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Crossed Corticospinal Facilitation between Arm and Trunk Muscles in Humans

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Abstract

44 A voluntary contraction of muscles with one arm increases corticospinal excitability of projections to the contralateral resting arm, a phenomenon known as crossed facilitation. 45 46 Although many motor tasks engage simultaneous activation of the arm and trunk, interactions 47 between corticospinal projections targeting these segments remain largely unknown. Using 48 transcranial magnetic stimulation over the trunk representation of the primary motor cortex 49 we examined motor evoked potentials (MEPs) in the resting erector spinae (ES) muscle when 50 the contralateral arm remained at rest or performed 20% of isometric maximal voluntary 51 contraction (MVC) into index finger abduction, thumb abduction, elbow flexion and elbow 52 extension. We found that MEP size in the ES increased during all voluntary contractions, 53 with greater facilitation occurring during elbow flexion and index finger abduction. To 54 further examine the origin of changes in MEP size we measured short-interval intracortical 55 inhibition (SICI) and cervicomedullary MEPs (CMEPs) in the ES muscle during elbow 56 flexion and index finger abduction and when the arm remained at rest. Notably, SICI 57 decreased and CMEPs remained unchanged in the ES during both voluntary contractions 58 compared with rest, suggesting a cortical origin for the effects. Our findings reveal crossed 59 facilitatory interactions between trunk extensor and proximal and distal arm muscles, 60 particularly for elbow flexor and index finger muscles, likely involving cortical mechanisms. 61 These interactions might reflect the different role of these muscles during functionally 62 relevant arm and trunk movements.

63	New and Noteworthy Section
64	Many of the tasks of daily life involve simultaneous activation of the arm and trunk.
65	We found that responses in the erector spinae muscles evoked by motor cortical stimulation
66	increased in size during elbow flexion and extension and during index finger abduction and
67	thumb abduction. Crossed facilitation with the trunk was more pronounced during elbow
68	flexion and index finger abduction. These results might reflect the different role of these
69	muscles during arm and trunk movements.
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Introduction

89 Interactions between arm and trunk muscles are evident in a number of activities of 90 daily living. For example, trunk muscles are activated prior to or concurrent with voluntary 91 arm movements (Hodges et al. 1992; Aruin and Latash 1995; Hodges and Richardson 92 1997a,b) and when individuals reach for objects beyond arm's length (Kaminski et al. 1995; 93 Levin 1996). Trunk muscles are involved in keeping the center of mass over the support 94 surface while arm muscles are more involved in countering reaction forces generated by limb 95 movement onset (van der Fits et al. 1998). Indeed, deficits in trunk control (Reft and Hasan 96 2002; Cacho et al. 2011) and afferent input from the trunk movement (Adamovich et al. 97 2001) can alter the trajectory of arm movements. Despite this evidence, the effect of 98 voluntary contraction of distal and proximal arm muscles on corticospinal projections 99 contributing to control trunk muscles, and its mechanisms of action, remains largely 100 unexplored.

101 Several lines of evidence suggest that physiological pathways controlling arm and 102 trunk muscles interact. Electrophysiological studies using transcranial magnetic stimulation 103 (TMS) over the primary motor cortex showed that the size of motor evoked potentials 104 (MEPs, reflecting changes in corticospinal excitability) in the erector spinae (ES) muscle 105 increases during contralateral shoulder abduction in standing and lying (Davey et al. 2002). 106 MEPs in the ES muscle also increase during a rapid shoulder flexion task that requires 107 postural control (Chiou et al. 2016). Note that the nature of these interactions can be 108 influenced by the task. For example, changes in dynamic elbow flexion but not elbow 109 extension changes MEP size in trunk muscles (Christmas et al. 2016). When muscles close to 110 the trunk play a postural role, corticospinal responses in a hand muscle increases when the 111 hand is involved in precise force control (Schieppatti et al. 1996). Furthermore, studies 112 showed that electromyographic (EMG) activity in the ES muscle increases according to

