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1 **TITLE**

2 Evidence of invariant lower-limb kinematics in anticipation of ground contact during drop-landing and  
3 drop-jumping.

4

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## 1 **ABSTRACT**

2 Gravity is a ubiquitous external force that must be considered when producing coordinated movements.  
3 Drop-landing is a popular task to study how humans cope with gravity, because anticipatory muscle  
4 activations can be released before the estimated ground contact. But the consequences of these  
5 anticipatory muscle activations have only been interpreted in terms of stiffening the lower-limbs in  
6 preparation for ground contact, without considering potential anticipatory kinematic consequences. The  
7 objective of this study is to quantify the kinematic consequences of anticipatory muscle activations in  
8 two different landing tasks, to clarify whether anticipatory muscle activations are adapted to cope with  
9 gravity, to the dynamic constraints of the movement to perform, or both.

10 Twenty young athletes performed drop-landing and drop-jumping from a 35 cm elevated platform.  
11 Sagittal angles and angular velocities of the hip, knee, and ankle joints, and acceleration of the foot were  
12 computed, as well as the onset of joint flexions and onset of foot vertical acceleration change.

13 We found the same pattern of anticipatory hip and knee flexion, both starting *before* ground contact in  
14 all participants and in both tasks. We found no anticipatory kinematics for the ankle joint. Consecutive  
15 to the hip and knee flexion, the foot accelerated upwards before ground contact.

16 Our results show that anticipatory muscle activations used by humans have systematic and invariant  
17 kinematic consequences during the air-time phase to cope with gravity: they initiate the hip and knee  
18 joints flexion *before* ground contact. This strategy likely limits the amount of ground reaction forces  
19 developed to oppose the gravity external force, and completes the stiffening role already described in  
20 the literature. These two complementary consequences —rotation and stiffening— seem to serve the  
21 same purpose of protecting the skeletal system. Since gravity is ubiquitous, these automated movements  
22 must be considered in other movements involving landing phases, such as heel strikes during gait.

23

## 24 **KEYWORDS**

25 Anticipation; Coordination; Neuromuscular; Kinematics; Landing.

## 26 INTRODUCTION

27 Gravity is a ubiquitous external force influencing all movements because it constantly accelerates our  
28 body downward. Muscle activations are thus necessary to oppose this force and remain upright while  
29 moving. Additionally, because gravity has always been present in their motor control development,  
30 humans have learnt to anticipate the consequences of gravity on their movements, by adapting their  
31 muscle activations to the intended task (White et al., 2020). Yet, there is only a partial understanding of  
32 how the nervous system anticipates the consequences of gravity to produce coordinated movements.

33 Drop-landing tasks are popular experimental paradigms to study how humans cope with gravity. During  
34 the air-time phase preceding ground contact, the whole-body centre of mass downward velocity  
35 increases linearly, which simplify the estimation of ground reaction forces (GRF) to produce, larger than  
36 that of body weight during ground contact, to accelerate the whole-body centre of mass upward and  
37 complete the transition from the drop movement to a standing posture (Dufek & Bates, 1991). Even  
38 larger GRF are required to accelerate the whole-body centre of mass upward and transition from the  
39 drop to another movement, such as during drop-jumping (i.e. a drop-landing immediately followed by  
40 a jump) (Dyhre-Poulsen et al., 1991).

41 Fifty years ago, Jones and Watt suggested that stretch reflex responses alone would occur too late to  
42 accelerate the whole-body upward during drop-landing (Jones & Watt, 1971b). In other words, the  
43 consequences of gravity must be anticipated by muscle processes engaged during the air-time phase.  
44 Accordingly, authors described activations of the main lower-limb muscles (e.g. rectus femoris, vastii,  
45 hamstrings, soleus, and gastrocnemii) during the air-time phase preceding ground contact of drop-  
46 landing tasks, and interpreted these activations as preparation for muscle to develop large forces starting  
47 from ground contact (Jones & Watt, 1971b, 1971a; Podraza & White, 2010). The amplitude of such  
48 anticipatory muscle activations are adapted to the whole-body velocity at ground contact because they  
49 increase with drop-height (Jones & Watt, 1971a; Santello & McDonagh, 1998). The literature proposed  
50 that the role of these anticipatory activations is to increase the muscle and joint stiffnesses to accelerate  
51 the whole-body centre of mass upward during ground contact (reviewed in (Santello, 2005). This  
52 assumption has been confirmed by musculoskeletal modelling, where co-activation of muscles around

53 the ankle joint was related to larger joint stiffness and smaller joint range of motion during contact  
54 (DeMers et al., 2017); and in animal models (turkey), where authors established a relationship between  
55 gastrocnemius anticipatory activations and gastrocnemius force (Konow & Roberts, 2024). During drop-  
56 jumping, larger amplitudes of anticipatory muscle activations were recorded compared to drop-landing,  
57 and they were also interpreted as preparation to increase muscle and joint stiffnesses (Dyhre-Poulsen et  
58 al., 1991). Moreover, the amplitude of anticipatory muscle activations increased with a decreased ground  
59 contact time (Arampatzis et al., 2001), and were correlated to the eccentric action of the muscle during  
60 ground contact (Avela et al., 1996). In summary, it is clear that humans use anticipatory muscle  
61 activations to prepare their muscles to decrease the amount of vertical velocity accumulated during the  
62 air-time phase of dropping movements.

