

Glenohumeral joint and muscles functions during a lifting task

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ABSTRACT

The mobility of the healthy shoulder depends on complex interactions between the muscles spanning its glenohumeral joint. These interactions ensure the stability of this joint. While previous studies emphasized the complexity of the glenohumeral stability, it is still not clear how the kinematics and muscles interact and adapt to ensure a healthy function of the glenohumeral joint. To understand the function of each muscle and degree of freedom of the glenohumeral joint in executing an above-the shoulder box handling task while ensuring stability, we adapted an index-based approach previously used to characterize the functions of the lower limb joints and muscles during locomotion. Forty participants lifted two loads (6 Vs. 12 kg) from hip to eye level. We computed the mechanical powers of the glenohumeral joint and its spanning muscles. We characterized the function of muscles and degrees of freedom using function indices. The function of the glenohumeral joint underlined its compliancy and design for a large range of motion, while the rotator cuff indices emphasized their stabilizing function. The overall muscle functions underlined the complexity of the glenohumeral stability that goes beyond the rotator cuff. Additionally, the load increase was compensated with changes in the functions that seem to favor joint stability. The implemented approach represents a synthesized tool that could quantify the glenohumeral joint and muscles behavior during tridimensional upper limb tasks, which might offer additional insight into motor control strategies and functional alterations related to pathologies or external parameters (e.g., load).

1 INTRODUCTION

2 The upper limb is regularly recruited in daily activities. However, due to its neuro-
3 musculoskeletal complexity, the understanding of its functional anatomy is still limited. With
4 the evolution of the erect posture in humans, the upper limb evolved to ensure dexterous
5 manipulation over a wide range of motion. Nevertheless, the upper limb is often recruited for
6 load bearing activities, particularly during occupational handling tasks. The shoulder healthy
7 function, particularly that of its glenohumeral joint depends on intricate interactions between
8 its various muscles (Inman et al., 1996). In order, for shoulder muscles, to actuate and actively
9 stabilize the glenohumeral joint throughout its large range of motion, they have long fascicle
10 lengths, such that their working range remains within the force-length curve middle section
11 (Veeger and van der Helm, 2007). While classical biomechanical approaches predict
12 coordinates and moments of each joint degrees of freedom (DOF), as well as muscle
13 activations and lengths, it is difficult to use their results to draw conclusions on the upper limb
14 joint DOF and muscle behaviors during a handling task. Indeed, the variation of muscle force
15 directions and moment arms during three-dimensional tasks hinders the identification of a
16 sole muscle function. Additionally, while muscle behavior is strongly dependent on the force-
17 length and force-velocity curves (Lappin et al., 2006; Richardson et al., 2005), using these
18 curves to infer muscle functions during a dynamic task remains difficult due to their complex
19 interactions. As muscle architectural features have an impact on its behavior, and thus on the
20 joint function (Biewener, 2016), an approach that synthesizes muscle forces and length
21 change is expected to shed a light on the upper limb function. According to
22 Dickinson et al. (2000), muscle function can be split into four categories: strut, spring, motor
23 and damper. A strut function expresses the capacity to generate large muscle forces (or joint
24 moments) with little change in muscle length (or joint angle). Such behavior would be
25 beneficial for rotator cuff muscles, particularly for their stabilizing action but not for joints

26 with large range of motion. A spring-like behavior expresses the capacity of a structure to
27 store and release elastic energy; a motor-like behavior characterizes a structure that generates
28 positive energy; while a damper-like behavior characterizes a structure that relies on muscle
29 contraction to absorb energy. These four behaviors have been quantified through indices
30 calculated using mechanical energy. While initially introduced for muscles, these categories
31 have also been extrapolated to describe joint behavior. Indeed, this approach successfully
32 identified lower limb joints and muscles functions during walking and running (Lai et al.,
33 2019; Qiao and Jindrich, 2016). Implementing such approach to study the glenohumeral joint
34 would shed a light on the upper limb motor strategies. However, as the healthy function of
35 this joint relies on muscle co-contraction, predicting muscle forces that express the
36 coactivation of muscles is critical to predict their function.

37 Our previous work on the effect of sex and load on the biomechanics of a lifting task
38 presented the complexity of the upper limb biomechanics, as well as the interactions of the
39 various biomechanical variables for a relatively straightforward lifting task (Bouffard et al.,
40 2019; Martinez et al., 2020, 2019). While sex-load interactions were found for joint
41 kinematics (differences linked to the load lifted by women), no sex-load interactions were
42 observed for muscles' activations estimated using musculoskeletal models, nor for their
43 electromyographic signals (EMG). Additionally, no load effect was observed for the relative
44 time spent beyond a critical shear-compression dislocation ratio for the glenohumeral joint
45 reaction force of all participants, despite the increased muscle activation. Local adaptations
46 within the glenohumeral joint could explain the disparity of these results. Indeed, for pointing
47 tasks, shoulder fatigue was reported to induce differences in the shoulder kinematics and in
48 those of the trunk and elbow (Yang et al., 2019). Accordingly, an analysis of the adaptations
49 within the glenohumeral DOF and muscle functions could explain why no changes are

50 observed for muscle activations and why seemingly the load does not impact the
51 glenohumeral risk of dislocation.

52 The objective of this study is to further understand the glenohumeral joint and its muscles
53 functions using an energy index-based approach during a lifting task. It was hypothesized
54 from observation of the shoulder structure and function (multiple joints with scapulohumeral
55 rhythm, large mobility range and muscles with long fascicles) that this approach should yield
56 a minimal strut behavior for the glenohumeral joint DOFs irrespective of sex and load. On the
57 other hand, scapulohumeral muscles, particularly the rotator cuff muscles that act as
58 stabilizers, should mainly have a strut behavior. A secondary objective of this study is to
59 analyze the effect of sex and load on the mechanical power and the predicted behaviors in
60 light of our previous results regarding biomechanical parameters during a lifting task
61 (Bouffard et al., 2019; Martinez et al., 2020, 2019). It is hypothesized that functional
62 adaptations to load within the glenohumeral joint and musculature would occur. Particularly,
63 an increase in the damper-like behavior of the joint DOFs and muscles is expected to counter
64 the increased risk of injury associated with the increased load, pointing out complex
65 adaptation strategies of the upper limb.