113	activation of different arm muscles during functional motor tasks involving the arm and trunk
114	(Marcolin et al. 2015). Even the onset of muscle activity in the ES has been shown to depend
115	on the direction of the arm movement (Hodges and Richardson 1997b). Crossed facilitatory
116	effects also differ when proximal and distal arm muscles are active. Evidence showed that
117	voluntary activation of elbow flexor muscles increased MEP size in hand muscles and that
118	contractions of hand muscles increased MEP size in homologous muscles on the contralateral
119	side (Bunday and Perez 2012; Bunday et al. 2013). Indeed, voluntary activation of elbow
120	flexors and extensor muscles has a different effect on pathways controlling contralateral
121	homologous and heteronymous muscles (Perez et al. 2014). Thus, we hypothesized that
122	voluntary activation of proximal and distal arm muscles would result in different
123	corticospinal facilitation in a trunk muscle. Evidence has shown that crossed corticospinal
124	facilitation can occur at the level of the primary motor cortex, spinal motoneurons, or at both
125	sites (Perez and Cohen 2008; Bunday et al. 2012). Therefore, we tested short-interval
126	intracortical inhibition (SICI) and motor evoked potentials (MEPs) elicited by TMS at the
127	primary motor cortex and cervicomedullary junction (CMEPs) respectively, to examine
128	cortical and subcortical mechanisms contributing to changes in MEP size in the ES muscle in
129	intact humans.
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Methods

139	Subjects. Sixteen healthy volunteers (8 female, 8 male; 1 left handed) with a mean (\pm SD) age
140	of 29.7±10.9 years participated in the study. All subjects gave informed consent to the
141	experimental procedures, which were approved by the local ethics committee at the
142	University of Pittsburgh. The study was performed in accordance with the Declaration of
143	Helsinki. Subjects were preselected out of a total of 25 subjects who were screened to ensure
144	that they showed visible MEPs elicited by TMS in the ES muscle across conditions tested.
145	All subjects confirmed that they were not taking any prescription drugs on a regular basis.
146 147	EMG recordings. EMG was recorded bilaterally from the ES and unilaterally from the first
148	dorsal interosseous (FDI), abductor pollicis brevis (APB), biceps (BB) and triceps (TB)
149	brachii of the dominant arm (Fig. 1A) through surface electrodes (Ag-AgCl; 10 mm
150	diameter) secured on the skin over the belly of each muscle. The signals were amplified
151	(x1000), filtered (30–1000 Hz), and sampled at 2 kHz for off-line analysis (CED 1401 with
152	Signal software, Cambridge Electronic Design, Cambridge, UK).
153 154	Experimental setup. Subjects were seated in an armchair with head supported by a headrest.
155	At the beginning of the experiment, all subjects performed 2-3 unilateral isometric maximal
156	voluntary contractions (MVCs) for 3-5 s into index finger and thumb abduction, and elbow
157	flexion and extension, separated by 30 s of rest. During maximal contractions subjects
158	received verbal encouragement to perform maximally. MVCs for the ES were collected in a
159	prone position with subjects' pelvis and legs secured by the investigators. Testing was
160	completed with the trunk resting on a chair (conditioned referred here as "rest") and when
161	subjects performed index finger abduction, thumb abduction, elbow flexion, and elbow
162	extension in a pseudo-randomized order. During index finger and thumb abduction, subjects
163	were instructed to press with their index finger or thumb against a custom lever in the

