a selective release of inhibition also facilitates improvements in synaptic 117 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 118 119 al. 2011, Bütefisch et al. 2000 Kleim et al. 2004).

Several frameworks have been proposed to explain the neurophysiological processes that underlie 121 122 motor performance. Short-term potentiation (STP), long-term potentiation (LTP) and long-term 123 depression (LTD) are activity-dependent cellular responses that occur following motor behaviour 124 (Bliss and Collingridge 1993). STP refers to a transient elevation in synaptic transmission that lasts 5 125 minutes to 3 hours. In turn, the removal of gamma aminobutyric acid-mediated inhibition unmasks 126 latent or dormant synapses of existing pyramidal tract neurons (Ziemann et al. 1998). The LTP results 127 in prolonged increases in the strength of synaptic connections lasting from hours to days and is 128 commonly attributed to structural neuroplasticity after neuronal stimulation (Monfils et al. 2005). 129 Training-induced LTP within neural networks, most notably the M1, has been proposed to occur via 130 the formation of new synapses (i.e., synaptogenesis) and the increase in the size of trained-limb 131 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 132 133 could down regulate specific synapses within existing structures and, in turn, allow for a continued 134 improvement in synaptic transmission (Purves et al. 2001).

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Improvements in motor performance are driven by use-dependent mechanisms, with motor skill 136 137 and resistance training demonstrating considerable short-and long-term neurological adaptations, 138 that occur at different segments of the neuroaxis (Mason et al. 2020; Tallent et al. 2017). The aim of 139 this review was to identify and compare the short-term and long-term corticospinal adaptations to 140 both motor skill and resistance training. It is suggested that there are similarities in corticospinal 141 adaptions associated with both motor skill and resistance training. However, several methodological 142 factors, such as the motor complexity, type of task, and length of the resistance training 143 intervention, will influence how corticospinal adaptations manifest and how they might explain 144 some of the highly-variable findings in the literature. For the purpose of this review, temporal corticospinal and spinal adaptations will be defined as: 145

- Acute responses following a single training session
- Short-term adaptations from 2 to 30 training sessions
- Long-term 3+ years training history
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151 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.

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160 Initial increases in strength are manifested as modulations in the nervous system (Sale 1988; Enoka 161 1997). Large increases in integrated surface electromyography (sEMG) of over 50% have been shown 162 in as little as four weeks (20 training sessions) of resistance training (Yue and Cole 1992). Whilst 163 much of this early work (Carolan and Cafarelli 1992; Behm 1995; Hakkinen et al. 1998) provided 164 evidence of the rapid plastic nature of the nervous system in response to resistance training, there is 165 still a lack of understanding regarding differences or similarities in resistance and motor skill training 166 adaptations. Early work indicated changes in muscle coordination strategies from resistance training 167 (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). 168 Earlier studies (Carolan and Cafarelli 1992; Behm 1995; Hakkinen et al. 1998) used sEMG to identify 169 170 neurological adaptations to resistance training and, consequently, could not identify specific 171 neurological sites of adaptations on the brain to muscle pathway. Only relatively recently have 172 researchers been able to identify segmental changes in the CNS using techniques such as 173 transcranial magnetic stimulation; TMS (Goodwill et al. 2012; Kidgell and Pearce 2010), peripheral 174 nerve stimulation; PNS (Tallent et al. 2017; Aagaard et al. 2002) and transcranial electric stimulation; 175 tES (Kobayashi et al. 2014; Carroll et al. 2002), that enables the assessment of the segmental 176 adaptations the occur between motor skill and resistance training.

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178 **3.1 Short-Term Corticospinal Adaptations (2-30 training sessions)**

179 TMS allows for the assessment between corticospinal excitatory and inhibitory synaptic activity 180 within the corticospinal tract (Hallett 2000). Jensen et al. (2005) originally used TMS to compare 181 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 182 183 potential (MEP_{MAX}) compared to a decrease following resistance training. Though visuomotor skill-184 based tasks have continually shown an increase corticospinal excitability from as little as a single 185 session (Kouchtir-Devanne et al. 2012; Tallent et al. 2012; Schmidt et al. 2011; Goodwill et al. 2015), 186 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 187 188 increase (Weier et al. 2012; Kidgell et al. 2010; Goodwill et al. 2012), and a decrease (Christie and 189 Kamen 2014; Jensen et al. 2005; Carroll et al. 2002). Despite these inconsistencies, a recent meta-190 analysis demonstrated that corticospinal excitability is increased from resistance training when 191 recorded during an active contraction (Siddique et al. 2020), possibly through a release of short-192 interval intracortical inhibition (SICI). Some of the inconsistencies in the resistance training literature 193 might be a result of the differences in the demands of the resistance training task, the total number 194 of resistance training sessions or the specificity of the assessment task (Brownstein et al. 2018), 195 though assessment during an active muscle contraction appears essential.

