1   **Title:** The observation of explicit and implicit visuomotor cues can drive predictive motor control

2   **Abbreviated title:** Observation of implicit cues mediates motor planning

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23   **Abstract**

24   Recent studies have highlighted that the observation of hand-object interactions can influence

25   perceptual weight judgements made by an observer. Moreover, observing explicit motor errors during

26   object lifting allows individuals to update their internal sensorimotor representation about object

27   weight. Embodying observed visuomotor cues for the planning of a motor command further enables

28   individuals to accurately scale their fingertip forces when subsequently lifting the same object. However,

29   it is still unknown whether observation of a skilled lift is equally able to mediate predictive motor control

30   in the observer. Here, we tested this hypothesis by asking participants to grasp and lift a manipulandum

31   after observing an actor's lift. The object weight changed unpredictably (light or heavy) every third to

32   sixth trial performed by the actor. Participants were informed that they would always lift the same

33   weight as the actor and that, based on the experimental condition, they would have to observe skilled or

34   erroneously performed lifts. Our results revealed that the observation of both skilled and erroneously

35   performed lifts allows participants to update their internal sensorimotor object representation, in turn

36   enabling them to predict force scaling accurately. These findings suggest that the observation of explicit

37   as well as implicit visuomotor cues are embodied in the observer's motor repertoire and can drive

38   changes in predictive motor control.

Introduction

Skilled hand movements are essential throughout our daily life. It has been well established that dextrous object manipulation not only relies on tactile feedback but also on anticipatory sensorimotor mechanisms. Performing hand-object interactions allows internal object representations to be formed. In turn, these internal sensorimotor representations can be retrieved to enable anticipatory planning of digit forces for future object manipulations (E.g. see Johansson & Westling, 1988). It has been argued that predictive force scaling requires an association between intrinsic object properties, for example size or texture, and the object weight, which are experienced by visual and tactile feedback respectively (Baugh, Kao, Johansson, & Flanagan, 2012). In addition, other research groups have demonstrated that object weight is not only perceived via somatosensory inputs but can also be retrieved through vision and that visual weight judgements are associated to the actual object weight (Bingham, 1987; Runeson & Frykholm, 1981). Finally, it has been established that the object lifting phase conveys critical information for mediating weight judgements: observers mostly rely on the duration of the lifting movement for generating weight perception (Hamilton, Joyce, Flanagan, Frith & Wolpert, 2007; Shim & Carlton, 1997).

The influence of action observation on both weight perception and lift performance was first investigated by Meulenbroek and colleagues: They demonstrated that, when both the actor and subject had an incorrect weight prediction, lifting performance errors made by the subject are reduced, but not eradicated, after observing the actor making typical lift errors (Meulenbroek, Bosga, Hulstijn, & Miedl, 2007). In addition, it was shown in a more recent study by Uçar and Wenderoth that observation of different types of hand movements can alter grip force generation during object grasping: Prior to grasping an object, subjects were asked to observe an actor either touching or squeezing an object. The latter condition led subjects to produce larger grip forces (Uçar & Wenderoth, 2012). Finally, it has been demonstrated that when individuals observe grasping errors, they are able to differentiate object weight based on kinematic cues and, in turn, to scale their fingertip forces more accurately in upcoming trials (Reichelt, Ash, Baugh, Johansson, & Flanagan, 2013). Although these studies have shed light on how action observation can mediate anticipatory motor control in the observer, they only focused on observation of explicit hand-object interactions (different movements [Uçar & Wenderoth, 2012] or salient movement errors [Meulenbroek et al., 2007; Reichelt et al., 2013]) and not on more subtle, implicit, skilled performance of hand movements.

To our knowledge, only a few studies have compared how observing erroneous and skilled object interactions can mediate predictive force scaling. For example, using the size-weight illusion, Buckingham and colleagues highlighted that predictive force scaling in the observer is significantly better

71 after observing erroneous compared to skilled lifting. That is, when participants had to lift a large, but

72 unexpectedly light object for the first time, those who observed typical overestimation errors on the

73 same object would predict the actual weight more accurately (Buckingham, Wong, Tang, Gribble, &

74 Goodale, 2014). Interestingly, when investigating how corticospinal excitability (CSE) was modulated

75 during lift observation, Buckingham et al. found that only during the observation of skilled lifts, CSE was

76 modulated by object size: CSE modulation was significantly higher in response to the observation of a

77 skilled lift of the larger object compared to the smaller one. However, during observation of erroneous

78 lifts on the same objects, the effect of object size on CSE modulation was eradicated (Buckingham et al.,

79 2014). As such, it seems that, when observing skilled object lifting, object size is the critical factor for

80 extracting object weight and driving CSE changes; while when observing erroneous lifts, kinematic cues,

81 not size, have a predominant effect. As a result, it seems plausible that when a lifting error is observed,

82 the unexpected object kinematics drive individuals to shift their attention towards the object kinematics

83 and not size, improving the observer's predictive force scaling and altering the underlying CSE

84 modulation.

85   In the current study, we aimed to specifically investigate whether observation of skilled object

86 lifting can drive changes in internal sensorimotor representations when a similar action observation

87 strategy is used for both erroneous and skilled lifts. For this reason, we emphasised on three factors

88 considering the aforementioned studies: (1) we used objects that are identical in appearance to exclude

89 that size and other visual cues could be used to predict object weight. (2) Similarly to the study of

90 Reichelt et al., participants were familiarized to the experimental protocol and object weights. (3) In

91 contrast to the study of Reichelt et al., subjects were informed that they would have to focus on the

92 observation of either skilled or erroneous object lifting. We argue that these factors would allow

93 participants to better understand the task goal and to specifically focus on the actor's movement

94 kinematics during both action observation conditions. Even though kinematic differences during skilled

95 movements are far more subtle than during erroneously performed movements (e.g. see Buckingham et

96 al., 2014), we hypothesized that observation of skilled lifts can mediate predictive force scaling similarly

97 to observation of explicit lift errors.

98

99   **Methods**

100   Participants

101   14 subjects (6 males and 8 females; mean age = 19.7 ± 2.9 years) were recruited from the student body

102   of KU Leuven to participate in the current study. All participants were right-handed (self-reported), had

103   normal or corrected-to-normal vision, were free of neurological disorders and had no motor

104   impairments of the right upper limb. The study was conducted in accordance with the declaration of

105   Helsinki and was approved by the local ethical committee of the Faculty of Biomedical Sciences, KU

106   Leuven. Subjects were financially compensated for their participation. Data of one participant were

107   rejected after the data analysis stage due to high inconsistencies in grasping pattern throughout the

108   experiment.