66 **METHODS**

67 *Data collection*

68 The raw data previously used by Martinez et al. (2020) was used. Forty participants who had
69 no history of upper limb diseases performed a box handling task. The research protocol was
70 approved by the University of Montréal ethics committee (n° 15-016-CERES-P). All
71 participants provided their informed consent prior to the experimentation. A brief presentation
72 of the experimental setup is described hereafter, see supplementary material for a detailed
73 description.

74 The kinematics of the participants' trunk and right upper limb, and that of the box were
75 tracked using 42 reflective markers. Bipolar surface EMG electrodes were used to measure
76 the activation of 10 muscles: anterior, median and posterior deltoids, biceps, triceps,
77 pectoralis major, latissimus dorsi, upper and lower trapezius and serratus anterior.
78 Infraspinatus, supraspinatus and subscapularis activations were recorded using indwelling
79 electrodes. The linear envelopes of the EMG signals were normalized to the maximal
80 voluntary contraction (Dal Maso et al., 2016). The participants moved a box (6 or 12 kg)
81 between two shelves from hip to eye level. Forces and moments between the right hand and
82 the box were measured using a six-dimensional force sensor.

83 *Neuro-musculoskeletal model*

84 A musculoskeletal model was developed in Opensim (Delp et al., 2007) from the shoulder
85 model of Wu (2016). The acromioclavicular and glenohumeral joints were both modelled as
86 3-DOF joints, while the sternoclavicular joint, the elbow and wrist were each modelled as 2-
87 DOF joint. The glenohumeral joint DOFs sequence was plane of elevation, elevation and axial
88 rotation (Wu et al., 2005). The generic model was first anthropometrically scaled to match the
89 markers positions during a static trial in the anatomical position. The joint angles and
90 moments were predicted using Opensim's inverse kinematics (a global optimization scheme
91 with higher weights for markers that are reported to have a minimal soft tissue artefact) and
92 inverse dynamics, respectively (Delp et al., 2007). Our study was focused on the
93 glenohumeral joint DOFs and the muscles acting on it. Out of the 17 musculotendon units
94 actuating the glenohumeral joint, three (teres major, teres minor and coracobrachialis) had no
95 experimental EMG. The scaled models were further personalized by calibrating their
96 neuromuscular parameters (e.g. optimal fiber length) using the CEINMS toolbox (Pizzolato et
97 al., 2015). The personalized models were then used to predict muscle forces and fiber
98 contraction velocities in CEINMS using an EMG-assisted scheme, while implementing a

99 fiber-tendon equilibrium constraint. The calibration and muscle force prediction processes are
100 described in supplementary material.

101 *Analysis*

102 We calculated the glenohumeral joint 3-DOF powers as the product of their respective
103 generalized moments and angular velocities. The muscle fiber power was calculated as the
104 product of the fiber's tension and its contractile velocity. DOF and fiber powers were reported
105 for men and women with both loads. To evaluate the function of each DOF and each fiber
106 during the box-handling tasks, we calculated four indices that describe the mechanical
107 behavior of an entity as a strut, a spring, a motor and a damper (i.e., function indices). The
108 indices were defined to have a cumulative sum of 100% and are fully described in Lai (2019)
109 and Qiao and Jindrich (2016). Further details about these indices can be found in
110 supplementary material. Briefly, an entity that has a dominant strut behavior would generate
111 large forces with little fluctuation in its length or angle. A spring-like behavior manifests itself
112 with energy storage or release often synchronized with the compression and extension phases
113 of the movement. Since the task of interest involved mainly a thoraco-humeral elevation, we
114 defined the compression phase as the phase beginning with the lifting of the box from the
115 shelf to the moment when the box is the closest to the participant, while the rest of the trial is
116 the extension phase. An entity, acting like a motor, would generate mainly positive work
117 throughout the task. Finally, a damper-like behavior would stand for a dominant negative
118 work generation. To obtain dimensionless indices for muscle fibers, the strut index was
119 normalized with respect to the fiber's optimal length obtained with the model calibration.

120 The effects of sex and load on the glenohumeral DOF and muscle fibers powers, as well as
121 their function indices were evaluated using a two-way nonparametric ANOVA with repeated
122 measures on the load (Pataky et al., 2015). Statistical significance was fixed at 0.05. For the
123 1D analysis, the family-wise error for all clusters was respected using a Bonferroni correction

124 to account for the number of DOFs and muscle. On the other hand, the p-values reported for
125 the function indices (OD analysis) are the ones obtained from a Holm-Bonferroni correction,
126 to maintain the power of the analysis, despite running the tests for four indices.

127 **RESULTS**

128 The sex had no significant effect on the joint power, while the load had a significant effect on
129 the power of the glenohumeral elevation ($p < 0.05$; Fig. 1). The glenohumeral plane of
130 elevation and axial rotation had power peaks higher than those calculated for the elevation.
131 These peaks occurred close to the transition from the compression to the extension phase (Fig.
132 1). The net joint power was mainly the result of the anterior deltoid, biceps and latissimus
133 dorsi fiber powers, followed by the infraspinatus and supraspinatus, two rotator cuff muscles
134 (Fig. 2). No major effects of sex, load, nor their interaction were observed on the fibers
135 power.

136 All glenohumeral DOF had a minimal strut-like behavior with no significant effect of sex or
137 load ($p > 0.05$; Fig. 3). The spring-like behavior was not a main function for any of the DOF;
138 however, it was usually more present in the glenohumeral axial rotation, irrespective of the
139 load or sex ($p > 0.05$). The load affected the elevation damper ($p = 0.012$) and motor ($p = 0.035$)
140 behaviors. Both men and women relied on their glenohumeral plane of elevation and
141 elevation as prime motors. For the 6 kg lifting task, women relied more on their plane of
142 elevation to drive the motion with a motor index of $66 \pm 15\%$, whereas men preferred their
143 glenohumeral elevation ($68 \pm 23\%$). For the 12 kg task, women did not change their power
144 strategy (glenohumeral plane motor index: $60 \pm 16\%$), while men moved the box by using
145 both their plane of elevation ($48 \pm 20\%$) and elevation ($46 \pm 28\%$) as motors. The damping
146 action was ensured by the glenohumeral axial rotation for women and men during the 6 kg
147 trial. However, as the load increased, so did the damping action of the two other DOFs.