164 abduction direction with the forearm pronated and the wrist restrained by straps. During 165 elbow flexion and extension testing, subjects were seated with both shoulders and elbows flexed to 90° and the forearm supinated. Here, a custom-built arm device was used to 166 167 maintain the position of the arm. Since a voluntary contraction of arm muscles can generate 168 EMG activity in the ES, in a preliminary study (n=8) we tested the effects of 10, 20 and 30% 169 of MVC with all arm muscles tested on background EMG activity in the ES muscle. We 170 found that subjects were able to maintain 20% of MVC with each of the muscles tested 171 without eliciting voluntary activity in the ES muscle. Thus, testing was performed at rest and 172 when the contralateral arm remained at rest or when performing 20% of MVC into index 173 finger and thumb abduction and elbow flexion and extension. EMG activity in the ES and in 174 the arm muscle tested were continuously displayed on an oscilloscope and verbal feedback 175 was provided to subjects to ensure that physiological measurements were acquired at similar 176 levels of background EMG activity. A total of 3.4±2.0% trials in which mean rectified EMG 177 activity exceeded 2 SD of the mean average rectified EMG, measured 100 ms before the 178 stimulus artifact, were excluded from further analysis (Bunday et al. 2012, 2013). 179 *TMS*. TMS pulses were delivered via a Magstim 200^2 monophasic stimulator (Magstim 180 181 Company) through a bat-wing (loop diameter, 90 mm; handle pointing backward and 45° 182 away from the midline) or a double-cone coil (loop diameter, 110 mm; handle pointing 183 vertically upwards). In individuals in whom an MEP could not be elicited in the ES muscle 184 with a bat-wing coil the double-cone coil was used. We determined the optimal position for 185 eliciting a MEP in the ES muscle (hot spot) by moving the coil in small steps along the area 186 corresponding to the primary motor cortex. The hot spot was defined as the region where the 187 largest MEP in the ES could be evoked with the minimum intensity (Rothwell et al. 1999). 188 With this coil position the current flowed in a posterior-anterior direction and probably 189 produced D and early I wave activation (Sakai et al. 1997). The TMS coil was held to the

head of the subject with a custom coil holder, while the head was firmly secured to a headrest
by straps. TMS was used to elicit MEPs, resting motor threshold (RMT), and short-interval
intracortical inhibition (SICI).

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194 MEPs. RMT [78.8±18.2% of the maximal stimulator output (MSO)] was defined as the 195 minimal stimulus intensity required to induce MEPs greater than 50 μ V peak-to-peak 196 amplitude in at least 3/5 consecutive trials in the relaxed ES muscle (Rothwell et al. 1999). 197 Based on our previous results (Chiou et al. 2018), we used a stimulus intensity needed to 198 elicit an MEP with a peak-to-peak amplitude of ~0.1 mV (89.7±12.7% MSO) in the ES 199 muscle in order to elicit responses in most subjects. Single TMS pulses were delivered at 4 s 200 intervals in sets of 10 separated by rest periods as needed. Twenty MEPs were tested during 201 each voluntary contraction.

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203 SICI. We observed that voluntary contraction into elbow flexion and index finger abduction 204 increased MEP size in the ES muscle to a larger extent than elbow extension and thumb 205 abduction. Therefore, we examined the contribution from the primary motor cortex to 206 changes in ES MEP size by testing SICI using a previously described method (Kujirai et al. 207 1993) at rest first and when subjects performed 20% of MVC into elbow flexion and index 208 finger abduction in a randomized order (n=8). A conditioning stimulus (CS) was set at an 209 intensity needed to elicit \sim 50% of SICI, which corresponded to \sim 70% of AMT (55.2±13.1% 210 MSO). This low-intensity stimulus allowed us to assess SICI independently of the effects on 211 short-intracortical facilitation at low contraction levels (Ortu et al. 2008). The same stimulus 212 intensity was used for the CS across conditions. The test stimulus (TS) was set at an intensity 213 needed to elicit an MEP with a peak-to-peak amplitude of ~0.1 mV (86.4±15.2% MSO). The 214 CS was delivered 2.5 ms before the TS. Previous studies showed that the size of the test MEP 215 can influence the magnitude of SICI (Roshan et al. 2003). Since our results from the single-

pulse TMS showed that ES MEPs became larger during the elbow flexion and index finger
abduction compared with rest, we adjusted the size of the test MEP by decreasing the TMS
stimulus intensity to match the size of the test MEP at rest. SICI was also tested by adjusting
the size of the test MEP to match that of the resting test MEP. SICI was calculated by
expressing the size of the conditioned MEP as a percentage of the size of the test MEP.
Twenty test MEPs and 20 conditioned MEPs were tested in each condition.