109   General procedure

110   Subject and actor were comfortably seated opposed to each other in front of a table (for the

111   experimental set-up see figure 1A). Participants were required to grasp and lift a manipulandum (see

112   'Data acquisition') that was placed in front of them (1) either repeatedly ('SOLO condition') or (2) in turns

113   with the actor ('dyadic conditions'). Participants and actor used their entire right upper limb to reach for

114   the manipulandum and were asked to grasp it with the thumb and index finger only (precision grip).

115   Subjects and actor were required to lift the manipulandum smoothly to a height of approximately 3 cm

116   and to keep the grasp-and-lift movement consistent throughout the entire experiment. Additionally,

117   subjects and actor were required to place their hand on a predetermined resting position on their side of

118   the table between trials, at a distance of approximately 25 cm from the manipulandum. This was done to

119   ensure consistent reaching movements across trials. Each trial initiated with a neutral sound cue ('start

120   cue') indicating that the movement could be initiated. Trials lasted 4 seconds to ensure that subjects and

121   actor had enough time to reach, grasp and lift the manipulandum smoothly at a natural pace. Inter-trial

122   interval was approximately 5 s during which the weight of the manipulandum could be changed. A

123   transparent switchable screen (Magic Glass), placed in front of the participants' face, became

124   transparent at trial onset and turned back to opaque at the end of the trial. The screen remained opaque

125   during the inter-trial interval.

126   ---------------------------

127   Figure 1

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129

130   Experimental conditions

131   We used an experimental set-up similar to the study of Reichelt et al. (Reichelt et al., 2013). Participants

132   always performed the solo condition first in order to be familiarized with the experiment. After this

133   condition, subjects performed two dyadic conditions, i.e. erroneous lift observation ('EO') and skilled lift

134   observation ('SO'). Each dyadic condition was performed two times in a counterbalanced order within

135   and across subjects.

136   *Solo condition ('SOLO').* Participants repeatedly lifted the manipulandum themselves, therefore

137   performing all trials. The weight of the object changed between 1.5 N (light, 'L') and 6.2 N (heavy, 'H')

138   after a pseudo-random amount of trials of the same weight. The number of trials per weight sequence

139   (i.e. sequential lifts of the same weight) varied randomly between 3 and 6 trials. Thus participants could

140   not predict when the weight change would occur based on the number of lifts. Subjects completed 8

141   transitions from each weight to the other (i.e. from 1.5 N to 6.2 N and vice versa). This provided 8 trials

142   per weight transition which were used to familiarize participants, assess baseline sensorimotor memory

143   effects (for example see: Johansson & Westling, 1984) and use for comparison with the dyadic

144   conditions.

145   *Dyadic conditions.* Between the end of the SOLO condition and the start of the first dyadic

146   condition, subjects were instructed on lifting errors i.e. incorrect scaling of fingertip forces due to wrong

147   estimation of object weight. They were told that in the dyadic conditions they would have to lift the

148   manipulandum in alternation with the actor and that the object weight presented in their trial would

149   always be identical to the weight lifted by the actor in the preceding trial. It was also mentioned that the

150   object weight would always change first for the actor and then would be the same for the subject.

151   Finally, subjects were asked to avoid making lifting errors and, importantly, they were told to use cues

152   from the actor's movement to estimate object weight. However which movement cues could be relevant

153   or which strategy could be used were not discussed. After receiving the task instructions, participants

154   performed the two dyadic conditions. As in the SOLO condition, there were 8 transitions from one

155   weight to the other after a pseudo-random amount of trials. During the dyadic conditions each weight

156   sequence consisted of an even amount of trials between 6 and 12. As such, both actor and participants

157   lifted the manipulandum between 3 and 6 trials within each weight sequence (i.e. the same amount as in

158   the SOLO condition for each person).

159   Because each dyadic condition took twice the amount of trials in comparison with the SOLO

160   condition, both dyadic conditions were divided into two blocks with a break in between them. This was

161   done to prevent fatigue affecting observation and movement performance. Dyadic block order was

162   counter-balanced within and between subjects. Although both dyadic conditions consisted of two

163   separated blocks, data is presented pooled per condition. In the SO condition, the actor always scaled his

164   fingertip forces correctly to the weight that was presented to him. As a result, the subject could only

165   extract information about object weight by observing skilled lifts. In the EO condition, the actor

166   incorrectly scaled his fingertip forces when the new weight was presented. This lifting error was made

167   only in the first trial after the weight change. In all other trials of the same weight sequence of the EO

168   condition, the actor would perform a skilled lift of the manipulandum. Thus in the EO condition,

169   participants could perceive a weight change by looking for lifting errors. Importantly, the lifting error

170   made by the actor was intentional due to the experimental set-up (see: 'data acquisition'). Lastly, one of

171   the authors (GR) served as an actor for all experiments.

172   Data acquisition

173   A grip-lift manipulandum consisting of two 3D force-torque sensors (Nano17, ATI Industrial Automation,

174   Apex, NC, USA) was attached to a custom-made carbon fibre basket in which different objects (cubes)

175   could be placed (For an example of the manipulandum see Fig. 1B). The total weight of the

176   manipulandum was 1.2 N. The graspable surface (17 mm diameter and 45 mm apart) of the force

177   sensors was covered with fine sandpaper (P600) to increase friction. The objects were 3D-printed cubes

178   of 5 × 5 × 5 cm, filled with different amounts of lead particles to create weights of 0.3 N ('light') and 5.1 N

179   ('heavy'), therefore the total weight were respectively 1.5 N and 6.3 N for the light and heavy weight. To

180   exclude all visual cues about weight, cubes were hidden under the same paper cover. It is noteworthy

181   that cubes were changed manually between each trials (even for trials without weight change) to ensure

182   participants could not use any sound cues to predict weight changes. Second, given the actor was

183   responsible for changing cubes between trials, he always knew what weight would be presented in the

184   upcoming trial. Therefore, the over- and underestimation lift errors related to object weight were made

185   intentionally by the actor and not by a wrong prediction of object weight. Custom-made scripts were

186   compiled in MATLAB (Mathworks) for both data acquisition and processing.

