1    **Title:** Motor resonance is modulated by an object's weight distribution

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20

**Abstract**

Transcranial magnetic stimulation (TMS) studies showed that corticospinal excitability (CSE) is modulated during observation of object lifting, an effect termed 'motor resonance'. Specifically, motor resonance is driven by movement features indicating object weight, such as object size or observed movement kinematics. We investigated in 16 humans (8 females) whether motor resonance is also modulated by an object's weight distribution. Participants were asked to lift an inverted T-shaped manipulandum with interchangeable center of mass after first observing an actor lift the same manipulandum. Participants and actor were instructed to minimize object roll and rely on constrained digit positioning during lifting. Constrained positioning was either collinear (i.e. fingertips on the same height) or noncollinear (i.e. fingertip on the heavy side higher than the one on the light side). The center of mass changed unpredictably before the actor's lifts and participants were explained that their weight distribution always matched the one of the actor. Last, TMS was applied during both lift observation and planning of lift actions. Importantly, our results revealed that CSE was similarly modulated during lift observation and planning: when participants observed or planned lifts in which the weight distribution was asymmetrically right-sided, CSE, recorded from the thumb muscles, was significantly increased compared to when the weight distribution was left-sided. Moreover, this increase seemed to be primarily driven by the observed and planned thumb positioning when lifting the right-sided asymmetrical weight distribution. In conclusion, our results suggest that complex intrinsic object properties such as weight distributions can be encoded by an individual's motor system during both observation and planning of lifting actions.

**Highlights**

- Motor resonance is observation-induced activity in the observer's motor system
- We used a dyadic lifting task of objects with asymmetrical weight distribution
- We investigated which movement features modulate motor resonance
- Motor resonance is modulated by the object's weight distribution
- Motor resonance is driven by observed and planned digit positioning

**Keywords**: Action observation; object lifting; dyadic interaction; motor planning; motor resonance

**Introduction**

55

56 Skilled object manipulation not only relies on tactile feedback but also on anticipatory mechanisms

57 (Johansson & Westling, 1988). When performing hand-object interactions, humans establish well-

58 learned size-weight and material-density associations, termed 'priors'. These priors can then be relied

59 upon to accurately estimate object weight (Baugh, Kao, Johansson, & Flanagan, 2012). However,

60 predictive lifting errors can be made when object weight is wrongly estimated (e.g. lifting an opaque box

61 with unknown amount of filling). Rather than updating the well-learned priors in these erroneous

62 situations, individuals update their 'sensorimotor memory' which contains short-term associations

63 between previous hand-object experiences and the visual object properties (Baugh et al., 2012). As such,

64 the sensorimotor memory can be flexibly updated and subsequently used for predicting object weight

65 and planning skilled hand-object interactions.

66 Importantly, skilled hand-object interactions not only require accurate planning for an object's

67 weight but also for its weight distribution. For instance, when having to avoid content spill, object roll

68 has to be minimized by generating appropriate compensatory torque to offset the external torque

69 induced by an unbalanced weight distribution. Lukos et al. (2007) showed that individuals can update

70 their sensorimotor memory for an object's weight distribution, in turn enabling them to predictively

71 generate appropriate compensatory torque. In addition, Fu et al. (2010) showed that individuals scale

72 their fingertip forces in function of their digit positioning: when digit positioning is constrained,

73 individuals scale their fingertip forces in function of these fixed contact points. Conversely, when digit

74 positioning is unconstrained, individuals scale their fingertip forces accurately in function of their self-

75 chosen contact points. However, it has been argued that, in line with these findings, object lifting with

76 unconstrained digit positioning relies on both predictive and feedback driven mechanisms: although

77 fingertips are positioned based on the initial motor command, trial-to-trial variability in actual

78 positioning is induced by contextual and executional noise. As a result, the initially planned fingertip

79 forces need to be updated in function of tactile feedback about the actual positioning (Mojtahedi et al.,

80 2015).

81 Although execution of hand-object interactions is pivotal in rapidly updating the sensorimotor

82 memory, other studies have shown that humans are able to generate similar representations during

83 observation of object lifting as well. For instance, Meulenbroek et al. (2007) demonstrated that when

84 two individuals incorrectly predict an object's weight, the second individual will make a smaller lifting

85 error after observing the first individual making one. These findings have been supported by other

86 studies (Buckingham, Wong, Tang, Gribble, & Goodale, 2014; Reichelt, Ash, Baugh, Johansson, &

87    Flanagan, 2013). In addition, it has been shown that observation of skilled lifting can improve predictive

88    object lifting as well, albeit in a smaller manner than observing lifting errors (Rens et al. 2020a; Rens and

89    Davare 2019).

90         It has been well-established that observing hand-object interactions not only alters sensorimotor

91    representations but also activates the observer's motor system (for a review see Naish et al. 2014).

92    Fadiga et al. (1995) were the first to demonstrate that corticospinal excitability (CSE), probed with

93    transcranial magnetic stimulation (TMS), is similarly modulated during the execution and observation of

94    hand actions. They argued that the motor system is potentially involved in action understanding through

95    a bottom-up mapping ('mirroring') of observed actions onto the same cortical areas involved in their

96    execution (for a review see: Rizzolatti et al., 2014). Consequently, action observation-driven modulation

97    of CSE has been termed 'motor resonance'. With specific interest to observation of object lifting, Alaerts

98    et al. (2009, 2010a, 2010b) demonstrated that motor resonance is modulated by observed movement

99    features indicating object weight, such as intrinsic object properties (e.g. size), muscle contractions and

100    movement kinematics. Specifically, CSE is increased when observing lifts of heavy compared to light

101    objects. Critically, other studies have shown that these motor resonance effects are not robust. For

102    instance, Buckingham et al. (2014) demonstrated, using the size-weight illusion, that CSE modulation is

103    driven by object size when observing skilled but not erroneous lifts. In addition, Tidoni et al. (2013)

104    showed that motor resonance is differently modulated when observing an actor with truthful or

105    deceptive intentions. Last, Rens et al. (2020) demonstrated that motor resonance is easily biased by

106    differences within the contextual setting even though the observed lifting actions are the same. In

107    addition, they showed that this bias was generated by top-down inputs from the posterior temporal

108    sulcus.

109         Although Alaerts et al. (2010) and Buckingham et al. (2014) highlight that motor resonance can

110    reflect simple object properties, it is unknown whether it can reflect more complex ones such as an

111    object's weight distribution. Due to the importance of accurately estimating an object's weight (i.e. avoid

112    damage) and weight distribution (i.e. avoid content spill), it is plausible that they rely on similar

113    mechanisms for estimating these properties. However, as minimizing object roll requires a valid digit

114    position-force coordination pattern, the observer's motor system should integrate both observed digit

115    positioning and forces (rather than solely encoding force) for accurately encoding the weight

116    distribution. As such, in this study we wanted to investigate whether the observer's motor system

117    encodes (a) observed force scaling, (b) observed digit positioning or (c) the weight distribution, as

118    indicated by a combination of these features. We asked participants to grasp and lift an inverted T-

119    shaped manipulandum with interchangeable (left, middle or right) center of mass after first observing an

120    actor lift the same manipulandum. Participants and actor were required to minimize object roll during

121    lifting by generating appropriate compensatory torque. The center of mass changed unpredictably

122    before the actor trials, but participants were informed that they would always lift the same weight

123    distribution as the actor. As such, participants could potentially estimate the object's center of mass

124    during lift observation and use this information to predictively plan their own lifts. For lifting the

125    asymmetrical weight distributions, we constrained digit positioning to two distinct possibilities: (1)

126    Placing the fingertips on the same height ('collinear positioning') or placing the finger on the heavy side

127    higher than the one on the light side ('noncollinear positioning'). Importantly, when compensatory

128    torque is generated for an asymmetrical weight distribution, the fingertip on the heavy side generates

129    more force when using a collinear positioning compared to a noncollinear one (Fu, Zhang, & Santello,

130    2010). By relying on these constrained digit positionings and the associated force requirements for

131    skilled lifting, we hypothesized that we could disentangle whether the motor system encodes force or

132    digit positioning during lift observation. For doing so, we used TMS to probe CSE during lift observation

133    and planning.

134        In line with Alaerts et al. (2010), we hypothesized that, if the observer's motor system encodes

135    force, motor resonance should be significantly increased when observing skilled lifts on the asymmetrical

136    weight distributions with collinear compared to noncollinear positioning. In contrast, if motor resonance

137    is primarily modulated by digit positioning, we would expect that motor resonance, when observing lifts

138    on the asymmetrical weight distribution, would be increased when observing lifts with noncollinear

139    compared to collinear positioning.

140

141    **Methods**

142    Participants

143    16 individuals participated in the present study (8 females; mean age = 24 ± 3 years). The Edinburgh

144    Handedness Questionnaire (Oldfield, 1971) revealed that all participants were strongly right-handed (>

145    90). Prior to participation, participants were required to fill in a TMS safety screen questionnaire based

146    on Rossi et al. (2011). Moreover, all participants had normal or corrected-to-normal vision, were free of

147    neurological disorders and had no motor impairments of the right upper limb. Participants gave written

148    informed consent and were financially compensated for their time. The protocol was in accordance with

149    the Declaration of Helsinki and was approved by the local ethical committee of KU Leuven, Belgium.