63 Minimising the impact GRF is important to protect the skeletal system and thus reduce injuries in drop-  
64 landing tasks (Devita & Skelly, 1992; Dufek & Bates, 1991). Consequently, a body of literature focused  
65 on kinematic landing techniques used by humans to minimise impact GRF. Authors showed that when  
66 humans land with larger hip and knee joint flexions at ground contact, they experience lower GRF and  
67 joint moments (Devita & Skelly, 1992; Podraza & White, 2010). Simulating single-leg landings,  
68 Wakabayashi et al., (2021) also found that increasing knee joint flexion at ground contact reduce the  
69 GRF. These studies suggest that the joint configuration at ground contact is a determinant factor to  
70 protect the skeletal system. However, these studies quantified kinematics only *starting from* ground  
71 contact. To reach the flexed lower-limb joints configuration described at ground contact, humans can  
72 either (i) spend the whole air-time phase with joints in the final desired flexed configuration or (ii)  
73 initiate joint flexions before ground contact. Only the ankle joint was characterised and showed little to  
74 no kinematic adjustments during the air-time phase before ground contact, suggesting the first solution  
75 is used for the ankle joint (Santello & McDonagh, 1998; Santello, 2005). However, potential anticipatory  
76 kinematics of the hip and knee joints before ground contact have not been characterised. One study  
77 reported possible hip and knee angular velocity at ground contact, negatively correlated to the peak of  
78 vertical GRF (Yu et al., 2006). However, the results reported in this paper indicate a large heterogeneity  
79 in the hip and knee angular velocity between participants: flexion angular velocity was not present in

80 every participant at ground contact, some participants even presented extension angular velocity at  
81 ground contact; and they did not quantify any anticipatory kinematics during the air-time phase. Yet,  
82 the presence of hip and knee angular velocity at ground contact might suggest that hip and knee joint  
83 flexions are initiated before ground contact. Hip and knee joint angles have been plotted during the last  
84 100 ms before ground contact, where they seem to flex before ground contact (Devita & Skelly, 1992;  
85 Horita et al., 2002). But these results were obtained from limited 2D kinematic chain models, with few  
86 markers, approximating the hip joint centre to the great trochanter, which can affect both hip and knee  
87 joint flexion angle computation (Della Croce et al., 2005). Thus, it remains to clarify whether  
88 anticipatory kinematic adjustments exist at the hip and knee joints, and if there is a relationship between  
89 the anticipatory muscle activations and the temporal evolution of these lower-limb joint kinematic  
90 adjustments before ground contact.

91 During drop-jumping (i.e. a drop-landing immediately followed by a jump), authors reported that hip  
92 and knee joint angles were more flexed at ground contact compared to drop-landing (Mache et al., 2013;  
93 Hovey et al., 2021). This joint configuration, associated with larger anticipatory muscle activations  
94 compared to drop-landing, may favour the quick extension of the lower limb to initiate the following  
95 jump. Horita et al., (2002) correlated knee flexion angular velocity before ground contact with drop-  
96 jumping performance, when producing large GRF is required, suggesting that possible anticipatory  
97 adjustments are adapted to the movement to perform. This result is in opposition with the result from  
98 (Yu et al., 2006), where hip and knee flexion angular velocity were negatively correlated with the peak  
99 of vertical GRF, suggesting that possible anticipatory adjustments are rather adapted to cope with  
100 gravity. Thus, it remains unclear whether the kinematic configuration at ground contact, and its temporal  
101 evolution during the air-time phase *before* ground contact, are adapted to cope with gravity, to the  
102 dynamic constraints of the movement to perform after ground contact, or both. One way to answer this  
103 question would be through the comparison of the temporal evolution of anticipatory lower-limb joint  
104 angles and angular velocities between drop-landing and drop-jumping, to identify whether joint  
105 kinematics differ between tasks.

106 To summarise, although the consequences of anticipatory muscle activations on biomechanical output  
107 seem to be well understood *during* the ground contact period, it remains largely unclear whether they  
108 have kinematic consequences *before* ground contact. The objective of this study is to characterise the  
109 kinematic consequences of anticipatory muscle activations before ground contact in two different  
110 landing tasks (i.e. drop-landing and drop-jumping), to determine whether anticipatory muscle  
111 activations are adapted to cope with gravity, to the movement to perform, or both. We hypothesise that  
112 hip and knee flexions would be initiated before ground contact, regardless of the landing task.  
113 Additionally, we hypothesise earlier flexions during drop-jumping as a solution to reach larger joint  
114 angles compared to drop-landing. To test these hypotheses, we quantified the onset time of lower-limb  
115 joint flexions to determine whether they arise from ground contact or from anticipatory muscle  
116 activations. We also quantified the foot kinematics to determine the impact of anticipated lower-limb  
117 joints rotations at the end of the kinematic chain.

## 118 **METHODS**

### 119 **PARTICIPANTS**

120 Twenty young, healthy adults (10 females, mean  $\pm$  standard deviation,  $24.0 \pm 4.1$  years old;  $172.9 \pm 7.6$   
121 m;  $65.3 \pm 8.1$  kg;  $21.9 \pm 2.3$  kg.m<sup>-2</sup> of body-mass index) practicing a physical activity including jumps,  
122 on a weekly basis, were recruited for this study. A priori power analysis, assuming a type I error of 0.05  
123 and a type II error rate of 0.20 (80% statistical power) indicated that 13 participants would be sufficient  
124 to detect statistically significant difference in knee flexion angle between drop-landing and drop-  
125 jumping at ground contact, based on data from Hovey et al., (2021). All participants gave informed  
126 consent to the protocol in accordance with the institutional guidelines set by the Declaration of Helsinki.  
127 Exclusion criteria were: any musculoskeletal injury of the lower-limb during the six months preceding  
128 the experiment, any neurological impairment that could affect balance and coordination, and any  
129 contraindication to the practice of physical activity. All procedures were approved by the University  
130 ethics committee (CER-TP 2022-04-02).