187   Data analysis

188   Force signals were sampled in 3 dimensions at 1000 Hz and smoothed using a 4th order, zero-phase lag,

189   low-pass Butterworth filter with a cut off frequency of 15 Hz. Grip force (GF) was defined as the exerted

190   force (on the force sensors) perpendicular to the normal force. Load force (LF) was defined as the

191   exerted force parallel to the normal force (Fig. 1B). GF and LF were computed as the sum of the

192   respective force components exerted on both sensors. Additionally, grip force rate (GFr) and load force

193   rate (LFr) were calculated by computing the first derivative of GF and LF. Finally, we calculated the

194   loading phase duration (LPD) by measuring the latency between LF onset (LF > 0.05 N) and an

195   approximation of object lift off (LF > 0.95 * total object weight) (Fig. 1C). Peak force rate values, not peak

196   force values, are presented in the results as it has been demonstrated that these force parameters are a

197   reliable indicator of predictive force scaling (Gordon, Forssberg, Johansson, & Westling, 1991; Johansson

198   & Westling, 1988). These force parameters were compared based on only the first and second trials after

199   the weight change for both subject and actor as it has been demonstrated that individuals adapt to the

200   actual object weight after one trial (Gordon, Westling, Cole & Johansson, 1993). As such, these trials

201   allowed us to investigate (1) the baseline for over- and underestimation of object weight by subjects

202   during the SOLO condition, (2) the movement kinematics of the actor in the EO and SO condition and (3)

203   whether the EO and SO conditions alter the typical over- and underestimation of object weight and could

204   mediate accurate predictive force scaling.

205

206   Statistical Analysis

207   For statistical analysis of peak force rate values, we normalized the data of all subjects; i.e. the peak

208   values and LPD of each trial were divided by the peak values and LPD of the last trial in the same weight

209   sequence (i.e. sequential lifts of the same weight). For example: If the subject had to grasp 5 heavy

210   weights repeatedly, all parameters of these 5 trials were divided by the parameter value recorded in the

211   fifth trial of the same sequence. The first 4 trials are expressed as a ratio to the fifth trial and the fifth

212   trial would have a value of 1 for each parameter. If any of the measured parameters in the last trial of

213   the weight sequence was an outlier relative to this condition (value larger or smaller than mean ± 2 SD's)

214   then the entire sequence of weight repetitions was discarded. We chose to compute ratios based on the

215   last trial of a weight sequence because the last trial can be considered as the most skilled due to the

216   repetition of lifts of the same weight (Reichelt et al., 2013). Secondly, some participants altered their

217   general force pattern over time during the experiment although they were informed to maintain a

218   consistent grasping pattern. Using this procedure, the over- and underestimations of object weight are

219   always expressed in relation to the force pattern of skilled lifting during that specific time point and take

220   these potential changes over time into account.

221   We performed repeated-measures ANOVAs to investigate differences in the weight change trials

222   between conditions. We used 2 within-subject factors: LIFT NUMBER (the first trial after weight change

223   and the second trial after weight change) and CONDITION (SOLO, SO, and EO). Importantly, when

224   investigating the actor's force parameters, we included the last trial of each weight sequence in the

225 factor LIFT NUMBER in order to investigate the actor's consistency. ANOVAs were performed separately

226 for heavy-to-light and for light-to-heavy weight changes. Comparisons of interest exhibiting statistically

227 significant differences (p ≤ 0.05) were further analysed using the Holm-Bonferroni test. All data

228 presented in the text are given as mean ± standard error of the mean (SEM).

229 **Results**

230 We aimed to investigate whether action observation can drive changes in internal sensorimotor

231 representations, which would further translate into changes in predictive motor control. To address this

232 issue, we compared 3 conditions. In the solo condition ('SOLO'), participants repeatedly lifted the objects

233 for familiarization purposes and to assess baseline sensorimotor memory effects caused by an

234 unexpected weight change. In the dyadic conditions, participants lifted series of objects in alternation

235 with an actor. Subjects were informed that they would always have to lift the same object weight as the

236 actor. For this reason, subjects could use observed kinematics to perceive object weight and

237 consequently update their internal sensorimotor representation. In the error observation condition

238 ('EO'), the actor would make a typical lifting error when the weight would change from light to heavy

239 (i.e. 'undershoot') or from heavy to light (i.e. 'overshoot'). The actor would then correctly scale his

240 fingertip forces in the following trials. In the skilled lift observation condition ('SO'), the actor would

241 always apply correct fingertip forces. These two action observation conditions allowed us to investigate

242 whether individuals respond differently to error vs. skilled actions in order to plan their own motor

243 command following an unexpected object weight change.

244

245 <u>Actor's lifting force parameters</u>

246 The actor only lifted the objects during action observation trials. In EO, we expected that the first trial

247 after a weight change would differ significantly from the following lifts of the same weight (i.e. explicit

248 lift error). In SO, we expected all trials, including the first lift after a weight change, to be performed with

249 comparable force parameters (i.e. skilled lift).

250   For all force parameters and both weight changes, except pLFr ($F_{(1,13)} = 0.54$, $p = 0.47$, *Fig. 3A*)

251 and LPD ($F_{(1,13)} = 2.71$, $p = 0.12$, *Fig.3C*) for the heavy-after-light weight changes, both main effects of

252 CONDITION and LIFT NUMBER as well as the CONDITION X LIFT NUMBER interaction were significant *(all*

253 *F-values > 8.39, all p-values < 0.01, Figures 2-3)*.

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257   Table 1

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259   Table 1 represents the actor's lifting performance, pooled across all participants. The force

260   pattern used by the actor in the first trial after the weight change in the EO condition was significantly

261   different from all other trials of both conditions: Post-hoc analyses for all force parameters revealed that,

262   except for pLFr in the heavy-after-light condition, that the first trial after the weight change in the EO

263   condition differed significantly from all other trials of both conditions (Figures 2 and 3).

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265   Figure 2 and 3

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267   In order to explain the lack of effect for pLFr in the heavy-after-light weight changes, we further

268   looked at the time-to-peak of pLFr. Post-hoc analysis of the significant interaction effect *(*CONDITION X

269   LIFT NUMBER *F-value = 4.83, p-value = 0.02)* revealed that the pLFr time-to-peak value was significantly

270   longer for the first trial after the weight change in the EO condition compared to all trials in all other

271   conditions. These analyses highlight that the actor's lifting performance was explicitly different for the

272   first trial after a weight change compared to the following trials, thus providing reliable lifting error cues

273   to the observer.

274   It is noteworthy that the lifting errors were made artificially by the actor as he always had prior

275   knowledge of the object weight. For this reason, errors were exaggerated in comparison with natural

276   lifting errors on similar weight differences (for example see: Reichelt et al., 2013). Hamilton and

277   colleagues showed that strong deviations in loading phase duration influence weight perception in the

278   observer (Hamilton et al., 2007), therefore it is plausible that subjects are still capable of deriving object

279   weight based on these artificial lifting errors. In addition, the EO condition was essentially added to

280   replicate the findings of Reichelt and colleagues (Reichelt et al., 2013). The main purpose of the current

281   study was to investigate whether skilled lift observation can mediate sensorimotor memory. Importantly,

282   our data revealed that the actor was consistent throughout the performance of skilled lifting as there

283   were only two cases for which LPD values were significantly different (light-after-heavy: first SO trial vs.