150

151                                      ----------

152                                      Figure 1

153                                      ----------

154 <u>Data acquisition</u>

155 For the present study, we used the same custom-built carbon fiber 'inverted T-shape' grip-lift

156 manipulandum (Arsalis, Belgium; for all object dimensions see: Figure 1) as in one of our previous studies

157 (Rens et al. 2020b). The manipulandum consisted of a horizontal basis and a vertical block to which two

158 3D force/torque (F/T) sensors were attached. A cover plate (height × width: 140 × 53 mm) with a central

159 protruding surface (height × width: 140 × 20 mm) was attached to each F/T sensor to block view on the

160 sensors. On each protruding surface, we attached two pieces of fine-grained sandpaper (p600) (height x

161 width: 20 x 20 mm). Both actor and participants were only allowed to place their fingertips on these

162 constrained locations. The distance between the bottom side of the upper piece and the upper side of

163 the lower piece of sandpaper on the same cover plate was 20 mm. As a result, the vertical distance

164 between the center points of the same-sided pieces was 40 mm. This vertical distance was based on a

165 preliminary investigation which showed that when lifting the asymmetrical weight distribution and

166 keeping the basis horizontal, the load force difference between the two fingertips was zero if the

167 fingertips were placed non-collinearly and distanced 40 mm from each other. The manipulandum's

168 horizontal basis was divided into three compartments enabling the placement of 3D-printed cuboids that

169 were visually identical (height x width x depth: 55 x 35 x 40 mm). One cuboid was filled with lead

170 particles and weighted 4.24 N, the other two were hollow and weighted 0.24 N each. Combined with the

171 manipulandum, the total weight amounted to 8.67 N. The external torque (i.e. torque induced by the

172 object's weight distribution) could be changed by inserting the heavy cuboid in the left, center or right

173 compartment and amounted to -245, 0 or + 245 Nmm, respectively (for the calculation of these values

174 see Rens et al., 2020b).

175      For collecting lifting-related parameters, we used two ATI mini-40 SI-40-2 F/T sensors (force

176 range: 40, 40 and 120 N for x-, y- and z-axes respectively; force resolution: 0.01 N; torque range: 2 Nmm;

177 torque resolution: 0.0005 Nmm) (ATI Industrial Automation, USA). F/T sensors were calibrated by the

178 developer in accordance with the applicable QTI procedures. The maximum amount of error for the

179 force and torque components were 1.50 % and 1.75 % respectively. Both F/T sensors were connected to

180 a NI-USB 6221 OEM board (National Instruments, USA) which was connected to a personal computer.

181 Data was acquired using a custom-written MATLAB script (Mathworks, USA) and sampled at 1 kHz.

182

183    TMS procedure and EMG recording

184    *General procedure*. Electromyography (EMG) recordings were performed using Ag-AgCl electrodes which

185    were placed in a typical belly-tendon montage over the right first dorsal interosseous muscle (FDI) and

186    abductor pollicis brevis (APB). A ground electrode was placed over the processus styloideus ulnae.

187    Electrodes were connected to a NL824 AC pre-amplifier (Digitimer, USA) and a NL820A isolation amplifier

188    (Digitimer, USA) which in its turn was connected to a micro140-3 CED (Cambridge Electronic Design

189    Limited, England). EMG recordings were amplified with a gain of 1000, high-pass filtered with a

190    frequency of 3 Hz, sampled at 3000 Hz using Signal software (Cambridge Electronic Design Limited,

191    England) and stored for offline analysis. For TMS stimulation, we used a DuoMAG 70BF coil connected to

192    a DuoMAG XT-100 system (DEYMED Diagnostic, Czech Republic). For M1 stimulation, the coil was

193    tangentially placed over the optimal position of the head (hotspot) to induce a posterior-anterior current

194    flow and to elicit motor evoked potentials (MEPs) in both right FDI and APB. Stimulation intensity (1 mV

195    threshold) for each participant was defined as the lowest stimulation intensity that produced MEPs

196    greater than 1 mV in both muscles and in at least four out of eight consecutive trials when stimulating at

197    the predetermined hotspot (average stimulation intensity = 54 ± 5.6 % of maximum stimulator output).

198    During the experiment, TMS was applied during both the actor (observation) and participant trials

199    (execution). During actor trials, TMS was applied 300 ms after the actor lifted the object from the table

200    (for definition of lift-off see: 'Data analysis'). This timing was based on earlier work from our group (Rens

201    et al. 2020a) which showed clear motor resonance effects 300 ms after observed lift-off. During

202    participant trials, TMS was applied 400 ± 100 ms (jitter) after object presentation. As participants were

203    instructed to only start reaching for the object after TMS was applied, the TMS stimulation was actually

204    applied during lift planning.

205

206    Experimental set-up

207    *Dyadic set-up.* As shown on figure 1C, participant and actor were comfortable seated at a square table

208    with their lower arm resting on the table. The actor was seated on the left side of the participants so that

209    the participant and actor were angled 90 degrees towards each other. The manipulandum was

210    positioned between both individuals so both individuals could comfortably grasp and lift it. When

211    grasping, both individuals were required to reach with their entire right upper limb causing their elbow

212    to lift from the table. The manipulandum was distanced approximately 30 cm from each individual. In

213    addition, participant and actor were asked to place their hand on a predetermined location in front of

214    them to ensure consistent reaching throughout the experiment. It is important to note that when the

215  actor reached for the manipulandum, their arm would move in front of the participant's upper body

216  (Figure 1C). Although this orientation likely occluded visual information about the left side of the

217  manipulandum, we opted for this positioning rather than opposing both individuals for two reasons.

218  First, Mojtahedi et al. (2017) showed that, when lifting an object together, individuals perform better

219  when seated next to each other compared to opposed to each other. Second, Alaerts et al. (2009)

220  showed that modulation of motor resonance is increased when observing actions from a first person

221  point of view compared to a third person one. For our study, we argued that this side-by-side

222  configuration would also enhance motor resonance effects in the participants. During the experiment, a

223  switchable screen (MagicGlass) was placed in front of the participant's face which was transparent

224  during trials and returned opaque during inter-trial intervals. This screen blocked vision on the

225  manipulandum when the experimenter would switch the cuboids between compartments, thus making

226  participants blind to the weight distribution change. Last, one trial consisted of one lifting movement

227  performed by either the actor or participant, thus being 'participant trials' or 'actor trials'. Trial duration

228  was 4 seconds and trial onset was indicated by the switchable screen turning transparent. Trial duration

229  was based on preliminary testing and showed that individuals had sufficient time to reach, grasp, lift and

230  return the object smoothly at a natural pace. Inter-trial interval was approximately 5 seconds during

231  which the screen was opaque and the center of mass could be changed. To end, a female master's

232  student was the actor for all participants.

233

234  Experimental procedure

235  *General procedure.* At the start of the session, participants gave written informed consent and were

236  prepared for TMS (see 'TMS procedure and EMG recording'). Afterwards, they were explained the

237  experimental task and received the following instructions regarding object lifting: (1) lift the inverted T-

238  shape to a height of approximately 5 cm at a smooth pace that is natural to you. (2) Only use thumb and

239  index finger of the right hand and only place them on the sandpaper pieces. (3) You are required to use

240  the same digit positioning the actor used in their preceding trial. (4) Keep the inverted T-shape's base as

241  horizontal as possible during lifting (i.e. 'try to minimize object roll'). (5) The center of mass in your trials

242  always matches the one in the actor's preceding trial. In sum, participants were explained that they

243  should try to minimize object roll during object lifting and could potentially rely on the observed lifting

244  performance of the actor to plan their own lifts. Importantly, participants were explicitly explained that

245  they were required to use the same digit positioning as the actor. This was done to ensure that we would

246  have enough trials per experimental condition (see below).

247        After task instructions, participants were allowed to perform 3 practice lifts on the symmetrical

248    weight distribution and 6 on each asymmetrical weight distribution (left or right). On half of the lifts with

249    the asymmetrical weight distribution, participants were required to position their fingertips on the same

250    height, i.e. 'collinear positioning'. In the other half, they were required to place their fingertips

251    'noncollinearly', i.e. the fingertip on the heavy side was positioned higher than the fingertip on the light

252    side (left asymmetrical: right thumb higher than right index; right asymmetrical: right thumb lower than

253    right index). When lifting the symmetrical weight distribution, no compensatory torque should be

254    generated. Accordingly, for this weight distribution participants were required to always place their

255    fingertips collinearly as noncollinear positioning would cause participants to automatically generate

256    compensatory torque. These practice trials were aimed to familiarize participants with the

257    manipulandum.

258        *Constrained digit positioning.* Fu et al. (2010) showed that appropriate compensatory torque can

259    be generated by many valid digit position-force coordination patterns. As motor resonance is driven by

260    movement features such as fingertip forces, we wanted to limit the digit positioning options in order to

261    reduce potential variability in motor resonance effects. We argued that constrained digit positioning and

262    limited experimental conditions would enable us to find more reproducible results. As mentioned

263    before, noncollinear positioning was defined based on the vertical difference between fingertips which

264    caused the load force difference to approximate zero. Collinear positioning was included as we

265    considered it a 'neutral' condition to contrast the noncollinear one. Because the fingertip on the heavy

266    side has to generate more force when positioned collinearly compared to noncollinearly, we argued that

267    these two conditions would allow us to disentangle whether the observer's motor system would encode

268    observed positioning or observed forces. When using collinear digit positioning, irrespective of the

269    weight distribution, actor and participant were required to place their fingertips on the upper sandpaper

270    pieces on each side (Figure 1B). When using noncollinear digit positioning for the asymmetrical weight

271    distribution, the finger on the heavy side was placed on the upper piece whereas the finger on the light

272    side was placed on the lower piece. For instance, when the heavy cuboid was inserted in the left

273    compartment, the thumb and index finger were placed on the upper and lower piece of their respective

274    side, respectively (Figure 1). The actor was instructed to use these digit positioning strategies which

275    ensured that participants would use the same digit positionings. We opted for these digit positionings

276    (primarily collinear positioning on the upper pieces instead of the lower ones) to protect the EMG

277    electrodes over the thumb muscle from rubbing over the manipulandum's base.