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197 Since the work of Jensen et al. (2005), limited literature has directly compared the neuroplastic 198 mechanisms underpinning muscular strength adaptations and compared these to skill training 199 adaptations. Leung et al. (2017) compared metronome-based resistance training, visuomotor skill 200 training and self-paced resistance training. The visuomotor skill training and metronome-based 201 resistance training required greater attention from the participant and, consequently, were 202 considered a more skill-based movement compared to self-paced resistance training. Following four 203 weeks of training (12 training sessions), there was an increase in corticospinal excitability and a 204 release in SICI in the visuomotor skill training and metronome-based group, but not the self-paced 205 resistance training group. In both the metronome and visuomotor skill groups, establishing the 206 correct motor commands with the perceived sensory cues is vital in the early stages of skill learning 207 (Halsband and Lange 2006). As the self-paced resistance training group was not exposed to the same 208 level of feedback and attention to the task, it could be proposed that increased corticospinal 209 excitability and release of SICI is amplified through motor skill acquisition. Interestingly, the cognitive 210 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. 211 212 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 213 214 increases in SICI were only observed during balance perturbation and not at rest, suggesting task-215 specific modulation of intra-cortical changes. Finally, from a limited number of studies, inconsistent 216 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 217 218 cervicomedullary excitability changes from visuomotor skill training, (Giesebrecht et al. 2012) does 219 not allow for any conclusive site-specific cervicomedullary adaptations to be presented in this 220 review.

The concepts of early and late phases of neuroplasticity have been well established within the 221 222 context of skill literature (Dayan and Cohen, 2011; Floyer-Lea & Matthews, 2005; Kleim et al. 2004). 223 For example, at first exposure to a novel task there is an improvement in synaptic efficacy mediated 224 through STP mechanisms (Coxon et al. 2014). As motor skill acquisition progresses from early to late 225 stages (i.e. with more training sessions), the mechanisms of neuroplasticity occur at a structural level 226 in the form of synapse formation (i.e. synaptogenesis) and an expansion of M1 movement 227 representations (Kleim et al. 2004). The developmental process of STP and LTP mechanisms allow for 228 continued and sustained improvements in motor performance (Romano et al. 2010). In particular, 229 online and offline adaptations have been proposed to explain the mechanisms of use-dependent 230 plasticity following motor skill training, and more recently applied to resistance training regimes 231 (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 232 233 representing changes that occur between sessions (Dayan and Cohen, 2011). Frameworks described 234 within the skill literature, in particular those associated to early and late stages of neuroplasticity, 235 may underpin improvements in strength following resistance training interventions. Mason et al. 236 (2020) observed increases in wrist flexor strength after three sessions of resistance exercise 237 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 238 239 to the initial three sessions. This indicates an early phase of strength development that is driven by 240 an improved efficacy of synaptic connections and is likely to occur online (Mason et al. 2020). The 241 increases in corticospinal excitability in the later stages of the intervention were attributed to offline 242 mechanisms, with synaptogenesis considered a dominant adaptation reflecting structural changes 243 (Kleim et al. 2004). This evidence demonstrates that the rapid cellular responses following a single 244 session of resistance training develop into structural adaptations across a short-term training period 245 that underpins increases in muscular strength. It therefore appears that early and late stages of 246 neuroplasticity are associated with strength developments and, interestingly, are similar to the 247 frameworks established in the context of skill literature.

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249 **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 254 individuals and highly motor skilled performers. There is a lack of change shown in corticospinal 255 excitability associated with long-term resistance trained individuals (Tallent et al. 2013; Philpott et 256 al. 2015; Fernandez del Olmo et al. 2006), nevertheless there is an increase in cervicomedullary-257 evoked potentials (Philpott et al. 2015). Clear indications of a long-term increase in M1 258 representation or excitability occur as a result of complex motor skill training and can be seen in 259 highly-skilled Paralympic congenital amputation athletes when compared to able-bodied controls 260 (Nakagawa et al. 2020). However, in able-bodied, highly-skilled individuals, an increase in cortical 261 movement representations and decrease in corticospinal excitability have been shown. For example, 262 in professional painters (Krings et al. 2000) and an international soccer player (Naito and Hirose 263 2014), a reduction in movement representation has been suggested, but conversely, musicians 264 (Bangert and Schlaug 2006) and racquet-based athletes (Pearce et al. 2000) have reported an 265 increase. Exact reasons for the differences are unclear, but the range of expertise and assessment 266 task could contribute to the discrepancies in the findings. Naito and Hirose (2014) and Krings et al. 267 (2000) attributed the decrease in movement-related cortical representation to improvements in 268 neural efficiency during the examination task. The increase in neural efficiency is likely a result of the 269 skill becoming more automated (Debarnot et al. 2014) or a reduction in the sensory activity, leading 270 to a reduced energy expenditure (Nakata et al. 2010; Zhang et al. 2019). Once a sustained synaptic 271 strength is reached, LTD probably down regulates specific synapses within existing structures 272 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 273 274 with the earlier stages of skill learning that plateau or reduce without the introduction of a further 275 novel task and new sensory information (Figure 1).