284   second EO trial, *p < 0.01*; heavy-after-light: second vs. last trial in the EO condition, *p < 0.01)*.

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287   --------------------------

288   Figure 4

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290   Observers' lifting force parameters: light-after-heavy weight changes

291   The left panel of Figure 4 shows the averaged force profiles of the first trial after the weight changed

292   from heavy to light in a typical subject. When a subject scales his fingertip forces in anticipation of a

293   heavy object, more force than required (overshoot) will be applied to lift the light object adequately

294   (Johansson & Westling, 1988). In addition, it has been demonstrated that after observing a lift error,

295   individuals are able to immediately scale their fingertip forces accurately (Reichelt et al., 2013).

296   Accordingly, Figure 4 reveals that the subject was able to downscale force parameters after observing a

297   lift error compared to the SOLO condition. It is noteworthy that the subject was also able to apply the

298   correct force scaling after observation of a skilled lift (SO). For data analysis purposes, we only included

299   the first and second trials following a light-after-heavy weight change. Considering that we processed the

300   data using ratio values (see 'Methods'), force scaling overestimation corresponds to peak force rates

301   with ratios larger than 1. As expected for light-after-heavy weight changes, these effects are the opposite

302   for the loading phase duration: A ratio value smaller than 1 indicates a faster increase in force generation

303   thus resulting in a shortened loading phase duration.

304   --------------------------

305   Figure 5

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307   *Load force rates.* Repeated-measures ANOVA for load force rates revealed that both main effects

308   were significant (*both F-values > 5.65; both p-values < 0.05*). The interaction effect was not significant

309   ($F_{(2, 22)} = 0.19$, $p = 0.83$). Firstly, as can be seen in Figure 5A, post-hoc analysis of the significant main

310   effects revealed that participants scaled their load forces with a significantly improved accuracy after

311   observing lifting errors in comparison with the SOLO condition *(p < 0.01)*. However, given that there was

312   no significant difference between the SO and SOLO conditions and between the SO and EO conditions *(p*

313   *> 0.31)*, this indicates that the SO condition is likely to mediate predictive force scaling as well albeit to a

314   lesser extent than the EO condition. Finally, considering the significant main effect of LIFT NUMBER, it is

315   clear that participants were able to predictively scale fingertip forces with increased accuracy in the

316   second trial after the weight change (*p = 0.01*).

317   *Grip Force rates.* The analyses for peak grip force rate revealed that both main effects and the

318   interaction effect were significant (*all F-values > 7.34; all p-values < 0.01)*. As can be seen in Figure 5B, it

319   is noticeable that participants scaled their grip forces with the highest accuracy after observing errors

320   (Ratio = 1.16 ± 0.08) in comparison with both the SO (Ratio = 1.77 ± 0.77) and the SOLO (Ratio = 2.17 ±

321   0.14) conditions (*both p-values < 0.001)*. In addition, the difference between the SO and SOLO conditions

322   neared significance *(p = 0.11)*, indicating, in line with the findings for LFr, that the observation of skilled

323   lifting might be able to mediate predictive force scaling. Finally, for all conditions, participants were

324   increasingly accurate in the second trial after the weight change as the analysis revealed no significant

325   differences between the SOLO, SO and EO second trials *(All p-values = 1)*.

326   *Loading phase duration.* Repeated-measures ANOVAs for the loading phase duration revealed

327   that both main effects and the interaction effect were significant *(all F-values > 8.18, all p-values < 0.05)*.

328   In Figure 5C, it is noticeable that participants had a significantly shorter loading phase duration in the SO

329   (Ratio for first trial of SO = 0.88 ± 0.03) and SOLO condition (Ratio for first trial of SOLO = 0.82 ± 0.05) in

330   comparison with all other trials of all conditions (*all p-values < 0.05*). This indicates that the observation

331   of lift errors allowed participants to lift the object accurately (Ratio for first trial of EO = 1.07 ± 0.05).

332   Finally, participants were able to adapt their LPD on a trial to trial basis as indicated by the ratio values

333   for the second trials of all conditions (Pooled ratio = 1.12 ± 0.03). However, it is noteworthy that

334   participants overcompensated in the second trial after the weight change. This is especially visible in the

335   SO condition (Ratio 2nd trial SO = 1.21 ± 0.04). In addition, although participants made a predictive error

336   in the first trial after the weight change in the SOLO and SO condition, participants were already able to

337   skilfully lift the object in the second trial after the weight change as can be seen in the significant

338   differences between the first and second trials in the SOLO and SO condition *(all p-values < 0.001)*. This

339   improvement was absent for the EO condition revealing that participants were already able to lift the

340   object accurately in the first trial after the weight change (*p-value = 0.92)*.

341   Altogether, our results for the light-after-heavy weight changes support the findings of Reichelt

342   et al. that observation of erroneous lifts enables the observer to accurately scale fingertip forces

343   according to the actual object weight (Reichelt et al., 2013). In addition, our results for light-after-heavy

344   weight changes suggest that when individuals observe skilled lifts, they might be able to improve their

345   predictive force scaling although to a lesser extent than after observing erroneous lifts.

346   <u>Observers' lifting force parameters: heavy-after-light weight changes</u>

347   The right panel of Figure 4 shows the averaged force profiles of the first trial after the object weight

348   changed from light to heavy in a typical subject. When a subject scales his fingertip forces in anticipation

349   of a light object, less force than required (undershoot) will be applied to lift the heavy object adequately

350   (Johansson & Westling, 1988). Figure 4 reveals that the subject upscaled his force generation after

351   observing an erroneous or skilled lift compared to the SOLO condition. In the case of heavy-after-light

352   weight changes, force parameters with ratios smaller than 1 indicate underestimation. As expected,

353   these effects are the opposite for loading phase duration: a ratio value >1 indicates a slower increase in

354   force generation resulting in a longer loading phase duration.