131 **PROCEDURE**

132 The participants first performed a standing trial designed to scale their anatomical posture to the generic  
133 whole-body kinematic chain model (Fig. 1.A). They then performed three functional movements  
134 bilaterally, rotating each degree of freedom of the hip, knee, and ankle to compute joint centres. After a  
135 10-minute warm-up consisting of articular, muscular and plyometrics movements of the lower-limb such  
136 as squats, lunges, and hops, the participants performed two dropping tasks from a height of 0.35 m: i)  
137 drop-landing and ii) drop-jumping; randomly presented. The participants performed three trials of each  
138 task. Participants initially stood in an upright standing posture on a rigid elevated platform, with feet  
139 apart at approximately shoulder width. They were instructed to always keep their hands on their hips,  
140 and to retrieve an upright standing posture at the end. The participants were instructed to leave the  
141 platform with both feet simultaneously, without jumping upwards, and to land evenly on both feet, with  
142 one foot on each force-plate embedded in the ground. For the drop-landing task, the participants were  
143 instructed to amortise their landing as much as possible. For the drop-jumping task, they were instructed  
144 to minimise the ground contact time. The participants familiarised themselves with the tasks and the  
145 instructions before any recording was taken.

146 **MEASUREMENTS**

147 Nine rectangular surface electromyographic (EMG) electrodes (Trigno, Delsys, Natick, USA) with a bi-  
148 polar parallel bar electrode configuration and an inter-electrode distance of 10 mm were used to record  
149 the electrical activity of lower-limb muscles (tibialis anterior, soleus, gastrocnemii medialis and lateralis,  
150 vastii medialis and lateralis, rectus femoris, biceps femoris long head, and semitendinosus, see Fig. 1.A)  
151 at 2000 Hz. Skin was shaved and cleansed with alcohol prior to EMG sensor placement. EMG sensors  
152 were positioned on the muscle belly so that the electrode bars were oriented perpendicular to the  
153 underlying muscle fibre direction (De Luca, 1997). After EMG sensors placement, a test muscle  
154 contraction was performed to confirm good position and skin-electrode contact. EMG Sensors were  
155 secured with adhesive surface interface strips (Delsys Natick, USA) and double-sided elastic tape. EMG  
156 sensors were placed only on the dominant lower-limb of each participant, identified as the one used to  
157 perform a high jump or a long jump.



158 The three-dimensional GRF and torques were recorded by four force plates (400 × 600 mm, Sensix,  
159 Poitiers, France) sampled at 2000 Hz: two force plates underneath the elevated platform, and two others  
160 in the landing area. The vertical GRF under the elevated platform was set to zero when the elevated  
161 platform was already in place, to not consider its weight. Thirty-six markers were placed on the  
162 participants' body, 22 on anatomical body landmarks and 14 as technical markers (Fig. 1.A). Their three-  
163 dimensional trajectories were recorded by an optoelectronic system composed of 19 cameras (T40,  
164 Vicon, Oxford, UK) sampled at 200 Hz. All three measurement systems were synchronised using Vicon  
165 Nexus 2.12 (Vicon, Oxford, UK).

## 166 **DATA ANALYSIS**

### 167 **Electromyography**

168 The EMG envelope was obtained with a second-order zero-phase low-pass Butterworth filter at 50 Hz.  
169 Onsets of muscle activations were computed using a double-threshold method (Hodges & Bui, 1996):  
170 to be considered active, the EMG muscle signal had to be larger than an activation threshold during at  
171 least 50 ms. The activation threshold of each participant was established as the average signal during a  
172 five-second period when the participant was resting, lying on the back. EMG onset detection was  
173 performed in a window starting from when the participants jumped off the elevated platform, i.e. when  
174 the vertical GRF under the elevated platform was lower than 20 N and ending at ground contact (see  
175 next paragraph for ground contact computation).

### 176 **Kinetics and Kinematics**

177 To avoid possible undershoot or overshoot of the data around ground contact, GRF and marker  
178 trajectories were filtered using a critically damped zero-phase low-pass filter at 50 and 20 Hz,  
179 respectively (Robertson & Dowling, 2003). For each task, ground contact was identified as the first  
180 instant when the vertical ground reaction force of the corresponding force plate exceeded 1 N (standard  
181 deviation of the weight-free platform filtered signal was around 0.5 N). Further analyses focused on the  
182 anticipatory phase, which corresponded to the air-time period preceding ground contact. For the Drop-  
183 Jumping task, only the anticipatory period preceding the first ground contact was analysed.

184 Functional movement trials were used to compute three joint centres. Hip joint centres were determined  
185 according to Halvorsen's method (Halvorsen, 2003). Knee joint centres were determined as being the  
186 middle of the femoral condyles, projected onto the axis of flexion, according to the Sara algorithm (Ehrig  
187 et al., 2007). Ankle joint centres were determined as the middle of both malleoli. We performed a multi-  
188 body kinematic optimisation to reduce the impact of soft-tissue artefacts (Lu & O'Connor, 1999), using  
189 a kinematic chain model developed in OpenSim 4.3 (Delp et al., 2007), based on the model developed  
190 by (Retailleau & Colloud, 2020). The model consisted of nine segments articulated by eight joints and  
191 24 degrees of freedom: the three positions and three orientations of the pelvis, and the 18 joint  
192 coordinates (three rotations for each joint) (Fig. 1.B). All marker data were then resampled at 2000 Hz,  
193 to have the same timescale as the force plates, and to avoid approximation of the ground contact time.