148 Most muscles had a mainly strut-like behavior, with rotator cuff muscles showcasing the
149 highest values (on average 90%). The biceps had, almost, no strut-like but a spring-like
150 behavior irrespective of the trial, followed by the posterior deltoid (Fig. 4). Following the
151 strut-like behavior, the muscles had either a damper or a motor-like tendencies, except for the
152 bicep's fibers. The clavicular head of the pectoralis major had a motor-like behavior for all
153 trials. The load also had an effect on the damping behavior of the latissimus dorsi and
154 subscapularis ($p < 0.015$), on the spring behavior of the posterior deltoid and the infraspinatus
155 ($p < 0.015$) and the strut behavior of the posterior deltoid, subscapularis and biceps ($p < 0.015$).
156 An effect of the interaction sex-load was only observed on the biceps strut behavior
157 ($p < 0.015$).

158 **DISCUSSION**

159 We implemented an analysis of the glenohumeral joint DOF and its muscle fibers based on
160 their mechanical energy to improve our understanding of the glenohumeral joint functions
161 during a lifting task. The predicted behavioral indices provided evidence supporting our
162 hypotheses regarding glenohumeral DOF and muscle functions. The limited strut indices of
163 the glenohumeral joint highlighted its large range of motion, whereas the large strut behavior
164 of muscle fibers, particularly the rotator cuff, emphasized their stabilizing function. Finally,
165 the predicted indices highlighted the sensitivity of kinematic and activation strategies to load
166 and sex.

167 *Glenohumeral joint: a design for a wide range of motion*

168 The complexity of the glenohumeral joint morphology has evolved to ensure a large range of
169 motion (Larson, 2009). With thoracohumeral elevation, the scapula is reoriented to maintain
170 congruency with the humeral head, and the humerus is externally rotated to avoid
171 impingement (Ludewig et al., 2009; Stokdijk et al., 2003). The effect of the scapula

172 orientation can be observed in the power evolution of the glenohumeral DOFs. While the task
173 involved mainly a change in potential energy of the box (thoracohumeral elevation)
174 (supplementary data, Fig. S3), the power of the glenohumeral elevation was smaller than the
175 other DOFs. Additionally, the occurrence of power peaks close to the transition between
176 pulling and pushing the box pointed out a strategy where participants relied on a sudden
177 increase in the box momentum to drive its elevation, confirmed by the change in box vertical
178 velocity. Women, who exhibit less upper body strength than men (Janssen et al., 2000), had a
179 steeper increase of the box vertical velocity at this transition (supplementary data, Fig. S4).
180 This could potentially explain the increased risk of injury for women, as the upper-arm
181 velocity was correlated with shoulder complaints (Balogh et al., 2019).

182 The design of the glenohumeral joint to cater to both mobility and stability can be observed in
183 its DOF strut coefficients. The box handling task did not reach extreme upper limb positions
184 yet was highly demanding of the shoulder. However, the strut index remained relatively low,
185 suggesting that the glenohumeral joint has a high compliancy, which would facilitate the
186 upper limb motor control and movement regulation. This is coherent with the glenohumeral
187 joint architecture that is optimal for large and precise displacements (Arias-Martorell, 2019).
188 This optimization impacted strongly the orientation of the scapula, which has been linked to
189 the throwing function of the upper limb, and enabled the use of elastic energy stored during
190 external rotation to increase the power generated for high-speed throwing (Roach et al.,
191 2013). This could possibly explain the high spring index observed for the humeral axial
192 rotation. Besides its spring function, the axial rotation behaved mainly as a damper, which
193 could point out functions of the passive structures (shoulder capsule and ligaments) that
194 would behave mostly as elastic components, stiffening with the glenohumeral axial rotation
195 (Burkart and Debski, 2002; Wilk et al., 1997). As the load increased, this passive damping
196 was probably no longer enough, thus the increase in the other DOFs input to the damping, and

197 possibly glenohumeral stability, at the expense of the elevation's motor behavior, and the box
198 vertical velocity.

199 *Adaptations to load within the joint*

200 The main motor behavior was ensured by the glenohumeral elevation and plane of elevation.
201 Women opted to use their glenohumeral plane of elevation to drive the movement. While their
202 strategy did not change between loads, men adapted theirs as the load increased, distributing
203 the motor load more equally between the actuators of the glenohumeral elevation and plane of
204 elevation. Participants have been reported to increase the use of their lower limbs with load
205 increase, with men relying on their hip vertical displacement more than women (Martinez et
206 al., 2020). The 12 kg task might have been taxing for both men and women's glenohumeral
207 joint. For men, however, relying on their lower limb, they decreased the motor demand on the
208 glenohumeral elevation, favoring stability. Women, on the other hand, might have already
209 strained their shoulder for the 6 kg task, which led them to seek assistance from their elbow
210 for the 12 kg one (Martinez et al., 2019). This observed adaptation could possibly shed a light
211 on neural control schemes that could start within the same structure (glenohumeral), before
212 seeking neighboring ones (distal joints). This points out the importance of the coupling of a
213 local and global kinematic analysis to gain a deeper understanding of the human motion.

214 *Fiber power adaptation to load*

215 Unlike joint power, the fiber powers did not have any significant increase with the load,
216 despite the significant muscle activation increase shown in Bouffard et al. (2019). This power
217 invariance pointed out a possible decrease in the fiber contraction velocity as the load
218 increased. This could be a direct effect of the decrease of the glenohumeral range of motion
219 with the load (Martinez et al., 2019). This decrease could also be linked to the change in
220 compliance of the muscle-tendon unit. As the load increased from 6 to 12 kg, the stiffness of
221 the tendon might have increased (Raiteri et al., 2018), impacting the fiber compliance, which

222 is reported to affect its power generation and efficiency (Fenwick et al., 2017). This potential
223 adaptation strategy would decrease injury risk at higher loads. As women have more
224 compliant tendons compared to men (Kubo et al., 2003), this could account in part for
225 women's higher injury rate, particularly as they rely more on speed to drive the box.