355   ---------------------------

356   Figure 6

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358   *Load force rate.* Analysis of peak load force rate revealed that both main effects of LIFT NUMBER

359   $(F_{1, 12} = 25.68; p < 0.001)$ and CONDITION $(F_{1, 12} = 5.92; p < 0.01)$ as well as the CONDITION X LIFT NUMBER

360   interaction $(F_{2, 24} = 3.72; p = 0.04)$ were significant. Our findings are interpreted in light of the significant

361   interaction effect. As can be seen in Figure 6A, post-hoc analysis revealed that subjects scaled their load

362   forces significantly more accurately in the EO *(Ratio: 0.96 ± 0.05)* and SO conditions *(Ratio: 0.98 ± 0.04)*

363   in comparison with the SOLO condition *(Ratio: 0.82 ± 0.05)* *(p < 0.05)*. These results indicate that

364   observation of both erroneous and skilled lifts allowed participants to anticipatory scale their fingertip

365   forces. When comparing with the second trials after the heavy-after-light weight change, it is noticeable

366   that the first and second trials of the EO condition do not differ significantly *(p = 1)* indicating that

367   participants were already scaling their load forces accurately in the first trial after the weight change. In

368   contrast, in the SOLO and SO conditions, participants significantly upscaled their load forces in the

369   second trial after the weight change *(both p-values < 0.01)*. Importantly, the significant difference

370   between the first and second trials for the SO condition is likely caused by participants

371   overcompensating in the second trial as shown by larger values for this trial *(Ratio: 1.22 ± 0.06)*.

372   *Grip force rate*. A significant main effect of LIFT NUMBER $(F_{1, 12} = 16.65; p < 0.01)$ but not of

373   CONDITION $(F_{2, 24} = 1.86; p = 0.17)$ was found. In addition, the CONDITION X LIFT NUMBER interaction

374   was not significantly $(F_{2, 24} = 1.44; p = 0.25)$. Accordingly, these results indicate that performance

375   significantly improved after the weight change from the first to the second trial but no differences were

376   found between conditions (Fig. 6B).

377   *Loading phase duration*. The repeated-measures ANOVA revealed that both main effects and the

378   interaction effect were significant *(all F-values > 8.22, all p-values < 0.01)*. As shown in Figure 6C, the

379   loading phase duration in the first trial after the weight change was significantly shortened for both EO

380   and SO conditions (Ratio for EO = 1.24 ± 0.05; Ratio for SO = 1.30 ± 0.04) compared to the SOLO

381   condition (Ratio = 1.58 ± 0.08) *(both p-values < 0.001).* In addition, the type of action observation (EO vs.

382   SO) did not affect anticipatory force scaling in the first trial after the weight change (*p = 1.00)*. With

383   respect to the second trials after the weight change, it is noticeable that for each condition, participants

384   had a significantly shorter loading phase duration in the second trials after the weight change *(all p-*

385   *values < 0.05)* indicating that independently of condition, subjects underestimated object weight in the

386   first trial and subsequently improved in the second trial. Lastly, the post-hoc analysis failed to reveal any

387   significant differences between the second trials of the three conditions (*all p-values = 1.00)* indicating

388   that the object internal sensorimotor representation was accurately updated independently of

389   condition.

390   Altogether, our findings for heavy-after-light weight changes show that observation of skilled lifts

391   enabled participants to improve their predictive force scaling as well as the observation of erroneous

392   lifts.

393

Discussion

395   The present study investigated whether observation of skilled object lifting allows individuals to update

396   their internal sensorimotor representations, which in turn might translate into changes in anticipatory

397   motor control. Importantly, our results not only corroborate recent findings regarding observation of

398   lifting errors (e.g. Buckingham et al., 2014; Reichelt et al., 2013) but also revealed that observation of

399   skilled hand movements can drive predictive motor control, albeit to a smaller extent than observation

400   of explicit movement errors. For this reason, our results not only support the current consensus that

401   grasp observation allows for accurate weight judgement (e.g. Meulenbroek et al., 2007; Shim & Carlton,

402   1997) but also sheds new light on the role of more implicit, natural, movement cues in mediating motor

403   planning in an observer (Buckingham et al., 2014; Reichelt et al., 2013; Uçar & Wenderoth, 2012).

404   The first aim of our study was to replicate the results of Reichelt and colleagues. Using a dyadic

405   setting, consisting of a participant and an actor, these researchers revealed that observation of lifting

406   errors can be used to perceive object weight and subsequently allow participants to scale their fingertip

407   forces accurately when lifting the object themselves. When an object with unknown weight was

408   presented, the actor would make a typical lifting error (over- or underestimation of object weight) as he

409   did not have prior knowledge about the object weight (Reichelt et al., 2013). It is plausible that

410   participants deduced object weight based on the observed kinematics: Firstly, it has been well

411   established that over- and underestimation of object weight respectively shortens or elongates the

412   lifting phase when lifting an object (for example see: Gordon et al., 1991; R S Johansson & Westling,

413   1988). Secondly, Hamilton and colleagues demonstrated that individuals will estimate an object to be

414   light when they observe a short lifting phase and, conversely, will estimate an object to be heavy when

415   observing a longer lifting phase (Hamilton et al., 2007). Our results are consistent with the findings of

416   Reichelt and colleagues: Participants in the current study were capable to predictively scale their

417   fingertip forces with significantly improved accuracy after observing lifting errors indicating a change in

418   object weight. It is noteworthy that in the current study a relatively large overestimation of object

419   weight remained present in the observer after observing the actor lifting the light object erroneously

420   whereas this effect was completely eradicated in the study of Reichelt et al. (Reichelt et al., 2013). This

421   discrepancy might be due to the different movement parameters investigated: While we used force

422   parameters (peak grip and load force rates), Reichelt and colleagues used lifting height as indicator of

423   predictive control. Since peak force rates occur before the time to reach lifting height, it is plausible that

424   subjects can use feedback mechanisms to update their lifting height, but not earlier force parameters,

425   which would therefore be not fully tuned to the current object weight.