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223 CMEPs. Since voluntary contraction into elbow flexion and index finger abduction increased 224 MEP size in the ES muscle to a larger extent than elbow extension and thumb abduction we 225 examined subcortical contributions to changes in ES MEP size during elbow flexion and 226 index finger abduction by stimulating the corticospinal tract at the cervicomedullary junction 227 using a circular magnetic coil (diameter, 90 mm;) located over one side of the neck, lateral or 228 near the inion with current flowing downward in the coil (Bunday et al. 2014; Taylor and 229 Gandevia 2004; Chiou et al. 2018). The position of the coil was marked on the subjects using 230 a removable marker pen once the optimal coil position for evoking the largest CMEP was 231 identified. The coil was held firmly to the back of the neck of the subject by one of the 232 experimenters and, since our voluntary contractions were isometric, there was very little head 233 displacement observed during the contractions. The latency of CMEPs was also monitored 234 frame-by-frame to ensure that the stimulation was consistent and accurate across trials. 235 Cervical root activation was investigated by increasing the intensity until an abrupt decrement 236 in latency occurred, then decreasing the intensity and verifying that the response was 237 potentiated by a small background contraction (Taylor, 2006). The latency of CMEPs was 238 significantly shorter than MEPs elicited by TMS (CMEP=10.2±1.2 ms, MEP=16.7±1.9 ms; 239 p<0.001) indicating that the stimulation activated corticospinal axons directly. CMEPs were 240 tested at rest and during 20% of MVC into elbow flexion or index finger abduction with the

241	contralateral arm (n=8) using an intensity needed to elicit a CMEP with a peak-to-peak
242	amplitude of ~0.1 mV (intensity: 92.2±6.7% MSO). Ten CMEPs were tested in each
243	condition.

245	Data analysis. Data were analyzed using SigmaPlot software (version 12.5, Systat Software,
246	Inc., San Jose California USA, 2011). Normal distribution and homogeneity of variances
247	were tested by the Shapiro-Wilk's test and by the Equal Variance test, respectively. If the data
248	failed the normality test (p<0.05), non-parametric tests were used. Repeated-measures
249	analysis of variance (ANOVA) was performed to determine the effect of CONDITION (rest,
250	elbow flexion, elbow extension, index finger abduction, and thumb abduction) on MEP size
251	and mean rectified EMG in the ES muscle, and the effect of MUSCLE (BB, TB, FDI, and
252	APB) on the level of muscle activity. Repeated-measures ANOVA was also used to examine
253	the effect of SUBCONDITION (rest, elbow flexion, and index finger abduction) on SICI
254	adjusted and unadjusted and CMEPs in the ES muscle. Paired-t tests were employed to
255	compare the latencies of MEPs elicited by TMS over the primary motor cortex and the
256	cervicomedullary junction. Holm-Sidak post hoc test was used to test for significant
257	comparisons. Significance was set at p<0.05. Group data are presented as the means \pm SD in
258	the text.
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261	Results
262	EMG
263	Repeated measures ANOVA showed no effect of CONDITION ($F_{4,60}=0.9$, p=0.47,
264	n=16; Fig. 2A) on mean rectified EMG activity in the contralateral ES muscle. This result
265	indicates that mean rectified ES EMG activity remains constant when the right arm was at