278     *Experimental task.* After task instructions, participants performed the object lifting task with the

279     actor. The actor would change the inverted T-shape's center of mass and verbally declare that she would

280     execute the next trial. Verbal declaration took place before switching of the cuboids. After trial

281     completion by the actor, participant performed 3 back-to-back trials with the same weight distribution

282     and using the same digit positioning as the actor. We decided to have participants perform 3 repetitions

283     based on Fu et al. (2010). To ensure that participants could not rely on sound cues potentially indicating

284     the new weight distribution, the experimenter always removed and replaced all 3 cubes after randomly

285     rotating the inverted T-shape prior to each actor trial. These actions were never done before participant

286     trials as they were explained that the center of mass in their trials would always match the one of the

287     actor's preceding trial.

288     During the object lifting task, the experimenter and participants performed 20 transitions from

289     the middle compartment (i.e. symmetrical weight distribution) to each side (i.e. asymmetrical weight

290     distributions). When the experimenter lifted the new asymmetrical weight distribution (e.g. left-sided),

291     she would use collinear positioning in 10 lifts and noncolinear positioning in the other 10. Trial amount

292     per experimental condition was based on Senot et al. (2011) who used 10 trials per TMS condition when

293     investigating motor resonance effects during lift observation. After 4 trials were performed on the

294     asymmetrical weight distribution (i.e. 1 actor and 3 participant trials), the experimenter would change

295     the object's weight distribution again. Most of these transitions were 'normal' and consisted of the actor

296     changing the heavy cuboid back to the middle compartment for washing out the internal representation

297     for the asymmetrical weight distribution. However, 10 transitions were 'catch transitions' in which the

298     asymmetrical weight distribution was first changed to the other side (e.g. left to right asymmetrical) and

299     only then to the middle compartment to wash out the internal representation for asymmetrical. We

300     included these catch transitions to ensure that participants would not anticipate the typical change from

301     asymmetrical to symmetrical even though we still wanted to wash out the internal representation for

302     asymmetrical. Catch transitions were inserted equally after each lifting sequence on each asymmetrical

303     weight distribution. Considering that we had a 2 (side: left or right asymmetrical) by 2 (positioning:

304     collinear or noncollinear) design when lifting the asymmetrical weight distribution, either 2 or 3 catch

305     transitions were performed after each lifting sequence (e.g. 2 catch transitions after the lifting sequence

306     with collinear positioning on the right asymmetrical weight distribution). The actor randomly decided

307     which digit positioning to use on the new asymmetrical weight distribution in the catch transitions. Last,

308     in both the normal and catch transition to symmetrical, the standard amount of trials (1 actor and 3

309     participant's trials) were performed after each weight distribution change.

310    The object lifting task was split over 4 experimental blocks with a short break between blocks.

311    For each participant, transition order was pseudo-randomized within each experimental block. As such,

312    each experimental block contained 5 transitions to left and right asymmetrical. In addition, either 2 or 3

313    of these transitions to each side were performed with one digit positioning type (e.g. collinear) and the

314    other 3 or 2 transitions with the other digit positioning type (e.g. noncollinear). Transitions to a specific

315    side (e.g. symmetrical to left-sided asymmetrical) would repeat maximally 2 times back to back and catch

316    transitions were spread equally over all blocks. The full experimental session lasted approximately 2 h.

317

318    Data analysis

319    *Behavioral data.* Data collected with the F/T sensors were sampled in 3 dimensions at 1000 Hz and

320    smoothed using a fifth-order Butterworth low-pass filter (cut-off frequency: 15 Hz). For each sensor, grip

321    force (GF) and load force (LF) were defined as the exerted force perpendicular to the normal force (Y-

322    direction on Figure 1) and the exerted force parallel to the normal force (X-direction on Figure 1),

323    respectively. Digit positioning was defined as the vertical coordinate (X-direction on Figure 1) of the

324    fingertip's center of pressure on each cover plate. The center of pressure was calculated from the force

325    and torque components measured from the respective F/T sensor relative to its frame of reference,

326    using formula 1.

327    $$COP = \frac{(T_y - F_x \, \delta)}{F_z} \tag{1}$$

328

329    In formula 1, COP = center of pressure, $T_y$ = Torque in the Y-direction, $F_x$ = Force in the X-direction, $F_z$ =

330    Force in the Z-direction, $\delta$ = cover plate thickness (1.55 mm). Compensatory torque was defined as the

331    net torque generated by an individual to offset the external torque caused by the object's weight

332    distribution and was calculated with formula 2 (we refer the reader to the supplementary materials of Fu

333    et al., 2010 for the detailed explanation of the formula).

334

335    $$T_{comp} = \frac{d}{2} \times (LF_{thumb} - LF_{index}) + (COP_{thumb} - COP_{index}) \times GF_{average} \tag{2}$$

336

337    In formula 2, $T_{comp}$ = Compensatory torque, d = horizontal distance between the digits (48 mm; Figure 1;

338    Y-direction), $LF_{thumb/index}$ = Load force generate by the thumb and index finger, respectively, $COP_{thumb/index}$ =

339    center of pressure of the thumb and index finger, respectively, $GF_{average}$ = averaged amount of GF exerted

340    by the thumb and index finger.

341      To investigate the effects of lift observation on the performance of the participants we used the

342      following variables: Digit positioning difference, defined as the difference between the COP of the thumb

343      and the index finger (positive values indicate a thumb placement higher than that of the index finger),

344      compensatory torque, total grip force, and load force difference, defined as the difference between load

345      forces generated by the thumb and index finger (positive values indicate the thumb generating more

346      load force than the index finger). We included difference in digit positioning to investigate whether actor

347      and participants placed their fingertips appropriately. However, it is important to note that during data

348      processing we excluded trials (both force and TMS data) in which fingertips were not placed on the

349      sandpaper pieces (< 1% of all trials). We considered compensatory torque as our key indicator of

350      performance as it results from the combination of grip and load forces as well as digit positioning and

351      because we explicitly asked participants to minimize object roll during lifting ('task goal'). Moreover, Fu

352      et al. (2010) showed a strong linear correlation between compensatory torque and peak object roll,

353      arguing its validity as our key indicator of performance. We included total grip force and load force

354      difference to explore their potential effect on CSE modulation during observation and planning. Last, it is

355      important to note that, for analysis purposes, we inversed the sign for compensatory torque for the right

356      asymmetrical weight distribution, which allows for better comparisons regarding performance between

357      the left and right side. We argued not to do so for load force and digit position differences for

358      interpretability with respect to motor resonance effects.

359      In line with Fu et al. (2010), we extracted digit positioning difference at early object contact,

360      which we defined as total GF > 1 N. Considering that we had no proxy of lift onset (again see Fu et al.

361      2010), we decided to approximate lift onset by using object lift-off instead. In line with our previous work

362      (Rens et al. 2020a; Rens and Davare, 2019), we defined lift-off as the time point where total load force >

363      0.98 x object weight. As such, we extracted total grip force, load force difference and compensatory

364      torque at object lift-off.

365      *EMG data.* From the EMG recordings, we extracted the peak-to-peak amplitude of the MEP using

366      a custom-written MATLAB script. All EMG recordings were visually inspected and afterwards analyzed in

367      the script. Trials were excluded when the MEP was visibly contaminated by noise (i.e. spikes in

368      background EMG) or when an automatic analysis found that background EMG was larger than 50 μV

369      (root-mean-square error) in a time window of 200 ms prior to the TMS stimulation. Last, for each

370      participant we excluded outliers which we defined as values exceeding the mean ± 3 SD's. The total

371      amount of removed MEPs was 1.68 %. For each participant, all MEPs collected during the experimental

372      task were z-score normalized for observation and planning separately. Last, we also assessed pre-

373     stimulation ('background') EMG by calculating the root-mean-square across a 100ms interval ending

374     50ms prior to TMS stimulation.

375

376     <u>Statistical analyses</u>

377     For statistical purposes, we did not include catch trials (center of mass change from side to side) and

378     trials in which the weight distribution changed from asymmetrical to symmetrical. First, we excluded

379     transitions to the symmetrical weight distribution as we had less than 10 MEPs for these conditions. As

380     mentioned before, we had 20 transitions to each asymmetrical weight distribution, 10 in which the actor

381     used collinear positioning and 10 in which she used noncollinear positioning. After performing this lifting

382     sequence, the weight distribution normally changed to symmetrical. However, as mentioned before, we

383     also included 10 catch transitions in which one asymmetrical weight distribution changed to the other

384     (i.e. 5 changes from left to right and 5 from right to left). Due to these 10 catch transitions, we had less

385     than 10 MEPs for each transition to symmetrical. For instance, when a lifting sequence was performed

386     on the right asymmetrical weight distribution with noncollinear digit positioning only 7 or 8 normal

387     transitions were performed in which the weight distribution changed directly back to symmetrical. Given

388     the limited amount of MEP data for these changes with respect to relevant motor resonance studies

389     (Alaerts et al. 2010; Buckingham et al. 2014; Senot et al. 2011) and the actor choosing her digit

390     positioning randomly in these catch transitions, we decided to not include these trials for analysis

391     purposes. Note that we included lifts for the symmetrical weight distribution lifts in the analysis of the

392     actor's performance, to compare this against the asymmetrical distributions. Second, we excluded catch

393     trials for analysis purposes due to the very limited amount we had.