226 *Fiber function between actuation and stability*

227 The highest strut like behavior in muscles was showcased by the infraspinatus and
228 subscapularis. This was consistent with their architecture, having relatively short fibers and
229 large physiological cross-sectional areas, which enables them to generate large forces over a
230 short range of deformation (Gobbi, 2017). Overall, most of the muscles displayed a strut-like
231 behavior for the studied task, which implies a high fiber force with a minimal length change,
232 which supports our initial hypothesis. Unlike most upper limb muscles, the biceps had a main
233 spring-like behavior, storing and releasing energy. This behavior is consistent with its
234 architecture, as slender muscles with long tendons are reported to be favorably designed for
235 energy saving (Biewener, 2009). However, mechanical energy storage remains costly from a
236 chemical energy perspective.

237 The muscle ability to quickly actuate a joint depends on the speed and the type of contraction.
238 As reported by Tillin et al. (2018) and Aagard et al. (2018), the change in fiber velocity per
239 degree of joint rotation is different depending on the type of contraction. They showed that
240 muscles would more efficiently generate a higher torque during concentric activations at
241 higher speeds (Tillin et al., 2018). This might explain the significant decrease in the motor
242 function of the clavicular head of the pectoralis major as the load increased, since the
243 contraction velocity decreased, limiting the fiber force potential. This could also explain why
244 women chose to approach the box to their trunk, as it gave them higher potential for a
245 concentric explosive contraction. However, an explosive contraction without sufficient
246 muscle strength and control, particularly for higher loads, might increase injury risk (Davies

247 and Matheson, 2001). This might explain why the damper behavior of some muscles
248 increased with the load, as this function should help in the stabilization of the humeral head.
249 The effect of the load on the strut, spring and damper behavior further points to the
250 complexity of the glenohumeral joint stabilization, as it involves more than just the rotator
251 cuff muscles (Lee and An, 2002; Yanagawa et al., 2008).

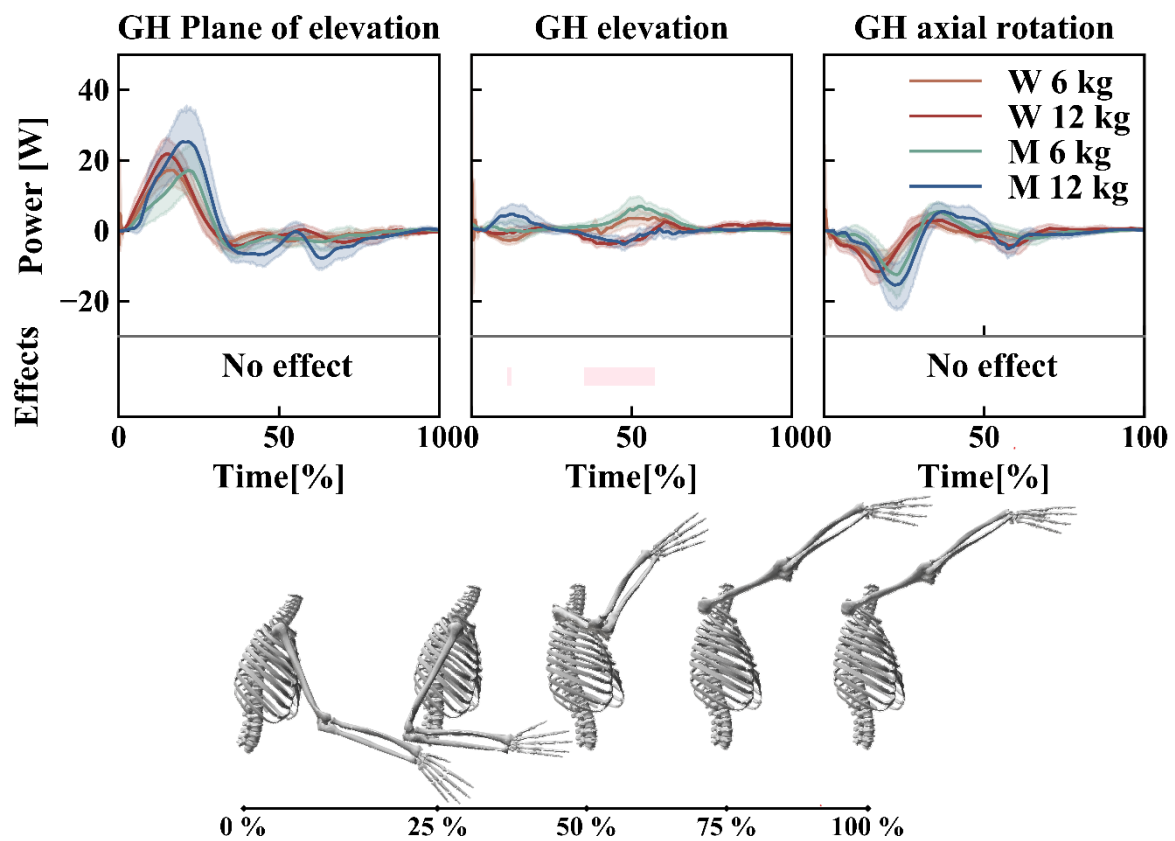
252 *Energetic approaches to complement the upper limb understanding*

253 The musculoskeletal structure is a transducer that converts chemical energy into mechanical
254 work (Wilkie, 1975). Accordingly, energetic approaches could potentially offer a
255 complementary and insightful understanding to the classical biomechanical analysis of forces
256 and kinematics (Guo et al., 2003; Siegel et al., 2004). Similarly, within our study, we could
257 gain insight into the intricate functions of the different glenohumeral joint DOF, without the
258 need to analyze unidirectional movements (Hawkes et al., 2019). The use of the four function
259 indices enabled a fair analysis of the different muscles within their physiological abilities.
260 Indeed, while the infraspinatus and subscapularis had low power magnitude, their role in
261 glenohumeral stability was emphasized by their strut index. This reinforces our understanding
262 of the stabilizing potential of the rotator cuff muscles, particularly as their characteristics are
263 still not well understood (Sangwan et al., 2015). These indices could also be used in the
264 development of ergonomic work strategies that go beyond the joint repartition (Martinez et
265 al., 2020) of the task.