266 rest or performed 20% of MVC into index finger abduction, thumb abduction, elbow flexion 267 and elbow extension. We also found no effect of MUSCLE ($F_{3,45}=2.1$, p=0.1, n=16; Fig. 2B) 268 on the level of muscle contraction exerted by each muscle tested across conditions. Further, 269 repeated measures ANOVA showed no effect of CONDITION (F_{4.60}=0.65, p=0.63, n=16) on 270 mean rectified EMG activity in the ipsilateral ES muscle. 271 272 273 **MEPs** 274 Figure 3A illustrates traces of averaged MEPs elicited by TMS over the primary 275 motor cortex in the ES muscle from a representative subject. Note that the size of MEP in the 276 ES muscle increased during all voluntary contractions compared with rest but to a larger 277 extent during elbow flexion and index finger abduction. 278 Repeated-measures ANOVA revealed an effect of CONDITION ($F_{4.60}$ =11.29; 279 p<0.001) on ES MEP size (n=16; Fig. 3B). Post hoc tests showed that ES MEP amplitude 280 increased during elbow flexion (164.31±48.58%, p<0.001; 16/16), elbow extension 281 (128.07±27.03%, p=0.04; 13/16), index finger abduction (160.73±51.39%, p<0.001; 15/16) and thumb abduction (130.36±40.10%, p=0.03; 14/16) compared with rest. Note that changes 282 283 in MEP size in the ES muscle were also larger during elbow flexion compared with elbow 284 extension (p=0.01) and thumb abduction (p=0.02). In addition, changes in MEP size in the 285 ES muscle were larger during index finger abduction compared with elbow extension (p=0.02) and thumb abduction (p=0.04). The majority of subjects showed larger ES MEP size 286 287 during elbow flexion (16/16) and during index finger flexion (15/16; Fig. 3C). No difference 288 was found in the amplitudes of the ES MEP between elbow flexion and index finger 289 abduction (p=0.9) or between elbow extension and thumb abduction (p=0.8). 290

291 **SICI**

292	Figure 4A illustrates averaged data from SICI measurements in a representative
293	subject. Note that the magnitude of SICI decreased during elbow flexion and index finger
294	abduction compared with rest. Repeated-measures ANOVA revealed an effect of
295	SUBCONDITIONS (F _{2,14} =11.8, p<0.001, n=8) on ES MEP size (Fig. 4B). Post hoc tests
296	showed that SICI in the ES decreased during the elbow flexion (p=0.008) and during the
297	index finger abduction (p=0.001; Fig 4B, left panel). Since MEP size increased during
298	voluntary contraction, SICI was also tested with an adjusted test stimulus intensity. Similarly,
299	there was a decrease in SICI _{adj} in the ES during elbow flexion ($p=0.002$) and during index
300	finger abduction (p=0.005) compared with rest (Fig. 4B, right panel). Note that SICI in the
301	ES was reduced in all participants (8/8) during elbow flexion and during index finger
302	abduction compared with rest (Fig. 4C). Mean background EMG in the ES was similar across
303	the conditions tested ($F_{2,14}=1.2$, p=0.3, n=8).

305 **CMEPs**

Figure 5A illustrates examples of averaged CMEPs in the ES muscle in a representative subject. Note that ES CMEP size remained similar during contralateral elbow flexion and index finger abduction compared with rest. Repeated-measures ANOVA revealed no effect of SUBCONDITIONS ($F_{2,14}=2.36$; p=0.13, n=8) on ES CMEP size, suggesting that the amplitude of CMEPs in the ES muscles remain the same at rest, during elbow flexion and index finger abduction. Mean background EMG in the ES was similar across the conditions tested ($F_{2,14}=2.07$; p=0.16, n=8).

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Discussion

319 Our findings demonstrate that corticospinal excitability of projections to a trunk 320 muscle increases during voluntary activation of proximal and distal arm muscles in intact 321 humans. Specifically, we found that MEP size in the ES muscle increased during elbow 322 flexion and extension and during index finger abduction and thumb abduction. Note that the 323 ES MEP facilitation was greater during elbow flexion and index finger abduction compared 324 with the other voluntary contractions. SICI decreased and CMEPs remain unchanged in the 325 ES during elbow flexion and index finger abduction compared with rest, suggesting that 326 crossed facilitatory interactions are mediated at the level of the motor cortex. We argue that 327 these findings might reflect the role of proximal and distal arm muscles during functionally 328 relevant arm and trunk movements.