194 Lower-limb segment coordinate systems were computed based on ISB recommendations (Wu et al.,  
195 2002), using a custom script (Matlab, MathWorks, version 2021b). They were used to compute lower-  
196 limb joint angles, which correspond to the Euler angles between the proximal and distal coordinate  
197 systems, following a Z (mediolateral axis) - X (anteroposterior axis) - Y (longitudinal axis) sequence.  
198 Angular velocities were then obtained by computing a simple left derivative of the joint angles to avoid  
199 any effect due to ground contact. The onset of joint flexion was determined as the first instant when the  
200 angular velocity was positive and continued to increase until ground contact.

201 The foot trajectory was characterised by the trajectory of the midpoint between the first and the fifth  
202 metatarsal markers in the global coordinate system, because it is approximately where the centre of  
203 pressure is located during ground contact (Gross & Nelson, 1988). Therefore, it represents the point of  
204 the whole-body in contact with the ground. From this trajectory, the foot vertical velocity and  
205 acceleration were computed using a simple left derivative. The foot was considered to be accelerated  
206 upwards relative to a free-falling object when its acceleration was larger (i.e. closer to zero) than the  
207 acceleration of gravity, and continued to accelerate until ground contact. The pelvis vertical velocity  
208 was computed at the origin of the pelvis segment coordinate system (i.e. the hip joint centre of the  
209 dominant lower-limb (Wu et al., 2002)), to represent a free-falling object.

210 For each participant, only the best trial of each task was analysed, and only the dependent variables from  
211 the dominant lower limb were extracted from that best trial. We chose to analyse one trial per participant,  
212 that was actually performed by our participants, and not an average of trials which could erase some  
213 strategies and filter out local maxima and timings (Kneip & Gasser, 1992). For the drop-landing, the  
214 best trial was the trial with the smallest vertical ground reaction force peak. For the drop-jumping, the  
215 best trial was the trial with the shortest ground contact time. Because the literature reported that muscles  
216 are activated 100 to 150 ms before ground contact (Ambegaonkar et al., 2011; Arampatzis et al., 2001;  
217 Santello & McDonagh, 1998), analyses of lower-limb kinematics were performed from 150 ms before  
218 ground contact to ground contact.

## 219 **STATISTICS**

220 All statistical tests were performed using Matlab (MathWorks, version 2021b). The normality of each  
221 dependent variable was checked using a Shapiro-Wilk test. Because most variables were not normally  
222 distributed, only non-parametric tests were used. The onset of muscle activations, the onset of joint  
223 flexions, the onset of foot acceleration, the joint angles, and the joint angular velocities at ground contact  
224 were compared between drop-landing and drop-jumping, using a Wilcoxon signed rank test. To test  
225 whether the foot kinematics were modified by the lower-limb kinematic adjustments, we compared the  
226 foot and pelvis vertical velocities at ground contact using the same test. We computed the effect size  $r$   
227 for non-parametric data according to (Fritz et al., 2012) as :  $r = \frac{z}{\sqrt{N}}$ , comprised between -1 and 1, with  
228  $|r| > 0.37$  corresponding to a large effect size and  $|r| > 0.51$  corresponding to a very large effect size.  
229 Moreover, we performed a non-parametric Statistical Parametric Mapping (SPM) (Pataky, 2010) to  
230 compare one-dimensional curves. For all tests, the significance threshold was set at 5%.

## 231 **RESULTS**

232 All recorded muscles were activated before ground contact (Table 1). There was no effect of the task on  
233 the activation timing of the selected muscles.

234 In both landing tasks, the hip and knee joints started the air-time phase by extending (Fig. 2). Then, we  
235 found a systematic (i.e. for each participant and each task) hip and knee flexion starting before ground

236 contact (Fig. 2), without any difference in timing between the two tasks ( $p = 0.89$ ,  $r = -0.03$  and  $p =$   
237  $0.70$ ,  $r = -0.07$ , respectively). The ankle joint started the air time phase by a plantarflexing motion, but,  
238 contrary to the hip and knee joints, no clear ankle dorsiflexion was observed before ground contact in  
239 both tasks. At ground contact, there was no difference in both the hip flexion ( $p = 0.35$ ,  $r = -0.15$ ) and  
240 ankle dorsiflexion ( $p = 0.17$ ,  $r = 0.22$ ) angles between the two tasks, whereas the knee was significantly  
241 more flexed in drop-jumping compared to drop-landing ( $p = 0.012$ ,  $r = -0.40$ ) (Fig. 2). For every lower-  
242 limb joint, there was no difference in angular velocity at ground contact ( $p = 0.26$ ,  $r = 0.18$ ;  $p = 0.55$ ,  $r$   
243  $= 0.09$  and  $p = 0.77$ ,  $r = 0.05$  for the hip, knee, and ankle joints, respectively) (Fig. 2). We did not find  
244 any difference before ground contact between the two tasks, for both the joint angle and joint angular  
245 velocity curves using the SPM.

246 The vertical velocity of the foot became larger (i.e. closer to zero) than the acceleration of gravity before  
247 ground contact for all participants and in both tasks (Fig. 3). Consequently, the foot vertical velocity  
248 was larger than the pelvis vertical velocity at ground contact in both tasks (Table 2). We did not find  
249 any difference before ground contact between the two tasks, for both the foot vertical velocity nor the  
250 foot vertical acceleration curves using the SPM.