394             We investigated whether the actor's and participants' performance changed between

395     experimental blocks. Considering we did not find any learning effects, we collapsed our data across

396     experimental blocks. All statistical analyses were performed in SPSS statistics version 25 (IBM, USA) and

397     are described below. For each parameter of interest, we performed a separate analysis. We used linear

398     mixed models (LMM) considering our coding for the noncollinear condition (left noncollinear: thumb

399     higher than index; right noncollinear: thumb lower than index). The reason hereof is that digit

400     positioning (i.e. noncollinear on left or right side) could potentially modulate motor resonance

401     differently.

402             For the actor's data (behavioral only), we used the factors SIDE (mid, left and right) and

403     POSITION (collinear and noncollinear which were coded as described in the preceding paragraph). We

404     included the actor's collinear lifts on the symmetrical weight distribution (i.e. mid) to investigate changes

405    in lift performance. Specifically, if the actor correctly planned to lift an asymmetrical weight distribution,

406    her lift performance should differ significantly from that when she planned to lift the symmetrical weight

407    distribution (Rens and Davare 2019). We included SIDE as a main effect and nested POSITION within SIDE

408    (i.e. POSITION$_{SIDE}$).

409         For the participants' data (behavioral and MEPs), we used the factors SIDE (left and right only),

410    POSITION (collinear and noncollinear) and REPETITION (first, second and third lift after the center of

411    mass change). Please note that the factor REPETITION and all its interaction effects described below

412    were only included during lift planning, not observation, which we investigated separately. SIDE and

413    REPETITION were included as main effects. Again, POSITION was nested within SIDE. For the participants'

414    data we also included the interaction effect SIDE X REPETITION as well as REPETITION X POSITION$_{SIDE}$.

415    Here, we did not include the lifts on the symmetrical weight distribution as lift performance of

416    participants can be investigated by comparing lifts without tactile feedback (i.e. first lift after lift

417    observation) to their own lifts on the same object with tactile feedback (second and third lifts). As such,

418    lift performance is quantified by comparing lifts without and with tactile feedback (Fu et al. 2010;

419    Reichelt et al. 2013; Rens and Davare 2019). To analyze motor resonance effects during lift observation,

420    we used the factors SIDE (left and right) and POSITION (collinear and noncollinear). We included SIDE as

421    a main effect and nested POSITION within SIDE (i.e. POSITION$_{SIDE}$).

422         For both the actor and participant data, we included the intercept in the model. Moreover, for

423    all participants' analyses we also included the participant's number as random effect. Last, we decided to

424    include the mixed model covariance structures as first-order autoregressive based on the assumption

425    that correlation in residuals between factor levels was identical across levels. We used type III sum of

426    squares and Maximum Likelihood (ML) for mixed model estimation and Bonferroni corrections for

427    pairwise comparisons. All data in text is presented as the mean ± SEM.

428                           ----------

429                        Figure 2

430                           ----------

431    **Results**

432    In the present study, we investigated how CSE is modulated when observing and planning lifts of objects

433    with an asymmetrical weight distribution. Participants performed an object lifting task in turns with an

434    actor and were required to lift a manipulandum with interchangeable center of mass as skillfully as

435    possible, i.e. minimize object roll by generating appropriate compensatory torque. When participants

436    were required to lift an object with unknown weight distribution, they first observed the actor lift the

437      new weight distribution. Afterwards, the participants lifted this weight distribution three times.

438      Importantly, participants were instructed to place their fingertips on the same constrained locations the

439      actor used. After participants performed their three lifts, the actor changed the weight distribution and

440      again lifted the new weight distribution. Accordingly, participants could potentially derive critical

441      information about the object's weight distribution by observing the actor's lifts. During the behavioral

442      task, TMS was applied during observed lifting (after observed lift-off) and during lift planning in the actor

443      and participant trials, respectively.

444           Traces of the included lifting parameters, when lifting an asymmetrical weight distribution, can

445      be found in figure 2, showing the difference between a single lift of the actor (solid lines) with collinear

446      (blue) and noncollinear positioning (green). In addition, the dashed traces represent a single first lift of a

447      participant after observing the actor's lift. As the actor could anticipate the object's weight distribution, she

448      would predictively generate compensatory torque to minimize object roll (Figure 2A; blue and green

449      solid traces). When the participants lifted the object after observing the actor, they were able to

450      generate appropriate compensatory torque after observing noncollinear positioning (green dashed

451      trace) but not after observing collinear one (blue dashed trace). Accordingly, the difference in lift

452      performance can be quantified through differences in compensatory torque. As mentioned before,

453      appropriate compensatory torque is the resultant of a valid digit positioning – force coordination pattern

454      (Fu et al., 2010). For instance, it can be seen in Figure 2B that in the actor's (blue solid) and participant's

455      lift (blue dashed), fingertips were positioned similarly. However, as the actor but not the participant

456      generated appropriate compensatory torque, it can be seen in Figure 2D that the load force difference

457      increased faster for the actor than the participant. Conversely, when lifting with noncollinear digit

458      positioning (green traces), the fingertip on the heavy side is positioned higher than the fingertip on the

459      light side (Figure 2B). Due to this vertical height difference, the fingertip on the heavy side does not have

460      to generate more load force than the fingertip on the light side (Figure 2D), resulting in a load force

461      difference close to zero. Last, as can be seen in Figure 2C, the fingertips generate more grip force when

462      positioned collinearly compared to noncollinear positioning.

463      ----------

464      Figure 3

465      ----------

466      <u>Actor's lift performance</u>

467      The actor's lift performance should have been consistent due to (a) our constrained positioning

468      conditions and (b) her changing the weight distribution. However, we decided to analyze her

469    performance for verification and to quantify which observed movement features might have been driven

470    motor resonance effects. We expected that the actor would comply with task instructions and would

471    always lift the manipulandum skillfully (i.e. generate appropriate compensatory torque).

472       *Compensatory torque at lift-off.* As the actor was not blinded to the weight distribution change,

473    she generated significantly more compensatory torque when lifting the asymmetrical weight

474    distributions (left = 232.56 ± 4.22 Nmm; right = 189.03 ± 3.39 Nmm) compared to the symmetrical one

475    (mean = 6.90 ± 1.38 Nmm*; both p < 0.001*) (SIDE: $F_{(2,80)} = 1135.70; p < 0.001$). Although the actor was

476    instructed to lift the asymmetrical weight distributions as skillfully as possible, she failed to do so when

477    using collinear positioning: as shown in Figure 3A, the actor generated more compensatory torque when

478    lifting asymmetrical weight distributions with noncollinear positioning (between adjacent bars: *each p <*

479    *0.001*) (POSITION$_{SIDE}$: $F_{(2,80)} = 518.184; p < 0.001$). Noteworthy, the performance when lifting

480    noncollinearly was similar between asymmetrical weight distributions (Figure 3A; between green bars: *p*

481    *= 1.00*). Last, the actor's lift performance was the least skillful when collinearly lifting the right

482    asymmetrical weight compared to all other asymmetrical conditions (*all p < 0.001*).

483       *Digit positioning at early object contact.* Although digit positioning was constrained to small

484    sandpaper pieces and we removed trials in which fingertips were not positioned correctly, we provide

485    these results for clarity. Please note that positive values for difference in digit positioning indicate that

486    the thumb was positioned higher than the index finger and negative values indicate that the index finger

487    was positioned higher than the thumb. Briefly, when the actor was instructed to use noncollinear

488    positioning, she appropriately placed her fingertips further apart compared to the collinear conditions

489    (Figure 3B; green compared to blue bars: *all p < 0.001*) and differently than the other noncollinear

490    condition (between green bars: *p < 0.001*) *(*POSITION$_{SIDE}$: $F_{(2,80)} = 2342.74, p < 0.001).$ Noteworthy, digit

491    positioning also differed significantly between all collinear conditions (*all p < 0.001)* which indicates that

492    the weight distribution caused subtle differences in the collinear digit positioning. However, considering

493    the magnitude of these differences between collinear conditions (Figure 3B; Mid col = 4.55 ± 0.24 mm;

494    Left col = 9.86 ± 0.25 mm; Right col = 0.32 ± 0.36 mm), it is unknown to which extent they were visible to

495    the participants.

496       *Total grip force at lift off*. When the actor lifted the asymmetrical weight distributions

497    noncollinearly, she used less grip forces than when lifting all weight distributions collinearly (Figure 3C;

498    green compared to blue bars: *all p < 0.001*) (POSITION$_{SIDE}$: $F_{(2,80)} = 405.68; p < 0.001$). Importantly,

499    differences between all conditions were significant (*all p < 0.001*) suggesting that the actor used a unique

500    amount of grip forces in each condition. It also important to note that the actor used, on average, more

501    grip forces when lifting the right asymmetrical weight distribution (mean = 24.12 ± 0.63 N) compared to

502    the left one (mean = 19.77 ± 0.52 N; *p < 0.001*) *(SIDE: $F_{(2,80)}$ = 46.13; p < 0.001)*.

503         *Load force difference at lift-off*. Please note that these values are expressed as the difference in

504    load force between the thumb and index finger therefore positive values indicate that the thumb

505    exerted more load force than the index finger and negative values indicate that the index finger exerted

506    more load force than the thumb. First, when the actor lifted the asymmetrical weight distributions, she

507    generated significantly more load force with the fingertip on the heavy side (left = 5.43 ± 0.18 N; right = -

508    8.91 ± 0.20 N) compared to lifting the same weight distribution noncollinearly (Figure 3D*; between*

509    *adjacent bars: p < 0.001)* and compared to all other conditions *(all p < 0.001)* (POSITION$_{SIDE}$: $F_{(2,80)}$ =

510    *877.52; p < 0.001)*. Second, the load force difference was different (borderline significant) when lifting

511    the asymmetrical weight distributions noncollinearly *(*Figure 3D; between green bars: *p = 0.09)* indicating

512    that small differences in load force scaling where present between the noncollinear conditions.