329

330 Crossed facilitation of a trunk muscle during arm voluntary contraction

331 Our results agree with a previous study showing that MEP size of the voluntarily 332 active ES muscle increases during strong levels of contralateral shoulder abduction when 333 tested in standing and lying postures (Davey et al. 2002). We extended these results and for 334 the first time examined crossed corticospinal facilitation between the trunk and different 335 proximal and distal arm muscles and the mechanisms contributing to this effect. We found 336 that MEPs in the ES muscle increased in size during elbow flexion and extension and during 337 index finger abduction and thumb abduction, with greater facilitation observed during elbow 338 flexion and index finger abduction. This agrees with topographical studies of the primary 339 motor cortex showing that motor cortical zones controlling various forelimb segments are 340 largely interconnected (Capaday et al. 1998; Huntley and Jones 1991). This is also consistent 341 with evidence showing that crossed corticospinal facilitatory effects are present not only 342 between contralateral homologous muscles but also between bilateral non-homologous 343 muscles (Hortobagyi et al. 2003; Perez and Cohen 2008; Zijdewind and Kernell 2011; Chiou

344 et al. 2013). An intriguing question is why ES MEPs were more facilitated by elbow flexion 345 than elbow extension. If the primary motor cortex controls different forelimb segments as a 346 whole rather than individually (Devanne et al. 2002) one might expect that all proximal 347 muscles will exert similar facilitatory effects on the size of MEPs in the ES muscle. Although 348 the representations of elbow flexor and extensor muscles in the primary motor cortex are 349 close in monkeys (Kwan et al. 1978) and humans (Penfield and Boldrey 1937) some 350 differences exist in the neural control of these muscles. For example, the intrinsic properties of human elbow flexor and extensor motor units differ (Wilson et al. 2015) and phase-351 352 dependent modulation of MEPs is present in elbow flexors but not in elbow extensors during 353 arm cycling (Spence et al., 2016), supporting the view that both muscles are subject to 354 different motor control principles. In addition, evidence showed that ipsilateral MEPs tested 355 by TMS over the primary motor cortex are frequently elicited in elbow flexors while they are 356 not present in elbow extensors (Ziemann et al. 1999). Thus, it is possible that elbow flexors 357 might be better suited to contribute to the stronger interaction with the back extensors 358 observed in this study. This is also consistent with evidence showing that dynamic elbow 359 flexion but not elbow extension changes MEP size of the ES muscle (Christmas et al. 2016). 360 It is important to note that crossed facilitatory effects are more pronounced during strong levels of voluntary activity (Muellbacher et al. 2000; Perez and Cohen 2008). However, it is 361 362 less likely that this factor contributed to our results since we found that the level of EMG 363 activity exerted during elbow flexion and extension was similar across voluntary 364 contractions.

A next important question is why ES MEPs were more facilitated by index finger abduction compared with thumb abduction. Electrophysiological and biomechanical studies suggest that the control of index finger and thumb muscles differ. In monkeys, a single corticomotoneuronal cell does not facilitate the FDI and APB muscles simultaneously (Buy et

369 al. 1986), which might contribute to relatively independent movements of these digits. In 370 humans, the size of MEPs in the FDI increased in accordance with the posture of the hand 371 during grasping but it remained unchanged in the APB (Perez and Rothwell 2015). Hand 372 trajectory during pointing is affected during reaching movements involving the trunk 373 (Adamovich et al. 2001). During a postural task involving the whole arm, MEPs in the FDI 374 were greater when the task involved precise force control with the hand (Schieppatti et al. 375 1996). Biomechanical studies also showed that during grasping the APB has a more 376 stabilizing role (Chao et al. 1976) while the FDI contributes to the fine grading of forces 377 (Maier and Hepp-Reymond, 1995). Therefore, it is possible that these physiological and 378 biomechanical features make the FDI more suitable to have stronger facilitatory interactions 379 with the ES muscle during arm movements.

