

1 **MOTOR STYLE AT REST AND DURING LOCOMOTION IN HUMAN**

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## SUMMARY

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97 Humans exhibit various motor styles that reflect their intra and inter-individual variability  
98 when implementing sensorimotor transformations. This opens important questions; such as, at  
99 what point should they be readjusted to maintain optimal motor control? Do changes in motor  
100 style reveal the onset of a pathological process and can these changes help rehabilitation and  
101 recovery? To further investigate the concept of motor style, tests were carried out to quantify  
102 posture at rest and motor control in 18 healthy subjects under four conditions: walking at three  
103 velocities (comfortable walking, walking at 4 km/h and race walking) and running at maximum  
104 velocity.

105 The results suggest that motor control can be conveniently decomposed into a static  
106 component (a stable configuration of the head and column with respect to the gravitational  
107 vertical) and dynamic components (head, trunk and limb movements) in humans, as in  
108 quadrupeds, and both at rest and during locomotion.

109 These skeletal configurations provide static markers to quantify the motor style of  
110 individuals because they exhibit large variability among subjects. Also, using four measurements  
111 (jerk, root mean square, sample entropy and the two-thirds power law), it was shown that the  
112 dynamics were variable at both intra- and inter-individual levels during locomotion.

113 Variability increased following a head to toe gradient. These findings led us to select  
114 dynamic markers that could define, together with static markers, the motor style of a subject.  
115 Finally, our results support the view that postural and motor control are sub-served by different  
116 neuronal networks in frontal, sagittal and transversal planes.

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119 Key words: perceptive-motor styles, sensorimotor, pathological process, locomotion, running

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#### NEW AND NOTEWORTHY

- During human locomotion, motor control can be conveniently decomposed into a static and dynamic components.
- Variable dynamics were observed at both the intra and inter-individual levels during locomotion. Variability increased following a head to toe gradient.
- Finally, our results support the view that postural and motor control are sub-served by different neuronal networks in the frontal, sagittal and transversal planes.

## INTRODUCTION

Balance maintenance and locomotion both involve complex sensorimotor transformations that require the integration of several sensory inputs and the coordination of multiple motor outputs to more than 600 muscles throughout the body (Ting & McKay, 2007; Guerraz & Bronstein, 2008). The coordination of posture and movement relies on anticipatory and reactive postural control mechanisms, that are both modulated by sensory inputs and influenced by learning and experience (Massion, 1994). With the complexity of these processes, it is not surprising that they exhibit great inter-individual variability whatever the topic studied, postural control, locomotion, post-lesional plasticity, which has led to the perceptive motor style concept.

The sensory side of the perceptive motor style originates from the fact that several systems are at play when representing the body in space and when generating the system of coordinates on which the body's postural control is processed (Merfeld et al., 1999). Visual information determines the orientation of objects in space and the detection of movements, including postural oscillations. Somatosensory information provided by muscular, joint, and cutaneous receptors encode data on relative head, trunk and limb position in space. Finally, vestibular information encodes head position along with linear and angular head accelerations, thus helping to inform the brain of body orientation and movement. The continuous reweighting of these three types of sensory information is required for efficient, flexible, context-dependent postural control, as shown by numerous studies since the pioneering publication of Nashner (1976). Hence, the perceptive style can differ considerably among individuals and during pathologies for the same person (Vibert et al. 2001, Sasaki et al., 2002, Lacour et al., 1997, Isableu et al., 2003). For instance, stroke patients have a strong dependence on visual, proprioceptive and vestibular information to control their standing posture, and they differ individually in their relative sensitivity to each type of sensory stimulation (Bonan et al., 2013, 2015).

The motor side of the perceptive motor style is of emerging interest and is a property of the large number of degrees of freedom of the musculo-skeletal system: a given motor action can be performed in several ways by different actuators. For instance, (Maselli et al., 2017) recently proposed a methodology to explore the nature of early kinematic cues that could inform an

162 observer on the future direction of a ball projected by an unconstrained overarm throw. The  
163 recorded kinematics showed that throwing styles differed considerably among individuals, with  
164 corresponding inter-individual differences in the spatio-temporal structure of the thrower's  
165 predictability. Also, the simple fact that identification can be achieved on the basis of variability  
166 in gait patterns among different people (Sprager & Juric, 2015) confirms that the perceptive  
167 motor style has a motor side.

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169 The existence of various motor styles among individuals is rooted in the large intra- and  
170 inter-variability in their motor control. Importantly, a recent review by (Sternad, 2018) underlined  
171 that variability and noise in motor performance is not only a nuisance but it is also a ubiquitous  
172 and informative biological feature that has meaning in itself. On the nuisance side, by causing  
173 changes both at the musculoskeletal and sensory receptor levels, the aging process can increase  
174 gait variability, which leads to instability and falls (Herssens et al., 2018a, Kikkert et al., 2016,  
175 Ayoubi et al., 2015), particularly in frail seniors (Schwenk et al., 2014, Dasenbrock et al., 2016,  
176 Mortaza et al., 2014, Herssens et al., 2018b). Gait variability also increases during various  
177 pathologies (Figueiredo et al., 2018) such as cerebellar and vestibular ataxia (Schniepp et al.,  
178 2017, Buckley et al., 2018) and neurological disorders with motor deficits (Y. P. Ivanenko et al.,  
179 2013, Moon et al., 2016). However, variability in motor performance can also be an asset and  
180 depends on the importance of the movements for the desired task: movements contributing to the  
181 intended outcome would be consistent, whereas the others would be more variable (Todorov &  
182 Jordan, 2002). During walking and running, differences in speed would drive changes in  
183 variability, but adopting different gaits would drive changes in how people regulate stepping  
184 (Dingwell & Cusumano, 2015, Dingwell et al., 2017, Möhler et al., 2020). Also, as shown by a  
185 comparison of experienced and novice runners, variability during task execution is linked to  
186 adaptability and flexibility, which may reduce the risk of running injuries (Mo & Chow, 2018,  
187 Hamill et al., 2012). Finally, variability can specifically contribute to the acquisition of  
188 perceptual-motor behaviors that are novel, such as walking on a split-belt treadmill in normal  
189 individuals (Van de Putte et al., 2006, Altman et al., 2012) and those with pathologies (Mawase  
190 et al., 2016). Variability of several gait metrics are also useful indicators for the study of  
191 development (Kraan et al., 2019).

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193 In summary, it is now well established that humans exhibit various perceptive-motor  
194 styles, which are based on 1) inter-individual variations in how they process sensorimotor  
195 transformations and 2) intra-individual fluctuations of sensory and motor control. In this  
196 context, characterizing and monitoring motor style is important for several reasons. First,  
197 early predictions formulated during an action are important to control several aspects of  
198 human behavior when individuals interact with others. This necessitates *a priori* knowledge  
199 of the information sources that are relevant for making reliable predictions, and which differ  
200 with the motor style of the person. Second, differences in motor style are idiosyncratic and/or  
201 detrimental, which raises the question of at what point should they be readjusted to maintain  
202 optimal motor control (see Moore, 2016 for a review concerning walking and running  
203 economy). Third, changes in motor style could reveal the onset of a pathological process and  
204 could help in following its recovery (König et al., 2016) using the thresholds to pathological  
205 variability during standing and walking.

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207 Nevertheless, despite its attractiveness, the concept of motor style remains relatively  
208 elusive, and this study is aimed at determining markers that could better define the motor  
209 style of a person. It is hypothesized that markers should have two characteristics: first, they  
210 should be idiosyncratic for a given person; that is, they should exhibit the lowest intra-individual  
211 variability possible; and second, they should be as different as possible between individuals; that  
212 is, they should exhibit the largest inter-individual difference possible. The motor style of a person  
213 shapes all his/her motor activities. This study is limited to markers characterizing an individual's  
214 postural control at rest and during locomotion because these behaviors are routinely monitored in  
215 clinics and sport. Furthermore, analysis of postural control at rest is restricted to the sagittal plane  
216 because of the low number of degrees of freedom of the skeletal systems in the frontal and  
217 transversal planes, when subjects were instructed to stand and gaze forward. Locomotion entails  
218 progression toward a goal (navigation), generation of locomotor patterns (dynamic components)  
219 and maintenance of a stable posture in different environments (static component), meaning that  
220 numerous markers are available to capture the various locomotor style facets. Here, a choice was  
221 made to study the body configuration maintained in the sagittal plane during walking and running  
222 and four dynamic parameters in three-dimensions: a smoothness measure expressed by the jerk, a  
223 variability measure expressed by the amount of movement given by the root mean square (RMS),

224 a regularity measure given by the sample entropy, and a measure of trajectory optimization given  
225 by the two-thirds power law.

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## METHODS

### PARTICIPANTS

Eighteen healthy volunteers (8 females and 10 males, 20-58 years old) participated in the trial. All participants were free of any diagnosed diseases. All participants were normal bodied ( $170 \pm 12$  cm and  $67 \pm 21$  kg, see Table I) with a body mass index ( $22.3 \pm 2$  kg/m<sup>2</sup>) corresponded to a “normal” range “body mass index (BMI) classification” and the Global Database on Body Mass Index (*WHO | The World Health Report 2006—Working together for health*, s. d.). A priori approval was gained from the University's Research board of the Plateforme d'Etudes de la Sensorimotricité and written informed consent was obtained from all participants.

### EXPERIMENTAL PROTOCOL

All the collected data was recorded on the Plateforme Sensorimotricité hosted by the Université Paris Descartes, in Paris. A Cybex 770T (0,8 à 20 km/h) treadmill was used to control walking and running in the laboratory. Linear acceleration and angular velocity of the head, lower back (L4-L5 vertebra) and both feet were collected using four inertial motion units (IMUs) and the Coda motion system. The IMUs included triaxial accelerometers, gyroscopes and magnetometers (XSens, Culver City, CA, USA, MTw Measurement Units, 3.5h LiPo battery, 27g, 3.5x5.8x1.0cm<sup>3</sup>,  $\pm 16$ g,  $\pm 1200$ deg/s, 100Hz, errors 0.003m/s<sup>2</sup> and 0.05deg/s). They were fixed with manufacturer-designed adhesive straps and connected to a computer via Wi-Fi. Measurements were performed using the Codamotion 3-D Analysis System (Charnwood Dynamics Ltd., Leicestershire, UK), which is composed of light-emitting diode (LED) markers, the Coda sensor module and the ODIN software suite. This system was used to measure the subjects at rest, during walking and running. Infrared light signals generated by the markers placed on the anatomical landmarks were captured by the Coda sensor module at a rate of 100 Hz. The data was processed with the Codamotion ODIN software running on a personal computer with a Microsoft Windows-based operating system. Twenty-four Coda active markers were placed on the subject body. Locomotion for 4 segments of the body was of interest: head, trunk, legs and feet, and a minimum of three markers were selected for each segment (see Figure 1). The markers were detected by four Coda CX1 units placed in the laboratory working space so as to cover the running range.

- Four markers were placed on the head (one, FH, on the forehead was placed on the Xsens sensor, two on the left LT and right RT temporal bones, and one on the external occipital protuberance BH).
- One marker was placed on the sternal notch (STE);
- Two markers were placed on the left and right acromion (LA, RA),

- 265
- One marker was placed on the spinous process of the 5th lumbar vertebra (L5)
- 266
- Two 4-Marker-Clusters were installed below the right and left lateral condyle of the tibia (LLT,
- 267
- RLT).
- 268
- Eight markers were placed on the feet (two markers on the left and right heel elbows (LHE, RHE),
- 269
- two on the left and right heels at low level (LHL, RHL), two on the left and right over the Xsens
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- sensor on the instep (LI, RI) and two on the right and left fifth metatarsal-phalangeal joint (LM,
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- RM).

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275 The trial protocol consisted of 5 stages:

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- 1) Static recordings: the subject stood on the non-moving treadmill for 30 seconds with eyes open
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- and then eyes closed.
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- 2) Comfortable walking: the participant set the treadmill velocity to what they considered to be
- 279
- comfortable walking (V1) and then continued to walk at V1 for 2 minutes.
- 280
- 3) Walking: the participant set the treadmill velocity at 4km/h (V2) (Long & Srinivasan, 2013)) and
- 281
- walked at V2 for 2 min.
- 282
- 4) Race walking: the participant increased the velocity until it reached his/her maximum walking
- 283
- velocity, (V3) and walked at V3 for 1 min.
- 284
- 5) Running: the participant increased the velocity up to his/her maximum running velocity (V4) and
- 285
- then ran at V4 for 2 minutes.

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## 288 **DATA PROCESSING**

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290 This section introduces the methodology used to quantify the motor style. This methodology involved three

291 steps: data pre-processing, extraction of static markers and then extraction of dynamic markers.

292

### 293 **Data pre-processing**

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295 Two preliminary remarks: first, Owings and Grabiner (Owings & Grabiner, 2004) have shown that

296 normalizing step length and width using body height is not advantageous in the statistical analysis of

297 locomotion. Therefore, this normalization was not used here. Second, Hafer et Boyer (Hafer & Boyer,

298 2017) found that at least ten treadmill walking and running strides are required to attain reliable measures

299 of a subject's coordination variability. The results obtained here are well above this limit with at least 70

300 strides for walking and running (Table II).

301

302 Two instants in the gait cycle were defined: Heel strike and Toe off, for each leg. Automatic identification  
303 of these instants was performed by peak detection in the LHL and RHL sensor signals for heel strike and  
304 the right and in the left fifth metatarsal-phalangeal joint (LM, RM) sensor signals for toe off.

305  
306 Two spatio-temporal parameters of interest were calculated from the detected heel strikes. First, the step  
307 width calculated as the maximal left/right distance (medio-lateral signal) reached for each step at heel  
308 contact. Second, the step length calculated as the distance between the right and left heels at the moment  
309 of a local maximum in the horizontal marker data.

310

### 311 **Extraction of static markers**

312

313 As illustrated in Figure 2, the skeletal configuration in the sagittal plane of the subjects at rest is defined  
314 using three reference points. The first point was determined using the sensor located at the spinous  
315 process of the 5th lumbar vertebra (L5). The second point was virtual (P1), and it was calculated using  
316 triangulation of the left and right acromion (LA and RA) sensors and the sternon notch (STE) sensor. The  
317 third point was also virtual and corresponded to the centroid of the 4 sensors positioned on the head (P2).

318

319 Then, in order to determine the skeletal configuration of each subject in the sagittal plane, three  
320 inclinations were calculated:

321 i) The trunk inclination was defined as the angle between the gravity vector passing through L5  
322 and the vector L5 - P1.

323 ii) The head inclination vector was defined as the angle between the gravity vector through P1  
324 and the vector P1 - P2.

325 iii) The leg inclination (right and left) was defined as the angle between the gravity vector through  
326 L5 and the vectors L5 - LHL, L5 - RHL.

327

328 The skeletal configuration in the sagittal plane was determined in the same way while the subject was  
329 walking or running. The angles between the body segments mentioned above were calculated at the four  
330 time instants corresponding to the right and left heel strikes and right and left toe off.

331

332

### 333 **Extraction of dynamic markers**

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#### 335 ***Jerk***

336

337 Jerk is the third time-derivative of position. It is a measure of the rate at which each part of the body is  
338 accelerated. First, the positional data for each marker was smoothed using a 4th order, zero-lag

339 Butterworth filter following the procedure described in Hreljac (2000). Second, the second derivative  
340 (acceleration) of the positional data was calculated using finite difference equations. Finally, the  
341 acceleration data was smoothed, and the first derivative of acceleration  $\frac{d(Acc)}{dt}$  (jerk) was calculated.

342

343 For the transversal plane Jerk was calculated as follows:

344

$$JERK = \frac{1}{2} \int_0^t \left( \frac{dAccX}{dt} \right)^2 + \left( \frac{dAccY}{dt} \right)^2$$

345

346 Where AccX corresponds to the obtained acceleration in the medio-lateral axis and AccY corresponds to  
347 the obtained acceleration in the antero-posterior axis. Jerk is calculated in the other planes by combining  
348 the acceleration in the other directions: AccX and AccZ for the frontal plane and AccY and AccZ for the  
349 sagittal plane.

350

### 351 **RMS**

352

353 The RMS of trunk acceleration is frequently used in gait analysis. For marker displacement, the Root-  
354 mean-square (RMS) amplitude represents the standard deviation of the marker displacement. This  
355 parameter measures the average absolute displacement around the mean marker and has been  
356 employed by numerous researchers. For example, a decrease in RMS amplitude of the Center of  
357 pressure (CoP) represents an increased ability to preserve an upright stance. An increased RMS value  
358 suggests a decreased ability to maintain postural control.

359

### 360 **Sample Entropy**

361

362 The sample entropy is a variation of the approximate entropy method. Sample entropy is the foundation  
363 for determining the complexity of both stationary and nonstationary signals. Sample entropy is the  
364 negative natural logarithm of the probability that two sequences will be similar for  $m + 1$  data points  
365 divided by the probability that two sequences will be similar for  $m$  data points. For two data points to match  
366 they need to be within a range of tolerance of  $\pm r$ , which is between 10% and 20% of the standard  
367 deviation of the original data set. The match of the template sequence to itself is excluded in this  
368 calculation. Elimination of this self-matching is the distinction between sample entropy and approximate  
369 entropy. The equation used to calculate the sample entropy of a time series data-set is as follows:

370

$$SampEnt = \ln \left( \frac{\sum_{i=1}^{N-m} n_i^m}{\sum_{i=1}^{N-m} n_i^{m+1}} \right)$$

371  
372 Where  $N$  is the number of points in the data set,  $n_i^m$  is the number of vector matches for vectors of length  
373  $m$  and  $n_i^{m+1}$  is the number of vector matches for vectors of length  $m+1$  (Costa et al., 2005).

### 374 375 **Two-Thirds Law**

376  
377 A mathematical equation known as the “Two-Thirds Power Law” was created by (Lacquaniti et al., 1983a)  
378 to demonstrate that the kinematics of many different human movements seem to follow a relationship  
379 between the velocity and the curvature of the motor trajectory. This law is stated as  $v = \gamma \kappa^{-\beta}$ , and  
380 represents a robust local relationship between the geometrical and temporal aspects of human movement,  
381 which is represented by curvature  $\kappa$  and speed  $v$ , with a piecewise constant  $\gamma$  and exponent value  $\beta = 1/3$ .

382  
383 This law has been partially demonstrated for the trajectory of the Centre of Mass (CM) of the human body  
384 during walking. In (Tesio et al., 2011) the trajectory of the CM was segmented in high and low curvature  
385 segments. The  $\beta$  coefficient was close to the expected  $1/3$  value if the complete trajectory was  
386 considered. In high-curvature segments the  $\beta$  coefficient is significantly higher ( $\beta = 0.486$ ). By contrast, in  
387 low-curvature segments the  $\beta$  coefficient is significantly lower ( $\beta = 0.185$ ).

388  
389 In an equivalent form, let  $\omega$  be the angular or curvilinear speed,  $r_c$  the radius of curvature,  $C=1/r_c$  the  
390 curvature, and  $k$  a constant. In its simplest form, the law predicts that  $\omega=kC^{2/3}$ , where  $k$  is a constant.  
391 Hence the popular term “2/3 power law”.

### 392 393 394 **Statistical Analysis**

395  
396 Continuous variables are presented as mean  $\pm$  standard deviation. Comparison between men and women  
397 was performed using the unpaired Mann Whitney Wilcoxon nonparametric test. Intra- and inter-variability  
398 are illustrated in figures 6, 7, 8 and 9. In these figures, the sensors are represented on the abscissa and  
399 they are numbered from 1 to 24. Sensors 1 to 4 were positioned on the head, sensors 5 and 6  
400 corresponded to the right and left acromion (LA and RA), 7 was positioned at the sternum notch (STE), 8  
401 at L5, sensors 9 to 16 are positioned on the legs and sensors 17 to 24 on the feet. In order to facilitate a  
402 macroscopic interpretation of the statistical analysis, the computed variables of each sensor were grouped  
403 by body parts and the mean value has been calculated. Head (1-4), Trunk (5-7), L5 (8), Leg (9-16), Feet  
404 (17-24). Comparison between different groups of sensors for evaluation of the intra- and inter-variability  
405 was performed using the Wilcoxon Sign rank nonparametric paired test and paired t-test. For all  
406 comparisons, a  $p$ -value  $\leq 0.05$  was considered to be statistically significant and the size effect was

407 provided through  $se^2 = z_{score}^2/N$  or a sign rank test and Cohen  $d$  for paired t-test (Fritz et al., 2012) for  
408 every p-value. The statistical analyses and variable computations were performed using MATLAB 2019.  
409  
410  
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## RESULTS

### Quantification of locomotor patterns

The mean and standard deviation of the speed, the step length and step width are presented in Table II for the 18 males and females.