276

277 3.3 Spinal Adaptations

278 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-279 280 wave). The H-reflex is a measure of la afferent monosynaptic reflex (Knikou 2008) that excludes 281 muscle spindle discharge (Zehr 2002). It reflects the motor neuron excitability and the presynaptic 282 inhibition of the la afferents reflex (Aagaard et al. 2002). V-wave is performed during maximal 283 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 284 285 antidromic action potentials that create a pathway for an evoked reflex, termed the V-wave. 286 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 288 289 V-wave, have shown evidence of short-term (Aagaard et al. 2002; Gondin et al. 2006; Del Balso and 290 Cafarelli 2007; Fimland et al. 2009a; Fimland et al. 2009b; Ekblom 2010; Vila-Cha et al. 2012; Tallent 291 et al. 2017) and long-term increases (Milner-Brown et al. 1975; Upton and Radford. 1975) from 292 resistance training. There also appear to be task-specific changes in V-wave with concentric and 293 eccentric resistance training showing greatest adaptations in V-waves when recorded during the 294 respective contractions (Tallent et al. 2017). Although there are no studies assessing changes in V-295 wave with motor skill training, it appears that there is an element of task specificity to the 296 contraction type that may be applicable for enhancing motor skill performance. Unlike changes in V-297 waves from resistance training that have been shown to increase (standardized mean difference = 298 1.04), a recent meta-analysis has shown no change in H-reflex following resistance training (Siddique 299 et al. 2020).

300

Long-term changes in motor skill training have been shown from evoked reflexes. Ballet dancers 301 302 have been reported to have a reduced H-reflex compared to well-trained controls (Nielsen et al. 303 1993). Classical ballet requires high volumes of high- and low-intensity landings (Shaw et al. 2020; 304 Wyon et al. 2011). It is proposed that the reduction in H-reflex is from an increase in presynaptic 305 inhibition that supresses the Ia afferent loop (Perez et al. 2005); this in turn causes a 306 desynchronization of the alpha motor neurons and increases muscle coordination. Consequently, it 307 is logical to suggest that there is a reduction in sensitivity of the la afferents to enhance the aesthetic 308 landing of the jump and improve the motor control of the task. Spinal changes, particularly spinal 309 reflex, seem therefore to adapt to the specific motor task.

310

311 Direct comparisons in animal models between motor skill and resistance training adaptations have 312 provided clear adaptive differences. Consistent with previous findings in humans (Nudo et al. 1996; 313 Karni et al. 1995), Remple et al. (2001) reported an increase in movement cortical representation in 314 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 315 316 multiple pasta strands or a single pasta strand. The notable differences between the resistance 317 trained and motor skill task occurred at a spinal level with the resistance trained group breaking 318 multiple pasta strands causing greater excitatory synapse expression onto the spinal motor neurons. 319 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.

325

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

327 Due to the relative ease of application compared to other neurophysiology techniques, the use of 328 non-invasive brain stimulation to enhance motor skill performance and resistance training has 329 received considerable attention in recent years (Cox et al. 2020; Ciechanski et al. 2019; Kim and 330 Wright 2020; Frazer et al. 2019). Non-invasive tES includes all methods of the non-invasive 331 application of electrical currents to the brain used in research and clinical practice (Guleyupoglu et 332 al. 2013). Transcranial direct current stimulation (tDCS) and transcranial alternating current 333 stimulation (tACS) are the most explored methods of tES and, consequently, this section will focus 334 on these methods.

335

336 Transcranial direct current stimulation consists of a constant low-intensity current (1 to 2mA) below 337 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). 338 339 Consequently, short-term adaptations are likely attributed to membrane polarity and more long-340 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 341 342 performance (Zhu et al., 2015) and more laboratory-based visuomotor skill training (Antal et al., 343 2004). Furthermore, tDCS has also been shown to enhance the motor skill training effects in clinical 344 populations such as stroke patients (Lefebvre et al. 2012).