380

381 Neuronal mechanisms

382 We found a decrease in intracortical inhibition in the ES muscle during contralateral 383 elbow flexion and index finger abduction. These results agree with previous findings 384 suggesting that intracortical circuits contribute to modulate crossed corticospinal facilitation 385 between arm muscles (Perez and Cohen 2008; Chiou et al. 2013). This agrees with lesion 386 experiments and single-unit recordings in monkeys suggesting that the primary motor cortex 387 is involved in the coordination of limb segments (Kalaska and Drew 1993). Since ~50% of 388 corticospinal neurons project to both proximal and distal arm muscles (McKiernan et al. 389 1998) it is possible that extensive intraspinal branching of corticospinal axons might also 390 contribute to interactions found in our study. Indeed, it could be also argued that changes in 391 spinal excitability might contribute to crossed facilitation in the ES muscle, since subcortical 392 mechanisms have been shown to be involved in some crossed corticospinal facilitatory 393 effects in intact humans (Muellbacher et al. 2000; Stedman et al. 1998). Since we found no 394 changes in the size of CMEPs, it is less likely that our results reflect changes in corticospinal

395 transmission or motoneuron excitability (Ugawa et al. 1994; Taylor and Gandevia 2004). 396 However, others have shown that crossed facilitatory effects also involve changes in spinal 397 reflexes (Hortobayi et al. 2003); then, this possibility cannot be completely excluded. The 398 latencies of CMEPs in the ES muscle were shorter than the latency of MEPs elicited by TMS 399 over the primary motor cortex, supporting the view that corticospinal axons were stimulated 400 directly. In addition, the location of magnetic stimulation was distant from the root outflow 401 for the ES at vertebral level T12, thus it is unlikely that any direct stimulation of the relevant 402 ventral roots innervating ES T12 occurred. Our results are also consistent with a previous 403 study showing a lack of contribution of subcortical pathways to crossed facilitation when 404 similar low levels of voluntary contraction were performed (Stedman et al. 1998).

405

406 Functional significance

407 It is possible that the observed crossed facilitatory effects are relevant to limb and 408 trunk interactions during unimanual and bimanual actions (Carson et al. 2008; Lee et al. 409 2010). Functional interactions between the trunk and arm muscles are well recognized with 410 ample evidence showing that when the arms are moved, trunk muscle activity increases 411 concurrently (Aruin and Latash 1995; Benvenuti et al. 1997; Bouisset and Zattara 1987; 412 Hodges and Richardson 1997b). Studies showed greater activation of the ES muscle when 413 different arm muscles are active during functional motor tasks such as pushups (Marcolin et 414 al. 2015). Even the onset of muscle activity in the ES has been shown to depend on the 415 direction of the arm movement (Hodges and Richardson 1997b). The greater facilitation from 416 elbow flexors to the ES can be used to support postural perturbations since arm flexion 417 movements are likely to cause anterior displacement of the center of mass that required 418 activation of the trunk extensors (i.e. ES) to minimize the postural displacement (Aruin and 419 Latash 1995; Hodges and Richardson, 1997b). The more pronounced facilitatory effects of the FDI to the ES can also be related to anticipatory postural adjustments needed to stabilize 420

421 the whole arm prior to upcoming finger activation (Caronni and Cavallari 2009). Indeed, the 422 earlier onset of anticipatory postural adjustments for proximal arm muscles has been 423 associated with higher precision of pointing movements (Bruttini et al. 2016). Altogether, our 424 findings support the view of strong interactions between the neural control of trunk and 425 proximal and distal hand muscles in intact humans. 426 These results may have clinical relevance since previous evidence suggests that 427 crossed corticospinal facilitatory effects might be beneficial in improving arm function in 428 patients with specific neurological disorders (Hamzei et al. 2012; Kowalczewski et al. 2011). 429 Since many patients with stroke (Verheyden et al. 2006) or spinal cord injury (Field-Fote and 430 Ray 2010) have reduced trunk control, the use of the arms to increase corticospinal 431 excitability of projections to trunk muscles may increase neural interactions, which could 432 contribute to improve functional outcomes. As such, crossed facilitation between arm and

trunk muscles might represent an opportunity for trunk rehabilitation and its effect on

434 functionally relevant motor tasks remain to be tested.