As expected, the locomotor patterns differed between males and females and for different walking paces. Variability expressed in terms of the coefficient of variation (or CV, ratio of the standard deviation to the mean) was higher for step width than for step length. Maximum CV occurred during running (40% for step width vs. 12% for step length). These results confirmed that step width was a more meaningful descriptor of the individual locomotion control than step length.

### Skeletal configuration in the sagittal plane

#### *At rest*

The average sagittal inclination for the eighteen subjects was  $11.0^\circ \pm 7.5^\circ$  for the head,  $11.6^\circ \pm 2.9^\circ$  for the trunk and  $1.8^\circ \pm 2.0^\circ$  for the legs. That is, the trunk and the head were aligned and were inclined forward, while the leg were aligned with the gravity vector.

Resting postures displayed distinct features when the subjects were considered separately. Figure 3 A illustrates schematically the various skeletal configurations adopted by the 18 subjects at rest. In order to further characterize these differences, the inclinations of the head, the trunk and the legs vs gravity vector were calculated for each subject. The results are illustrated in Figure 3 B.

#### *During locomotion*

The skeletal configuration of the subjects during locomotion was quantified at the time of heel strike for each foot. Figure 4 illustrates three subjects walking and running at self-selected speeds. For each subject, recordings of 30 superimposed strides for the left (in red) and right leg (black) are shown. Clearly, the skeletal configuration varied for a given subject at each strike and was different for each subject. The variability of each stride is seen as the heel strikes touch the ground at different positions for each leg (left in red, right in black). It was generally found that the skeletal configuration variability increased with velocity, as illustrated for subjects 6 and 13 by the forward inclination of the trunk, which was more important than head inclination. However, there were exceptions to this rule, as illustrated for subject 17 in Figure 4. While running at 6.5 km/h, which was the lowest running speed of all the subjects in this study, the subject presented large head and trunk inclinations for increased velocity.

449  
450 Detailed analysis of head, trunk and leg inclinations in the sagittal plane at the time of heel strike is  
451 presented in Figure 5. Leg inclinations increased progressively for all subjects with respect to the static  
452 case when the subjects walked comfortably, walked at 4 km/h and race walking i.e. when velocity  
453 increased (comfortable walk versus all the other speeds - pairwise, all  $p < 0.001$ ,  $se^2 > 0.5$ ). Then, an abrupt  
454 increase in leg inclination in the sagittal plane took place during running. No significant differences in  
455 head inclination were found in any exercise, while trunk inclinations were significantly higher during race  
456 walking and running ( $p < 0.001$ ,  $se^2 > 0.7$ ) compared to standing and walking ( $p = 0.002$ ,  $se^2 = 0.49$ ). Finally  
457 (see Figure 5), head and trunk inclinations were more variable than leg inclination among subjects for all  
458 tasks ( $p < 0.01$ ,  $se^2 > 0.36$ ).

459  
460 The variability of the skeletal configuration in the 18 subjects was quantified by calculating the CV for each  
461 body segment (intra-individual). The average head inclination CVs were 0.43, 0.30, 0.11 and 0.22,  
462 respectively, for walking, walking at 4km/h, race walking and running. This amounted to CVs equal to  
463 0.08, 0.08, 0.07 and 0.07 for the trunk inclination and 0.05, 0.03, 0.02 and 0.04 for the leg inclination.  
464 Altogether, variability in head inclination is much larger than for trunk and legs. All body parts, but  
465 especially average CV of the head inclination, tend to gain in stability with increasing locomotion speed.

466

## 467 **Dynamics of locomotion**

468

469 In contrast to the static analysis, the quantification of dynamic parameters was performed for the three  
470 anatomical planes: sagittal, frontal and transversal planes. As hypothesized in the introduction, features  
471 that adequately determine the motor style should have two characteristics: a low intra-individual variability  
472 and a high inter-individual variability during locomotion.

473

### 474 *Intra-individual variability*

475

476 In order to quantify the intra individual variability of the body segment movements during locomotion, each  
477 exercise was separated into strides and the CV for the motion of each sensor was calculated. This  
478 procedure was performed for each plane in the space and the results of these calculations are  
479 illustrated in Figure 6. Each row represents a subject (from 1 to 18) and each column represents a  
480 sensor (from 1 to 24). The different protocol phases are illustrated in four different panels from top  
481 to bottom. The data for each plane in space are illustrated from left to right. The CVs are  
482 expressed with a color code ranging from 0 to 0.7. Average head and trunk intra-individual  
483 variability was found to be significantly lower ( $p < 0.001$ ,  $se^2 > 0.41$ ) compared to the leg and feet

484 intra-variability for all the exercises and all planes. Interestingly, head intra-variability was found to  
485 be statistically lower compared to trunk intra-variability during: a- running in the transversal plane  
486 ( $p < 0.001$ ,  $se^2 = 0.73$ ), b- all exercises in the sagittal plane ( $p < 0.05$ ,  $se^2 > 0.27$ ) and c- race walking  
487 and running in the frontal plane ( $p < 0.001$ ,  $se^2 > 0.77$ ).

488  
489  
490 As already seen qualitatively for three subjects in Figure 4, Figure 6 shows quantitatively three  
491 distinct locomotion features:

- 492 • First, the head and trunk movements (sensors from 1 to 8) of each subject and for each plane  
493 in space displayed very little intra-individual variability between strides. This is especially true  
494 in the frontal plane.
- 495 • Second, there is clearly a gradient in the CVs from the head to the leg, with the head  
496 movements being the least variable.
- 497 • Third, given the intra-individual variability of the feet movements, they should not be chosen  
498 as a marker to determine the motor style of each subject.

499  
500

### 501 *Inter-individual variability*

502  
503 Figures 7, 8 and 9 respectively summarize the computed results for jerk, RMS and sample entropy. For  
504 each of these three figures, the average values of jerk, RMS and sample entropy are displayed in the left  
505 column and the coefficient of variation in the right column. The jerk (Figure 7), RMS (Figure 8) and sample  
506 entropy (Figure 9) were calculated independently for each sensor in each plane and for the four protocol  
507 phases. In figures 7, 8 and 9, each square represents the data recorded from one sensor averaged over  
508 the 18 subjects, i.e. for a specific body location. The ordinate represents the four different conditions. The  
509 blue to red color gradient indicates an increase in the represented numerical variable. In the case of the  
510 CV, blue represent a small variability among the subjects while red represents a high variability among the  
511 subjects.

512  
513 *Analysis of the jerk:* As illustrated in Figure 7, higher average values of the jerk were observed in the  
514 sagittal and frontal planes for the sensors placed on the head, which reflected important changes in the  
515 acceleration patterns during the four investigated types of locomotion. Average head jerk of the individuals  
516 was found to be significantly higher ( $p < 0.001$ ,  $se^2 > 0.77$ ) compared to the average trunk, leg and feet jerks  
517 in the frontal and sagittal planes, in all four exercises. Lower average values were observed in the frontal

518 plane at the lower part of the body (L5, legs and feet). For the transversal plane, jerk was moderate and  
519 similar for all sensors and protocol phases.

520  
521 The CV of the lower trunk movement at L5 (sensor 8) was significantly higher (in all exercises) with  
522 respect to the sensors on the upper part of the body ( $p < 0.05$ ,  $d > 2$ ) in the frontal plane, and the difference  
523 tended to decrease while the subjects were running. Also, in the frontal plane, the sensors positioned on  
524 the anterior left and anterior right tibial crest (sensors 13 and 14) showed large CV variation during  
525 walking and racing and this increased when subjects ran (for sensor 13,  $p < 0.05$ ,  $d > 2$  when compared to  
526 average variation of head, trunk, feet, for sensor 14,  $p < 0.05$ ,  $d > 2$  when compared to average variation of  
527 head and feet). For the sagittal and transversal planes, a low jerk variability was observed for the upper  
528 part of the body for the four protocol phases, while large jerk variability was observed at feet level.

529  
530 Overall, by comparing Figures 6 and 7, the best markers for the determination of the motor style based on  
531 the jerk appear to be the marker at L5 and those on the anterior left and anterior right tibiae in the frontal  
532 plane.

533  
534 *Analysis of the RMS:* As illustrated in Figure 8, the quantity of motion increased progressively from head  
535 to feet in the sagittal and transversal planes, but remains quite low in the frontal plane. The average head  
536 RMS of the individuals was found to be significantly lower ( $p < 0.001$ ,  $se^2 > 0.77$ ) compared to average leg  
537 and feet RMS in sagittal and transversal plane, in all four exercises. On the other hand, the average head  
538 RMS was found to be significantly lower ( $p < 0.01$ ,  $se^2 > 0.6$ ) compared to average trunk RMS only while the  
539 subjects were running in the frontal plane. No specific pattern was observed concerning the inter-  
540 variability (as shown by the CV) in the frontal plane. In contrast, an important inter-individual variability  
541 was observed in sensors located on the upper part of the body (head and trunk versus leg and feet,  
542 pairwise  $p < 0.001$ ,  $se^2 > 0.77$ ) in the sagittal and transversal planes.

543  
544 Overall, by comparing Figures 6 and 8, the best markers for the determination of the motor style based on  
545 the RMS appeared to be the markers on the head and trunk in the transversal plane.

546  
547 *Analysis of the Sample Entropy:* As illustrated in Figure 9, the sample entropy is quite uniform and low for  
548 markers in the transversal plane. However, the transversal average head entropy was significantly lower  
549 ( $p < 0.001$ ,  $se^2 > 0.69$ ) compared to trunk, leg and feet, for all the exercises. In contrast, frontal and sagittal  
550 average head and trunk entropies were both found to be significantly higher ( $p < 0.001$ ,  $se^2 > 0.53$ )  
551 compared to those derived from leg and feet in all exercises, reflecting the low locomotion regularity, even  
552 more so during race walking and running. The CVs were found to be large for the upper part of the body  
553 (pairwise comparison of head and trunk versus leg and feet ( $p < 0.01$ ,  $se^2 > 0.50$ ), for the sagittal (except for  
554 running) and transversal planes and for the lower part of the body and the frontal plane (head and trunk  
555 versus feet,  $p < 0.05$ ,  $se^2 > 0.39$ ).

556  
557 Overall, by comparing Figures 6 and 9, the best markers for the determination of the motor style based on  
558 the sample entropy appeared to be the markers on the upper part of the body for the sagittal and  
559 transversal planes and on the lower part of the body for the frontal plane, except during running.

560  
561 *Analysis of body segment trajectories*

562  
563 The trajectory of each sensor was separated into stride segments in the different planes. Figures 10 and  
564 11 show typical examples of the L5 and left ankle markers' trajectories for the 18 subjects while walking at  
565 a comfortable speed and running. Trajectories are shown in the three different planes. As can be  
566 observed, the trajectories were qualitatively similar among subjects in the sagittal plane for L5. The  
567 trajectories were more complex when subjects ran. In contrast, the trajectories were dissimilar among the  
568 subjects in the frontal and transversal planes. For the ankle, as for L5, similar trajectories were observed  
569 among the subjects in the sagittal plane. The trajectories also largely differed in the frontal and transversal  
570 planes.

571  
572 Description of all trajectories in the various protocol phases for every marker in the three planes of space  
573 would require too much space. As a rule, however, the trajectories always qualitatively differed in shape  
574 amongst the subjects for every marker, every protocol phase and every plane in space. For the sagittal  
575 and transversal planes the trajectories could be similar in shape or not depending on the markers. It  
576 remains that quantitatively, every marker differed amongst the subjects for every protocol phase and every  
577 plane of space, as illustrated in Figures 10 and 11.

578  
579 The trajectories for all sensors were analyzed to check if they obeyed the two thirds law. For each stride,  
580 the curvature and the angular velocity were calculated and the slope of their relationship ( $\beta$  factor) was  
581 expressed in a logarithmic scale. This is illustrated in Figure 12 for the sensor located at L5 with a subject  
582 walking at preferred speed and running.

583  
584 Figure 13 illustrates the distribution of the  $\beta$  factor for the different walking and running speeds in the three  
585 different planes. The red line in each boxplot represents the median  $\beta$  factor of each distribution. The  
586 edges of the box represent the 25<sup>th</sup> and 75<sup>th</sup> percentile of the data point. The lines emanating from each  
587 box extent to the most extreme data point not considered to be part of the outliers. The outliers are  
588 represented by red crosses. For example, in the transversal plane, the head  $\beta$  factors are significantly  
589 lower ( $p < 0.001$ ,  $se^2 > 0.48$ ) than those of the lower body during all exercises, except for running. In the  
590 sagittal plane, feet  $\beta$  factors are significantly higher ( $p < 0.001$ ,  $se^2 > 0.46$ ) than those of the other markers  
591 during every protocol phase. In the frontal plane, the feet  $\beta$  factors are significantly lower ( $p < 0.001$ ,  
592  $se^2 > 0.52$ ) than those of the other markers during every protocol phase. In summary,  $\beta$  factors may vary  
593 with the considered body segment and velocity of locomotion. The  $\beta$  factors for the lower body (feet and

594 legs) were significantly lower ( $p < 0.01$ ,  $se^2 > 0.32$ ) in the frontal plane compared to transversal and sagittal  
595 planes for each protocol except for running, where only feet maintain a significant difference. In contrast,  
596 head was significantly higher ( $p < 0.05$ ,  $se^2 > 0.28$ ) in the frontal plane compared to transversal and sagittal  
597 in higher-speed protocols (race walking and running).

598  
599 Finally, as illustrated in Figures 10 and 11, the trajectories and therefore the  $\beta$  factors appeared to be  
600 valuable candidates for definition of the motor style of every individual, independent of protocol phase,  
601 marker and spatial plane.

602

## DISCUSSION

The current results confirm that when at rest and during locomotion, motor control in humans can be decomposed into stable configurations of the head and column with respect to the gravitational vertical and dynamic components (head, trunk, arms and limb movements). By quantifying and comparing these skeletal configurations and four dynamic features (jerk, RMS, sample entropy and two-thirds power law) at rest and during locomotion in 18 subjects, it was possible to propose a set of markers that define the locomotion motor styles. The markers are summarized in Table III.

Finally, previous studies have suggested that postural and motor control are sub-served by different neuronal networks in the frontal, sagittal and transversal planes. Our results support this view by showing that the dynamic markers used to describe locomotion and running differ markedly by plane in space.

### **Static markers of the motor style**

Motor control is characterized by a finite number of skeletal configurations in quadrupeds. At rest and during circling, a quadruped's skeletal system adopts a stereotypical posture S-shaped configuration (Vidal et al., 1986)(Vidal et al., 2004)(Graf et al., 1995). During trotting and running, the column degrees of freedom are redistributed: the atlanto-occipital joint and the cervico-thoracic junction are fully extended and the thoraco-lumbar kyphosis decreases markedly relative to at rest. A remarkable feature of these behaviors is the stability of the head and the entire column relative to space (Vidal et al., 2004). In contrast, in standing humans, the column exhibits limited degrees of freedom in the frontal plane. In addition, in the present study, subjects were asked to maintain their gaze in the straight-ahead direction. Hence, our subjects exhibited little inter-individual variability in skeletal configuration in the transverse and frontal planes at rest, which explains why the analysis was focused on motor control at rest in the sagittal plane.

### *Sagittal skeletal configurations at rest*

All subjects aligned their posture with gravity, which is not surprising. However, as illustrated in Figure 3, the orientation versus gravity of the head, trunk and legs in the sagittal plane, as defined by three real and one virtual marker (heel, L5, sternum and centroid of the

635 head), differed among the subjects. To best characterize this variability, it was postulated that the  
636 two optimal characteristics of any feature defining the motor style of an individual should be low  
637 intra-individual variability and large inter-individual variability. Using these criteria it was shown  
638 that the orientation of the head and trunk in space and the orientation of the head versus the trunk  
639 in the sagittal plane seemed to be important markers for identification of individuals at rest (see  
640 Table III). These results agree well with a recent study by (Khalil et al., 2018), who found large  
641 differences in inter-individual strategies for maintaining horizontal gaze in asymptomatic  
642 subjects.

643

#### 644 *Skeletal configurations during locomotion*

645 Figures 4 and 5 show that during locomotion, as at rest, all subjects adopted idiosyncratic  
646 skeletal configurations and could be divided in two groups. Three subjects increased their trunk  
647 and head inclinations during walking but decreased them during running to values similar to at  
648 rest. Interestingly these subjects were not habitual runners, but more detailed study would be  
649 needed to relate posture to skill during running. In the 15 remaining subjects the forward trunk  
650 inclination increased with locomotion velocity, including during running, which displaced the  
651 center of mass forward. This forward displacement is an advantageous biomechanical feature that  
652 is likely to facilitate locomotion. A precise quantification of the relationship between trunk  
653 inclination and locomotion velocity would require a larger sample of subjects and velocities, so  
654 this was not attempted here. The leg angles versus the vertical also increased with velocity, but in  
655 contrast to the progressive inclination of the trunk orientation, this angle increased sharply by 10  
656 degrees during running. Altogether, compared to the strategy adopted by quadrupeds, the ability  
657 to alter the inclination of the body segments during locomotion in the sagittal plane can be  
658 considered an optional attribute of bipedalism. For the intra-individual variations, the coefficient  
659 of variation (CV) for the whole sample was low except for the two legs during running.

660 Finally, the skeletal configurations adopted during locomotion at the head and trunk levels  
661 were stable enough for a given subject to be used as an index of his/her motor style (see Table  
662 III). This result agrees with the finding of Newell et al. (2018), who showed that head posture,  
663 cervical spine alignment and muscle activation levels differed significantly while moving, in  
664 comparison with resting upright.

665

666 **Dynamic markers of the motor style**

667

668 *Intra-individual variability*

669 As illustrated in Figure 6, a clear gradient of variability of the body movement versus  
670 space is observed for each stride and in each tested subject, and this variability increased from the  
671 head to the tip of the feet for any considered plane in space. Due to bipedalism developing on  
672 uneven ground, it may be not surprising that looser limb control is maintained while the trunk and  
673 head are stabilized in space. For inter-individual variability, four types of dynamic markers were  
674 investigated.

675

676 *Jerk*

677 According to Flash and Hogan (T. Flash & Hogan, 1985), the “minimization of mean-  
678 squared jerk is a mathematical model of one movement objective, the production of smooth,  
679 graceful movements” (p. 1698), where jerk is defined as the rate of change of acceleration  
680 (Viviani & Flash, 1995)(Hreljac & Martin, 1993)(Hreljac, 2000). A decrease in jerk cost, which  
681 indicates increased smoothness, takes place in practiced movements both at the level of the upper  
682 limbs (Schneider & Zernicke, 1989) and the lower limbs (Hreljac, 1993). Also, aging is  
683 associated with slower and less smooth movements (Yan, 2000). To the authors’ knowledge, this  
684 study is the first to quantify jerk systematically for the head, trunk and leg movements during  
685 locomotion in the three spatial planes. The minimum jerk cost was increased with increasing  
686 stride length and walking speed of the subjects. Indeed, the normalized jerk increased for the  
687 head and upper trunk (sternum marker) in the frontal and sagittal planes, while it was low in the  
688 transversal plane for every part of the body and for the four velocities tested. That is,  
689 smoothness and economy are not always optimized in humans as is the case in quadrupeds  
690 (Vidal et al., 2004).

691

692 Could jerk be used as a motor style marker during locomotion? As illustrated in Figure  
693 7, the normalized jerk in the frontal plane at the trunk and legs levels could be useful (see Table  
694 III) because of the small intra-individual variability (Figure 6) and the large inter-individual  
695 variability (right panel in Figure 7).