513                                                    ----------

514                                                    Figure 4

515                                                    ----------

516    Participants' lift performance

517    We included the participants' lifting parameters to investigate their lift performance after lift

518    observation (first lift) and haptic feedback (second and third lifts) and how it might have affected CSE

519    modulation during lift planning. Based on our previous work (Rens et al. 2020b), we expected that lift

520    performance would be suboptimal after lift observation. That is, participants would perform better in

521    their second and third lifts compared to their first ones.

522         *Compensatory torque at lift-off.* Our results revealed that there were large differences in lift

523    performance between digit positioning conditions. When participants used noncollinear positioning,

524    they overcompensated for the asymmetrical weight distribution and generated more compensatory

525    torque (left = 319.50 ± 5.68 Nmm; right = 321.57 ± Nmm; Figure 4A green lines) than required (245

526    Nmm). In contrast, when lifting collinearly, participants could not generate appropriate compensatory

527    torque (left = 133.35 ± 6.73 Nmm; right = 48.14 ± 4.14 Nmm; Figure 4A blue lines). Although lift

528    performance did not differ between the noncollinear conditions (*p = 1.00*), it did differ between

529    noncollinear and collinear ones *(all p < 0.001)*. In addition, participants performed worse when

530    collinearly lifting the right asymmetrical weight distribution compared to all other conditions *(all < 0.001)*

531    (*POSITION$_{SIDE}$: $F_{(2,179)}$ = 1571.60; p < 0.001)*. When participants lifted the asymmetrical weight

532    distributions noncollinearly, they did not generate more compensatory torque over repetitions (*between*

533    *green connected scatters: all p = 1.00*) indicating that their lift performance was similar after lift

534    observation (first repetition) and after having tactile feedback (second and third repetitions)

535    (REPETITION X POSITION$_{SIDE}$: $F_{(4,179)} = 4.99; p < 0.001$). In contrast, when using collinear positioning,

536    participants performance improved over repeated lifts. This increase was significant from their first to

537    second lift (*both p < 0.009*), but not significant from their second to third lift (*both p > 0.54*) (Figure 4A

538    blue connected scatters).

539        *Digit positioning at early object contact.* As participants were instructed to imitate the actor's

540    constrained digit positioning and we excluded trials with incorrect digit positioning, we primarily report

541    digit positioning for transparency reasons. As shown in Figure 4B, participants did not change their digit

542    positioning over the multiple repetitions within each condition (REPETITON X POSITION$_{SIDE}$: $F_{(4179)} = 0.75;$

543    *p = 0.56*). This indicates that they adhered to the constrained digit positionings. Logically, when lifting the

544    left asymmetrical weight distribution noncollinearly, participants placed their thumb higher than their

545    index finger (mean = 48.22 ± 0.1.06 mm) and vice versa for the right asymmetrical weight distribution

546    (mean = -42.45 ± 0.84 mm; *p < 0.001)*. These noncollinear positionings also differed significantly from

547    those when lifting collinearly *(all p < 0.001)* (POSITION$_{SIDE}$: $F_{(2,179)} = 3605.93; p< 0.001$). Noteworthy,

548    collinear digit positioning for the left (mean = 5.80 ± 0.67 mm) and right (mean = 1.62 ± 0.54 mm)

549    asymmetrical weight distributions also differed significantly (*p = 0.003;* effect of POSITION$_{SIDE}$).

550    Considering the magnitude of this difference, it is improbable that participants planned their positioning

551    this accurately. Arguably, it is more likely that this difference between sides is driven by skin deformation

552    due to the different weight distributions.

553        *Total grip force at lift-off.* As shown by the green line plots in 4C, participants scaled their grip

554    forces similarly when using noncollinear positioning for both weight distributions and all repetitions *(all p*

555    *= 1.00)* (REPETITION X POSITION$_{SIDE}$: $F_{(4,179)} = 5.53; p < 0.001$). In contrast, this lifting consistency was

556    lower when using collinear digit positioning. When they lifted the right asymmetrical weight distribution

557    collinearly, participants significantly increased their grip forces from their first lift (mean = 23.95 ± 0.95

558    N) to their second one (mean = 27.92 ± 0.77 N; *p < 0.001*) but not from their second to third one (mean =

559    28.74 ± 0.74 N; *p = 1.00*). Conversely, when lifting the left asymmetrical weight distribution collinearly,

560    participants did not significantly increase their grip forces from their first (mean = 24.10 ±0.98 N) to

561    second lift (mean = 26.40 ± 0.98 N; *p = 0.51*). To end, as shown in Figure 4C, the amount of grip forces

562    applied when lifting collinearly or noncollinearly differed significantly for both weight distributions and

563    all repetitions *(all p < 0.001).*

564          *Load force difference at lift-off.* Based on our experimental set-up and constrained positioning,

565     we expected that noncollinear positioning would lead to a load force difference close to zero.

566     Conversely, collinear positioning would lead to the fingertip on the heavy side scale its load force larger

567     than the finger on the light side. As shown in Figure 4D, when participants used noncollinear positioning,

568     the load force difference was significantly different for the left (mean = -1.65 ± 0.24 N) and right (mean =

569     2.82 ± 0.24 N; *p < 0.001*) asymmetrical weight distributions (POSITION$_{side}$: $F_{(2,179)}$ = *667.79; p < 0.001*). This

570     difference was not only present during their first lift but persisted during their second and third lifts (*all p*

571     *< 0.001)* (REPETITION X POSITION$_{SIDE}$: $F_{(4,179)}$ = *3.69; p = 0.006)*. This indicates that participants did not

572     alter their load force difference based on tactile feedback. In line with our expectations, our results show

573     that when participants used collinear positioning, they exerted more load force with the finger on the

574     heavy side (left: mean = 3.01 ± 0.21 N; right: mean = -5.10 ± 0.38 N; between sides: *p < 0.001*).

575     Moreover, when using collinear positioning for each weight distribution, the load force difference

576     became larger from the first to the second lift (left: *p < 0.001;* right: *p = 0.06*) which indicates participants

577     altered their load force difference based on tactile feedback. This effect further increased from the

578     second to third lift for the left (*p < 0.001*) but not right *(p = 0.26)* asymmetrical weight distribution.

579                                     ----------

580                               Figure 5

581                                   ----------

582   <u>Corticospinal excitability during lift observation</u>. As mentioned before, we hypothesized that modulation

583     of motor resonance would be driven by specific observed movement features (i.e. digit positioning or

584     muscle contraction).

585          *First dorsal interosseus muscle (FDI).* As shown in Figure 5A, both the effect of SIDE and

586   POSITION$_{SIDE}$ were not significant *(both F < 0.94, both p > 0.91)*. As such, our results provide no evidence

587     that corticospinal excitability was differently modulated during the different observation conditions

588     when being recorded from the FDI muscle.

589          *Abductor pollicis brevis (APB)*. In contrast to our findings for the FDI muscle, both the effects of

590   SIDE and POSITION$_{SIDE}$ were significant *(both F > 5.19, both p < 0.008)*. As can be seen in Figure 5B, when

591     participants observed the actor lifting the right-sided asymmetrical weight distribution, CSE was

592     significantly larger (mean = 0.15 ± 0.06) compared to when participants observed lifts on the left-sided

593     weight distribution (mean = -0.07 ± 0.04) *(p = 0.013)*. Post-hoc exploration of the nested effect

594     (POSITION$_{SIDE}$) showed that this was driven by the noncollinear condition on the right-sided weight

595     distribution. Although borderline significant, when participants observed lifts with noncollinear digit

596     positioning on the right-sided weight distribution (mean = 0.30 ± 0.09), CSE was larger than when

597     participants observed non-collinear and collinear digit positioning on the left asymmetrical weight

598     distribution (non-collinear: mean = -0.09 ± 0.06; *p = 0.079;* collinear: mean = -0.05 ± 0.05; *p = 0.056)*. In

599     sum, these findings indicate that, CSE was significantly facilitated when observing lifts with an

600     asymmetrical weight distribution that was right-sided.

601

602     Corticospinal excitability during lift planning.

603     Although this study was aimed to investigate motor resonance effects, we expected that CSE modulation

604     would be similar (i.e. driven by the same movement features) as during lift observation.

605             *First dorsal interosseus muscle (FDI).* All effects were not significant *(all F < 1.42, all p > 0.24)*. As

606     such, our results provide no evidence that CSE was differently modulated during the different lift

607     planning conditions when being recorded from the FDI muscle (Figure 5C).

608             *Abductor pollicis brevis (APB)*. As shown in Figure 5D, in line with our findings for CSE modulation

609     during lift observation, the effect of SIDE was significant $(F_{(1,192)} = 16.23, p < 0.001)$ although all other

610     effects were not *(all F < 2.06, all p > 0.13)*. When participants planned to lift the right asymmetrical

611     weight distribution (mean = 0.11 ± 0.04), CSE was significantly larger compared to when they planned to

612     lift the left-sided one (mean = -0.08 ± 0.03). As such, these findings indicate that, irrespective of digit

613     positioning, CSE was significantly facilitated when planning for lifts with a right asymmetrical weight

614     distribution.

615

616     Background EMG during the experiment

617     To ensure that between-group and between-condition differences were not driven by differences in

618     hand relaxation during lift observation and planning, we investigated potential differences in background

619     EMG. For this we used the same statistics as the ones we used for lift observation and lift planning.

620             *Background EMG during lift observation*. For both the FDI and APB muscle, all effects were not

621     significant *(all F < 0.68, all p > 0.42)*. As such, these findings provide no evidence that background EMG

622     different significantly between conditions when participants observed lifts on the asymmetrical weight

623     distributions.