426   The second aim of our study was to test whether observation of skilled lifts mediates predictive

427   motor control as equally as observation of movement errors. With respect to both weight changes, it is

428   interesting to note that predictive scaling of the load force and loading phase after observing skilled

429   lifting significantly improved compared to the SOLO condition but was not as efficient as the observation

430   of lift errors, in particular for light object lifts. This indicates that observation of skilled movement

431   performance can also convey critical information about object weight but to a smaller extent than error

432   observation. It is noteworthy that our results about skilled grasp observation are in contrast with the

433   study of Buckingham et al. Indeed, their study revealed that error, but not skilled lift observation,

434   significantly reduced the learning that is required to grasp a novel, surprisingly light object (Buckingham

435   et al., 2014). Importantly, there are two major considerations to take into account while comparing the

436   results of the Buckingham study and ours. Firstly, while we used two differently weighted object with

437   identical appearance, Buckingham and colleagues used two objects that were identical in weight but

438   different in size (i.e. 'Size-Weight Illusion'). It is likely that this size difference caused a strong initial bias

439   regarding weight expectations towards the objects (for example see: Gordon et al., 1991; Peters, Ma, &

440   Shams, 2016). Secondly, in the Buckingham study, participants were not familiarized with the objects

441   prior to observing object lifting videos. This lack of familiarization and the presence of a size-weight

442   illusion might cause a different action observation strategy for extracting information from skilled or

443   erroneous lifting: When lifting skilfully, the kinematics of the lifting phase tend to have a similar duration

444   regardless of object weight (Gordon et al., 1991). According to this, it is likely that participants presumed

445   that weight and size were congruent when observing skilled object lifting, therefore leading them to

446   focus mostly on the size cue. In contrast, the observation of lifting errors reveals an incongruence

447   between size and expected weight which likely led participants to not only focus on size but also on the

448   movement kinematics. In our study, participants could only rely on the observed movement kinematics

449   to assess object weight as we excluded other visuals cues indicating object weight. Interestingly,

450   participants could estimate object weight during both the observation of skilled and erroneous lifting.

451   For observation of errors, it is likely that participants perceived object weight by focusing on the lifting

452   phase duration and grasp duration (hand-object contact without movement) (Hamilton et al., 2007;

453   Roland S. Johansson & Flanagan, 2009). Having experienced these typical lifting errors in the SOLO

454   condition, participants were likely to interpret the lifting errors made by the actor and adjust their

455   internal sensorimotor representation accordingly. In contrast, when observing skilled lifting, the

456   kinematic profiles of a heavy or light lift are more similar compared with lifting errors on the same

457   objects. It is therefore possible that participants developed an observational strategy emphasising on

458   other parameters to differentiate between weights such as the hand contraction state (Alaerts, Senot, et

459   al., 2010; Uçar & Wenderoth, 2012), the reaching phase (Ansuini, Cavallo, Bertone, & Becchio, 2014) or

460   the intention of the actor (Cavallo, Koul, Ansuini, Capozzi, & Becchio, 2016; Wasmuth & Lima, 2016).

461   The neural substrate responsible for the sensorimotor mapping of observed actions into one's

462   own motor repertoire is likely to be supported by the 'mirror neuron system', located in a subset of

463   sensorimotor brain areas (Giacomo Rizzolatti & Craighero, 2004). Mirror neurons were found to

464   discharge both when a monkey performs a goal-directed hand action and when observing another

465   individual performing the same action (Buccino, Binkofski, & Riggio, 2004; di Pellegrino, Fadiga, Fogassi,

466   Gallese, & Rizzolatti, 1992; G Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; Umiltà et al., 2001). More

467   importantly, it has recently been demonstrated that the action observation-induced increase of

468   excitability in the primary motor cortex, so called 'motor resonance', reflects specific parameters during

469   grasp observation such as the hand contraction state (Alaerts, Swinnen, & Wenderoth, 2010) or

470   observed movement kinematics, indicating object weight (Alaerts, Swinnen, et al., 2010; Senot et al.,

471   2011), object shape (Buckingham et al., 2014) and even the intentions of the observed actor (Wasmuth

472   & Lima, 2016). In the current study, participants were not able to perceive object weight via intrinsic

473   object properties. For this reason, it is plausible that participants had access to information about object

474   weight by mapping onto their own motor repertoire observed visuomotor cues such as object kinematics

475   and hand contraction states.

476   In conclusion, participants in the present study were familiarized to two different object weights

477   and generated a sensorimotor repertoire for skilled lifting (by applying accurate forces following

478   consecutive lifts of a same object) and for lifting errors (by over- or underestimating forces after a weight

479   change). After this initial process, participants lifted objects in turns with an actor. In this dyadic setting,

480   the only way individuals could extract information about weight, and in turn plan their subsequent

481   motor command, was by embodying the observed visuomotor cues into their own sensorimotor

482   repertoire. Our results not only support recent findings regarding the effect of observation of explicit

483   movement errors on mediating predictive motor control but also highlight that the observation of skilled

484   movements, carrying more implicit visuomotor cues, can also drive motor planning. Interestingly,

485   anticipatory force scaling in the first trial following skilled lift observation was not as accurate as

486   following error observation, and still improved in the second trial. This highlights that different action

487   observation mechanisms could contribute to mediating anticipatory motor control in an observer when

488   surprising or erroneous movements are performed (Cretu, Ruddy, Germann, & Wenderoth, 2019).

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563

564 **Table caption**

565 *Table 1.* The actor's lifting performance, pooled across participants, is presented as mean ± SEM. Values
566 represent the peak load force rate (pLFr; N/s²), peak grip force rate (pGFr; in N/s²) and loading phase
567 duration (LPD; in ms) for the first, second and last trials of the weight sequence blocks of both dyadic
568 conditions (SO: skilled lift observation, EO: erroneous lift observation). As the actor only made lifting
569 errors during the first trial of the EO condition, this trial should significantly differ from the parameters of
570 all other trials of both the SO and EO condition. *indicates whether the first trial of the EO condition
571 differs significantly from the same parameters of all other trials.

572 **Figure captions**

573 *Figure 1.* **A.** Experimental set-up: The participant and actor are seated opposite each other at a table on
574 which the manipulandum was positioned and a screen was placed in front of the participant's face. **B.**
575 Photo of the grip-lift manipulandum used in the experiment. Load force (LF: blue) and grip force (GF: red)
576 vectors are indicated. **C.** GF and LF typical traces (upper) and their derivatives (lower) for a skilled lift.
577 Circles denote first peak values used as parameters. Loading phase duration (LPD) is indicated on the
578 upper panel.

579 *Figure 2.* Averaged lift performance for the actor pooled across all participants for light object lifts either
580 after a heavy lift (left bars) or a light one (right bars). A, B and C show averaged data for peak LF rate
581 (LFr), peak GF rate (GFr) and LPD, respectively. Green bars represent lifts performed by the actor in the
582 skilled condition and red bars represent the error condition. All data is presented as the pooled mean ±
583 SEM. ***$p<0.001$, **$p<0.01$, *$p<0.05$. When the asterisk is placed above one bar only, this indicates that
584 this condition significantly differed from all others.

585 *Figure 3.* Averaged lift performance for the actor pooled across all participants for heavy object lifts
586 either after a light lift (left bars) or a heavy one (right bars). A, B and C show averaged data for peak LF
587 rate (LFr), peak GF rate (GFr) and LPD, respectively. Green bars represent lifts performed by the actor in
588 the skilled condition and red bars represent the error condition. All data is presented as the pooled mean
589 ± SEM. ***$p<0.001$, **$p<0.01$, *$p<0.05$. When the asterisk is placed above one bar only, this indicates
590 that this condition significantly differed from all others.