696

697 *RMS*

698 Head and trunk stabilization in space are required to maintain balance of the whole-body  
699 during locomotion (Pozzo et al., 1990)(Maslivec et al., 2018). Head stabilization is achieved by  
700 cyclically counteracting the body movements with coordinated trunk movements (Kavanagh et  
701 al., 2006). As a result, head accelerations can be as low as 8% of the ankle accelerations  
702 (Ratcliffe & Holt, 1997) and are unaffected when walking on an irregular surface, despite greater  
703 pelvis accelerations (Menz et al., 2003). Clearly, the lower limbs and the column are efficient  
704 shock absorbers, together with anticipatory postural adjustments and vestibulo-collic and cervico-  
705 collic synergies. Nevertheless, locomotion is characterized by its variability, as described in the  
706 Introduction. As shown by Toda et al. (Toda et al., 2016) for five walking speeds, vertical  
707 acceleration variability was the smallest in all body parts, and the walking speed effect  
708 demonstrated laterality. Antero-posterior acceleration variability was significantly associated  
709 with walking speed at sites other than the head. Variability of medio-lateral acceleration of the  
710 bilateral hip alone was smaller than antero-posterior variability. Also, Owings and Grabiner  
711 (Owings & Grabiner, 2004) showed that step width variability represented the more sensitive  
712 descriptor of locomotion control in young and old adults during treadmill locomotion at a self-  
713 selected walking speed. Our data confirms and extends these results. As illustrated in Figure 8,  
714 both head and trunk movements were by far the more stable segments of the body, and these  
715 were not observed to vary statistically for any spatial plane or type of locomotion investigated  
716 here. Nevertheless, a detailed analysis revealed subtle differences. The mobility versus space of  
717 the legs, heels and tips of the feet increased in that order for all of the walking and running  
718 velocities of the subjects and the spatial plane investigated. In summary, all subjects displayed a  
719 bottom-up gradient of mobility of the body versus space that decreased from the tip of the feet to  
720 the head, which fits with the existence of the same gradient for the skeletal configuration (see  
721 above).

722

723 Could RMS be used as a marker of motor style during locomotion? As illustrated in  
724 Figure 8, the RMS in the transversal plane at the head and trunk levels could be useful (see  
725 Table III) because of the small intra-individual variability (Figure 6) and the large inter-  
726 individual variability (right panel in Figure 8).

727

728 *Sample entropy*

729 Gait variability in a given individual was assessed using linear approaches to evaluate  
730 global variability, usually with the standard deviation (SD) and CV. In addition, non-linear  
731 approaches were used to explore the time-dependent nature of walking and running by including  
732 long-range correlation (Hausdorff, 2007)(De La Cruz et al 2018) . Using entropy, Estep et al. (   
733 2018) found that lower-limb kinematics of running was more variable than walking in healthy  
734 adults. This difference may reflect an adaptive ability, affording the person greater flexibility to  
735 accommodate changes and perturbations during running (see also Jordan et al., 2009). This  
736 hypothesis was also put forward by Dingwel et al. ( 2018), who found that when running, people  
737 corrected deviations both more quickly and more directly, each indicating tighter control,  
738 compared to walking. Thus, gait differences determined how stride-to-stride fluctuations were  
739 regulated, and this is independent of speed. These results are confirmed and extended here:  
740 sample entropy increases with locomotion velocity for each body segment (see Figure 9 left  
741 panel).

742

743 Could sample entropy be used as a motor style marker during locomotion? As illustrated  
744 in Figure 9, the sample entropy in the sagittal and transversal plane at the head and trunk levels  
745 and for the frontal plane at the leg and feet levels (except during running) could be useful (see  
746 Table III) because of the small intra-individual variability (Figure 6) and large inter-individual  
747 variability (right panel in Figure 9).

748

749 *Two-thirds power law*

750 In recent years, several behavioral and neurophysiological studies have shown that  
751 common rules may govern motor control. The relationship between velocity and curvature of the  
752 endpoint path was described using the two-thirds power law. In humans, the law holds true for  
753 drawing (Francesco Lacquaniti et al., 1983b) (Schaal & Sternad, 2001), pursuit eye movements  
754 (de'Sperati & Viviani, 1997), foot trajectory during swing phase (Ivanenko et al.,  
755 2002a)(Ivanenko et al., 2002b), body center of mass (Tesio et al., 2011), and the head (Olivier &  
756 Cretual, 2007a) during walking and during walking around ellipses drawn on the ground  
757 (Vieilledent et al., 2001a) and around a single turn (Olivier & Cretual, 2007b) but not complex  
758 curved paths (Hicheur et al., 2005) (Vieilledent et al., 2001b). It is still debated whether the

759 power law is a byproduct of the mechanical properties of the body or an epiphenomenon of  
760 planning strategies based on trajectory optimization (maximum smoothness, minimum variance  
761 etc.) or whether it could be centrally implemented (F. Lacquaniti et al., 2002) (Tamar Flash &  
762 Hochner, 2005) (Tamar Flash et al., 2013).

763  
764 Our results agree with those from the studies quoted above and generalize them when  
765 monitoring every segment of the body while walking and running on a treadmill. As shown in  
766 Figure 13, the two-thirds power law applies to every marker, hence the two-thirds law applies all  
767 body segments and every condition tested (two walking speeds, racing and running). In addition,  
768 as shown in Figure 13, several features emerged when the data for every marker is displayed in  
769 the three spatial planes.

770  
771 First, the average  $\beta$ -exponents were stable in the sagittal plane but increased with speed in  
772 the frontal and transversal planes. That is, the tangential velocity for the same radius of curvature  
773 increased as the subjects accelerated, which makes sense from a functional point of view. Of  
774 note, the  $\beta$ -exponents for the head, trunk and leg levels increased with subject velocity but also  
775 tended to converge on similar values during running, which may also optimize motor control.

776  
777 Second, differential motor control in the three spatial planes was suggested by significant  
778 differences in upper and lower body-part  $\beta$ -exponents (see Figure 13) between all planes.  
779 However, although different, Figure 13 revealed interesting couplings between the transversal  
780 and sagittal planes (see the evolution of body-part  $\beta$ -exponents with increased speed) and an  
781 inverse coupling between the frontal plane and the two other planes (especially the sagittal).

782  
783 Third, although the two-thirds law held true for all subjects and for each body segment,  
784 the exponent SDs were large. In fact, when comparing the subjects and body segments two by  
785 two, some but not all of the sensor trajectories were statistically different. Thus, the inter-  
786 individual disparities of the two-thirds power law at different body segments may help define a  
787 personal motor style (see Table III).

788

789 Fourth, the Lissajous model implies that curvature increases with decreasing velocity, as  
790 is the case during locomotion. (Viviani & Stucchi, 1989) suggested that only Lissajous elliptic  
791 motions look natural. Therefore, it is considered that this may be a key element for the visual  
792 system to identify “natural” human and/or animal movement. To the extent that individual  
793 differences in the exponents of the two-thirds power law among individuals are shown, the law  
794 may also help to identify a given individual, after a period of training, based on his/her pattern of  
795 locomotion.

796

### 797 **Plane-specific control for locomotion**

798

799 Multidirectional perturbations at the base of sustentation revealed that postural control in  
800 both humans (Maki et al., 1994) (Carpenter et al., 2001) and quadrupeds (Rushmer et al., 1988)  
801 was distinct in the anteroposterior and midlateral planes. It has been shown that selective lesions  
802 of the vestibular system (de Waele et al., 2017) and the dopaminergic system (Herbin et al.,  
803 2016) further support the notion that postural control is sub-served by different neuronal  
804 networks in the frontal, sagittal and transversal planes. Here, this hypothesis is confirmed by  
805 showing that the different features explored during locomotion and running obeyed different  
806 logics in the frontal, sagittal and transversal planes, as summarized qualitatively in Table III.

807

### 808 **Limitations**

809

810 There were a limited number of subjects, and this set was deliberately heterogeneous in  
811 terms of age, weight, sex, etc.,. The aim was to investigate personal motor style using the CODA  
812 motion system and 24 markers. The discussion and conclusions were based on the most  
813 statistically significant measures ( $p < 0.001$ ) and measures with higher p-values were left for  
814 future verification. It is thought that once a large number of subjects are explored using simpler  
815 and more automatized recording methods, such as IMU, mining of these databases may also  
816 reveal a taxonomy of the motor basis based on weight, morphology, sex, racial and cultural  
817 background. The use of the treadmill may provide a good representation of overground walking  
818 but it may also be limiting. On the one hand, Owings & Grabiner (2004) and (Grabiner & Troy,  
819 2005) stated that treadmill walking may be an acceptable representation of overground walking

820 with respect to the variability of spatial and temporal step kinematics. Also, (Fellin et al., 2010)  
821 found kinematic curves for overground and treadmill running to be generally similar when  
822 averaged across subjects. On the other hand, the treadmill itself implies great unnatural  
823 constraints and requires increased voluntary control. Hence, the quantification of gait dynamics  
824 by treadmill running does not entirely reflect movement in overground settings (Van  
825 Caekenberghe et al., 2013)(Lindsay et al., 2014)(García-Pérez et al., 2013).

826

827

828

829 **References**

830

831 Altman, A. R., Reisman, D. S., Higginson, J. S., & Davis, I. S. (2012). Kinematic comparison of  
832 split-belt and single-belt treadmill walking and the effects of accommodation. *Gait &*  
833 *Posture*, *35*(2), 287-291. <https://doi.org/10.1016/j.gaitpost.2011.09.101>

834 Ayoubi, F., Launay, C. P., Annweiler, C., & Beauchet, O. (2015). Fear of Falling and Gait  
835 Variability in Older Adults: A Systematic Review and Meta-Analysis. *Journal of the*  
836 *American Medical Directors Association*, *16*(1), 14-19.

837 <https://doi.org/10.1016/j.jamda.2014.06.020>

838 Bonan, I. V., Marquer, A., Eskizmirli, S., Yelnik, A. P., & Vidal, P.-P. (2013). Sensory  
839 reweighting in controls and stroke patients. *Clinical Neurophysiology*, *124*(4), 713-722.

840 <https://doi.org/10.1016/j.clinph.2012.09.019>

841 Bonan, I. V., Gaillard, F., Ponche, S. T., Marquer, A., Vidal, P. P., & Yelnik, A. P. (2015). Early  
842 post-stroke period: A privileged time for sensory re-weighting? *Journal of Rehabilitation*  
843 *Medicine*, *47*(6), 516-522. <https://doi.org/10.2340/16501977-1968>

844 Buckley, E., Mazzà, C., & McNeill, A. (2018). A systematic review of the gait characteristics  
845 associated with Cerebellar Ataxia. *Gait & Posture*, *60*, 154-163.

846 <https://doi.org/10.1016/j.gaitpost.2017.11.024>

847 Carpenter, M. G., Frank, J. S., Silcher, C. P., & Peysar, G. W. (2001). The influence of postural  
848 threat on the control of upright stance. *Experimental Brain Research*, *138*(2), 210-218.

849 <https://doi.org/10.1007/s002210100681>

850 Costa, M., Goldberger, A. L., & Peng, C.-K. (2005). Multiscale entropy analysis of biological  
851 signals. *Physical Review. E, Statistical, Nonlinear, and Soft Matter Physics*, *71*(2 Pt 1),  
852 021906. <https://doi.org/10.1103/PhysRevE.71.021906>

853 Dasenbrock, L., Heinks, A., Schwenk, M., & Bauer, J. M. (2016). Technology-based  
854 measurements for screening, monitoring and preventing frailty. *Zeitschrift Für*  
855 *Gerontologie Und Geriatrie*, *49*(7), 581-595. <https://doi.org/10.1007/s00391-016-1129-7>

856 De La Cruz J, Gómez-Herreros F, Rodríguez-Galán O, Begley V, de la Cruz Muñoz-Centeno  
857 M, Chávez S (2018). Feedback regulation of ribosome assembly. *Curr Genet*. *64*(2):393-  
858 404. <https://doi.org/10.1007/s00294-017-0764>

859 De'Sperati, C., & Viviani, P. (1997). The relationship between curvature and velocity in two-  
860 dimensional smooth pursuit eye movements. *The Journal of Neuroscience: The Official*

861 *Journal of the Society for Neuroscience*, 17(10), 3932-3945.

862 De Waele, C., Shen, Q., Magnani, C., & Curthoys, I. S. (2017). A Novel Saccadic Strategy  
863 Revealed by Suppression Head Impulse Testing of Patients with Bilateral Vestibular Loss.  
864 *Frontiers in Neurology*, 8, 419. <https://doi.org/10.3389/fneur.2017.00419>

865 Dingwell, J. B., Bohnsack-McLagan, N. K., & Cusumano, J. P. (2018). Humans control stride-to-  
866 stride stepping movements differently for walking and running, independent of speed.  
867 *Journal of Biomechanics*, 76, 144-151. <https://doi.org/10.1016/j.jbiomech.2018.05.034>

868 Dingwell, J. B., & Cusumano, J. P. (2015). Identifying stride-to-stride control strategies in human  
869 treadmill walking. *PloS One*, 10(4), e0124879.  
870 <https://doi.org/10.1371/journal.pone.0124879>

871 Dingwell, J. B., Salinas, M. M., & Cusumano, J. P. (2017). Increased gait variability may not  
872 imply impaired stride-to-stride control of walking in healthy older adults. *Gait & Posture*,  
873 55, 131-137. <https://doi.org/10.1016/j.gaitpost.2017.03.018>

874 Estep, A., Morrison, S., Caswell, S., Ambegaonkar, J., & Cortes, N. (2018). Differences in  
875 pattern of variability for lower extremity kinematics between walking and running. *Gait &*  
876 *Posture*, 60, 111-115. <https://doi.org/10.1016/j.gaitpost.2017.11.018>

877 Fellin, R. E., Manal, K., & Davis, I. S. (2010). Comparison of lower extremity kinematic curves  
878 during overground and treadmill running. *Journal of Applied Biomechanics*, 26(4),  
879 407-414. <https://doi.org/10.1123/jab.26.4.407>

880 Figueiredo, J., Santos, C. P., & Moreno, J. C. (2018). Automatic recognition of gait patterns in  
881 human motor disorders using machine learning: A review. *Medical Engineering & Physics*,  
882 53, 1-12. <https://doi.org/10.1016/j.medengphy.2017.12.006>

883 Flash, T., & Hogan, N. (1985). The coordination of arm movements: An experimentally  
884 confirmed mathematical model. *The Journal of Neuroscience*, 5(7), 1688-1703.

885 Flash, T., & Hochner, B. (2005). Motor primitives in vertebrates and invertebrates. *Current*  
886 *Opinion in Neurobiology*, 15(6), 660-666. <https://doi.org/10.1016/j.conb.2005.10.011>

887 Flash, T., Meirovitch, Y., & Barliya, A. (2013). Models of human movement: Trajectory  
888 planning and inverse kinematics studies. *Robotics and Autonomous Systems*, 61(4),  
889 330-339. <https://doi.org/10.1016/j.robot.2012.09.020>

890 Fritz, C. O., Morris, P. E., & Richler, J. J. (2012). Effect size estimates: Current use, calculations,  
891 and interpretation. *Journal of Experimental Psychology. General*, 141(1), 2-18.

892 <https://doi.org/10.1037/a0024338>

893 García-Pérez, J. A., Pérez-Soriano, P., Llana, S., Martínez-Nova, A., & Sánchez-Zuriaga, D.  
894 (2013). Effect of overground vs treadmill running on plantar pressure: Influence of fatigue.  
895 *Gait & Posture*, 38(4), 929-933. <https://doi.org/10.1016/j.gaitpost.2013.04.026>

896 Grabiner, M. D., & Troy, K. L. (2005). Attention demanding tasks during treadmill walking  
897 reduce step width variability in young adults. *Journal of Neuroengineering and*  
898 *Rehabilitation*, 2, 25. <https://doi.org/10.1186/1743-0003-2-25>

899 Graf, W., de Waele, C., & Vidal, P. P. (1995). Functional anatomy of the head-neck movement  
900 system of quadrupedal and bipedal mammals. *Journal of Anatomy*, 186 ( Pt 1), 55-74.

901 Guerraz, M., & Bronstein, A. M. (2008). Mechanisms underlying visually induced body sway.  
902 *Neuroscience Letters*, 443(1), 12-16. <https://doi.org/10.1016/j.neulet.2008.07.053>

903 Hafer, J. F., & Boyer, K. A. (2017). Variability of segment coordination using a vector coding  
904 technique: Reliability analysis for treadmill walking and running. *Gait & Posture*, 51,  
905 222-227. <https://doi.org/10.1016/j.gaitpost.2016.11.004>

906 Hamill, J., Palmer, C., & Van Emmerik, R. E. A. (2012). Coordinative variability and overuse  
907 injury. *Sports Medicine, Arthroscopy, Rehabilitation, Therapy & Technology: SMARTT*,  
908 4(1), 45. <https://doi.org/10.1186/1758-2555-4-45>

909 Hausdorff, J. M. (2007). Gait dynamics, fractals and falls: Finding meaning in the stride-to-stride  
910 fluctuations of human walking. *Human Movement Science*, 26(4), 555-589.  
911 <https://doi.org/10.1016/j.humov.2007.05.003>

912 Herbin, M., Simonis, C., Revéret, L., Hackert, R., Libourel, P.-A., Eugène, D., Diaz, J., de  
913 Waele, C., & Vidal, P.-P. (2016). Dopamine Modulates Motor Control in a Specific Plane  
914 Related to Support. *PLoS One*, 11(5), e0155058.  
915 <https://doi.org/10.1371/journal.pone.0155058>

916 Herssens, N., Verbecque, E., Hallemans, A., Vereeck, L., Van Rompaey, V., & Saeys, W.  
917 (2018a). Do spatiotemporal parameters and gait variability differ across the lifespan of  
918 healthy adults? A systematic review. *Gait & Posture*, 64, 181-190.  
919 <https://doi.org/10.1016/j.gaitpost.2018.06.012>

920 Herssens, N., Verbecque, E., Hallemans, A., Vereeck, L., Van Rompaey, V., & Saeys, W.  
921 (2018b). Do spatiotemporal parameters and gait variability differ across the lifespan of  
922 healthy adults? A systematic review. *Gait & Posture*, 64, 181-190.

923 <https://doi.org/10.1016/j.gaitpost.2018.06.012>

924 Hicheur, H., Vieilledent, S., Richardson, M. J. E., Flash, T., & Berthoz, A. (2005). Velocity and  
925 curvature in human locomotion along complex curved paths: A comparison with hand  
926 movements. *Experimental Brain Research*, *162*(2), 145-154.  
927 <https://doi.org/10.1007/s00221-004-2122-8>

928 Hreljac, A. (1993). Preferred and energetically optimal gait transition speeds in human  
929 locomotion. *Medicine and Science in Sports and Exercise*, *25*(10), 1158-1162.

930 Hreljac, A., & Martin, P. E. (1993). The relationship between smoothness and economy during  
931 walking. *Biological Cybernetics*, *69*(3), 213-218. <https://doi.org/10.1007/bf00198961>

932 Isableu, B., Ohlmann, T., Crémieux, J., & Amblard, B. (2003). Differential approach to strategies  
933 of segmental stabilisation in postural control. *Experimental Brain Research*, *150*(2),  
934 208-221. <https://doi.org/10.1007/s00221-003-1446-0>

935 Ivanenko, Y. P., Cappellini, G., Solopova, I. A., Grishin, A. A., Maclellan, M. J., Poppele, R. E.,  
936 & Lacquaniti, F. (2013). Plasticity and modular control of locomotor patterns in  
937 neurological disorders with motor deficits. *Frontiers in Computational Neuroscience*, *7*,  
938 123. <https://doi.org/10.3389/fncom.2013.00123>

939 Ivanenko, Y. P., Grasso, R., Macellari, V., & Lacquaniti, F. (2002). Control of Foot Trajectory in  
940 Human Locomotion: Role of Ground Contact Forces in Simulated Reduced Gravity.  
941 *Journal of Neurophysiology*, *87*(6), 3070-3089. <https://doi.org/10.1152/jn.2002.87.6.3070>

942 Ivanenko, Y. P., Grasso, R., Macellari, V., & Lacquaniti, F. (2002). Two-thirds power law in  
943 human locomotion: Role of ground contact forces: *Neuroreport*, *13*(9), 1171-1174.  
944 <https://doi.org/10.1097/00001756-200207020-00020>

945 Jordan, K., Challis, J. H., Cusumano, J. P., & Newell, K. M. (2009). Stability and the time-  
946 dependent structure of gait variability in walking and running. *Human Movement Science*,  
947 *28*(1), 113-128. <https://doi.org/10.1016/j.humov.2008.09.001>

948 Kavanagh, J., Barrett, R., & Morrison, S. (2006). The role of the neck and trunk in facilitating  
949 head stability during walking. *Experimental Brain Research*, *172*(4), 454-463.  
950 <https://doi.org/10.1007/s00221-006-0353-6>

951 Khalil, N., Bizdikian, A. J., Bakouny, Z., Salameh, M., Bou Zeid, N., Yared, F., Otayek, J.,  
952 Kharrat, K., Kreichati, G., Ghanem, I., Lafage, R., Lafage, V., Obeid, I., & Assi, A. (2018).  
953 Cervical and postural strategies for maintaining horizontal gaze in asymptomatic adults.