## 251 **DISCUSSION**

252 Our objective was to characterise the kinematic consequences of anticipatory muscle activations before  
253 ground contact during two different landing tasks (i.e. drop-landing and drop-jumping), to determine  
254 whether anticipatory muscle activations are adapted to cope with gravity, to the movement to perform,  
255 or both. Analysis of the temporal evolution of lower-limb joint angles revealed that anticipatory muscle  
256 activations have anticipatory kinematic consequences, because hip and knee joint flexions were initiated  
257 *before* ground contact for all participants, and without difference between both tasks. This suggests that  
258 these anticipatory joint flexions are not adapted to the dynamic constraints of the movement.  
259 Consecutive to these flexions, the foot started to be accelerated upward *before* ground contact. The  
260 systematicity of these results among all participants, despite different objectives between the tasks,  
261 suggests that these anticipatory joint flexions are a common strategy used by the nervous system to cope  
262 with gravity.

263 **KINEMATIC CONSEQUENCES OF ANTICIPATORY MUSCLE ACTIVATIONS**

264 Our results showed that the hip and knee joints started flexing systematically before ground contact (Fig.  
265 2) for all participants, and in the two landing tasks. Such anticipatory joint flexions can also been seen  
266 in Devita & Skelly, (1992) and in Horita et al., (2002), but they did not discuss this result. These  
267 anticipatory hip and knee flexions started after onsets of muscle activation (Table 1). The onsets of  
268 muscle activations we found were similar to those described in previous studies (Ambegaonkar et al.,  
269 2011; Arampatzis et al., 2001; Santello & McDonagh, 1998), but they did not report anticipatory joint  
270 flexion either. Although a direct relationship between EMG and joint rotations cannot be made, the joint  
271 rotations we observed here are likely to result from the anticipatory muscle activations. In light of the  
272 available evidence, it seems reasonable to suggest that the actions of the rectus femoris (and the iliopsoas  
273 that we could not record) are responsible for hip flexion, while biceps femoris long head, and  
274 semitendinosus are responsible for knee flexion. However, this remains a hypothesis that is yet to be  
275 confirmed.

276 Our results showed that the flexed hip and knee joints at ground contact are achieved through joint  
277 flexions initiated shortly before ground contact (Fig. 2). By anticipating joint flexions that would have  
278 been induced by ground contact, the hip and knee joints displayed no distinct change of angular velocity  
279 shortly after ground contact, contrary to the ankle joint (Fig. 2). The flexion of the hip and knee joints  
280 at the beginning of ground contact, without a distinct change in angular velocity, helps to limit any  
281 sudden increase in the upward acceleration of the whole-body centre of mass, which is limited by the  
282 neuromuscular strategy. These neuromuscular adaptations, driven by anticipatory muscle activations,  
283 may contribute to reduce the GRF magnitude at initial contact. According to Newton's second law, a  
284 lower upward acceleration of the whole-body centre of mass should correspond to a reduced GRF.  
285 Contrary to the study of Yu et al., (2006), all our participants landed with flexion angular velocity at  
286 ground contact, for both the knee and hip joints. This result suggests that presence of angular velocity  
287 is important in minimising the magnitude of GRF, in complement to the flexed-joint configurations  
288 previously described in the literature (Devita & Skelly, 1992; Podraza & White, 2010; Wakabayashi et  
289 al., 2021). These joint flexions, initiated before ground contact, may contribute to protect the skeletal

290 system by avoiding any joint extension movements that could lead to joint injury and/or imbalance  
291 during contact. The absence of difference between landing tasks is contrary to the findings of Horita et  
292 al., (2002), which suggested that knee angular velocity at ground contact is related to drop-jumping  
293 performance. Along with the systematicity of the anticipatory joint flexions, our results suggest that  
294 these flexions are an invariant component of the landing task selected by the nervous system to cope  
295 with gravity, regardless of the upcoming movement to perform.

296 Due to the multi-body structure of the human skeletal system, any kinematic adjustments influence the  
297 position and orientation of the segment located at the end of the open kinematic chain, the foot in our  
298 study. Despite no noticeable change in the ankle angle before ground contact (Fig. 2), an upward  
299 acceleration of the foot started before ground contact in both tasks and for all participants (Fig. 3),  
300 leading to a larger vertical velocity for the foot, compared to the pelvis. The larger vertical velocity of  
301 the foot reduces the velocity differential between the foot and the ground at ground contact (Table 2).  
302 Simultaneous to the flexing hip joint we recorded (Fig 1), the flexing knee joint accelerates the foot  
303 downward. Thus, the hip flexion mainly contributes to the upward foot acceleration and counteracts the  
304 downward effect of the knee flexion. The combined hip and knee flexions leading to an upward  
305 acceleration of the foot, regardless of the landing task (Fig. 3), reduce the upward foot acceleration that  
306 will be required during contact. This biomechanical solution seems efficient to limit the impact GRF  
307 during the beginning of ground contact.

308 The anticipatory joint rotations we quantified seem to complement the stiffening role of anticipatory  
309 muscle activations extensively described in the literature. In particular, only the ground contact induced  
310 ankle dorsiflexion (Fig. 2), confirming that the ankle muscles were anticipatorily co-contracted to  
311 increase ankle joint stiffness (Santello & McDonagh, 1998). This result is consistent with previous  
312 studies, which suggested that landing with a plantarflexed ankle joint enables landing on the forefoot,  
313 using a large ankle range of motion after ground contact to amortise (Gross & Nelson, 1988; Santello,  
314 2005). Given the results we have presented here, the hip and knee joint kinematic behaviours can also  
315 be interpreted as stiffening in preparation for ground contact. Indeed, maximal angular velocities  
316 occurred shortly after ground contact in both joints (Fig. 2), and could not be the result of a stretch reflex

317 (Jones & Watt, 1971b), indicating that muscle activations contributing to limit joint excursions are  
318 voluntarily-initiated (Zuur et al., 2010). Based on this interpretation, we suggest that the anticipatory  
319 muscle activations need to be precisely timed and coordinated according to the expected instant of  
320 ground contact: early activations enable the initiation of joint flexions, while latter activations stiffen  
321 joints to limit angular velocities shortly after ground contact, without causing an abrupt change of  
322 angular velocity. Thus, we suggest anticipatory muscle activations have two complementary  
323 consequences, joint flexing *and* stiffening, that seems to serve the same purpose of coping with gravity  
324 to protect the skeletal system.