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622 **Figure legends**

623 Figure 1. (A) Schematic illustration of the coil position (when the cone coil was used) and the electrodes over the erector spinae (ES) muscle at the 12th thoracic vertebral level. Raw 624 625 motor evoked potential (MEP) trace elicited in the ES muscle by transcranial magnetic 626 stimulation (TMS) over the primary motor cortex from a representative subject (20 stimuli, 627 averaged unrectified). The arrow indicates the TMS pulse and the dotted line indicates the 628 onset of the MEP. (B) Raw rectified electromyographic (EMG) activity from each of the 629 muscles tested during 20% of maximal voluntary contraction (MVC) into elbow flexion 630 (recording from the biceps brachii, BB), elbow extension (recording from the triceps brachii, 631 TB), index finger abduction (recording from the first dorsal interosseous, FDI), and thumb 632 abduction (recording from the abductor pollicis brevis, APB).

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634 Figure 2. Electromyography (EMG). (A) Group data showing background EMG in ES 635 across voluntary contractions (n=16). Testing was completed with the trunk resting on a chair (conditioned referred here as "rest") and when subjects performed index finger abduction, 636 637 thumb abduction, elbow flexion, and elbow extension in a pseudo-randomized order. The 638 abscissa shows the condition tested (rest, elbow flexion, elbow extension, index finger abduction, and thumb abduction) and the ordinate shows the mean background EMG activity 639 640 in the ES muscle (as a % of MVC). (B) Group data showing the background EMG in each 641 muscle tested during 20% of MVC (n=16). The abscissa shows the muscle tested [biceps 642 brachii (BB), triceps brachii (TB), first dorsal interosseous (FDI) and abductor pollicis brevis 643 (APB)] and ordinate the contraction level (as a % of MVC). Note that individual data is 644 shown for each condition. Error bars indicate the SD *p<0.05.



648 (black traces) and during 20% of MVC (grey traces). (B) Group data (n=16) showing MEPs 649 in ES across conditions. The abscissa shows the condition tested (elbow flexion, elbow 650 extension, index finger abduction, and thumb abduction) and the ordinate shows the size of 651 the ES MEP during 20% of MVC (as a % of the ES MEP obtained at rest). The horizontal 652 dashed line represents the size of the ES MEP at rest. Note that the amplitudes of MEP in the ES muscle increased during all voluntary contractions, with greater facilitation observed 653 654 during elbow flexion and index finger abduction. (C) Note that that majority of participants 655 show increases in ES MEPs during all voluntary contractions compared with rest. Error bars 656 indicate the SD. *p<0.05, comparison between voluntary contractions. ¥p<0.05, comparison 657 between rest and all voluntary contractions.

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Figure 4. Short-interval intracortical inhibition (SICI). (A) SICI recorded from the ES 659 660 muscle of a representative subject. Traces show the average of 20 test MEPs (black traces) 661 and conditioned MEPs (Cond. MEP, grey traces) indicated by arrows. (B) Group data showing SICI in the ES (n=8). The abscissa shows the subconditions tested in the unadjusted 662 663 (rest, elbow flexion and index finger abduction) and adjusted (rest, elbow flexion adj. and 664 index finger abduction adj.) conditions. The ordinate shows the size of the conditioned MEP expressed as a % of the test MEP. The horizontal dotted line shows SICI at rest. Note that 665 666 SICI decreased (increased conditioned MEP size) during elbow flexion (grey bars) and index 667 finger abduction (grey bars) when SICI was tested with an adjusted and unadjusted test MEP 668 size. (C) Note that all participants show reduction in SICI during elbow flexion (solid lines) and index finger abduction (dotted lines) compared with rest. Error bars indicate the SD. 669 670 *p<0.05, comparison between subconditions.

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Figure 5. Cervicomedullary MEPs (CMEPs). (A) CMEPs recorded from the ES muscle of
a representative subject. Traces show the average of 10 CMEPs. (B) Group data (n=8). The

674	abscissa shows the conditions tested (elbow flexion and index finger abduction). The ordinate
675	shows the size of the CMEPs (as a % of the test CMEP). The horizontal dashed line
676	represents the size of the CMEP at rest. Note that individual data is shown for each condition.
677	Error bars indicate the SD. *p<0.05, comparison between subconditions.
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Figure 2

Figure 3



Figure 4