345

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 352 353 weeks (9 sessions) of resistance training with tDCS or a sham condition. Despite superior cortical 354 plastic responses between the two groups, there were no differences in the strength changes. 355 Similarly, in stroke patients where the resistance training was conducted at a lower intensity, tDCS 356 and resistance training had no superior gains in strength compared to resistance training alone 357 (Beaulieu et al. 2019), though there is evidence that tDCS may improve the retention of motor based 358 tasks in stroke patients (Goodwill et al. 2016). Whilst there is a lack of evidence suggesting a longer-359 term enhancement in strength using tDCS, rehabilitation programmes require the enhancement in 360 motor skills and force-generating capacity of the muscle (Abbruzzese et al. 2016; Rio et al. 2016). 361 Consquently, any possible improvement in strength or motor skills will speed up recovery and 362 therefore, the use of tDCS could be a worthwhile tool to augment the rehabilitation process.

363

364 Compared to tDCS, tACS has been suggested to be a more-targeted approach to brain stimulation as 365 the oscillation can match the natural frequency of certain regions of the brain (Antal and Herrmann 366 2016). Transcranial alternating current stimulation has also shown an increase in motor performance 367 that is accompanied by an increase in corticospinal excitability and a reduction in intracortical 368 inhibition (Naro et al. 2017; Giustiniani et al. 2019; Wessel et al. 2020). Similar to tDCS, tACS has 369 been shown to improve motor skill performance through intrinsic changes in the micro-circuits of 370 the M1 (Wischnewski et al. 2019). This, accompanied with the lack of negative effect on resistance 371 training reported and possible facilitation, suggest that both tACS and tDCS could be useful tools, 372 particularly in the early stages of skill learning or resistance training. Future research may want to 373 consider stimulation between training sessions rather than during.

374

375 Finally, repetitive transcranial magnetic stimulation (rTMS) might also provide an additional tool to 376 augment motor skill or resistance training adaptions. High-frequency rTMS above 1 Hz has been 377 shown to increase corticospinal excitability and low-frequency rTMS below 1 Hz has been shown to 378 decrease corticospinal excitability (Pascual-Leone et al. 1998). More specifically, rTMS has been 379 suggested to cause LTP of GABAergic synaptic strength that can modulate cortical excitability or 380 inhibition (Lenz and Vlachos 2016). Motor performance and strength gains have been shown to 381 suppress (Hortobagyi et al. 2009; Carey et al. 2006) and enhance (Rumpf et al. 2020) motor skill 382 training/learning depending on the between-pulse frequency and the distribution of pulses across a 383 session. rTMS has also been shown to have positive effects in enhancing the rehabilitation process in 384 stroke patients (Fisicaro et al. 2019).

385 5. Implications For Rehabilitation And Athletic Performance

386 A reduction in strength and neuromuscular coordination are associated with injury (Wilson et al. 387 2020; Harput et al. 2020; Ward et al. 2015) and disease (Milosevic et al. 2017; Stock et al. 2019), 388 whilst strength is a key quality of athletic performance (Joffe and Tallent 2020). Consequently, the 389 enhancement of strength and neuromuscular coordination through maximising neurological 390 adaptation is vital. In clinical rehabilitation, enhancing recovery from disease or injury is not only 391 important for patients, but greater optimisation of exercise prescription can have positive financial 392 implications and reduce the resource demands on health services. For example, a reduction in 393 inpatient or outpatient rehabilitation time through effective and efficient exercise prescription, can 394 decrease the short-term care duration, long-term costs and secondary complications associated with 395 disease and injury (Morrison et al. 2018). Similarly, reducing the time lost from injury in sport 396 through reducing the rehabilitation time has implications for performance (Tallent et al. 2020), and 397 also reduce the financial costs to the organisation (Marshall et al. 2016).

398

Following injury, both clinical (Hansen et al. 2019) and athletic rehabilitation programmes 399 400 (Maestroni et al. 2020) are focused on restoring strength and motor skills (Hardwick et al. 2017; 401 Gokeler et al. 2019; Hansen et al. 2019). Within rehabilitation and athletic-performance training 402 programmes, understanding neurological motor skill and strength adaptations is vital in prescribing 403 the most efficient and targeted exercise programme. In clinical neurological conditions such as stoke 404 that require a dynamic interplay between numerous descending neurological processes (Xu et al. 405 2017), exercise programmes should target inefficiencies in the brain to muscle pathway that will 406 enhance recovery. Whilst similarities in neurological adaptations appear between strength and 407 motor skill training, a comprehensive motor skill and strength programme should be prescribed to 408 maximise adaptations. Figure 2 is a continuum of higher- to lower-force gym-based exercises of the 409 lower limb with the suggested contribution of motor skill efficiency to maximal force output. We 410 propose that, to maximise corticospinal and spinal adaptations, practitioners need to consider the 411 prescription of movements across a continuum of simple movements with high-force outputs, to 412 low-force outputs with highly coordinated movements. It has to be noted that complex highly 413 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). 414 415 However, these often require years of practice over 1000's of resistance training sessions. 416 Understanding the complexity of the task, novelty of movement, and force associated with the 417 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).