### 325 **GENERAL IMPLICATION OF ANTICIPATORY KINEMATIC ADJUSTMENTS**

326 In this study, we used landing tasks to investigate how humans anticipate the consequences of gravity  
327 and/or the consequences of the motor task. The invariance of the anticipatory kinematic adjustments we  
328 recorded across landing tasks, together with their precise timing relative to ground contact, and the fact  
329 that they were recorded in experienced athletes, reflect automaticity (i.e. the ability to perform actions  
330 with little to no conscious attention) (Shiffrin & Schneider, 1977). Because these adjustments are  
331 programmed depending on the expected instant of ground contact, our findings are relevant for sports-  
332 injury prevention. Future studies should assess the underlying mechanisms mobilised by an athlete to  
333 accurately predict ground contact, especially when the athlete is disturbed during the air-time phase,  
334 when injuries such as anterior cruciate ligament ruptures frequently occur (Krosshaug et al., 2007).

335 Since gravity is a ubiquitous external force, these automatic anticipatory kinematic adjustments may  
336 look similar in other types of movement. For instance, similar observations have been reported during  
337 walking in different contexts. During unperturbed flat gait, the vertical velocity of the foot decreases  
338 before ground contact, notably through the knee flexion preceding heel-strike (Winter, 1992). During a  
339 step-down task, the knee flexion angle at ground contact was reported to be larger than during flat gait  
340 (Müller et al., 2014), suggesting that lower-limb joint flexion that accelerates the foot upward before  
341 ground contact is an efficient biomechanical solution adopted by humans when downward vertical  
342 velocity increases. Thus, our findings encourage future research to continue studying how humans cope

343 with gravity, and to clarify whether these anticipatory kinematics adjustments are part of a universal  
344 strategy to protect the skeletal system from injuries.

### 345 **LIMITATIONS**

346 This study has several limitations. First, the positive upward acceleration of the foot started shortly  
347 before ground contact (median of 21 ms, Fig 3). This result depends on many different factors, such as  
348 the sampling frequency of kinematic data, the filtering procedure, and the soft tissue artefacts produced  
349 by lower-limb movements. Yet, the use of a left-derivative should have helped avoiding potential errors  
350 from ground contact (i.e. avoiding future position when computing linear velocity). Second, the study  
351 of EMG signals often results in large variance among different participants. In particular, both the cut-  
352 off frequency and the thresholds selected to obtain the envelop and the onset of muscular activations  
353 can introduce variabilities (Hodges & Bui, 1996). Nevertheless, threshold methods, as the one we used,  
354 remain the most used method in the research literature (Carvalho et al., 2023), with the advantages that  
355 results can be verified visually and our results remain consistent with previous studies (Ambegaonkar  
356 et al., 2011; Arampatzis et al., 2001; Santello & McDonagh, 1998). Third, we did not consider trunk  
357 segment motion. A relationship between hip, knee and trunk flexion during contact was established  
358 (Blackburn & Padua, 2008), and may also exist before contact. Determining whether the trunk segment  
359 is anticipatorily mobilised to cope with gravity remains to be investigated in landing tasks.

### 360 **CONCLUSION**

361 Our results show that anticipatory muscle activations used by humans have systematic and invariant  
362 kinematic consequences during the air-time phase: they initiate the hip and knee joints flexion *before*  
363 ground contact. Together with the stiffening function described in previous studies, the anticipatory joint  
364 flexions also contribute to preparing the skeletal system for landing. As a direct consequence of these  
365 anticipatory kinematic adjustments, the foot is accelerated upward to decrease its upcoming deceleration  
366 due to ground contact. These anticipatory kinematic adjustments were invariant across the studied  
367 landing tasks, suggesting that this is an efficient biomechanical solution selected by the nervous system  
368 to provide favourable biomechanical conditions for coping with gravity.



369 **TABLES**

370 **Table 1:** Timing of EMG activation onset relative to ground contact (median [1st and 3rd quartile]). A  
 371 negative value indicates an activation onset before ground contact. TA = Tibialis Anterior, SOL =  
 372 Soleus, GM = Gastrocnemius Medialis, GL = Gastrocnemius Lateralis, VM = Vastus Medialis, VL =  
 373 Vastus Lateralis RF = Rectus Femoris, BF = Biceps Femoris, ST = Semitendinosus.