624             *Background EMG during lift planning*. For both the FDI and APB muscle, all effects were not

625     significant *(all F < 0.69, all p > 0.60)*. As such, these findings provide no evidence that background EMG

626     different significantly between conditions when participants planned to lift the asymmetrical weight

627     distributions.

628    **Discussion**

629    In the present study, we investigated how CSE is modulated during observation of object lifting (i.e.

630    'motor resonance'). Although we were initially interested in motor resonance effects only, we also

631    recorded CSE during lift planning. Considering that participants performed an object lifting task in turns

632    with an actor, we were able to probe CSE modulation during lift planning as well. Participants were asked

633    to lift a manipulandum after observing an actor lift it. The object's center of mass could be changed by

634    placing a heavy cuboid in one of three compartments (Figure 1A). The object's weight distribution could

635    be 'symmetrical', by inserting the heavy cuboid in the middle compartment, or left- and right-sided

636    'asymmetrical', by inserting the heavy cuboid in the left or right compartment, respectively. Participants

637    and actor were instructed to lift the object skillfully, i.e. generate appropriate compensatory torque to

638    minimize object roll. Moreover, when lifting the asymmetrical weight distributions, digit positioning was

639    constrained to two specific digit positioning strategies and, as mentioned before, TMS was applied

640    during both observation and planning. Our results indicate that the participants' lift performance was

641    suboptimal as they were not able to generate appropriate compensatory torque (Figure 4A).

642    Noteworthy, the actor was also not able to do so when using collinear digit positioning on the

643    asymmetrical weight distributions. As such, suboptimal lift performance might have been caused by

644    limitations in our experimental set-up. However, our results indicate that CSE modulation during both lift

645    observation and planning was driven by the object's asymmetrical weight distribution. That is, when

646    participants observed or planned a lift on the right asymmetrical weight distribution, CSE recorded from

647    the APB muscle was significantly increased compared to observing or planning a lift on the left

648    asymmetrical one. During lift observation CSE modulation seemed to be primarily driven by an observed

649    change in digit positioning (i.e. the thumb moving to the lower constrained location; Figure 4B). During

650    lift planning, CSE modulation seemed to be more generally increased for both constrained digit

651    positioning conditions on the right asymmetrical weight distribution (5D). In line with previous work of

652    our group (Rens et al. 2020), these findings indicate that motor resonance can be modulated by

653    movement features within observed actions.

654          Previous studies have shown that CSE is modulated during lift observation ('motor resonance').

655    For instance, Alaerts et al. (2010a, 2010b) showed that motor resonance during lift observation reflects

656    object weight as indicated by visual object properties (i.e. degree of filling), muscle contraction or

657    movement kinematics. In addition, Buckingham et al. (2014) showed that motor resonance is driven by

658    object size when observing skilled, but not erroneous lifts. Last, Rens et al. (2020a), showed that motor

659    resonance is modulated by object weight but can be strongly biased by contextual cues. Our findings

660  corroborate these studies by showing that motor resonance was modulated by the intrinsic object

661  properties. Specifically, CSE recorded from the APB muscle was increased when observing lifts in which

662  the object's weight was asymmetrically distributed to the right side (Figure 4). Importantly, participants

663  could not rely on visual object-related information. As such, motor resonance should have been solely

664  driven by movement features within the observed lifts on the right asymmetrical weight distribution.

665  When the actor had lifted the symmetrical weight distribution and would then lift the right

666  asymmetrical one with noncollinear positioning, she would shift her thumb on the light side to the lower

667  constrained location whereas the index finger stayed on the same upper one. It is likely that this shift in

668  digit positioning increased motor resonance when observing noncollinear lifts on the right asymmetrical

669  weight distribution whereas the other movement features contributed arguably less. That is, when the

670  actor lifted both asymmetrical weight distributions noncollinearly, she generated similar compensatory

671  torques (Figure 3A). In addition, the actor used higher grip forces when lifting the asymmetrical weight

672  distributions with collinear positioning (Figure 3C) and she scaled her thumb load forces higher when

673  lifting the left-sided asymmetrical weight distribution with noncollinear positioning (Figure 3D). As such,

674  only when observing noncollinear lifts on the right asymmetrical weight distribution did the thumb

675  positioning change whereas the other movement features (i.e. force and compensatory torque) in this

676  condition were similar to those in the noncollinear left asymmetrical condition. Given the change in digit

677  positioning and the overlap in other movement features, it is likely that motor resonance effects in this

678  condition were primarily driven by the observed digit positioning.

679  In contrast to our initial hypotheses motor resonance effects were statistically driven by

680  differences in the asymmetrical weight distribution rather than constrained positioning conditions

681  (Figure 5). Accordingly, motor resonance should also have been increased when observing lifts on the

682  right asymmetrical weight distribution with collinear positioning. There are several factors that could

683  have driven this increase in motor resonance. First, in this condition, the actor's performance was the

684  worst as she generated the least amount of compensatory torque (Figure 3A). Second, in this condition

685  she scaled her grip forces higher than in all other conditions (Figure 3C). Third, the thumb had to

686  generate almost no load force as this was done by the index finger on the heavy side (Figure 3D). Last,

687  digit positioning did not deviate strongly from those in the other collinear conditions. As such, motor

688  resonance effects when observing collinear lifts on the right asymmetrical weight distribution should

689  could have been driven by object roll (due to the inappropriate amount of compensatory torque) or the

690  observed grip forces. Arguably, the contribution of the observed grip forces on motor resonance is

691  debatable. Specifically, when the actor lifted the left asymmetrical weight distribution with collinear

692 positioning, she generated more load forces with her thumb compared to when she used the same

693 positioning for the right asymmetrical weight distribution (Figure 3D). As such, this 'force interpretation'

694 would suggest that observed grip forces modulate motor resonance whereas observed load forces do

695 not. Although Alaerts et al., (2010b) have demonstrated that CSE is modulated during observed

696 squeezing (i.e. visible muscle contraction: grip forces) and during observed lifting when the hand

697 contraction cannot be seen (i.e. movement kinematics: indicative of the load forces), it is still unsure how

698 these force parameters converge in modulating CSE during observed lifting. To our knowledge, the

699 differential muscle contractions of grip and load forces on CSE modulation have not been disentangled

700 yet.

701 To end, we initially hypothesized that motor resonance would be selectively modulated by either

702 observed digit positioning or muscle contractions. However, our results suggest that modulation of

703 motor resonance was more generally modulated by movement features indicating the object's right

704 asymmetrical weight distribution. Indeed, motor resonance was primarily increased when observing a

705 visible shift in digit positioning in the right noncollinear condition and by the largest object roll, caused by

706 inappropriate compensatory torque, in the right collinear condition.

707 Based on previous findings of our group (Rens et al. 2020a), it is plausible that digit positioning

708 and object roll could have modulated motor resonance. In that study, we highlighted that motor

709 resonance is only modulated by object weight when the actual object weight would always match the

710 participants' weight expectations. However, when the participants' weight expectations could be

711 incorrect, motor resonance was rather driven by a mechanism monitoring these expectations. Those

712 findings have been supported by a reasoning within the review of Amoruso and Finisguerra (2019). They

713 argued that motor resonance reflects the inner replica of the observed action when observed in isolation

714 but can be altered by higher-level factors (such as contextual cues) when present. In sum, both these

715 works indicate that motor resonance can be flexibly driven by different movement features during action

716 observation. In the current study, participants were asked to minimize object roll during lift observation.

717 This contextual importance of accurately estimating the weight distribution during lift observation might

718 have caused motor resonance to be driven by 'salient' movement features indicating the object's weight

719 distribution. Arguably, it is plausible that participants focused on shifts in digit positioning and visible

720 object roll to perceive the weight distribution which in turn modulated their motor resonance.

721 Critically, we did not find similar modulation of CSE recorded from the FDI muscle. This was likely

722 caused by experimental limitations. When the inverted T-shape manipulandum was placed in front of

723 the participant, it was rotated (< 45 degrees) according to the participants' preferences. As most

724    participants found the manipulandum relatively heavy, the rotated position enabled them to reduce

725    wrist overextension, improving lifting comfort. Due to the object rotation, the index finger was hidden

726    behind the manipulandum and participants had no vision on the index finger during both lift observation

727    and execution. These visiblity limations might have completely eradicated any CSE modulation recorded

728    from the FDI muscle. It is also possible that similar visiblity limitations drove the selective modulation of

729    motor resonance for the right but not left asymmetrical weight distribution. When the actor lifted the

730    manipulandum (see dyadic positioning; Figure 1C), she would reach with her arm in front of the

731    participant blocking vision on the manipulandums left side with her lower arm. Because of these visiblity

732    limitations, participants might have primarily focused on thumb actions and the right side of the

733    manipulandum. However, it is important to note that the participant' lift performance for the

734    noncollinear conditions did not differ between asymmetrical weight distributions. Furthermore, when

735    using collinear positioning, participants performed worse on the right asymmetrcial weight distribution

736    compared to the left one. As such, even though motor resonance was selectively modulated for the right

737    asymmetrical weight distribution, participants perceived both weight distributions similarly during lift

738    observation as indicated by their own lift performance after lift observation. However, future research is

739    necessary to fully disentangle the contributing effects of the intrinsic object properties and observed

740    movement features on motor resonance.

741        To our knowledge, only Davare et al. (2019) investigated CSE modulation during lift planning and

742    execution on objects with an asymmetrical weight distribution. In their study, participants were required

743    to reach, grasp and lift an object with right asymmetrical weight distribution using either constrained or

744    unconstrained noncollinear digit positioning. In addition, participants received TMS mid-reach or after

745    object contact. Importantly, they found that after object contact, CSE was increased in the unconstrained

746    compared to constrained condition. Accordingly, the authors argued that the sensorimotor uncertainty

747    regarding digit positioning in the unconstrained condition drove CSE modulation. However, it is

748    noteworthy that they did not find similar effects during mid-reach indicating a time-specific effect. As

749    both TMS timings and digit postioning strategies differed between our and their study, it is impossible to

750    make further comparsisons between both studies.