591 *Figure 4.* Typical traces showing the evolution of the different force profiles over time for one subject for
592 the three conditions: grasping with incorrect weight expectations (SOLO), grasping after observing a
593 skilled lift (SO) and grasping after observing a lifting error (EO). From top to bottom: Grip force (GF), load
594 force (LF), grip force rate (GFr) and load force rate (LFr) for light-after-heavy (left panel) and heavy-after-
595 light (right panel).

596 *Figure 5.* **Light-after-Heavy weight changes:** Subject group averages for the first and second trials after
597 the weight changed from heavy-to-light for the three conditions [grasping with incorrect weight
598 expectations (SOLO), grasping after observing a skilled lift (SO) and grasping after observing a lifting error
599 (EO)]. **A.** Peak load force rates, **B.** Peak grip force rates and **C.** Loading phase durations. All data is
600 represented as a ratio (normalized to skilled lifting, light-after-heavy and light-after-light divided by the
601 last light-after-light lift of the same weight sequence block). A ratio > 1 for peak grip force rates and peak
602 load force rates (and a ratio < 1 for loading phase durations) indicates that subjects overestimated object
603 weight. All data is presented as the pooled mean ± SEM. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

604   *Figure 6.* **Heavy-after-Light weight changes:** Subject group averages for the first and second trials after
605   the weight changed from light-to-heavy for the three conditions [grasping with incorrect weight
606   expectations (SOLO), grasping after observing a skilled lift (SO) and grasping after observing a lifting error
607   (EO)]. **A.** Peak load force rates, **B.** Peak grip force rates and **C.** Loading phase durations. All data is
608   represented as a ratio (normalized to skilled lifting, i.e. heavy-after-light and aeavy-after-heavy divided
609   by the last heavy-after-heavy lift of the same weight sequence block). A ratio < 1 for peak grip force rates
610   and peak load force rates (and a ratio > 1 for loading phase durations) indicates that subjects
611   underestimated object weight. All data is presented as the pooled mean ± SEM. *** p < 0.001, ** p <
612   0.01, * p < 0.05.

Table 1. Mean peak force rates and loading phase duration for the lifting movements performed by the actor.

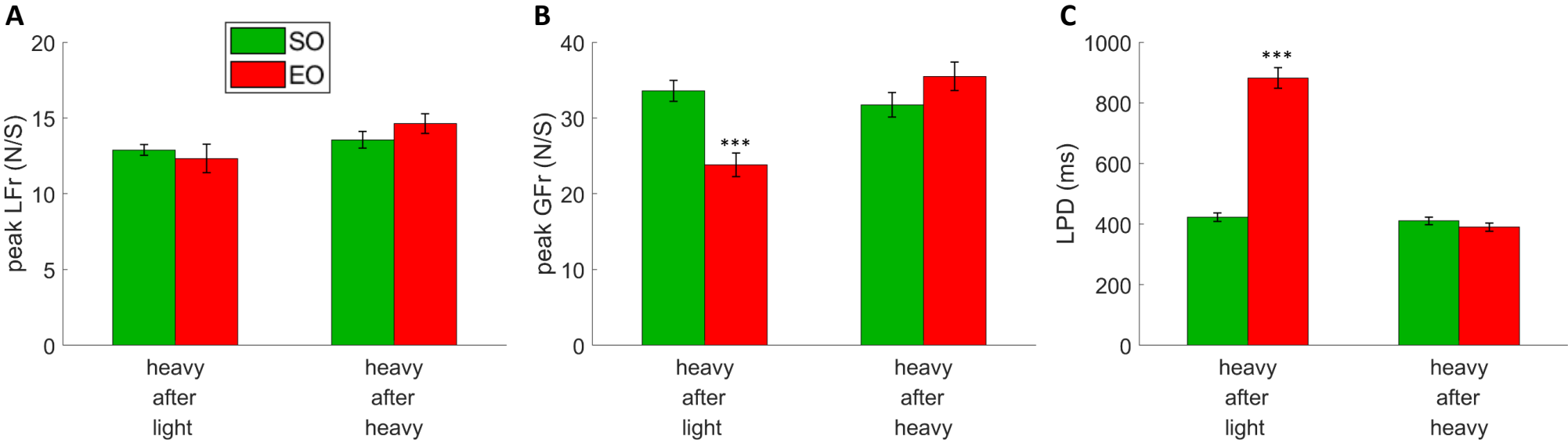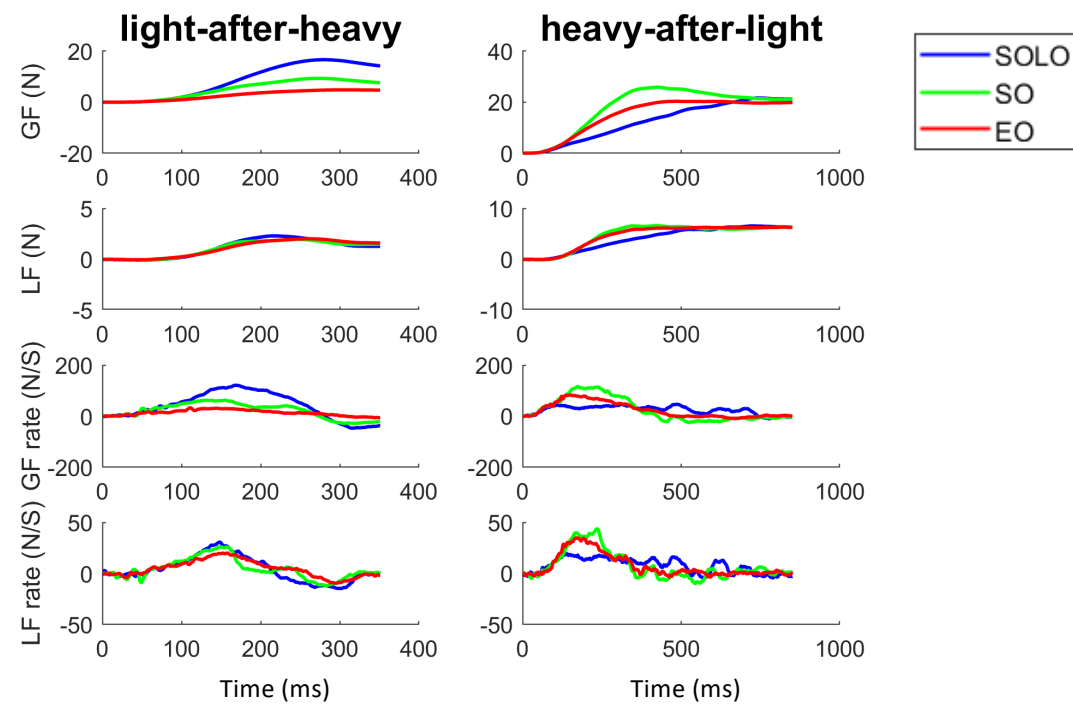|		Skilled lift observation			Erroneous lift observation		
		Trial 1	Trial 2	Last trial	Trial 1	Trial 2	Last trial
Light	pLFr	4.70 ± 0.26	5.27 ± 0.33	5.03 ± 0.29	59.38 ± 4.48*	5.22 ± 0.25	5.19 ± 0.31
after	pGFr	9.30 ± 1.19	9.52 ± 0.74	8.59 ± 0.52	50.50 ± 3.97*	11.01 ± 0.58	11.53 ± 1.36
heavy	LPD	356.63 ± 19.78	316.65 ± 15.75	315.10 ± 16.44	65.46 ± 10.05*	284.4 ± 18.5	306.16 ± 15.38
Heavy	pLFr	12.89 ± 0.38	13.56 ± 0.58	12.30 ± 0.46	12.32 ± 0.98	14.63 ± 0.67	12.03 ± 0.5
after	pGFr	33.59 ± 1.43	31.75 ± 1.69	30.90 ± 2.22	23.82 ± 1.61*	35.50 ± 1.97	31.20 ± 2.56
light	LPD	422.83 ± 14.57	410.39 ± 13.00	453.37 ± 15.45	881.8 ± 35.34*	389.95 ± 14.2	474.45 ± 16.08