266 Our study had some limitations. We chose to normalize the shelves height to the participants
267 to reduce bias against women. For an energetic approach, this led to differences in the
268 potential energy of the box. However, it was expected that the gender-related differences
269 would only be exacerbated in a working environment. The use of an energetic approach is
270 also limited by the power magnitude sensitivity to the scapula kinematic errors, particularly
271 those related to the soft tissue artefact (Blache et al., 2016). As for the indices' definition, the

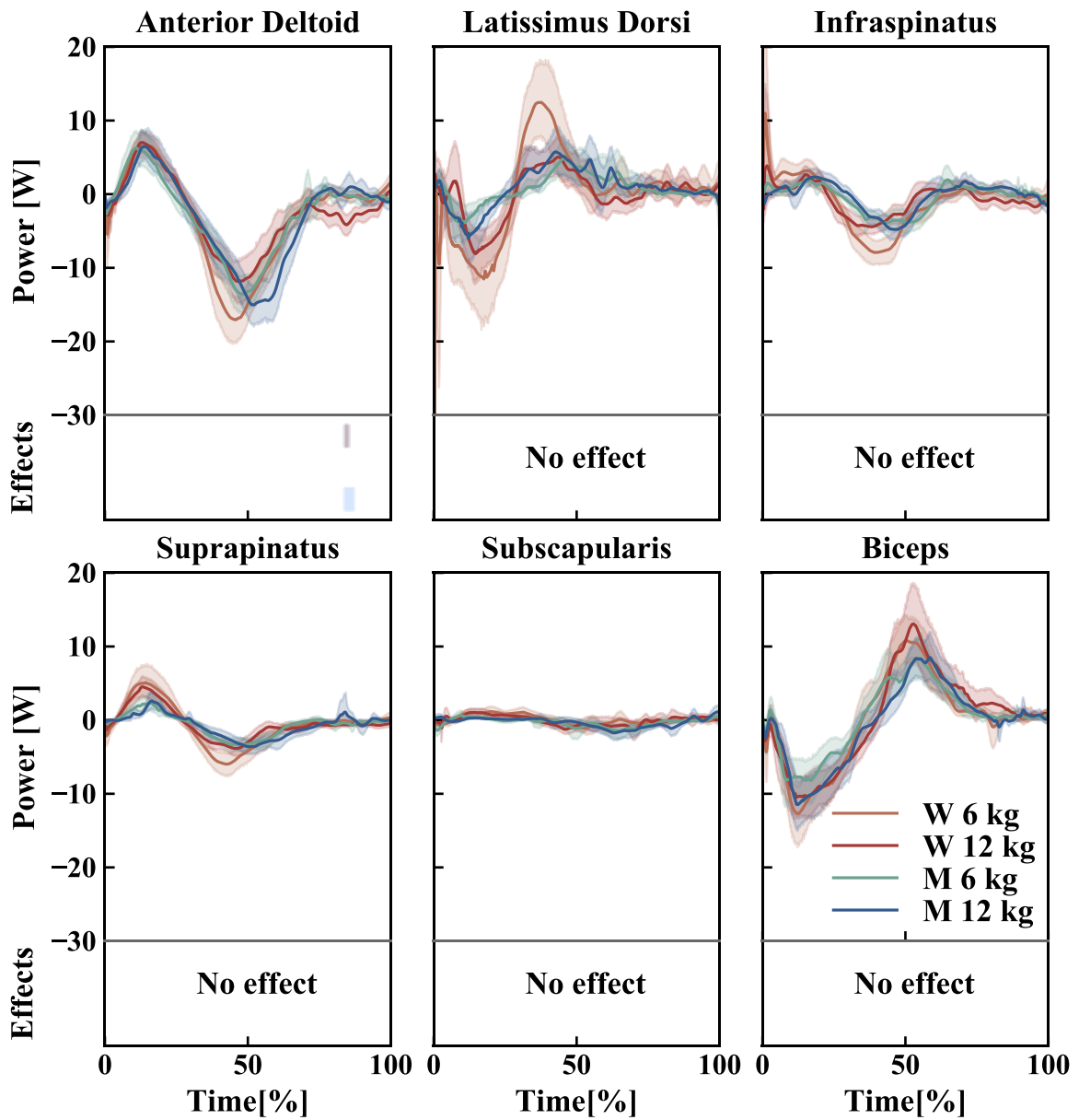
272 main limitation relied in the need of a compression and extension phases within the studied
273 trial. While this could be relatively easy to define for cyclic tasks: such as handcycling, it is
274 less straightforward for the majority of the upper limb tasks. Finally, the strut index is defined
275 relatively to a given length that could change the overall distribution of the muscle functions.
276 Unlike in Lai et al. (2019), there is no specific known behavior of the upper limb tendons or
277 muscles. Accordingly, we decided to use the fiber optimal length to make the strut index
278 dimensionless. This choice should circumvent introducing any task, participant or muscle
279 induced bias to the study. In the future, more research needs to be done to find an optimal
280 parameter for normalizing the upper limb strut index.

281 The implemented index-based approach enabled a more comprehensive understanding of the
282 upper limb motor control strategies during a box handling task and a summarized insight in the
283 function of the various muscles. The indices highlighted particularities of the glenohumeral
284 joint (large range of motion) and its muscles (stabilizing function), as well as sex-dependent
285 adaptation strategies to load, supporting our initial hypotheses. This approach might improve
286 our understanding of the upper limb by offering additional insight into its motor control
287 strategies, its components functional alterations related to pathologies or its adaptations to
288 external parameters.