954 *European Spine Journal*, 27(11), 2700-2709. <https://doi.org/10.1007/s00586-018-5753-3>

955 Kikkert, L. H. J., Vuillerme, N., van Campen, J. P., Hortobágyi, T., & Lamoth, C. J. (2016).  
956 Walking ability to predict future cognitive decline in old adults: A scoping review. *Ageing*  
957 *Research Reviews*, 27, 1-14. <https://doi.org/10.1016/j.arr.2016.02.001>

958 König, N., Taylor, W. R., Baumann, C. R., Wenderoth, N., & Singh, N. B. (2016). Revealing the  
959 quality of movement: A meta-analysis review to quantify the thresholds to pathological  
960 variability during standing and walking. *Neuroscience & Biobehavioral Reviews*, 68,  
961 111-119. <https://doi.org/10.1016/j.neubiorev.2016.03.035>

962 Kraan, R. B., Beers, L., van de Pol, D., Daams, J. G., Maas, M., & Kuijer, P. P. (2019). A  
963 systematic review on posterior circumflex humeral artery pathology: Sports and professions  
964 at risk and associated risk factors. *The Journal of Sports Medicine and Physical Fitness*,  
965 59(6), 1058-1067. <https://doi.org/10.23736/S0022-4707.18.08579-1>

966 Lacour, M., Barthelemy, J., Borel, L., Magnan, J., Xerri, C., Chays, A., & Ouaknine, M. (1997).  
967 Sensory strategies in human postural control before and after unilateral vestibular  
968 neurotomy. *Experimental Brain Research*, 115(2), 300-310.

969 Lacquaniti, F., Ivanenko, Y. P., & Zago, M. (2002). Kinematic control of walking. *Archives*  
970 *Italiennes De Biologie*, 140(4), 263-272.

971 Lacquaniti, F., Terzuolo, C., & Viviani, P. (1983a). The law relating the kinematic and figural  
972 aspects of drawing movements. *Acta Psychologica*, 54(1-3), 115-130.  
973 [https://doi.org/10.1016/0001-6918\(83\)90027-6](https://doi.org/10.1016/0001-6918(83)90027-6)

974 Lacquaniti, F., Terzuolo, C., & Viviani, P. (1983b). The law relating the kinematic and figural  
975 aspects of drawing movements. *Acta Psychologica*, 54(1-3), 115-130.  
976 [https://doi.org/10.1016/0001-6918\(83\)90027-6](https://doi.org/10.1016/0001-6918(83)90027-6)

977 Lindsay, T. R., Noakes, T. D., & McGregor, S. J. (2014). Effect of Treadmill versus Overground  
978 Running on the Structure of Variability of Stride Timing. *Perceptual and Motor Skills*,  
979 118(2), 331-346. <https://doi.org/10.2466/30.26.PMS.118k18w8>

980 Long, L. L., & Srinivasan, M. (2013). Walking, running, and resting under time, distance, and  
981 average speed constraints: Optimality of walk-run-rest mixtures. *Journal of the Royal*  
982 *Society, Interface*, 10(81), 20120980. <https://doi.org/10.1098/rsif.2012.0980>

983 Maki, B. E., Holliday, P. J., & Topper, A. K. (1994). A prospective study of postural balance and  
984 risk of falling in an ambulatory and independent elderly population. *Journal of*

985 *Gerontology*, 49(2), M72-84. <https://doi.org/10.1093/geronj/49.2.m72>

986 Maselli, A., Dhawan, A., Cesqui, B., Russo, M., Lacquaniti, F., & d'Avella, A. (2017). Where  
987 Are You Throwing the Ball? I Better Watch Your Body, Not Just Your Arm! *Frontiers in*  
988 *Human Neuroscience*, 11. <https://doi.org/10.3389/fnhum.2017.00505>

989 Maslivec, A., Bampouras, T. M., Dewhurst, S., Vannozzi, G., Macaluso, A., & Laudani, L.  
990 (2018). Mechanisms of head stability during gait initiation in young and older women: A  
991 neuro-mechanical analysis. *Journal of Electromyography and Kinesiology*, 38, 103-110.  
992 <https://doi.org/10.1016/j.jelekin.2017.11.010>

993 Massion, J. (1994). Postural control system. *Current Opinion in Neurobiology*, 4(6), 877-887.  
994 [https://doi.org/10.1016/0959-4388\(94\)90137-6](https://doi.org/10.1016/0959-4388(94)90137-6)

995 Mawase, F., Bar-Haim, S., Joubran, K., Rubin, L., Karniel, A., & Shmuelof, L. (2016). Increased  
996 Adaptation Rates and Reduction in Trial-by-Trial Variability in Subjects with Cerebral  
997 Palsy Following a Multi-session Locomotor Adaptation Training. *Frontiers in Human*  
998 *Neuroscience*, 10, 203. <https://doi.org/10.3389/fnhum.2016.00203>

999 Menz, H. B., Lord, S. R., & Fitzpatrick, R. C. (2003). Acceleration patterns of the head and  
1000 pelvis when walking on level and irregular surfaces. *Gait & Posture*, 18(1), 35-46.  
1001 [https://doi.org/10.1016/S0966-6362\(02\)00159-5](https://doi.org/10.1016/S0966-6362(02)00159-5)

1002 Merfeld, D. M., Zupan, L., & Peterka, R. J. (1999). Humans use internal models to estimate  
1003 gravity and linear acceleration. *Nature*, 398(6728), 615-618. <https://doi.org/10.1038/19303>

1004 Mo, S., & Chow, D. H. K. (2018). Stride-to-stride variability and complexity between novice and  
1005 experienced runners during a prolonged run at anaerobic threshold speed. *Gait & Posture*,  
1006 64, 7-11. <https://doi.org/10.1016/j.gaitpost.2018.05.021>

1007 Möhler, F., Marahrens, S., Ringhof, S., Mikut, R., & Stein, T. (2020). Variability of running  
1008 coordination in experts and novices: A 3D uncontrolled manifold analysis. *European*  
1009 *Journal of Sport Science*, 1-10. <https://doi.org/10.1080/17461391.2019.1709561>

1010 Moon, Y., Sung, J., An, R., Hernandez, M. E., & Sosnoff, J. J. (2016). Gait variability in people  
1011 with neurological disorders: A systematic review and meta-analysis. *Human Movement*  
1012 *Science*, 47, 197-208. <https://doi.org/10.1016/j.humov.2016.03.010>

1013 Moore, I. S. (2016). Is There an Economical Running Technique? A Review of Modifiable  
1014 Biomechanical Factors Affecting Running Economy. *Sports Medicine*, 46(6), 793-807.  
1015 <https://doi.org/10.1007/s40279-016-0474-4>

- 1016 Mortaza, N., Osman, N. A. A., & Mehdikhani, N. (2014). Are the spatio-temporal parameters of  
1017 gait capable of distinguishing a faller from a non-faller elderly? *European Journal of*  
1018 *Physical and Rehabilitation Medicine*, 50(6), 15.
- 1019 Nashner, L. M. (1976). Adapting reflexes controlling the human posture. *Experimental Brain*  
1020 *Research*, 26(1), 59-72.
- 1021 Newell, R. S., Blouin, J.-S., Street, J., Cripton, P. A., & Siegmund, G. P. (2018). The neutral  
1022 posture of the cervical spine is not unique in human subjects. *Journal of Biomechanics*, 80,  
1023 53-62. <https://doi.org/10.1016/j.jbiomech.2018.08.012>
- 1024 Olivier, A.-H., & Cretual, A. (2007a). Velocity/curvature relations along a single turn in human  
1025 locomotion. *Neuroscience Letters*, 412(2), 148-153.  
1026 <https://doi.org/10.1016/j.neulet.2006.11.005>
- 1027 Olivier, A.-H., & Cretual, A. (2007b). Velocity/curvature relations along a single turn in human  
1028 locomotion. *Neuroscience Letters*, 412(2), 148-153.  
1029 <https://doi.org/10.1016/j.neulet.2006.11.005>
- 1030 Owings, T. M., & Grabiner, M. D. (2004). Step width variability, but not step length variability  
1031 or step time variability, discriminates gait of healthy young and older adults during  
1032 treadmill locomotion. *Journal of Biomechanics*, 37(6), 935-938.  
1033 <https://doi.org/10.1016/j.jbiomech.2003.11.012>
- 1034 Pozzo, T., Berthoz, A., & Lefort, L. (1990). Head stabilization during various locomotor tasks in  
1035 humans. I. Normal subjects. *Experimental Brain Research*, 82(1), 97-106.  
1036 <https://doi.org/10.1007/bf00230842>
- 1037 Ratcliffe, R. J., & Holt, K. G. (1997). Low frequency shock absorption in human walking. *Gait &*  
1038 *Posture*, 5(2), 93-100. [https://doi.org/10.1016/S0966-6362\(96\)01077-6](https://doi.org/10.1016/S0966-6362(96)01077-6)
- 1039 Rushmer, D. S., Moore, S. P., Windus, S. L., & Russell, C. J. (1988). Automatic postural  
1040 responses in the cat: Responses of hindlimb muscles to horizontal perturbations of stance in  
1041 multiple directions. *Experimental Brain Research*, 71(1), 93-102.  
1042 <https://doi.org/10.1007/bf00247525>
- 1043 Sasaki, O., Usami, S., Gagey, P.-M., Martinerie, J., Le Van Quyen, M., & Arranz, P. (2002). Role  
1044 of visual input in nonlinear postural control system. *Experimental Brain Research*, 147(1),  
1045 1-7. <https://doi.org/10.1007/s00221-002-1170-1>
- 1046 Schaal, S., & Sternad, D. (2001). Origins and violations of the 2/3 power law in rhythmic three-

1047 dimensional arm movements. *Experimental Brain Research*, 136(1), 60-72.  
1048 <https://doi.org/10.1007/s002210000505>

1049 Schneider, K., & Zernicke, R. F. (1989). Jerk-cost modulations during the practice of rapid arm  
1050 movements. *Biological Cybernetics*, 60(3), 221-230. <https://doi.org/10.1007/bf00207290>

1051 Schniepp, R., Möhwald, K., & Wuehr, M. (2017). Gait ataxia in humans: Vestibular and  
1052 cerebellar control of dynamic stability. *Journal of Neurology*, 264(S1), 87-92.  
1053 <https://doi.org/10.1007/s00415-017-8482-3>

1054 Schwenk, M., Howe, C., Saleh, A., Mohler, J., Grewal, G., Armstrong, D., & Najafi, B. (2014).  
1055 Frailty and Technology: A Systematic Review of Gait Analysis in Those with Frailty.  
1056 *Gerontology*, 60(1), 79-89. <https://doi.org/10.1159/000354211>

1057 Sprager, S., & Juric, M. B. (2015). Inertial Sensor-Based Gait Recognition: A Review. *Sensors*  
1058 (*Basel, Switzerland*), 15(9), 22089-22127. <https://doi.org/10.3390/s150922089>

1059 Sternad, D. (2018). It's Not (Only) the Mean that Matters: Variability, Noise and Exploration in  
1060 Skill Learning. *Current Opinion in Behavioral Sciences*, 20, 183-195.  
1061 <https://doi.org/10.1016/j.cobeha.2018.01.004>

1062 Tesio, L., Rota, V., & Perucca, L. (2011). The 3D trajectory of the body centre of mass during  
1063 adult human walking: Evidence for a speed–curvature power law. *Journal of Biomechanics*,  
1064 44(4), 732-740. <https://doi.org/10.1016/j.jbiomech.2010.10.035>

1065 Ting, L. H., & McKay, J. L. (2007). Neuromechanics of muscle synergies for posture and  
1066 movement. *Current Opinion in Neurobiology*, 17(6), 622-628.  
1067 <https://doi.org/10.1016/j.conb.2008.01.002>

1068 Toda, H., Nagano, A., & Luo, Z. (2016). Analysis of walking variability through simultaneous  
1069 evaluation of the head, lumbar, and lower-extremity acceleration in healthy youth. *Journal*  
1070 *of Physical Therapy Science*, 28(6), 1801-1805. <https://doi.org/10.1589/jpts.28.1801>

1071 Todorov, E., & Jordan, M. I. (2002). Optimal feedback control as a theory of motor coordination.  
1072 *Nature Neuroscience*, 5(11), 1226-1235. <https://doi.org/10.1038/nn963>

1073 Van Caekenberghe, I., Segers, V., Willems, P., Gosseye, T., Aerts, P., & De Clercq, D. (2013).  
1074 Mechanics of overground accelerated running vs. Running on an accelerated treadmill. *Gait*  
1075 *& Posture*, 38(1), 125-131. <https://doi.org/10.1016/j.gaitpost.2012.10.022>

1076 Van de Putte, M., Hagemester, N., St-Onge, N., Parent, G., & de Guise, J. A. (2006).  
1077 Habituation to treadmill walking. *Bio-Medical Materials and Engineering*, 16(1), 43-52.

1078 Vibert, N., MacDougall, H. G., de Waele, C., Gilchrist, D. P., Burgess, A. M., Sidis, A.,  
1079 Migliaccio, A., Curthoys, I. S., & Vidal, P. P. (2001). Variability in the control of head  
1080 movements in seated humans : A link with whiplash injuries? *The Journal of Physiology*,  
1081 532(Pt 3), 851-868.

1082 Vidal, P. P., Graf, W., & Berthoz, A. (1986). The orientation of the cervical vertebral column in  
1083 unrestrained awake animals. I. Resting position. *Experimental Brain Research*, 61(3),  
1084 549-559.

1085 Vidal, P.-P., Degallaix, L., Josset, P., Gasc, J.-P., & Cullen, K. E. (2004). Postural and locomotor  
1086 control in normal and vestibularly deficient mice. *The Journal of Physiology*, 559(Pt 2),  
1087 625-638. <https://doi.org/10.1113/jphysiol.2004.063883>

1088 Vieilledent, S., Kerlirzin, Y., Dalbera, S., & Berthoz, A. (2001a). Relationship between velocity  
1089 and curvature of a human locomotor trajectory. *Neuroscience Letters*, 305(1), 65-69.  
1090 [https://doi.org/10.1016/s0304-3940\(01\)01798-0](https://doi.org/10.1016/s0304-3940(01)01798-0)

1091 Vieilledent, S., Kerlirzin, Y., Dalbera, S., & Berthoz, A. (2001b). Relationship between velocity  
1092 and curvature of a human locomotor trajectory. *Neuroscience Letters*, 305(1), 65-69.  
1093 [https://doi.org/10.1016/s0304-3940\(01\)01798-0](https://doi.org/10.1016/s0304-3940(01)01798-0)

1094 Viviani, P., & Flash, T. (1995). Minimum-jerk, two-thirds power law, and isochrony: Converging  
1095 approaches to movement planning. *Journal of Experimental Psychology. Human*  
1096 *Perception and Performance*, 21(1), 32-53. <https://doi.org/10.1037//0096-1523.21.1.32>

1097 Viviani, P., & Stucchi, N. (1989). The effect of movement velocity on form perception:  
1098 Geometric illusions in dynamic displays. *Perception & Psychophysics*, 46(3), 266-274.  
1099 <https://doi.org/10.3758/bf03208089>

1100 WHO | *The World Health Report 2006—Working together for health*. (s. d.). WHO. Consulté 17  
1101 février 2020, à l'adresse <https://www.who.int/whr/2006/en/>

1102 Yan, J. H. (2000). Effects of aging on linear and curvilinear aiming arm movements.  
1103 *Experimental Aging Research*, 26(4), 393-407.  
1104 <https://doi.org/10.1080/036107300750015778>

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Figure legends

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*Figure 1. Illustration of 24 Markers*

*Figure 2. Schematic representation of a subject in a static position. The trunk inclination was defined as the angle between the gravity vector passing through L5 and the vector L5 - P1 (V4 green vector). The head inclination vector was defined as the angle between the gravity through P1 and the vector P1 – P2 (V3 red vector). The leg inclination (right and left) was defined as the angle between the gravity vector passing through L5 and vector L5 - LHL (V5 blue vector).*

*Figure 3.*

*A- Skeletal postural configuration at rest for the 18 subjects in the sagittal view. Bold red horizontal bars indicate the head while the rest indicate trunk and leg positioning;*

*B- Angle inclination in degrees for trunk, head and legs among participants in the sagittal plane at rest.*

*Figure 4.*

*Skeletal postural configurations of three characteristic subjects performing walking and running in the sagittal view. Bold red horizontal bars indicate the head while the rest indicate trunk and leg positioning. The configurations have been acquired at the time of heel strike for each foot (red and black overlapped leg configurations). From left to right: comfortable walk, walk at 4 km/h, race walking and running. From top to bottom: A- subject 6; B- subject 11; C- subject 17.*

*Figure 5. Variability in inclination of trunk, head and legs during the protocol phases. Each line represents a subject and its respective average inclination angle.*

*Figure 6 Intra-individual variation expressed in terms of variation coefficient for the different sensors and walking and running speeds for each subject. Reading these graphs from left to right (upper to lower body sensors: Head (1-4), shoulders(5-6), trunk (7-8), legs(9-16) and feet (18-24)), average head and trunk intra individual variability was found to be significantly lower ( $p < 0.001$ ) compared to the leg and feet intra-variability for all the exercises and all planes. Interestingly, head intra-variability was found to be significantly lower compared to trunk intra-variability in: A) Running in transversal plane ( $p < 0.001$ ), B) All exercises in sagittal plane ( $p < 0.05$ ), C) Race walking and running in frontal plane ( $p < 0.001$ ).*

1145 *Figure 7 A) Average jerk among the different sensors and walking and running speeds. Reading all planes*  
1146 *(frontal, sagittal, transversal) from left to right (upper body to lower body), average head jerk of individuals*  
1147 *was found to be significantly higher ( $p < 0.001$ ) compared to average trunk, leg and feet jerks in frontal and*  
1148 *sagittal planes, for all four exercises. B). Coefficient of Variation of Jerk among the different sensors and*  
1149 *walking and running speeds. Reading all planes (frontal, sagittal, transversal) from left to right (upper body*  
1150 *to lower body), frontal plane had a significantly high anterior left and anterior right tibia and trunk L5 (see*  
1151 *red lines) compared to others while sagittal and transversal planes had a low jerk variability for the upper*  
1152 *part of the body for the four protocol phases.*

1153  
1154 *Figure 8 a) Average RMS for the different sensors and walking and running speeds. Reading all planes*  
1155 *(frontal, sagittal, transversal) from left to right (upper body to lower body), Average head RMS was found*  
1156 *to be significantly lower ( $p < 0.001$ ) compared to average leg and feet RMS in sagittal and transversal*  
1157 *plane, for all four exercises. On the other hand, average head RMS was significantly lower ( $p < 0.05$ )*  
1158 *compared to average trunk RMS only while running. b) RMS Coefficient of Variation (CV) for the different*  
1159 *sensors and walking and running speeds. No specific pattern was observed concerning the inter-variability*  
1160 *in the frontal plane. By contrast, an important inter-individual variability was observed for sensors located*  
1161 *on the upper part of the body (head and trunk versus leg and feet, pairwise  $p < 0.001$ ) in sagittal and*  
1162 *transversal plane.*

1163  
1164 *Figure 9 a) Average sample entropy for each sensor and walking and running speeds. Reading all planes*  
1165 *(frontal, sagittal, transversal) from left to right (upper body to lower body), average head entropy was*  
1166 *significantly lower ( $p < 0.001$ ) compared to trunk, leg and feet, for all the exercises. b) Coefficient of*  
1167 *Variation (CV) of Sample Entropy for the different sensors and walking and running speeds. High CVs*  
1168 *were observed for the upper part of the body (pairwise comparison head and trunk versus leg and feet,*  
1169  *$p < 0.05$ ), for the sagittal and transversal planes and for the lower part of the body in the frontal plane (head*  
1170 *and trunk versus feet,  $p < 0.05$ ).*

1171  
1172  
1173 *Figure 10. Average dynamic trajectories of 18 participants (P1 to P18 - sagittal, frontal and transversal*  
1174 *planes) acquired from the sensor placed on the lower back (L5) during comfortable walking and running.*

1175  
1176 *Figure 11. Average dynamic trajectories of 18 participants (P1 to P18 - sagittal, frontal and transversal*  
1177 *planes) acquired from the sensor placed on the left ankle during comfortable walking and running.*

1178  
1179  
1180

1181 Figure 12. A trajectory of the sensor located at L5 during a stride and its respective relationship between  
1182 angular velocity and curvature on a log scale. (left) walking, (right) running.