751        Our results indicate that modulation of CSE during planning and observation of lifts is not

752    associated with the participants' lift performance. Although CSE during observation and planning was

753    modulated similarly for collinear and non-collinear lifts on the right center of mass, participants did not

754    lift the right asymmetrical weight distribution skillfully with collinear digit positioning (Figure 5A).

755    Arguably, considering that the actor also performed worse in the collinear condition and participants

756    were not even able to collinearly lift the asymmetrical weight skillfully in their second and third lifts,

757    which they should have been based on the findings of Fu et al. (2010), these findings suggest that

758    collinear lifts of the asymmetrical weight distribution might have been challenging to execute properly.

759    Accordingly, CSE modulation might still have reflected the object's weight distribution but proper

760    planning of the collinear lifts might have been challenging. As such, future research might be required to

761    disentangle how motor resonance relates to motor planning and proper execution.

762         Motor resonance has been argued to rely on mirror neurons. Mirror neurons are similarly

763    activated when executing or observing the same action and have been argued to be involved in action

764    understanding by "mapping" observed actions onto the cortical representations involved in their

765    execution (Rizzolatti, Cattaneo, Fabbri-Destro, & Rozzi, 2014). Mirror neurons are primarily located in

766    M1, the ventral premotor cortex (PMv) and the anterior intraparietal area (AIP) (Rizzolatti et al., 2014).

767    Importantly, these regions also constitute the cortical grasping network which is pivotal in planning and

768    executing grasping actions (for a review see Davare et al. 2011) further substantiating these neurons

769    involvement in action understanding. Our findings corroborate mirror neuron functioning by showing

770    that CSE was similarly modulated during lift observation and planning. Interestingly, even though our

771    motor resonance findings might have been partially driven by the experimental context (Rens et al.

772    2020a), CSE modulation was similar during planning, which substantiates that the same mechanisms

773    underlied CSE modulation in our experiment. To end, CSE modulation being similarly increased for the

774    right asymmetrical weight distribution during both observation and planning indicates that the motor

775    system encoded the same object-related information during both planning and observation.

776         A limitation of the present study is that we did not find modulation of CSE recorded from the FDI

777    muscle. As mentioned before, this might have been caused by the non-visiblity of the index finger during

778    lift observation and planning. During lift observation, this issue could have been solved by placing the

779    actor opposite of the participant. However, we decided to place the actor at the side of the participant

780    as Alaerts et al. (2009) showed that motor resonance effects are stronger when executed actions are

781    observed from a first person point of view. Another limitation is the erroneous lifting performance on

782    the asymmetrical weight distribution when using collinear digit positioning: Buckingham et al. (2014)

783    showed that motor resonance can be differently modulated when observing skilled or erroneous actions.

784    As such, having decreased the object weight, thus making lifts on the asymmetrical weight distributions

785    less challenging, could have removed the potential confouding effect of lifting performance between

786    conditions. It is important to note that in previous work of our group (Rens et al. 2020b), we found that

787    observing skilled lifts of asymmetrical weight distributions did not enhance predictive lift planning in the

788    observer. In the present study, we found that participants generated more compensatory torque after

789    observing skilled lifts with noncollinear digit positioning, contrasting the findings of our previous study.

790    Arguably, this difference is driven by constraining and not constraining digit positioning in this and the

791    previous study, respectively. More research is required to investigate the effects of constraining digit

792    positioning on predictive lift planning.

793          In conclusion, the present study investigated how CSE is modulated during the observation and

794    planning of lifts with an asymmetrical weight distribution. Our findings revealed that CSE modulation

795    during observation was driven by the object's weight distribution as potentially indicated by digit

796    positioning and object roll (i.e. inappropriate compensatory torque). During lift planning, CSE was

797    similarly modulated as during lift observation indicating that the same neural mechansims are involved

798    in CSE modulation during lift observation and planning. As such, our findings provide novel insights in the

799    involvement of the hMNS in observation and planning lifts on objects with complex intrinsic properties.

800

801    **Bibliography**

802    Alaerts, K., Heremans, E., Swinnen, S. P., & Wenderoth, N. (2009). How are observed actions mapped to

803          the observer's motor system? Influence of posture and perspective. *Neuropsychologia*, *47*(2), 415–

804          422. https://doi.org/10.1016/j.neuropsychologia.2008.09.012

805    Alaerts, K., Senot, P., Swinnen, S. P., Craighero, L., Wenderoth, N., & Fadiga, L. (2010). Force

806          requirements of observed object lifting are encoded by the observer's motor system: a TMS study.

807          *European Journal of Neuroscience*, *31*(6), 1144–1153. https://doi.org/10.1111/j.1460-

808          9568.2010.07124.x

809    Alaerts, K., Swinnen, S. P., & Wenderoth, N. (2010). Observing how others lift light or heavy objects:

810          Which visual cues mediate the encoding of muscular force in the primary motor cortex?

811          *Neuropsychologia*, *48*(7), 2082–2090. https://doi.org/10.1016/j.neuropsychologia.2010.03.029

812    Amoruso, L., & Finisguerra, A. (2019). Low or High-Level Motor Coding? The Role of Stimulus Complexity.

813          *Frontiers in Human Neuroscience*, *13*(October), 1–9. https://doi.org/10.3389/fnhum.2019.00332

814    Baugh, L. a., Kao, M., Johansson, R. S., & Flanagan, J. R. (2012). Material evidence: interaction of well-

815          learned priors and sensorimotor memory when lifting objects. *Journal of Neurophysiology*, *108*,

816          1262–1269. https://doi.org/10.1152/jn.00263.2012

817    Buckingham, G., Wong, J. D., Tang, M., Gribble, P. L., & Goodale, M. A. (2014). Observing object lifting

818          errors modulates cortico-spinal excitability and improves object lifting performance. *Cortex*, *50*,

819          115–124. https://doi.org/10.1016/j.cortex.2013.07.004

820   Davare, M., Kraskov, A., Rothwell, J. C., & Lemon, R. N. (2011). Interactions between areas of the cortical

821      grasping network. *Current Opinion in Neurobiology*, *21*(4), 565–570.

822      https://doi.org/10.1016/j.conb.2011.05.021

823   Davare, M., Parikh, P. J., & Santello, M. (2019). Sensorimotor uncertainty modulates corticospinal

824      excitability during skilled object manipulation. *Journal of Neurophysiology*, *121*(4), 1162–1170.

825      https://doi.org/10.1152/jn.00800.2018

826   Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor Facilitation During Action Observation: a

827      Magnetic Stimulation Study. *Journal of Neurophysiology*, *73*(6), 2608–2611.

828   Fu, Q., Zhang, W., & Santello, M. (2010). Anticipatory Planning and Control of Grasp Positions and Forces

829      for Dexterous Two-Digit Manipulation. *Journal of Neuroscience*, *30*(27), 9117–9126.

830      https://doi.org/10.1523/JNEUROSCI.4159-09.2010

831   Johansson, R., & Westling, G. (1988). Coordinated isometric muscle commands adequately and

832      erroneously programmed for the weight during lifting task with precision grip. *Experimental Brain*

833      *Research*, *71*(1), 59–71.

834   Lukos, J., Ansuini, C., & Santello, M. (2007). Choice of contact points during multidigit grasping: effect of

835      predictability of object center of mass location. *The Journal of Neuroscience*, *27*(14), 3894–3903.

836      https://doi.org/10.1523/JNEUROSCI.4693-06.2007

837   Meulenbroek, R. G. J., Bosga, J., Hulstijn, M., & Miedl, S. (2007). Joint-action coordination in transferring

838      objects. *Experimental Brain Research*, *180*(2), 333–343. https://doi.org/10.1007/s00221-007-0861-z

839   Mojtahedi, K., Fu, Q., & Santello, M. (2015). Extraction of Time and Frequency Features from Grip Force

840      Rates for Identification of Control Mechanisms for Dexterous Manipulation. *IEEE Transactions on*

841      *Biomedical Engineering*, *62*(5), 1–3.

842   Naish, K. R., Houston-price, C., Bremner, A. J., & Holmes, N. P. (2014). Neuropsychologia Effects of action

843      observation on corticospinal excitability : Muscle specificity , direction , and timing of the mirror

844      response. *Neuropsychologia*, *64*, 331–348. https://doi.org/10.1016/j.neuropsychologia.2014.09.034

845   Reichelt, A. F., Ash, A. M., Baugh, L. A., Johansson, R. S., & Flanagan, J. R. (2013). Adaptation of lift forces

846      in object manipulation through action observation. *Experimental Brain Research*, *228*(2), 221–234.

847      https://doi.org/10.1007/s00221-013-3554-9

848   Rens, & Davare. (2019). Observation of both skilled and erroneous object lifting can improve predictive

849      force scaling in the observer. *Frontiers in Human Neuroscience*, *13*(October), 1–13.

850      https://doi.org/10.3389/fnhum.2019.00373

851   Rens, G., Orban de Xivry, J., Davare, M., & Van Polanen, V. (2020). Lift observation conveys object weight

852        distribution but partly enhances predictive lift planning. *BioRxiv Preprint*, 1–31.

853    Rens, G., Van Polanen, V., Botta, A., Gann, M., Orban de Xivry, J., & Davare, M. (2020). Sensorimotor

854        expectations bias motor resonance during observation of object lifting: The causal role of pSTS.