290

291 *Fig. 1. Glenohumeral joint power generated by women (W) and men (M) during the box (6 or*292 *12 kg) lifting tasks: solid line: mean value, hue: 95% confidence interval. In the bottom part of*293 *the graphs, pink bands correspond to the load effect.*

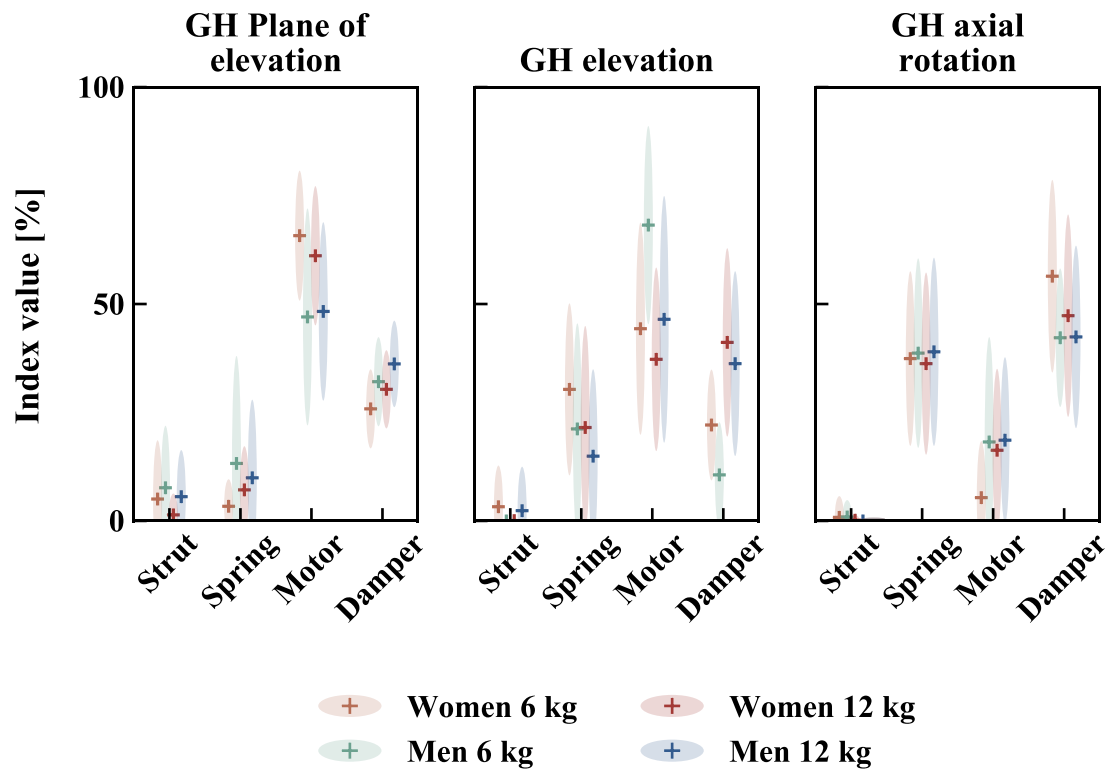


295

296 *Fig. 2. Power generated by muscle fibres during the box (6 and 12 kg) lifting tasks for women*

297 *(W) and men (M); solid line: mean value, hue: 95% confidence interval, blue bands: sex effect,*