1183  
1184

1185 Figure 13. The average exponent  $\beta$  for the relationship between curvature and angular velocity in the  
1186 trajectories of different parts of the body for the 18 subjects identified per plan and walking and running  
1187 speeds. In the transversal plane, the  $\beta$  exponents for the head are significantly lower ( $p < 0.001$ ) than those  
1188 for the lower body during all exercises except for running. In sagittal plane,  $\beta$  exponents for feet are  
1189 significantly higher ( $p < 0.001$ ) than those of the other markers during every protocol phase. In the frontal  
1190 plane, the  $\beta$  exponents for lower body (feet and legs) are significantly lower ( $p < 0.001$ ) than those of the  
1191 other markers during every protocol phase.

1192  
1193  
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1195

1196 Table I. Subject characteristics

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1198

1199 Table II. Mean and standard deviation of spatio-temporal characteristics obtained in the protocol. \*

1200 Indicates statistically significant difference between male and female participants.

1201

1202

1203 Table III. Summary of features used to define the motor style.

1204

1205

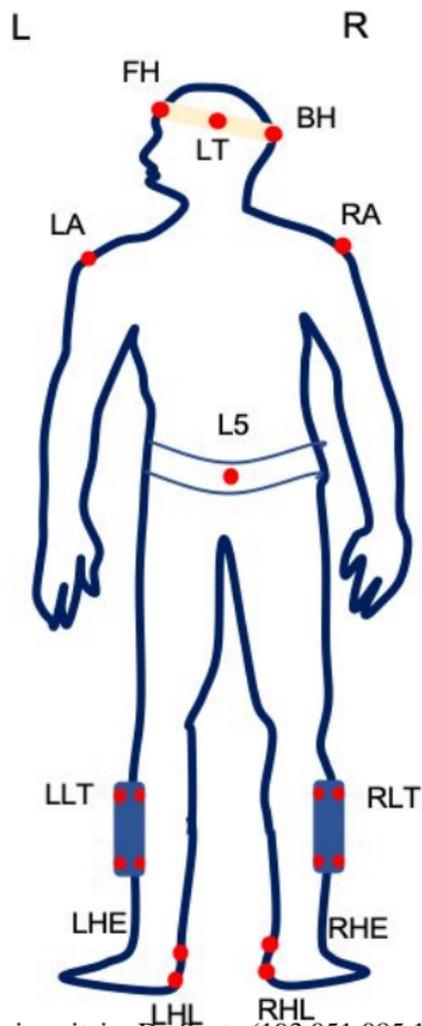
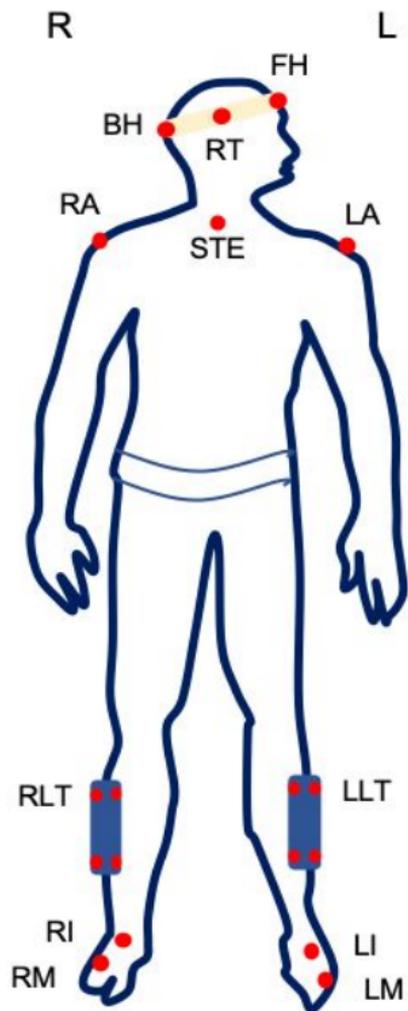
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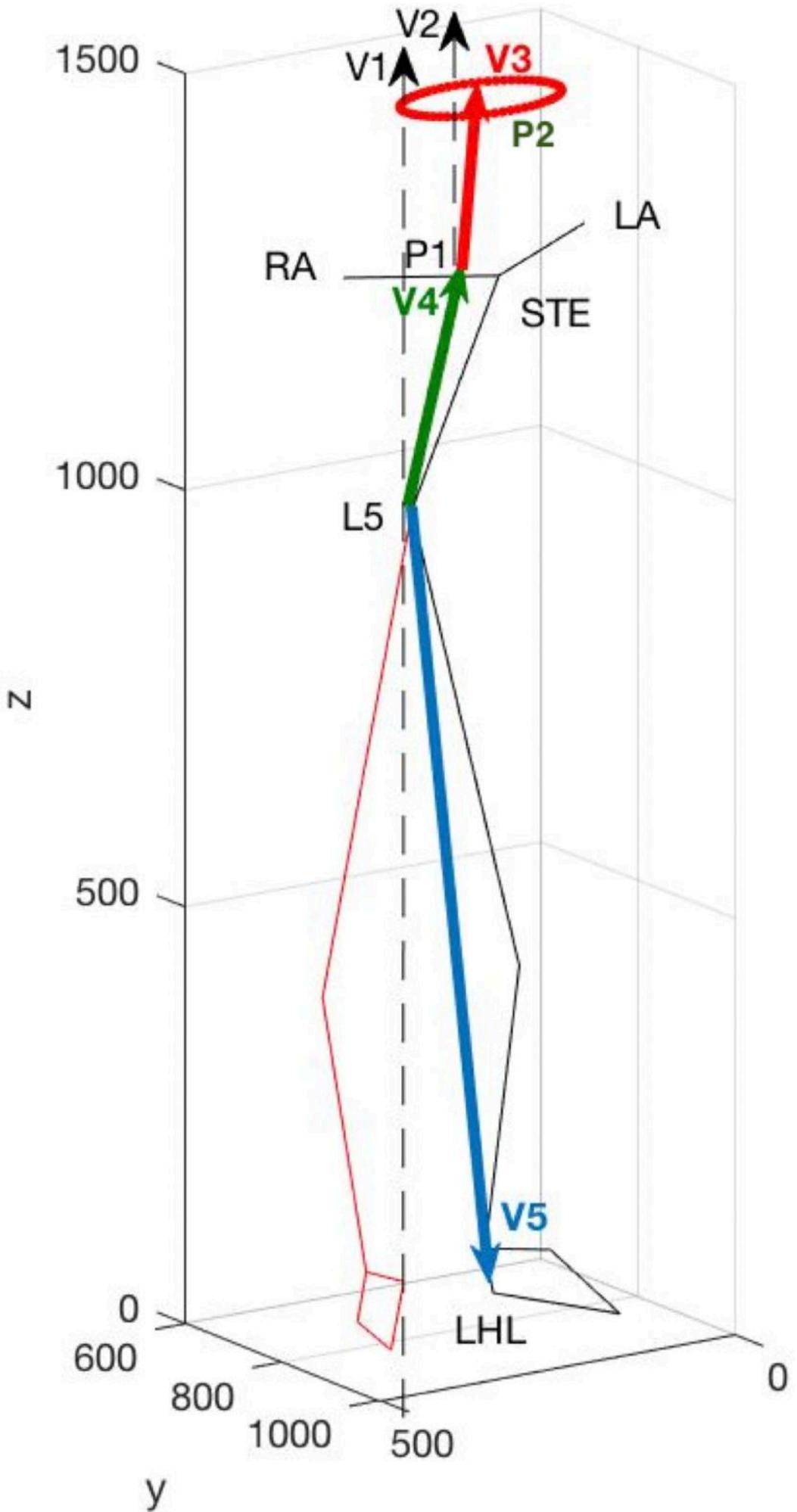
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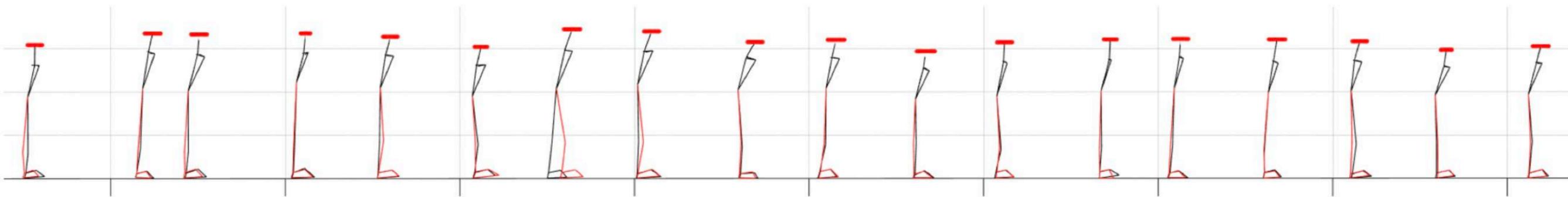
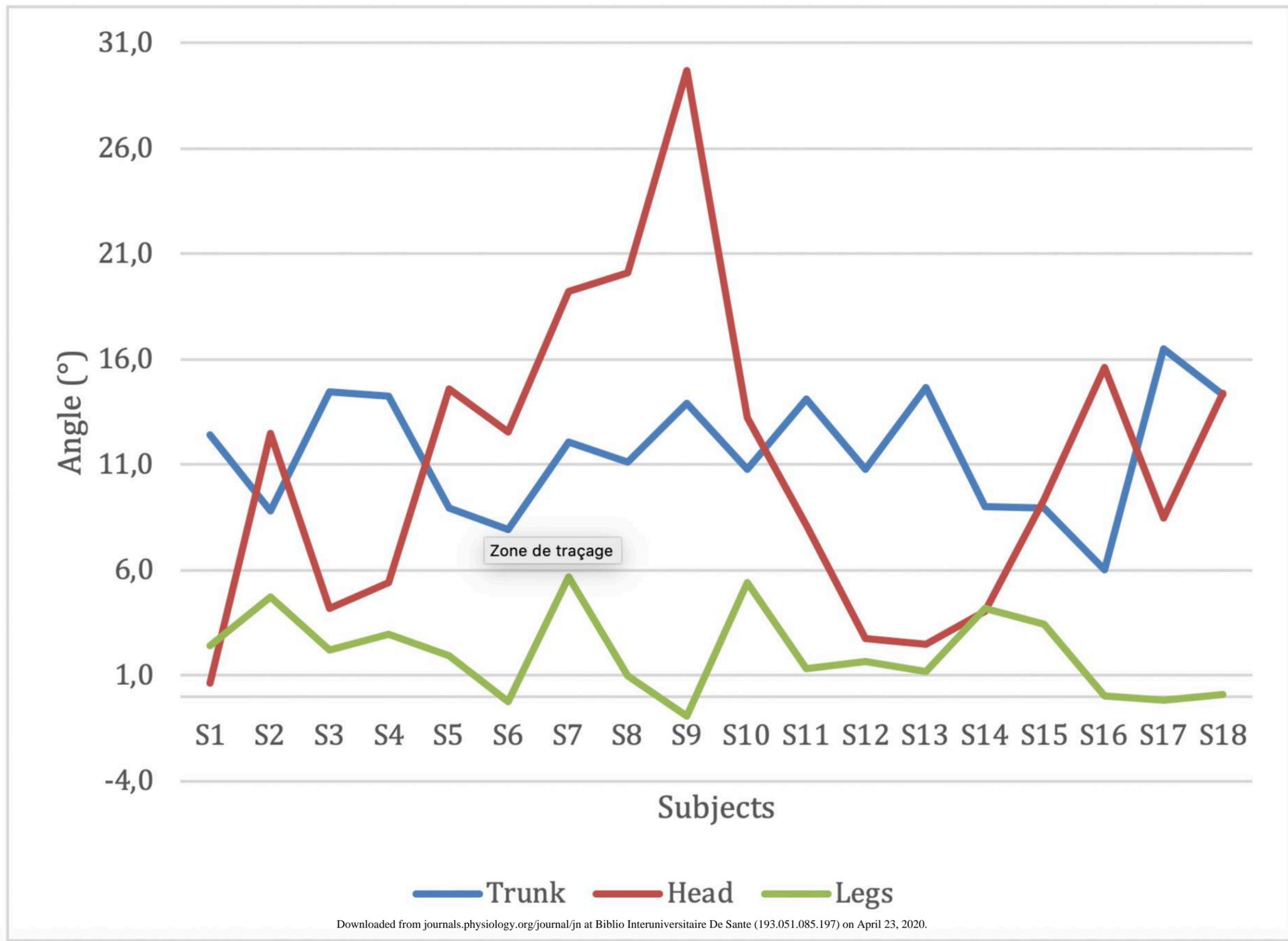
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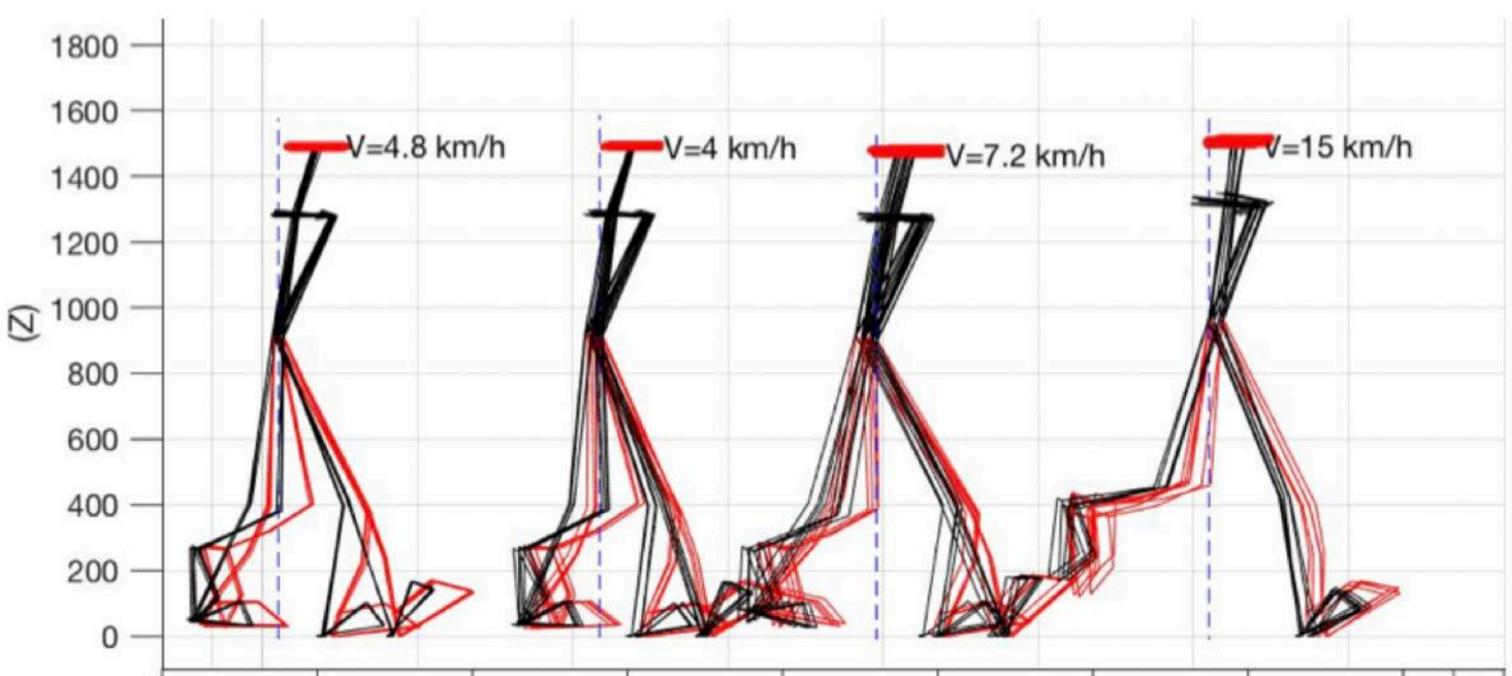
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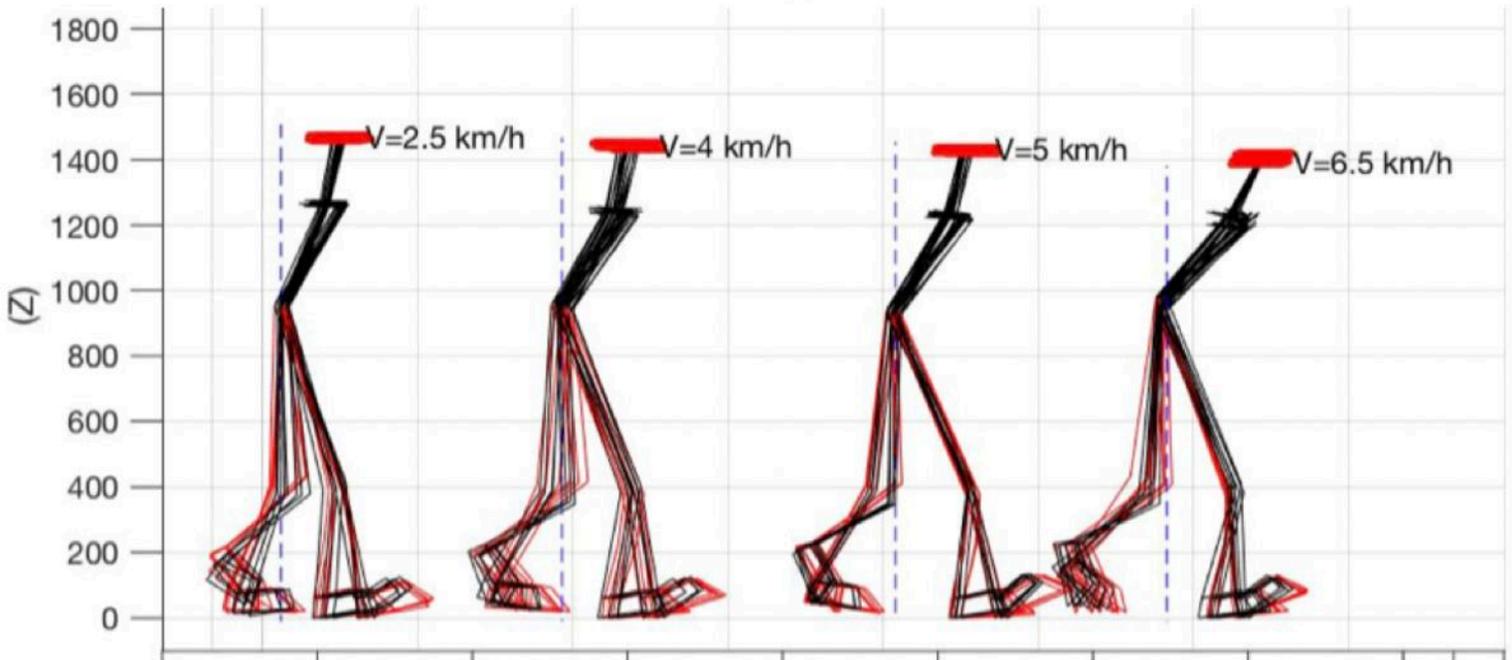