423 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.

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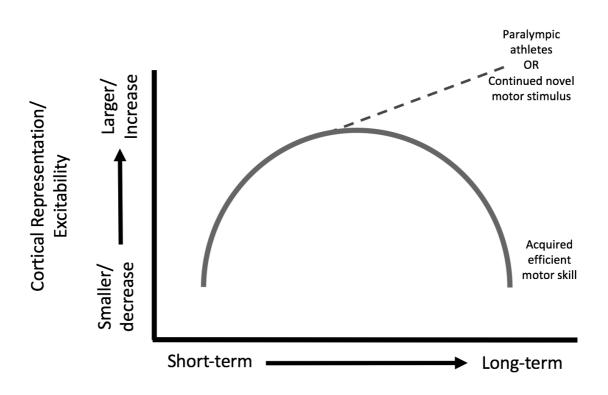
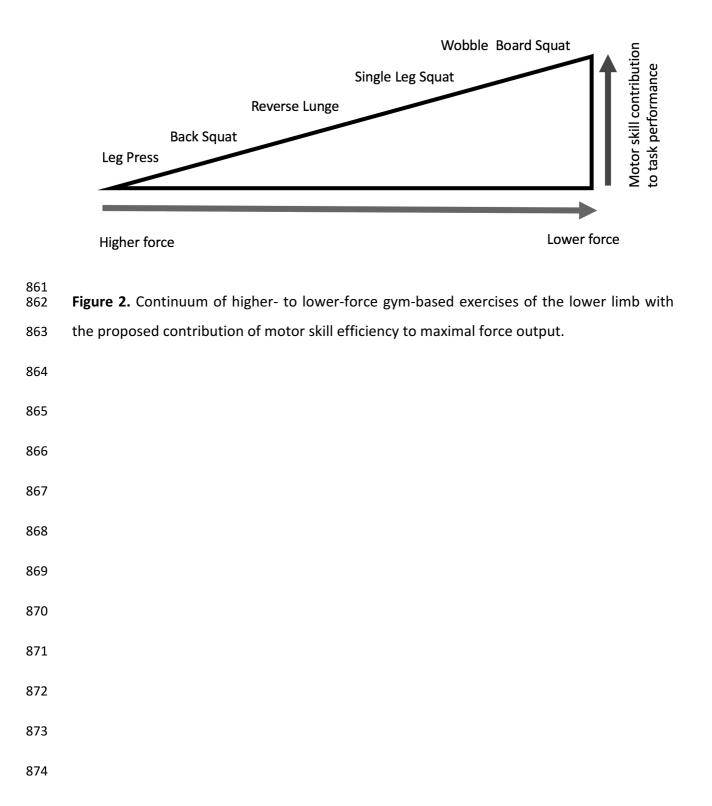




Figure 1. Longitudinal changes in cortical representation/excitability from motor skill training. Corticospinal excitability increases and then decreases as the motor skill is acquired. Continued increases in corticospinal excitability with a novel motor stimulus or in highly-skilled Paralympic congenital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



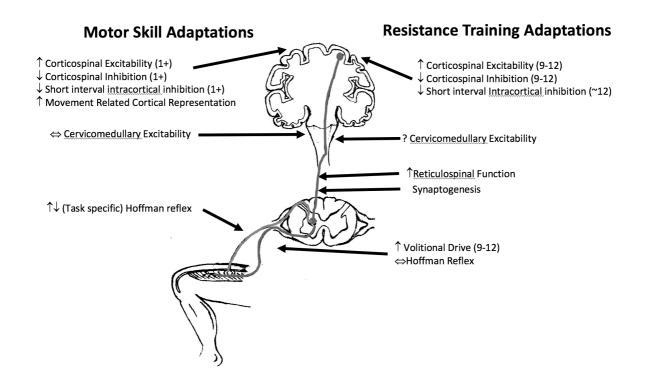


Figure 3. Proposed corticospinal and spinal adaptations to motor skill and strength training, with the number of sessions needed for the adaptation in brackets based on the findings from the literature. With the relatively limited number of studies investigating the timecourse adaptations to resistance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