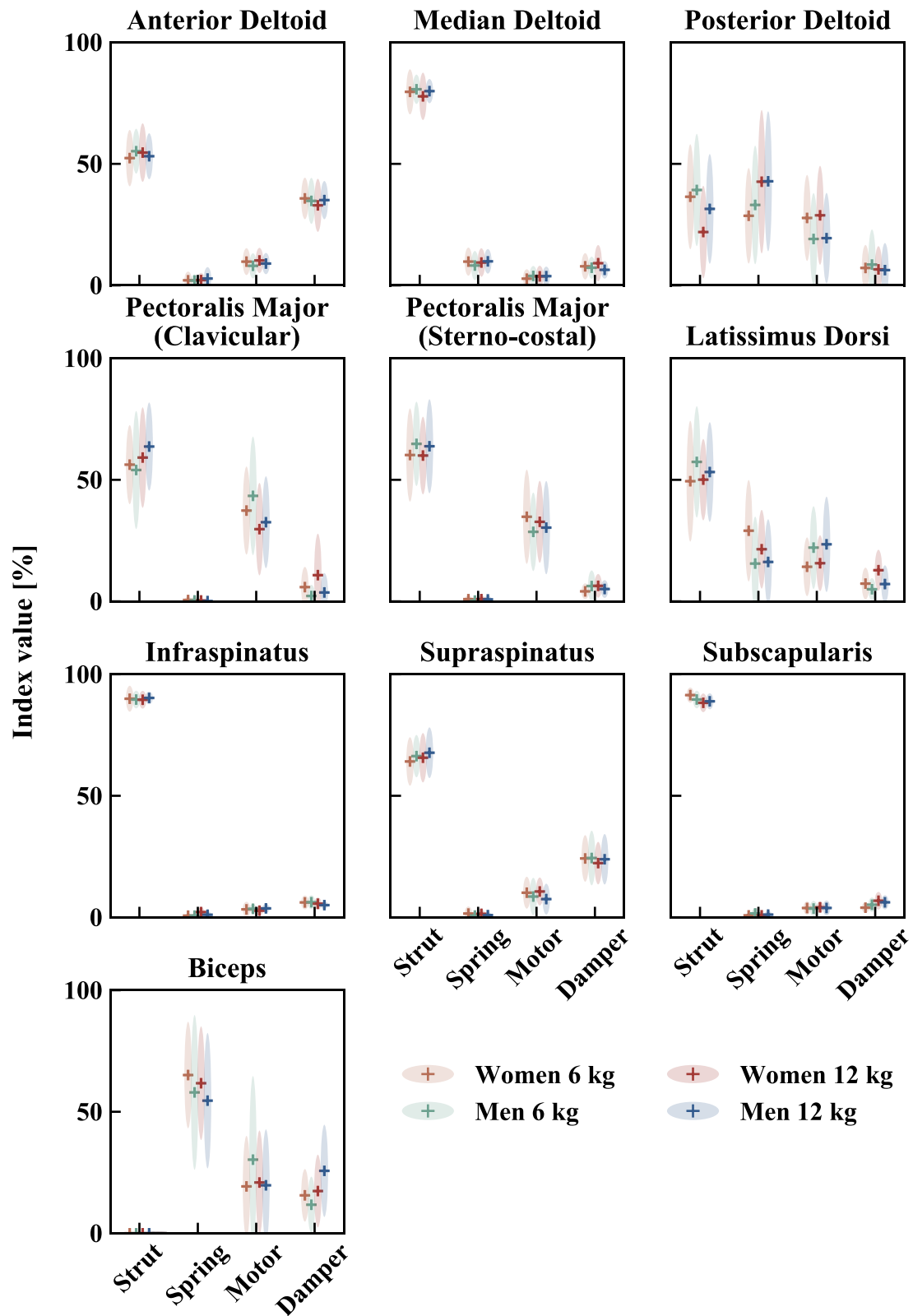
298 *purple bands: sex-load effect.*



300

301 *Fig. 3. Mean values of the four joint indices with a load of 6 and 12 kg for women and men.*

302



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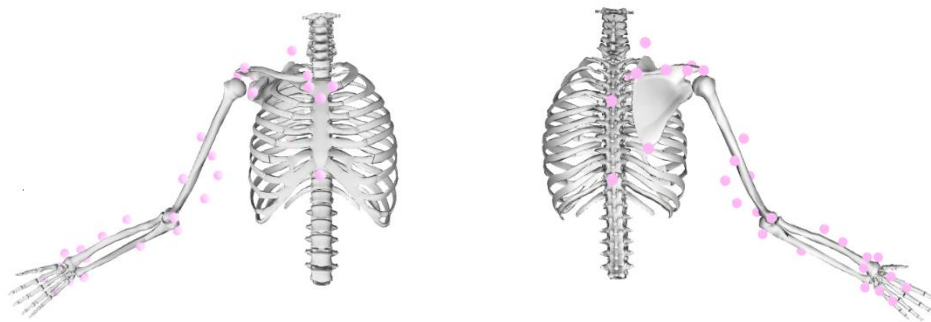
304 *Fig. 4. Mean values of the four muscle fiber indices with a load of 6 or 12 kg for women and*

305 *men.*

306 **SUPPLEMENTARY MATERIAL**

307 *Data collection*

308 Forty participants (20 women; 23.12 ± 3.1 years; 173.5 ± 9.5 cm; 68.1 ± 12.7) took part in this
309 study. They did not suffer from any significant disability related to their upper limbs or backs.
310 The participants first performed a static trial to anthropometrically scale the musculoskeletal
311 model. Then, they moved a box from a shelf at hip level to a shelf at eye level. The shelves
312 heights were adjusted to the height of each participant. The participants performed three lifts
313 for each mass (6 and 12 kg). The order of the lifts was randomized. A 30 s rest period
314 between lifts was given for recovery with increased time if needed. Assuming symmetry
315 between the right and left side during this task, only the right side was analyzed. A 6-degree-
316 of-freedom force sensor (Sensix, Poitiers, France) was mounted on the right handle of the box
317 to measure the contact forces between the box and the participant's hand. A threshold of 5 N
318 was used to detect the start and end of each trial. Following the recommendations of Jackson
319 et al. (2012), 34 reflective markers were used to track the trunk and upper limb kinematics
320 (Fig. S1). Eight markers positions on the box corners were used to track the box kinematics.



321

322 *Fig. S1. The position of the markers used to track the trunk and upper limb kinematics.*

323 *Neuro-musculoskeletal model*

324 To personalize the neuro-musculoskeletal model, the various parameters involved in the
325 activation and contraction dynamics were calibrated using experimental EMG, namely:

326 - The two recursive coefficients of the second-order differential system that relates the
327 excitation to the neural activation

328 - The shape factor that related the neural activation to the muscle activation

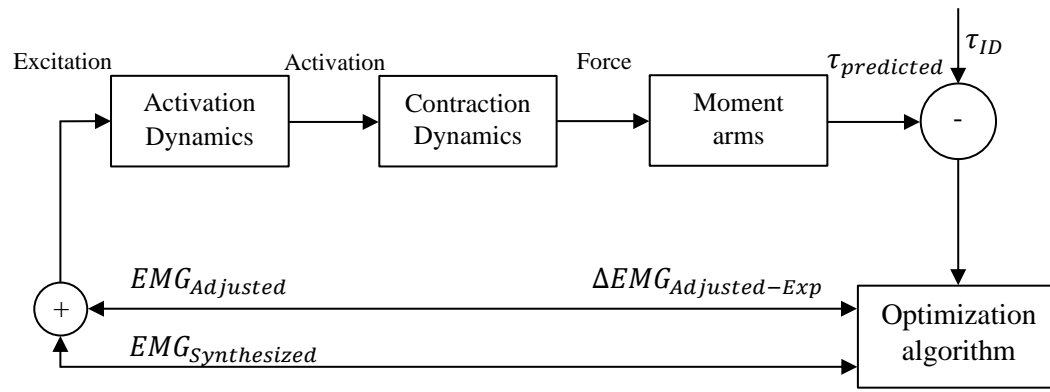
329 - The fiber optimal length

330 - The tendon slack length

331 - The isometric maximal force.

332 One trial per participant lifting a 6 kg load was used for calibration. The calibration aimed to
333 find musculo-tendon parameters that simultaneously minimized the inverse dynamic torques
334 tracking quadratic error and the ratio of the glenohumeral joint shear to compressive contact
335 forces, while driving the model using the experimental EMG. A penalty was used to avoid
336 normalized fiber length outside the physiological range throughout the calibration trial. This
337 objective function enabled the respect of the glenohumeral joint non-dislocation constraint
338 without the need to explicitly include it in the muscle force prediction algorithm (Assila et al.,
339 2020).