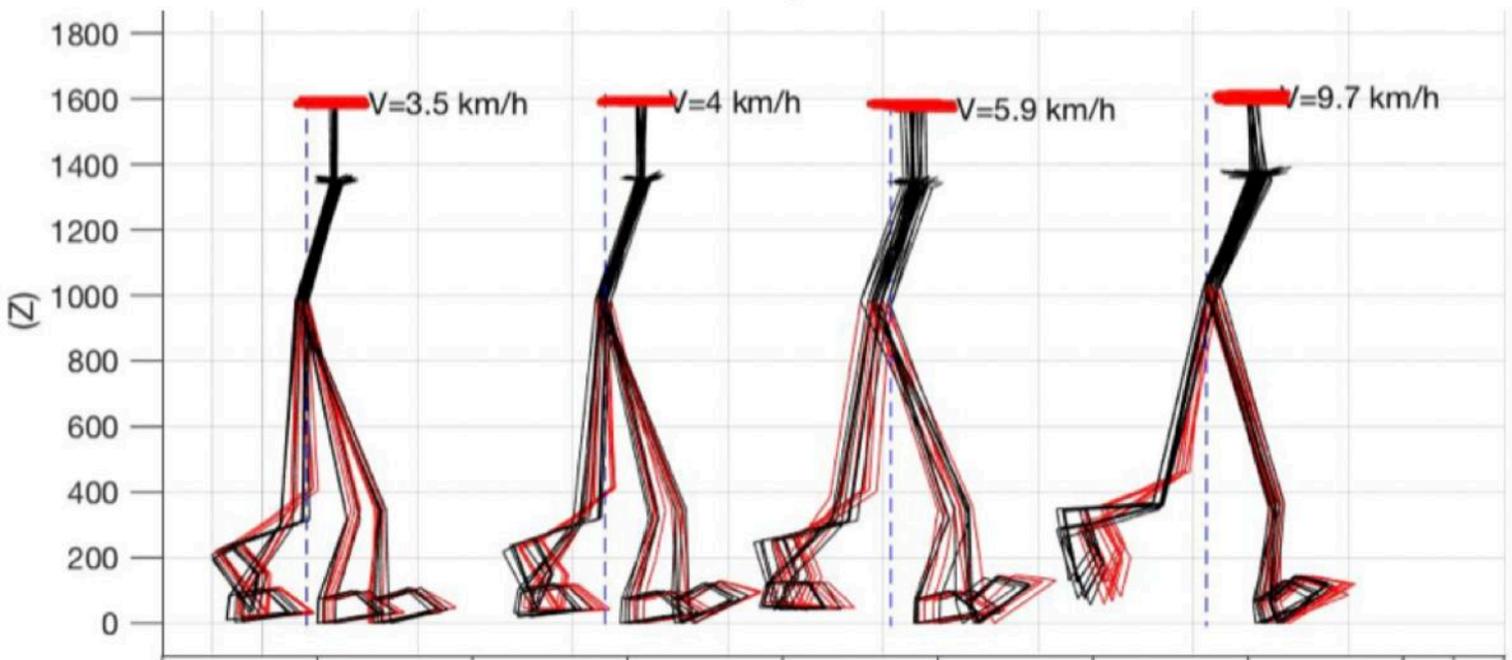
**A****B**



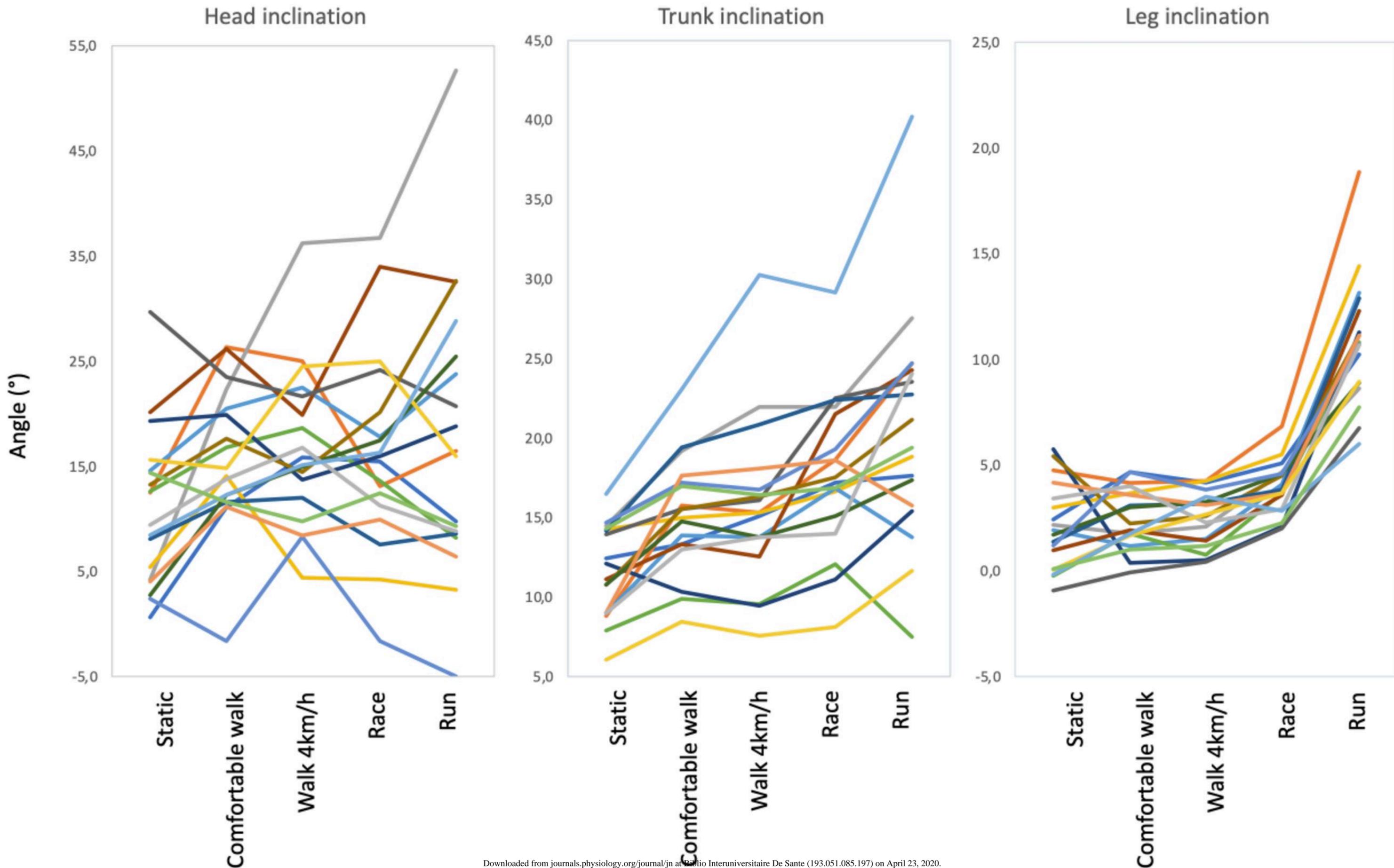
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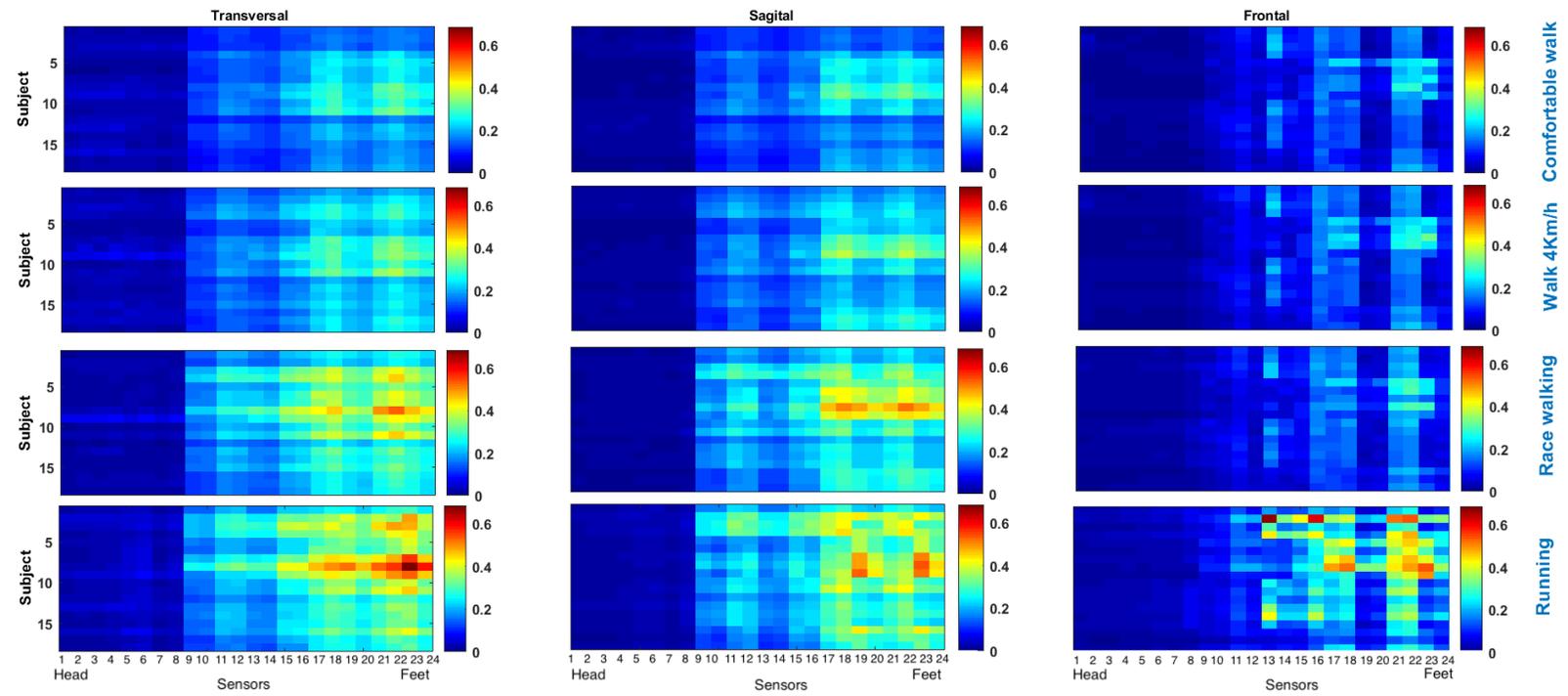


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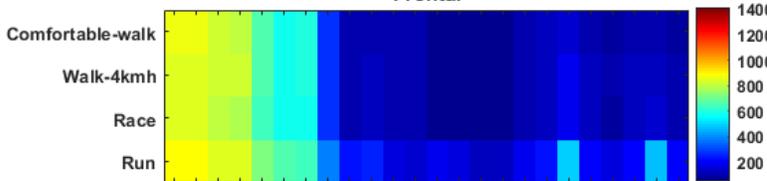
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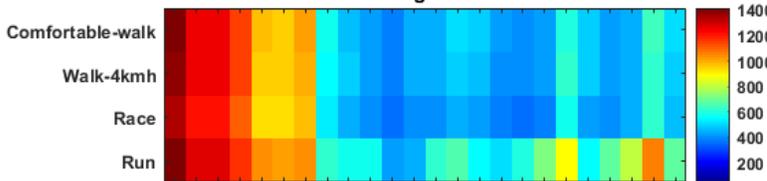


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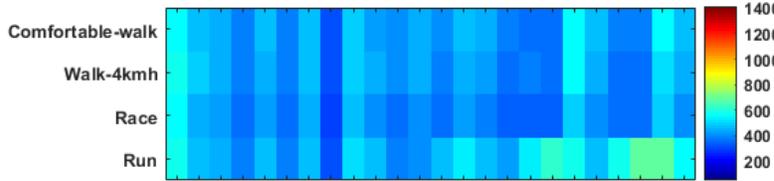
Frontal