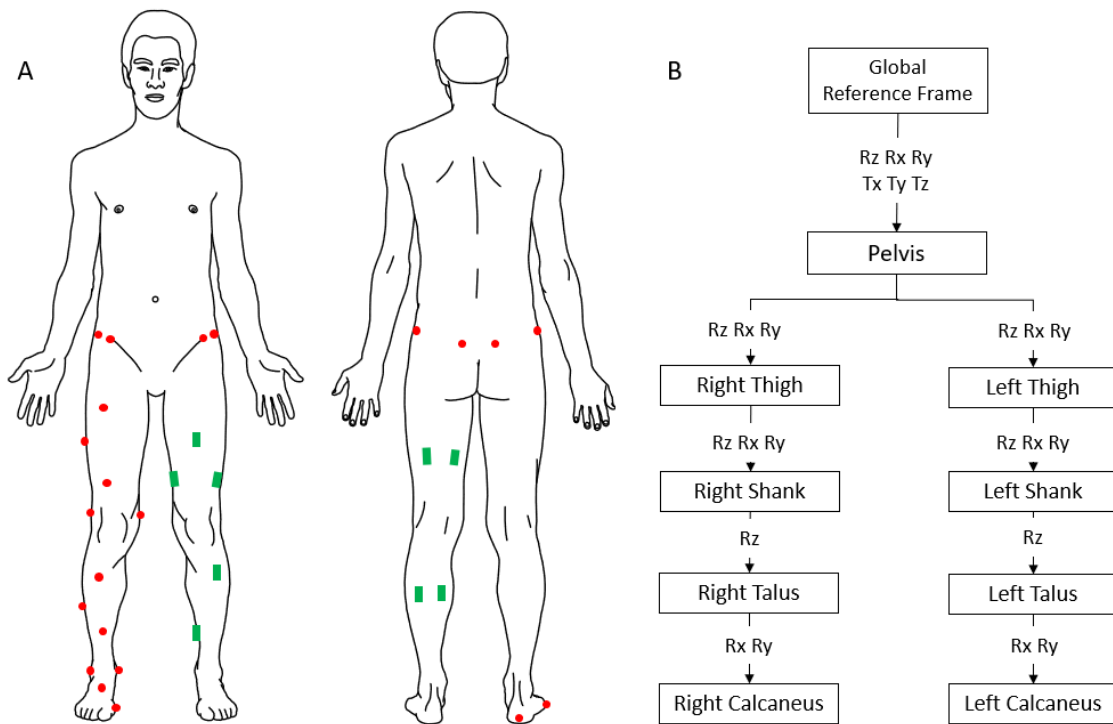
<b>Muscles</b>	<b>Drop-landing (ms)</b>	<b>Drop-jumping (ms)</b>	<b>p-value</b>	<b>Effect size</b>
TA	-109 [-75, -142]	-116 [-82, -128]	0.46	0.12
SOL	-99 [-72, -129]	-116 [-82, 128]	0.30	0.17
GM	-140 [-115, -175]	-134 [-114, -158]	0.09	0.27
GL	-157 [-128, -179]	-143 [-126, -180]	0.21	0.19
VM	-77 [-59, -90]	-71 [-50, -97]	0.35	0.15
VL	-72 [-57, -83]	-61 [-54, -99]	0.53	0.10
RF	-74 [-55, -104]	-54 [-46, -77]	0.11	0.25
BF	-61 [-13, -95]	-79 [-49, -119]	0.25	-0.18
ST	-99 [-13, -95]	-80 [-49, -119]	0.19	-0.21

374

375 **Table 2** Comparison between pelvis and foot vertical velocity at ground contact for drop-landing and  
 376 drop-jumping (median [1<sup>st</sup> and 3<sup>rd</sup> quartile]). Negative values for vertical velocities indicate a downward  
 377 velocity. Bold rows indicate a significant difference between the pelvis and foot vertical velocity at  
 378 ground contact for the associated condition.

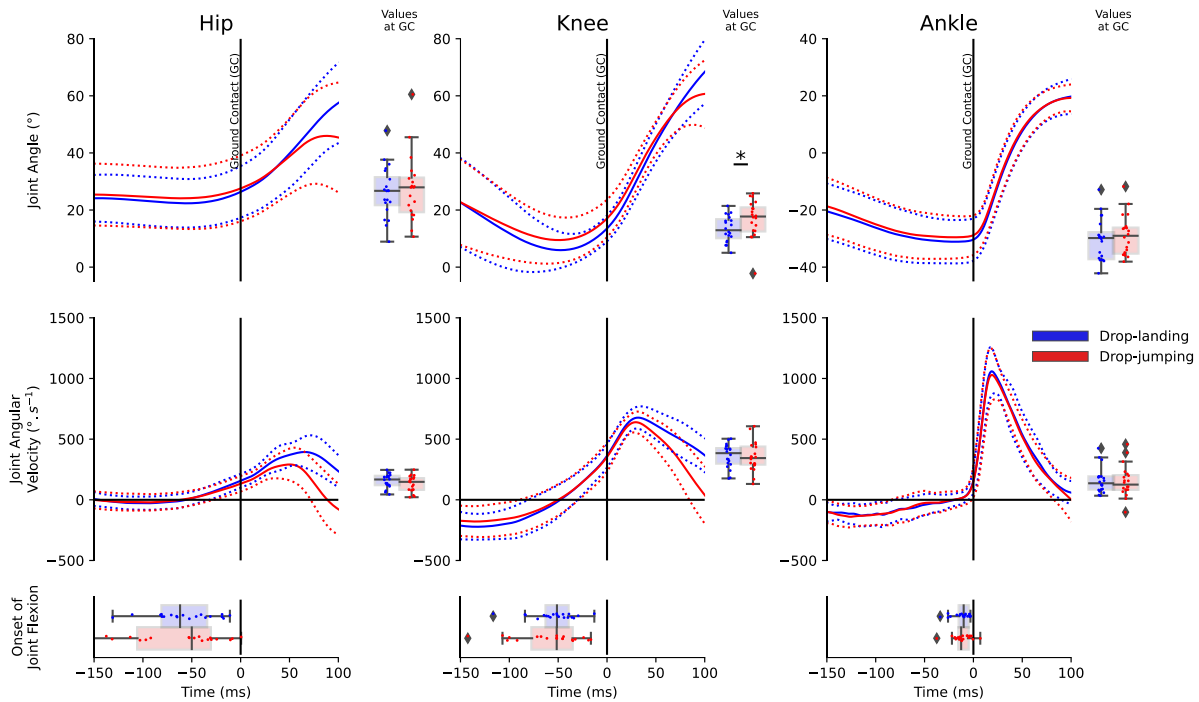
	<b>Pelvis vertical velocity at ground contact (m.s<sup>-1</sup>)</b>	<b>Foot vertical velocity at ground contact (m.s<sup>-1</sup>)</b>	<b>p value</b>	<b>Effect size</b>
Drop-landing	<b>-2.38 [-2.47, -2.28]</b>	<b>-2.09 [-2.17, -1.91]</b>	<b>&lt; 0.01</b>	<b>-0.61</b>
Drop-jumping	<b>-2.41 [-2.44, -2.32]</b>	<b>-2.11 [-2.18, -1.95]</b>	<b>&lt; 0.01</b>	<b>-0.57</b>