340 The calibrated models were then used to predict muscle forces through an EMG-informed
341 algorithm (Fig. S2). The optimization scheme adjusted the available experimental EMG
342 envelopes and synthesized the excitations that were not measured experimentally. The adjusted
343 and synthesized excitations minimized three terms: 1- inverse dynamics joint moments tracking
344 error, 2- experimental envelopes tracking error, 3- the sum of squared excitations for all lines
345 of actions. The weights used for the various terms were chosen to achieve a good balance
346 between joint moments and excitations tracking (Sartori et al., 2014). At the contraction
347 dynamics stage, the muscle-tendon equilibrium is accounted for by solving the equality of the
348 tendon and fiber forces with the fiber length as parameter. The root of this equation is found
349 using Brent's method (Brent, 1973).



350

351 *Fig. S2. Overview of the muscle force prediction algorithm. τ_{ID} is the moment obtained from inverse*
 352 *dynamics that the algorithm tries to track, $EMG_{Adjusted}$ is the adjusted excitation of the muscles that*
 353 *had experimental data, whereas $EMG_{Synthesized}$ is the excitation of the muscles that had no*
 354 *experimental data.*

355 *Function indices*

356 The function indices calculation was based on the formulae presented in (Lai et al., 2019; Qiao
 357 and Jindrich, 2016). The strut index is the ratio of the mechanical work generated by the entity
 358 during the box lifting task to the sum of the force norm generated. Accordingly, the index can
 359 be defined as follows:

$$360 \quad I_{strut,DOF} = \max \left(1 - \frac{(t_{end} - t_{beg}) \int_{t_{start}}^{t_{end}} |P_{DOF}| dt}{\int_{t_{start}}^{t_{end}} |M_{DOF}| dt}, 0 \right) \times 100\%$$

$$364 \quad I_{strut,muscle} = \max \left(1 - \frac{(t_{end} - t_{beg}) \int_{t_{start}}^{t_{end}} |P_{muscle}| dt}{l_{opt} \int_{t_{start}}^{t_{end}} |F_{muscle}| dt}, 0 \right) \times 100\%$$

361 with P_{DOF} and P_{muscle} the mechanical powers of the DOF and the fiber, respectively; M_{DOF} the
 362 DOF moment and F_{muscle} the fiber force. The optimal length of the fiber (l_{opt}) was used to
 363 obtain a dimensionless index. The lifting task started at t_{beg} and finished at t_{end} .

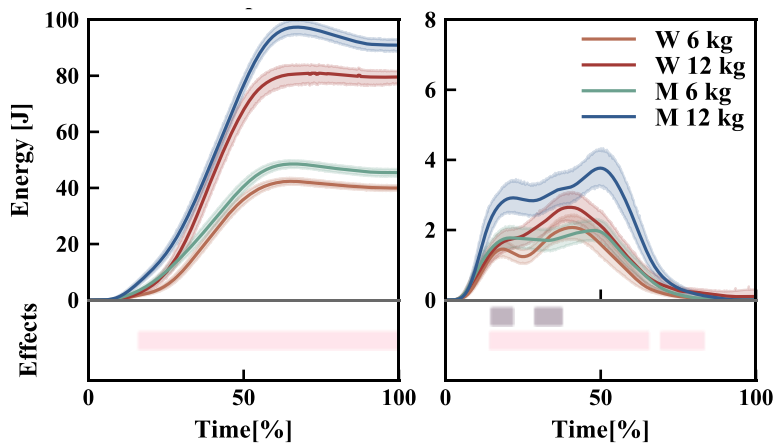
365 The other indices were calculated similarly for both the glenohumeral DOFs and muscles. They
 366 were calculated as follows:

367
$$I_{spring} = \frac{2 \cdot \min(|W_{com}^-|, |W_{ext}^+|)}{|W_{tot}^+| + |W_{tot}^-|} \times (100\% - I_{strut})$$

368
$$I_{motor} = \frac{|W_{tot}^+| - \min(|W_{com}^-|, |W_{ext}^+|)}{|W_{tot}^+| + |W_{tot}^-|} \times (100\% - I_{strut})$$

369
$$I_{damper} = \frac{|W_{tot}^-| - \min(|W_{com}^-|, |W_{ext}^+|)}{|W_{tot}^+| + |W_{tot}^-|} \times (100\% - I_{strut})$$

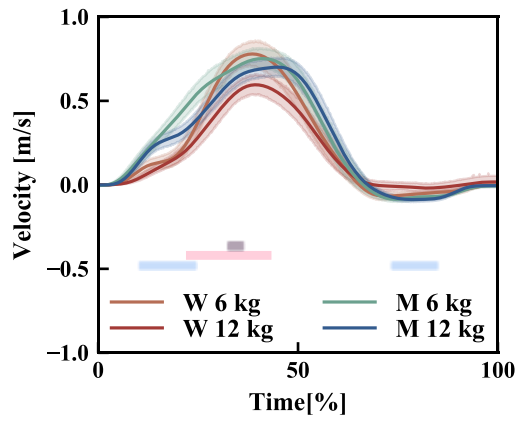
370 where $|W_{tot}^+|, |W_{tot}^-|$ were respectively the total positive and negative works generated by the
371 entity. $|W_{com}^-|$ and $|W_{ext}^+|$ where respectively the negative work during the compression phase
372 and the positive work during the extension phase.



373

374 *Fig. S3. Left: potential energy of the box with reference at hip level solid line, right: Kinetic*
 375 *energy of the box with the box state at t=0 as reference value: mean value, hue: 95% confidence*
 376 *interval, pink bands: load effect, purple bands: sex-load effect.*

377 *Note: The difference in potential energy between men and women was due to the height of the*
 378 *shelves that has been normalized to participants height (women: 167.7 ± 7.1 cm, men: 179.3 ± 7.9*
 379 *cm).*



380

381 *Fig. S4. Vertical velocity of the box (6 or 12 kg) for women (W) and men (M): solid line: mean value,*

382 *hue: 95% confidence interval, blue bands: sex effect, pink bands: load effect, purple bands: sex-load*

383 *effect.*

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389 **CONFLICT OF INTEREST**

390 The authors do not have any conflict of interest that could inappropriately influence this manuscript.

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