Sagittal



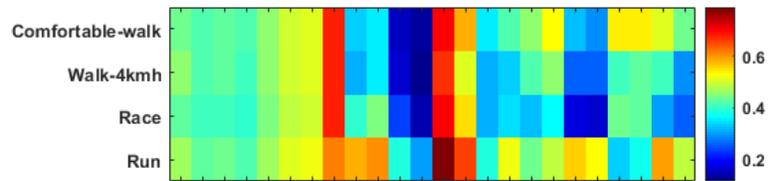
Transversal



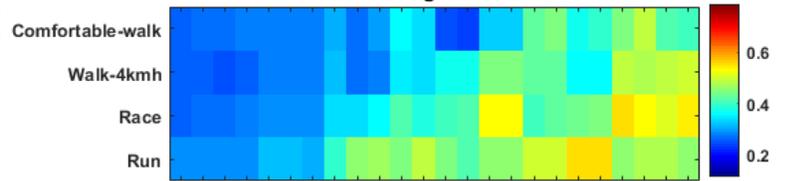
Sensors

b) Coefficient of Variation of Jerk

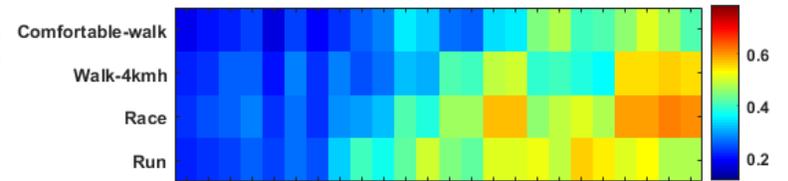
Frontal



Sagittal



Transversal

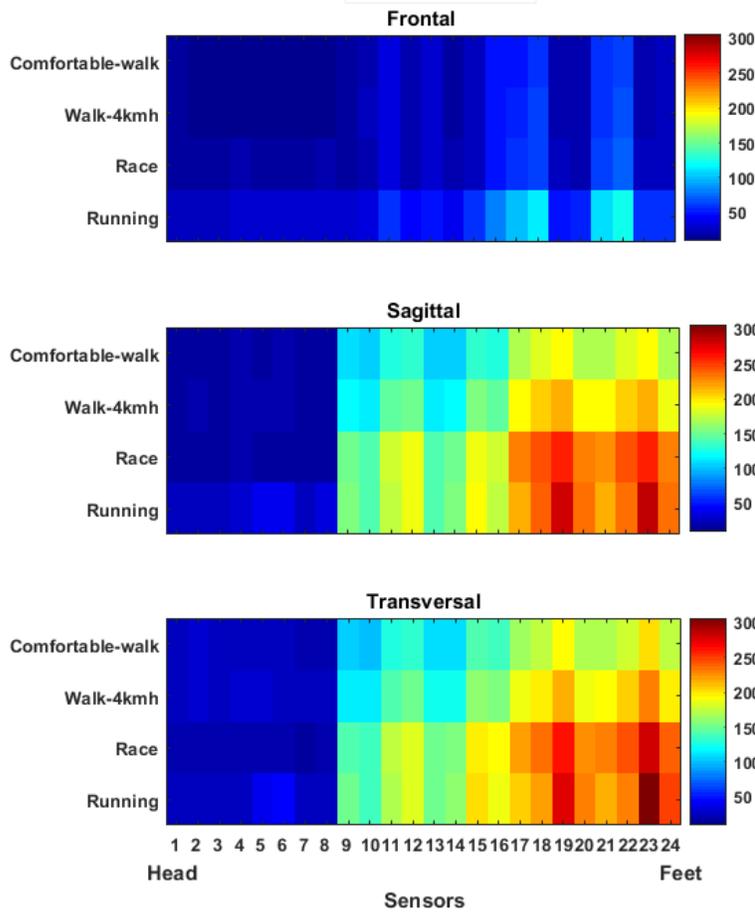


Head

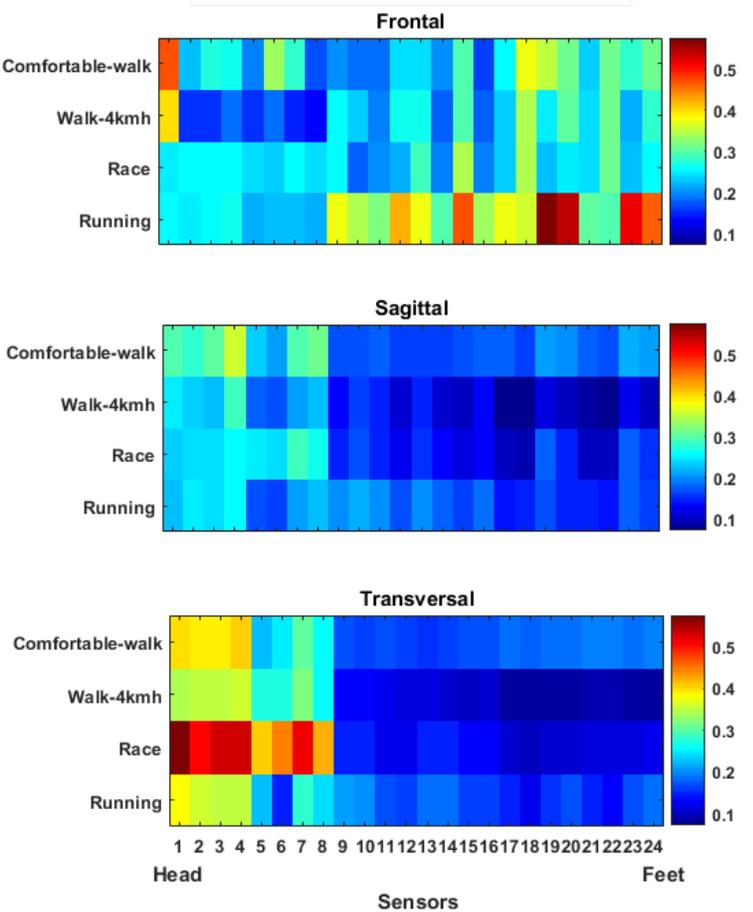
Sensors

Feet

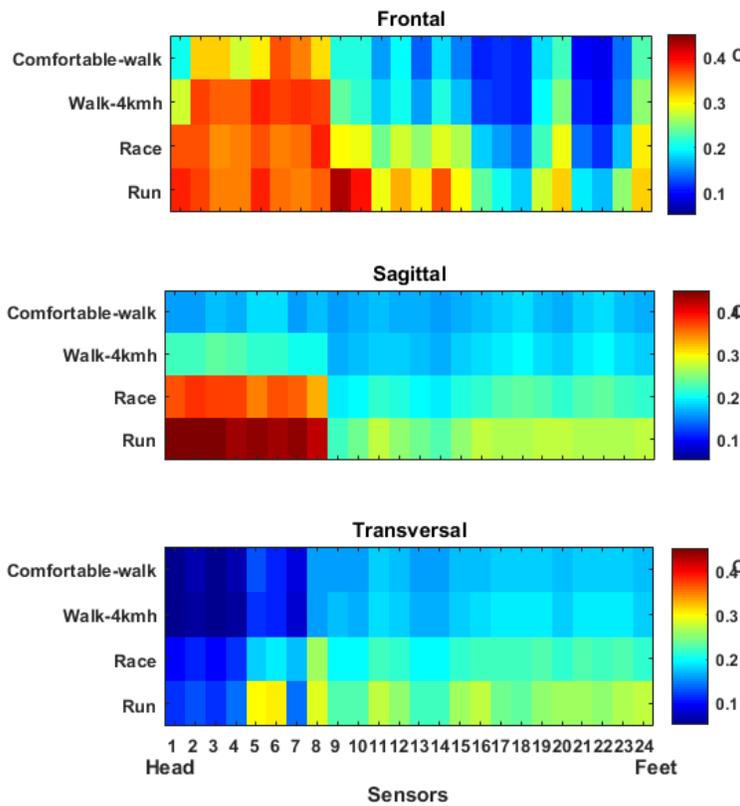
a) Average



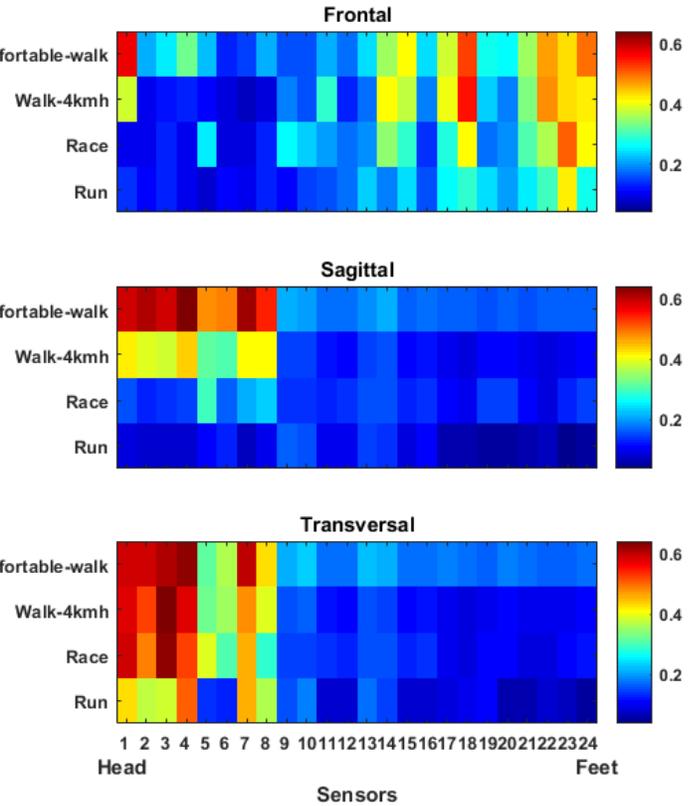
b) Coefficient of Variation of RMS



a) Average



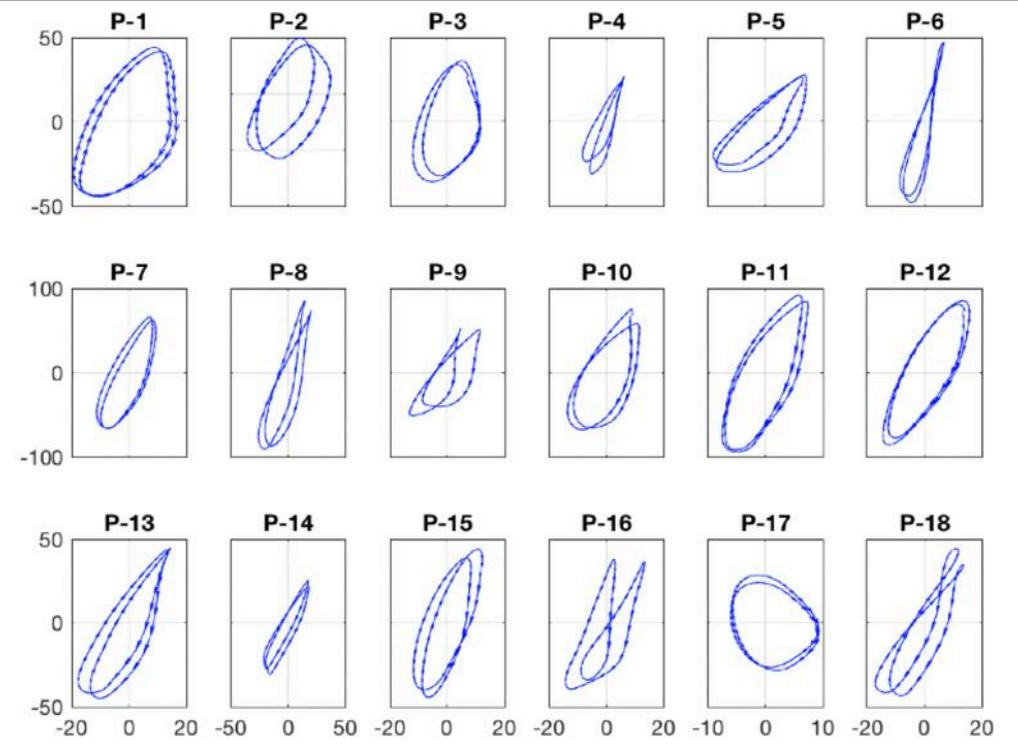
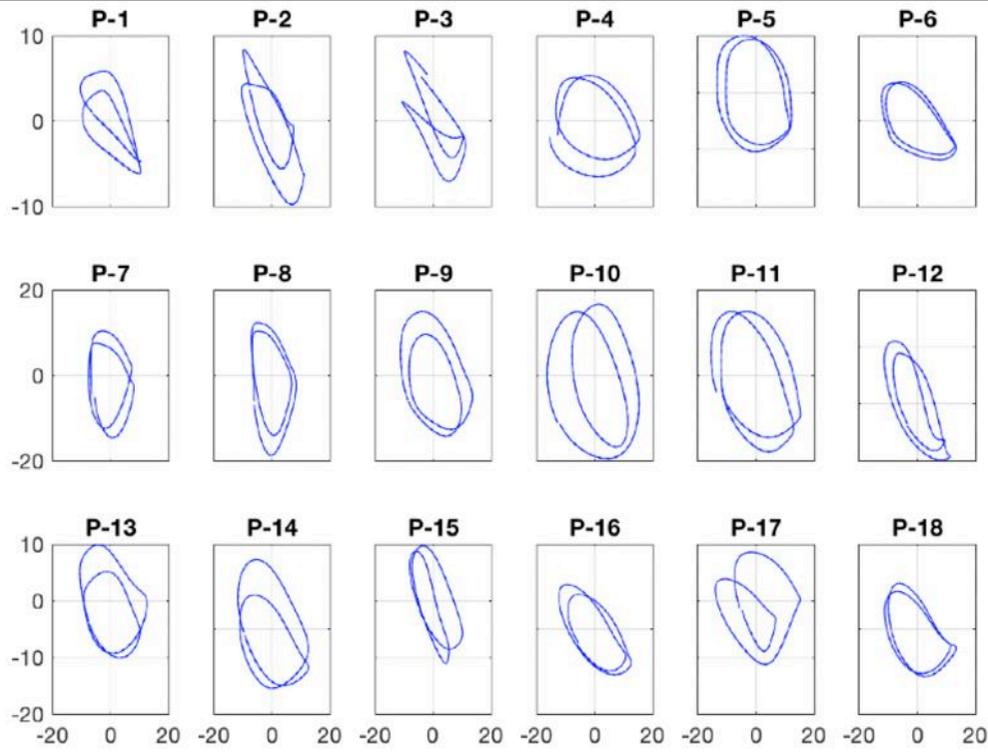
b) Coefficient of Variation of Sample Entropy



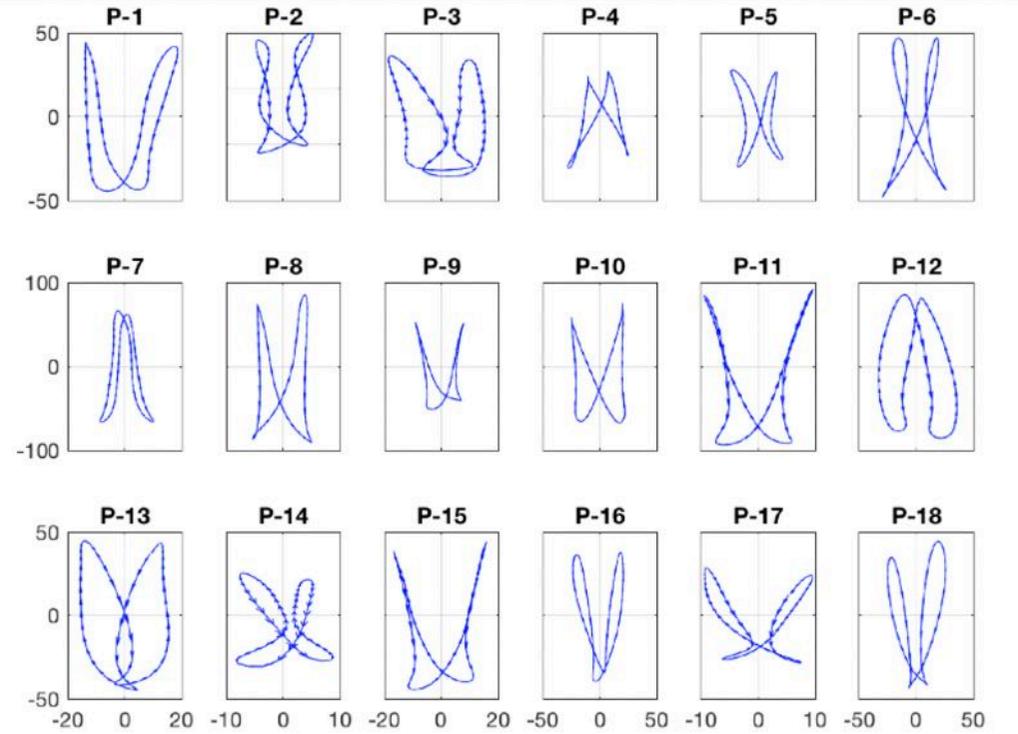
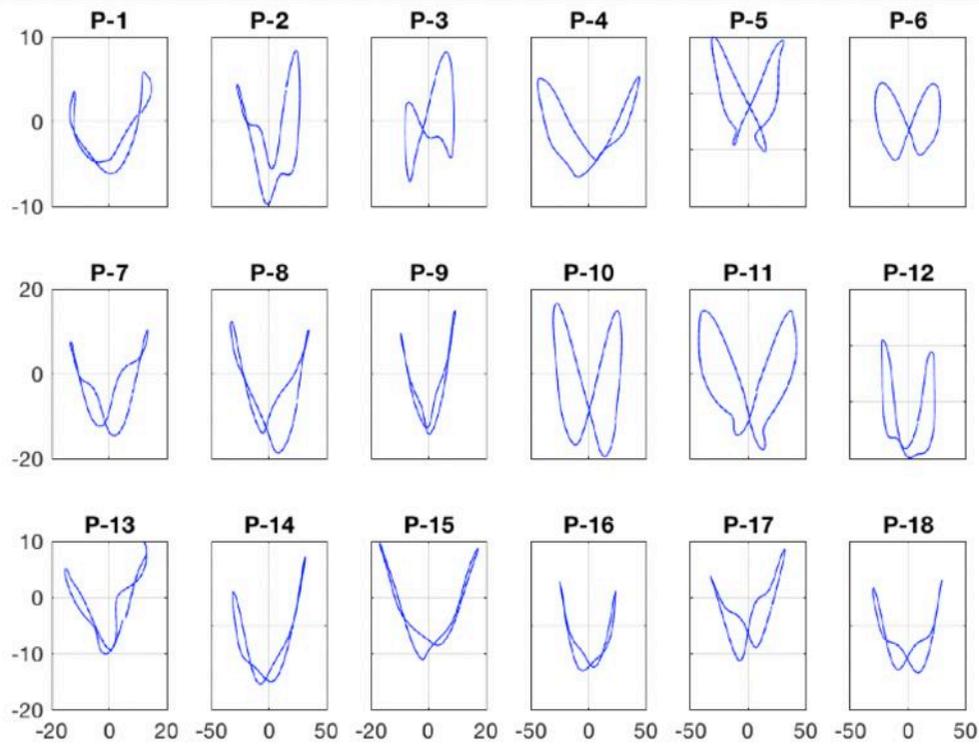
# Comfortable Walk

# Running

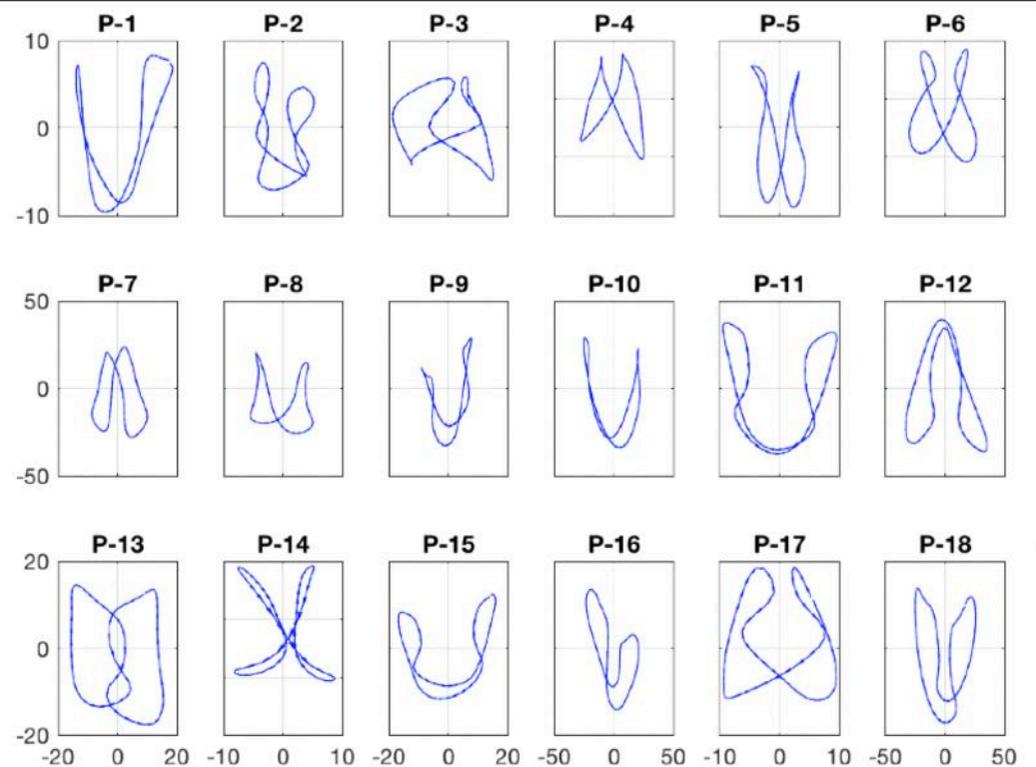
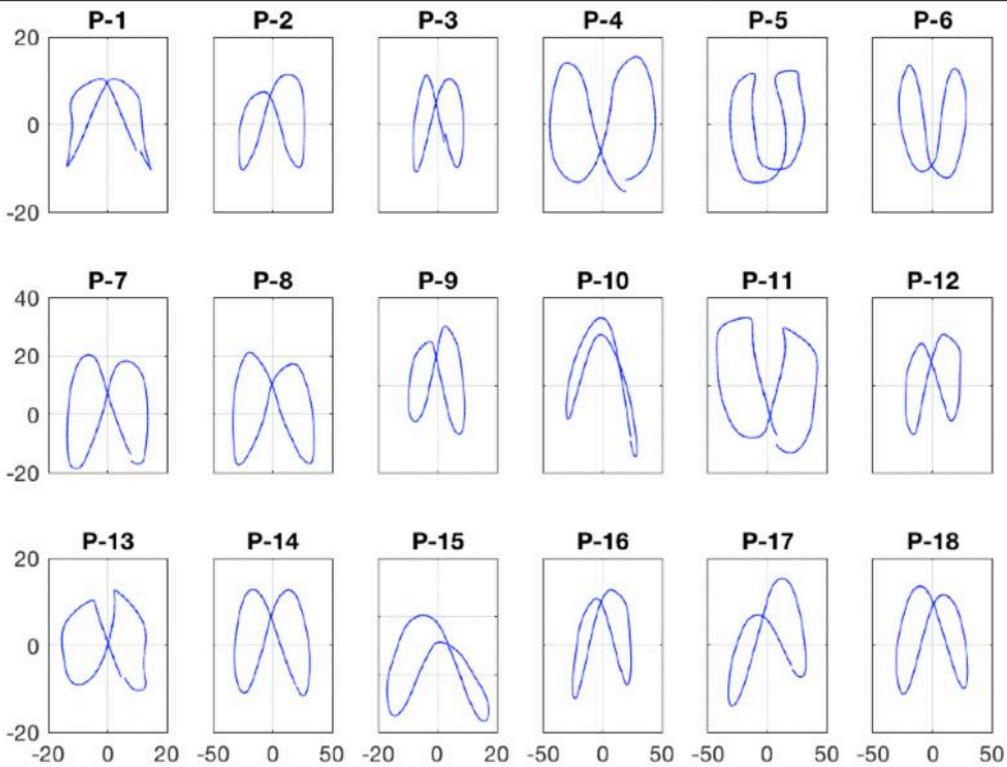
Sagittal



Frontal



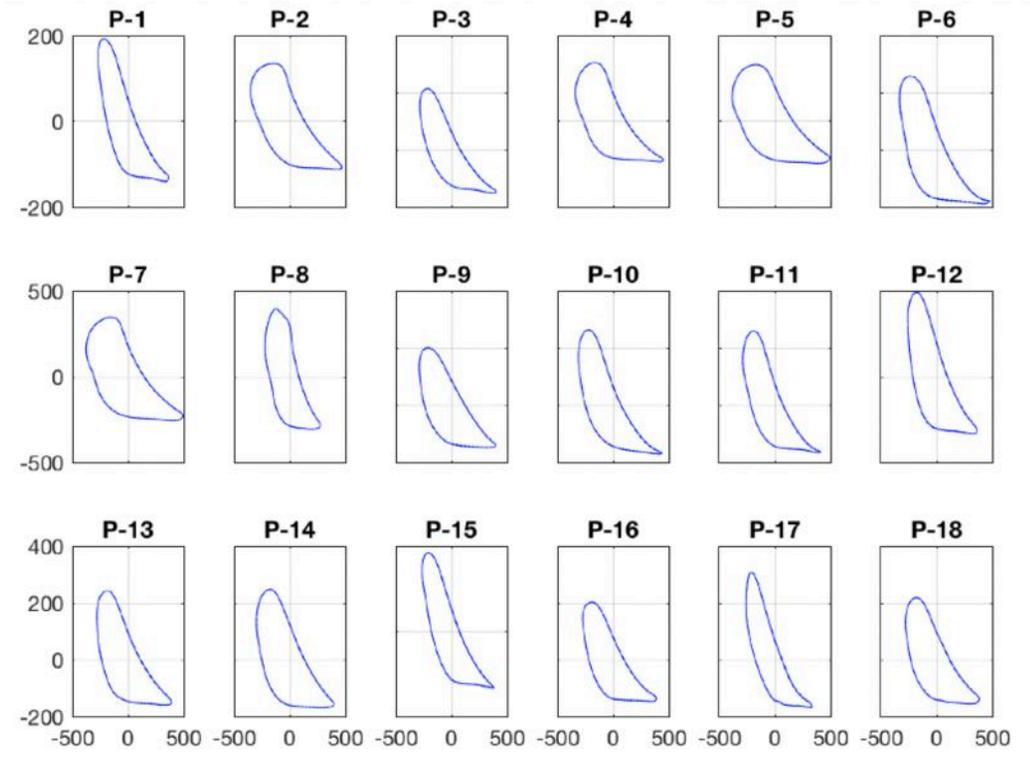
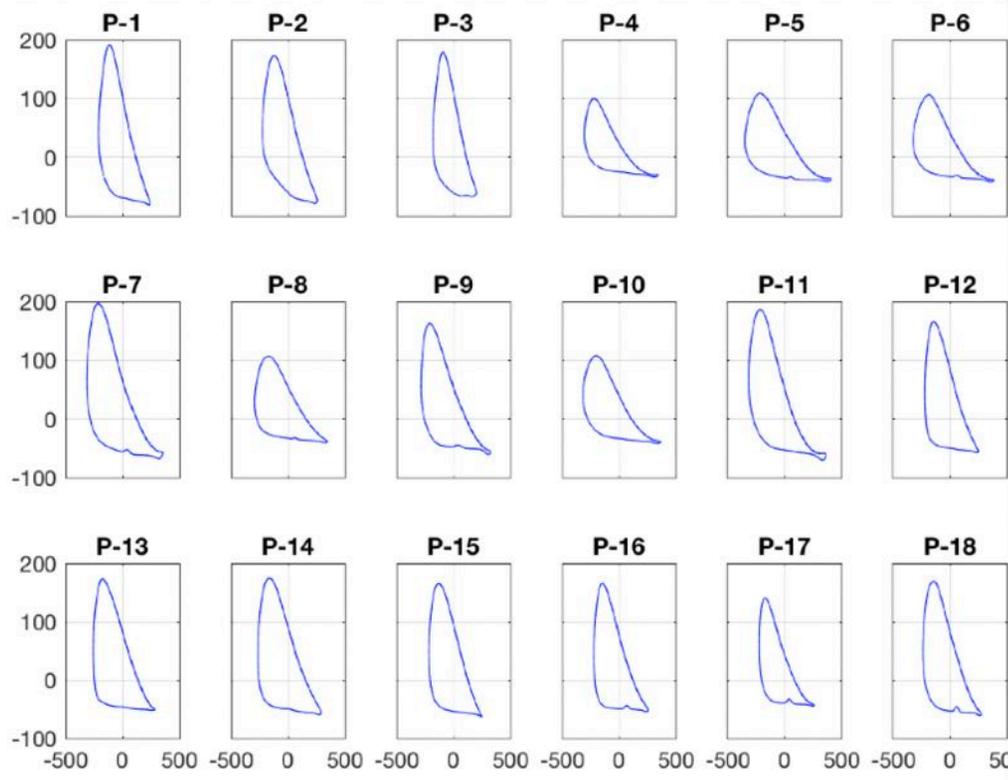
Transversal