Figure 1
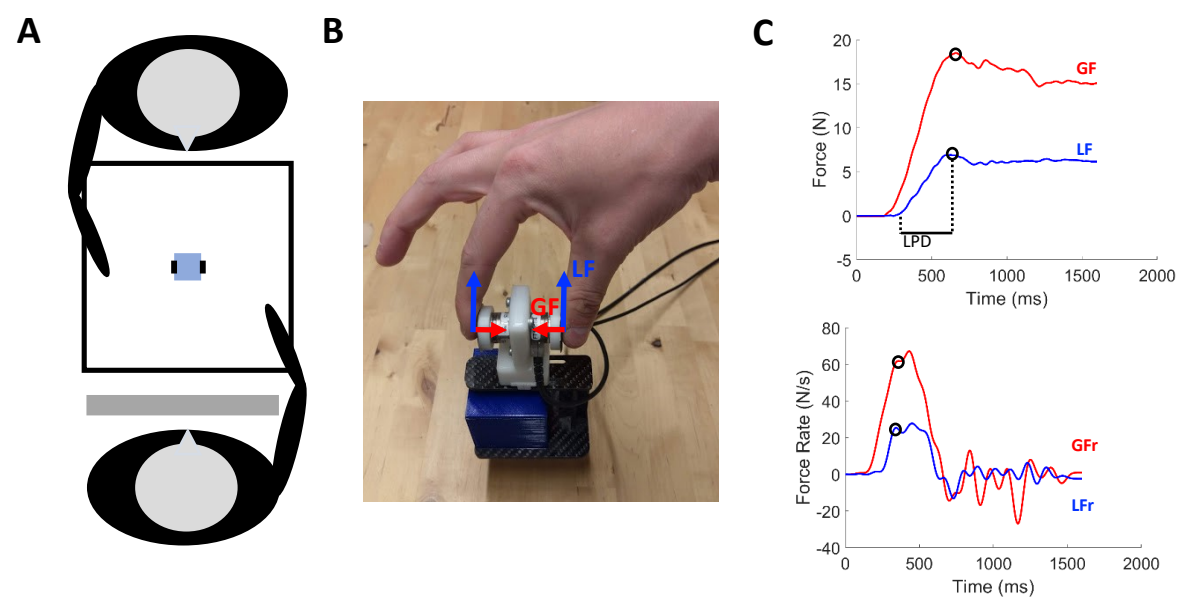
Figure 2
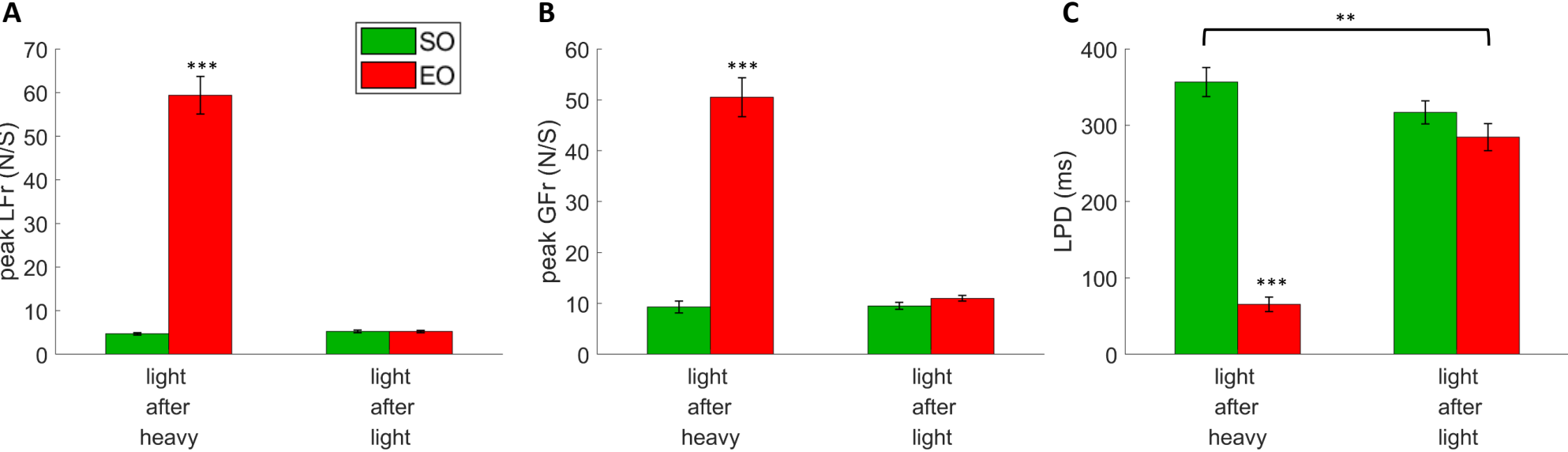
Figure 3

Figure 4

Figure 5

Figure 6