379

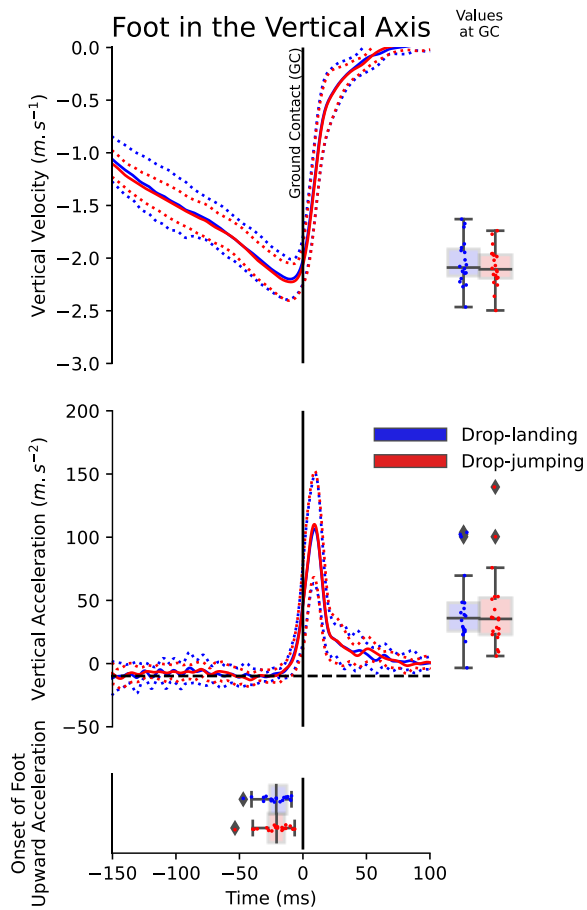
380 **FIGURES**

381

382 **Fig. 1** (A) Anterior and posterior view of the placement of markers (red dots) and EMG sensors (green  
 383 rectangles). Markers are only represented in the right lower limb in the figure, but were placed  
 384 bilaterally. Markers used in this study were placed on the pelvis (8), thigh ( $2 \times 5$ ), shank ( $2 \times 5$ ), and  
 385 foot ( $2 \times 4$ ). EMG sensors were placed on the dominant lower-limb of each participant (see Methods  
 386 section). (B) Details of the lower-limb kinematic model adapted from (Retailleau & Colloud, 2020) and  
 387 developed in OpenSim 4.3 (Delp et al., 2007), with the degrees of freedom allowed between the different  
 388 segments. Abduction-adduction, internal-external rotation, and flexion-extension are noted  $R_x$ ,  $R_y$  and  
 389  $R_z$ , respectively. Accordingly, translations are noted  $T_x$ ,  $T_y$  and  $T_z$ .



390  
 391 **Fig. 2** Sagittal kinematic results in the two landing tasks (drop-landing in blue, drop-jumping in red) for  
 392 the three lower-limb joints: hip (left), knee (middle), and ankle (right) during the [-150 to +100 ms] time  
 393 interval. Thick lines represent results averaged across all participants ( $n = 20$ ), and dotted lines represent  
 394 one standard deviation from the mean. The first row presents the joint angles (in  $^{\circ}$ ), the second row  
 395 presents the joint angular velocities (in  $^{\circ}\cdot s^{-1}$ ), and the third row presents the onset of joint flexion (in  
 396 ms), corresponding to the first instant when the angular velocity was positive with individual values.  
 397 Each vertical boxplot on the right side of each graph presents results at ground contact in the two landing  
 398 tasks, with individual values (joint angles for the first row, joint angular velocities for the second row).  
 399 A star indicates a significant difference between the two landing tasks.



400

401 **Fig. 3** Foot vertical kinematic results in the two landing tasks (drop-landing in blue and drop-jumping  
 402 in red) during the [-150 to +100 ms] time interval. Thick lines represent mean results across all  
 403 participants ( $n = 20$ ), while dotted lines represent one standard deviation from the mean. The first row  
 404 presents the foot vertical velocity (in  $m \cdot s^{-1}$ ), the second row presents the foot vertical acceleration (in  
 405  $m \cdot s^{-2}$ ), and the third row presents the onset of foot upward acceleration (in ms), corresponding to the  
 406 first instant when the foot acceleration was larger than the acceleration of gravity, represented by the  
 407 horizontal dotted line in the second row, with individual values. Each vertical boxplot on the right side  
 408 of each graph represents results at ground contact in the two landing tasks, with individual values  
 409 (vertical velocity for the first row, vertical acceleration for the second row).

410

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