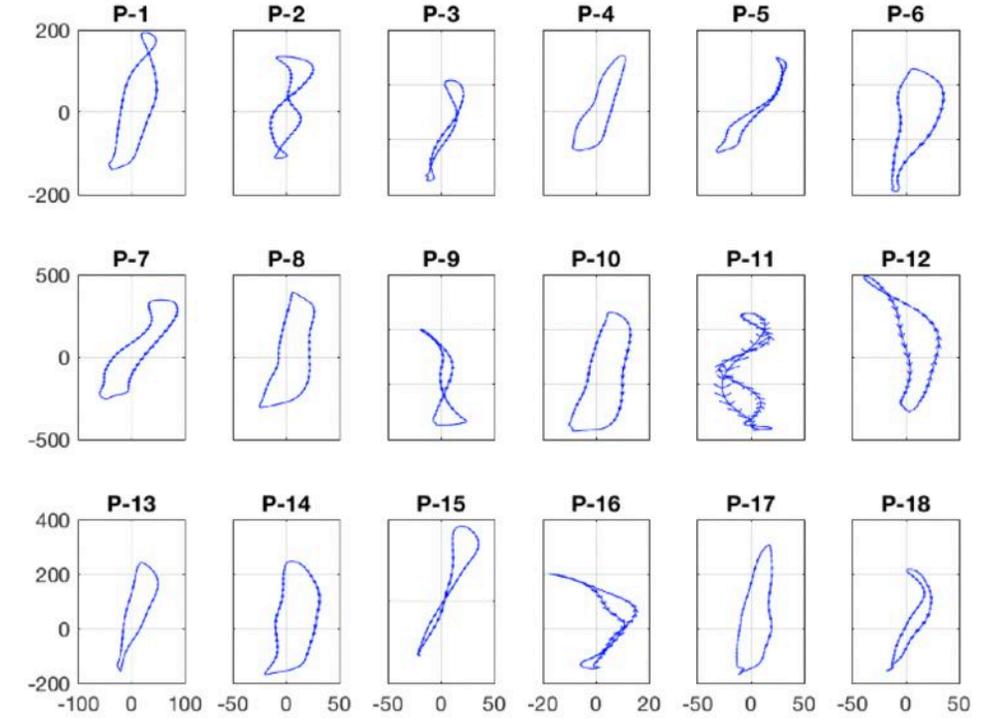
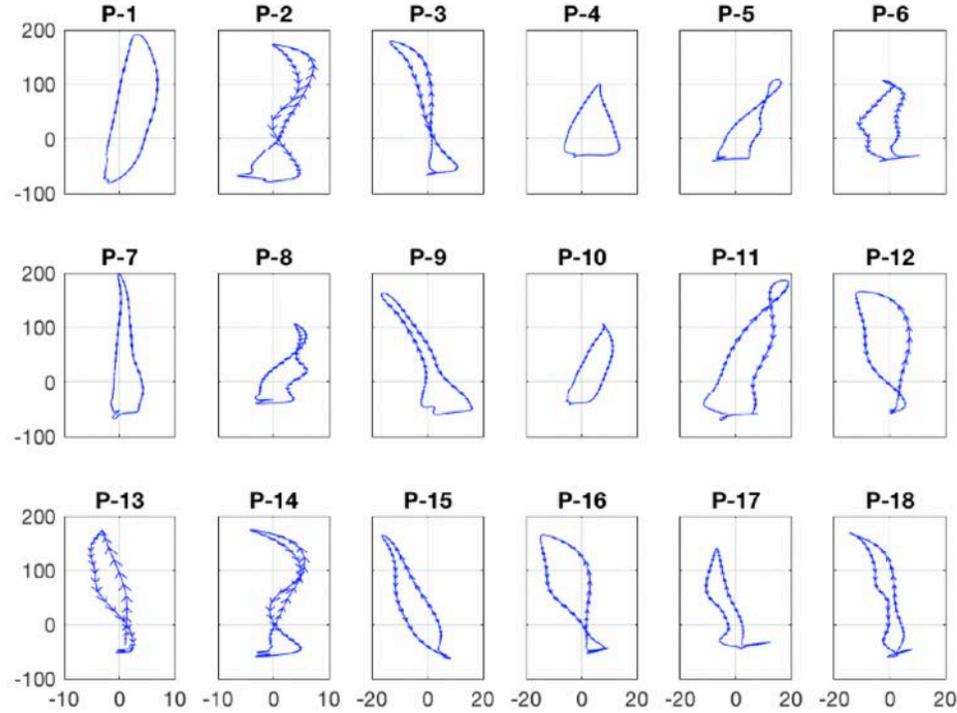
# Comfortable Walk

# Running

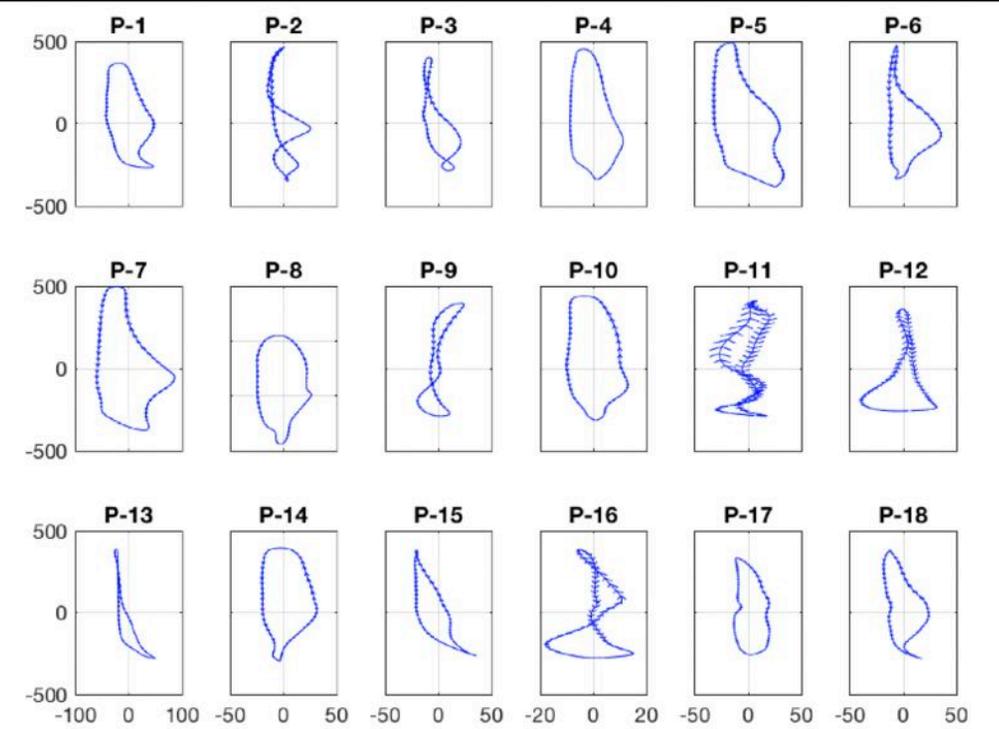
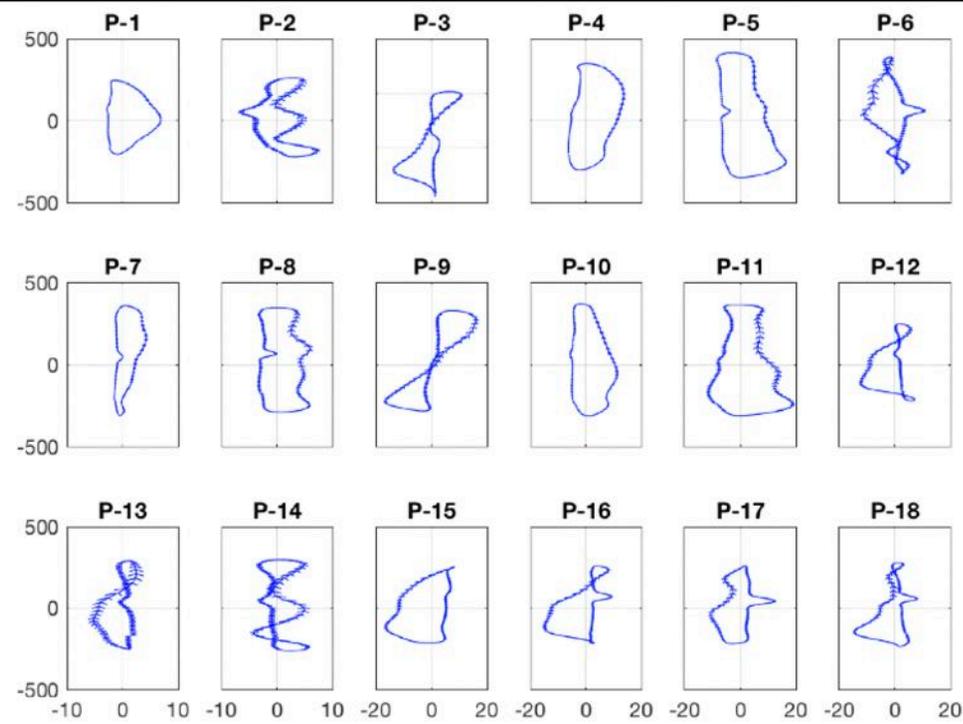
Sagittal



Frontal

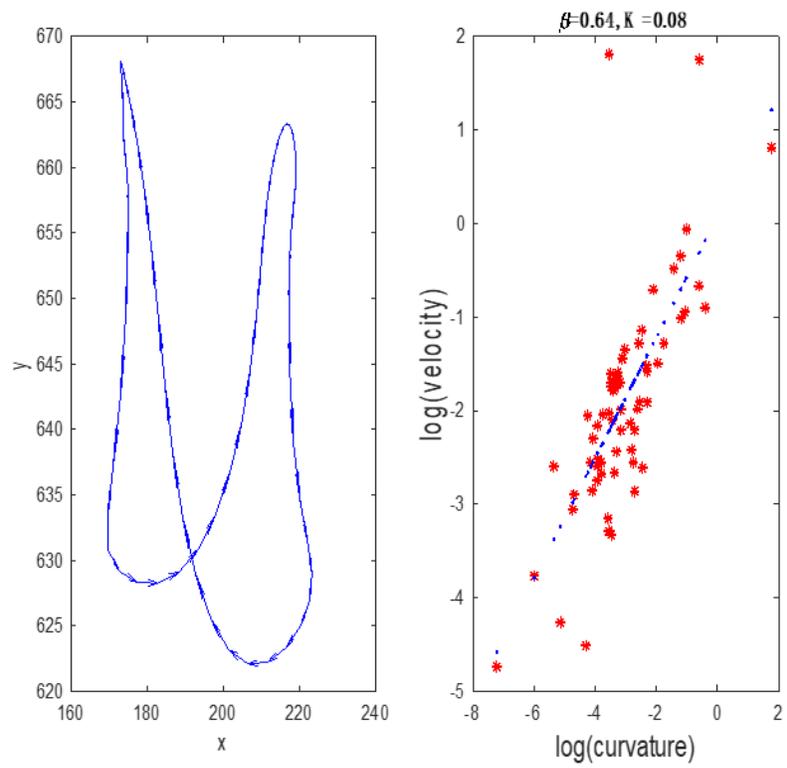
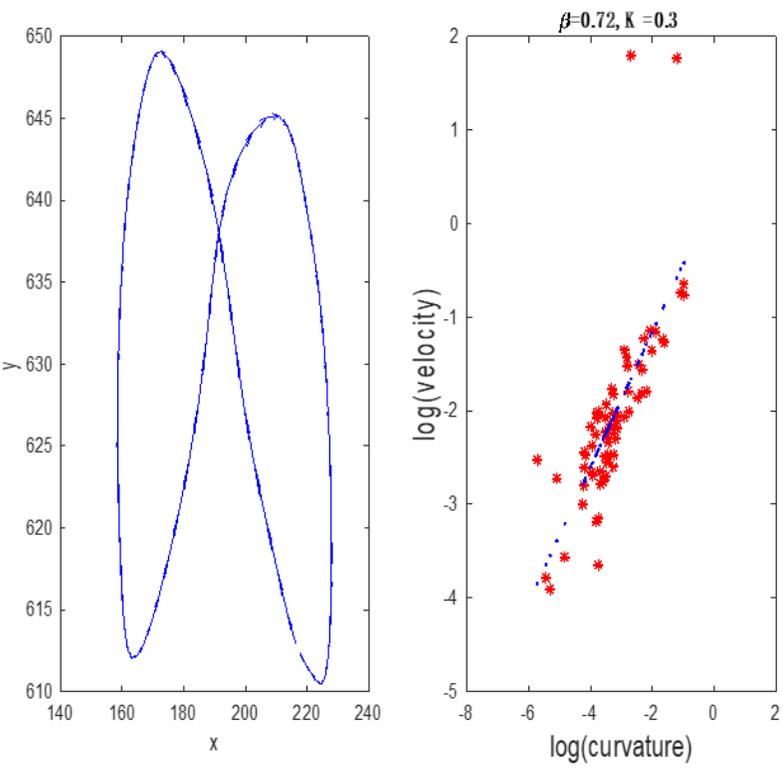


Transversal



Subject8- Transversal plan -8. Low back -Confortable-walk

Subject8- Transversal plan -8. Low back -Running



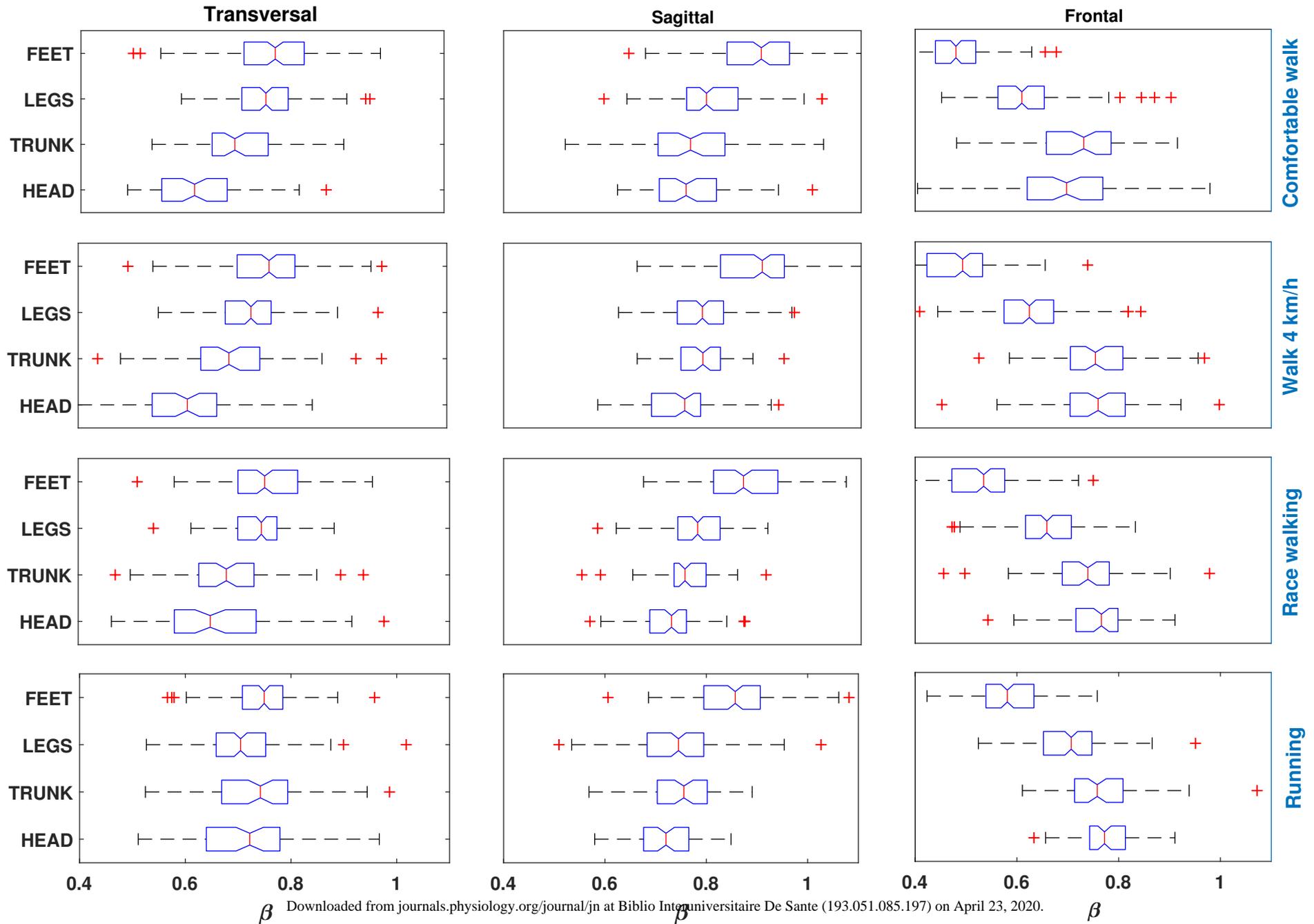


Table I. Subject characteristics

<b>Gender</b>	<b>n</b>	<b>Weight kg (std)</b>	<b>Height cm (std)</b>	<b>Age years (std)</b>
<b>M</b>	10	68,2 (9,22)	173,1 (7,47)	30,2 (9,51)
<b>F</b>	8	51,2 (3,69)	163,8 (4,64)	34,75 (14,55)

Table II. Mean and standard deviation of spatio-temporal characteristics obtained in the protocol. \* Indicates statistically significant difference between male and female participants.

Variable	Gender	Comfortable Walk	Walk 4 km/h	High speed walk	Running
Speed km/h	M	3,38 (0,81)	4	6,66 (1,02)*	12,51 (2,91)*
	F	2,93 (0,55)	4	5,6 (0,33)	9,475 (1,47)
Step length cm	M	53,50 (10,63)	60,00 (4,28)*	78,52 (8,11)*	<b>78,68 (10,06)*</b>
	F	45,30 (6,53)	55,22 (2,55)	66,77 (3,46)	65,39 (3,77)
Step width cm	M	7,01 (2,32)	6,76 (1,78,)*	7,65 (2,08)	<b>6,10 (2,62)</b>
	F	8,69 (1,72)	8,68 (1,09)	8,60 (1,02)	7,23 (1,10)

Table III. Summary of features to define the motor style.

	FRONTAL				SAGITTAL				TRANSVERSAL			
	HEAD	TRUNK	LEGS	FEET	HEAD	TRUNK	LEGS	FEET	HEAD	TRUNK	LEGS	FEET
<b>Inclination at rest</b>					+	+						
<b>Inclination during locomotion</b>					+	+						
<b>JERK</b>		+	+									
<b>RMS</b>									+	+		
<b>ENTROPY</b>			+	+	+	+			+	+		
<b><math>\beta</math> factor</b>	+	+	+	+	+	+	+	+	+	+	+	+