855        *Journal of Neuroscience*.

856    Rizzolatti, G., Cattaneo, L., Fabbri-Destro, M., & Rozzi, S. (2014). Cortical mechanisms underlying the

857        organization of goal-directed actions and mirror neuron-based action understanding. *Physiological*

858        *Reviews*, *94*(2), 655–706. https://doi.org/10.1152/physrev.00009.2013

859    Rossi, S., Hallett, M., Rossini, P. M., & Pascual-leone, A. (2011). Screening questionnaire before TMS: An

860        update. *Clinical Neurophysiology*, *122*(8), 1686. https://doi.org/10.1016/j.clinph.2010.12.037

861    Senot, P., D'Ausilio, A., Franca, M., Caselli, L., Craighero, L., & Fadiga, L. (2011). Effect of weight-related

862        labels on corticospinal excitability during observation of grasping: A TMS study. *Experimental Brain*

863        *Research*, *211*(1), 161–167. https://doi.org/10.1007/s00221-011-2635-x

864    Tidoni, E., Borgomaneri, S., di Pellegrino, G., & Avenanti, A. (2013). Action simulation plays a critical role

865        in deceptive action recognition. *Journal of Neuroscience*, *33*(2), 611–623.

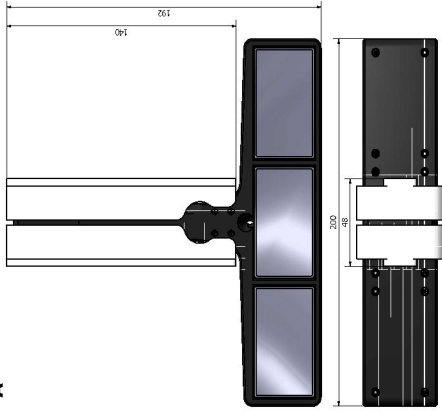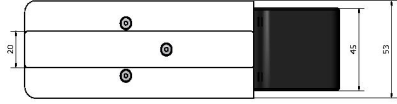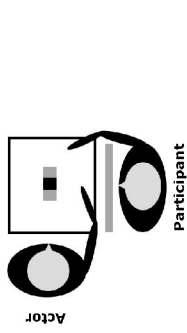866        https://doi.org/10.1523/JNEUROSCI.2228-11.2013

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868

869 **Figure captions**

870 **Figure 1. Experimental set-up. (A)** Left: Frontal, side and top down view of the 'inverted T-shape'
871 manipulandum with dimensions (in mm). **(B)** Schematic drawing of the manipulandum with the three
872 compartments indicated with L, C and R standing for left, central and right respectively. In red, the
873 constrained locations are marked. X, Y and Z indicates the frame of reference for the force/torque
874 sensors in the vertical component. **(C)** Dyadic positioning at a square table with the manipulandum
875 placed in between the actor and participant. Figure modified from and reprinted with permission from
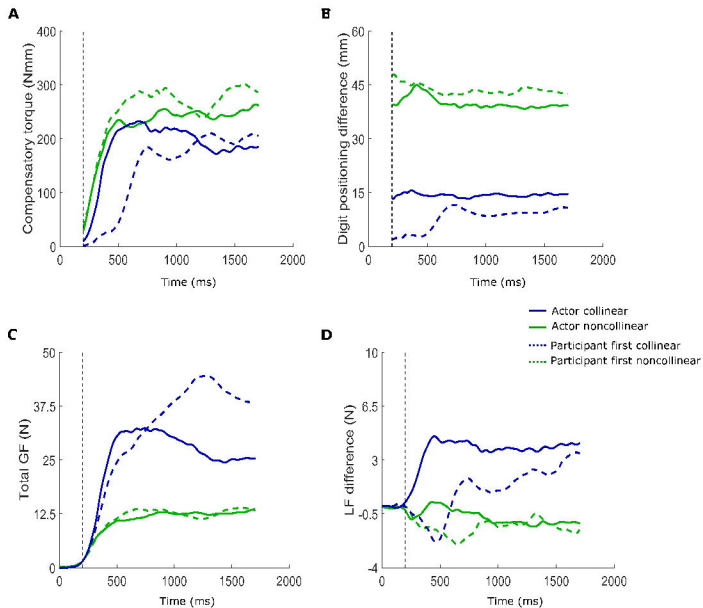876 Rens et al. (2020b)

877 **Figure 2. Example parameter traces.** One lift example of performance on a left-sided asymmetrical
878 weight distribution for the actor (solid traces) and first lift of a participant (dashed traces). These traces
879 show the typical evolution of different parameter profiles over time for a lift with fingertips positioned
880 on the same height ('collinear'; in blue) or with fingertips positioned on different heights ('noncollinear';
881 in green). **(A)** Compensatory torque (in Nmm). **(B)** Digit positioning difference, i.e. vertical height
882 difference in center of pressure of the fingertips (position thumb - position index finger; in mm). **(C)** Total
883 grip force (in N). **(D)** Load force difference (load force thumb – load force index finger; in N). Vertical
884 dashed line on each figure indicates object contact. We cleared compensatory torque and digit
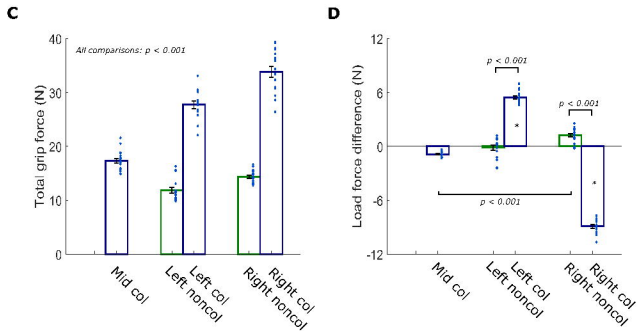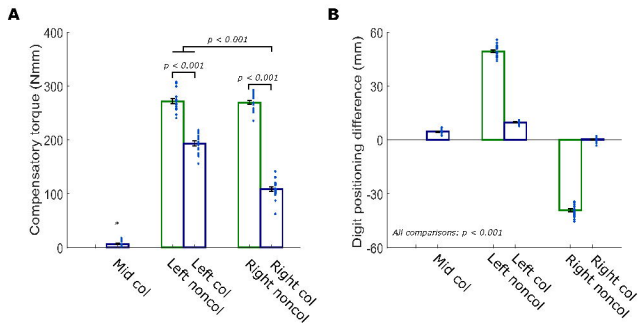885 positioning difference values before object contact as they are highly contaminated by noise.

886 **Figure 3. Lift performance of the actor.** The actor's averaged lift performance. The actor used either
887 collinear (col; blue) or noncollinear (noncol; green) digit positioning to the object. Each scatter dot
888 represents the averaged performance of the actor as observed by one participant. **(A)** Compensatory
889 torque (in Nm). **(B)** Digit positioning difference (in mm). **(C)** Total amount of grip force (in N). **(D)** Load
890 force difference (in N). All data is presented as the mean ± SEM. An asterisk above/within a bar indicates
891 that this condition differed significantly from all other conditions with a p < 0.001.
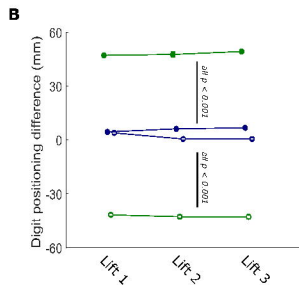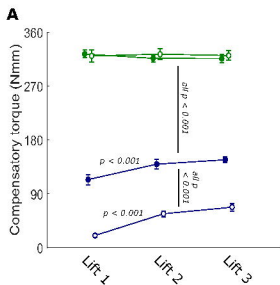
892 **Figure 4. Lift performance of the participants.** Connected scatterplot showing the averaged lift
893 performance of the participants for their three lift repetitions. Performance is shown for when the
894 weight distribution was left (solid scatter) or right (empty scatter**)** asymmetrical. Participants used either
895 collinear (blue) or noncollinear (green) digit positioning for lifting. **(A)** Compensatory torque (in Nmm).
896 **(B)** Digit positioning difference (in mm). **(C)** Total grip force (in N). **(D)** Load force difference (in N). All
897 data is presented as the mean ± SEM. Vertical lines with a p-value indicate that all scatters above this line
898 differ significantly from all scatters below. P-values between two connected scatters indicate that those
899 two differ significantly from each other.

900 **Figure 5. Corticospinal excitability during lift observation and planning.** Average motor evoked
901 potential (MEP) values (z-score normalized) during lift observation **(top row)** and lift planning, pooled for
902 REPETITION, **(bottom row)** recorded from first dorsal interosseous muscle **(FDI; panels A and C)** and
903 from the abductor pollicis brevis muscle **(APB; panels B and D)**. The actor and participants used either
904 collinear (col; blue) or noncollinear (noncol; green) digit positioning to lift the asymmetrical weight
905 distributions (left or right). Each dot on top of each bar represents the average MEP value for one
906 participant for that respective condition during lift observation and planning. All data is presented as the
907 mean ± SEM.

A

B

$x$ $z$ $y$

Roll  +  −

Index finger

Thumb

$T_{comp}$  −  $T_{comp}$  +

L  C  R

C

Actor

Participant

**A**

Compensatory torque (Nmm)

**B**

Digit positioning difference (mm)

**C**

Total GF (N)

**D**

LF difference (N)

Time (ms)

— Actor collinear
— Actor noncollinear
···· Participant first collinear
···· Participant first noncollinear

**A** Compensatory torque (Nmm)

**B** Digit positioning difference (mm)

**C** Total grip force (N)

**D** Load force difference (N)

Legend:
- ● Left noncollinear
- ● Left collinear
- ○ Right noncollinear
- ○ Right collinear