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Sintesi

A statistical approach for investigating the law of intersegmental coordination in animal locomotion

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Sintesi

Locomotion is a unique feature of animal kingdom. To move, animals control multiple degrees of freedom of the body and coordinate multi-segment limb motion.

The aim of this study was to use the basic mathematical framework and analytical tools to investigate the ‘rules’ or ‘laws’ of the inter-segmental coordination during walking in different animals.

The focus has been placed on terrestrial locomotion of vertebrates including humans and a characterization of both bipedal (birds, human) and quadrupedal locomotion. On the whole, I recorded walking in humans and 17 animals (5 birds and 12 mammals). The basic analysis consisted in two main parts: 1) reconstruction of angular motion of limb segments from the optoelectronic systems and 2) application of the principal component analysis for characterising the inter-segmental coordination, performed in Matlab.

Neurophysiology and biomechanics of animal locomotion

Walking, in bipedal and quadrupedal animals, involves rhythmic behaviour of the body and limb. These movements depend on the precise regulation of the timing and the strength of contractions in numerous muscles. Centrally located neuronal circuits, known as central pattern generators, (CPGs) (Grillner 1981), can generate the basic motor pattern of locomotion.

Systems motor physiologists aim at understanding the organization and production of movements in terms of the elementary components, that is, the basic control units with which the Central Nervous System (CNS) constructs a movement and controls multiple degrees of freedom of the body (Lacquaniti, Ivanenko, and Zago 2012).

It has been previously suggested that covariation of limb segment motion might simplify the control of both posture and locomotion by reducing the effective degrees of freedom. Thus an understanding of this phenomenon might provide some basic understanding about how the CNS controls legged terrestrial locomotion.

To define the segments, the elevation angles and the joint angle now it has been assumed that, in the sagittal plane, the right side of the subject, in our case human or animal subject, is being viewed as she or he or it progresses from left to right (Fig. 1). So, the two-dimensional model of the body of a quadrupeds consists of one forelimb, trunk, and one hindlimb. Each hindlimb comprised of four segments which are thigh, shank, tarsals and digits, and each forelimb comprised of other four segments which are upper arm, forearm, carpals and digits. Each segments is assumed to be a rigid body. Segments are linked by frictionless hinge joints. Thus, the limb is modelled as an interconnected chain of rigid segments. The main axis for each limb is defined as the segments between the hip and the ankle for the

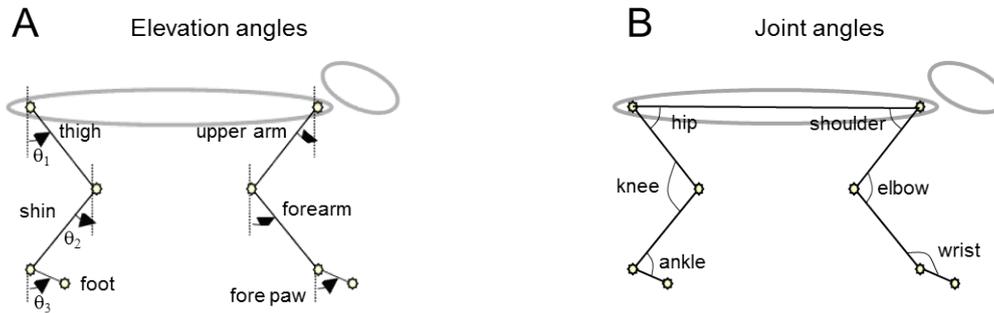


Figure 1: Elevation and joint angles.

hindlimb, and as the segment between the shoulder and the metacarpal joint.

An *elevation angle* (Fig. 1) of a limb segment is defined as the orientation of the segment with respect to the vertical and the walking direction (e.g., positive when the distal joint moves in the forward direction). Elevation angles are considered in the sagittal plane only since segment motion in the lateral direction and/or its rotation is much smaller. Finally, considering two consecutive segments, the *joint angles* are the angles between the higher segments and the lower.

Comparison of locomotion in animals of different size

During walking, in the swing face the leg swings around the hip, as a regular pendulum. In the stance face our leg moves like an inverted pendulum: we pivot around the foot that is on the ground, as if we were using that leg to pole-vault, and our center of mass, somewhere in the belly, describes an arc. As we plant a foot on the ground in front of us, the ground exerts a force back up our leg that slows us down, and we continue slowing as we rise up on that foot to the top of our arc. At that point our kinetic energy is at a minimum, but our potential energy is at a maximum. As we fall forward into the next step, that stored potential energy is converted back into kinetic energy, and we accelerate again.

In the nineteenth century, the nautical engineer William Froude introduced a dimensionless variable to help him to produce model ships that maintained the same propulsion dynamics as full-size vessels. He came out with the intuition that such a model depends on the interchange between the kinetic and potential energy of the water caused by the ship progression. The Froude number is

$$Fr = \frac{v^2}{gl}$$

where v is the progression speed ($\frac{m}{s}$), g is the acceleration of gravity ($9.81 \frac{m}{s^2}$) and l is the vertical distance of the centre of mass from a given reference altitude (m).

Since the pendulum dynamics is controlled by the continuous interchange between potential and kinetic energy, as in the wave generated by ship progression, it is possible to exactly predict the motion of differently sized pendula by using the Froude number.

One important consequence of the presence of gravitational forces is a pendulum-like behaviour of our limbs. This behaviour is inherently linked to the optimization of movement in animals. Accordingly, gravity plays an essential role in terrestrial locomotion. Alexander and Jayes 1983 formulated the hypothesis that similar animals of different sizes, travelling over land at equal Froude numbers, would tend to move in dynamically similar fashion.

Alexander and Jayes 1983 that in a system, like walking and running, where gravitational forces are important, dynamic similarity is possible if the two systems have equal Froude numbers, $\frac{v^2}{gl}$.

He also observed that bipeds generally seem to use about the same duty factors as quadrupeds at the same Froude number and also, in many respects, he saw that the techniques of walking and running of bipedal mammals and birds are much as would be predicted extending the dynamic similarity hypotheses to them.

Summarizing, dynamic similarity implies that the recovery of mechanical energy in subjects of short height, such as children, pygmies, and dwarfs, is not different from that of normal-sized adults at the same value of Fr . At $Fr = 0.25$, an optimal exchange between potential and kinetic energies of the COM occurs. Other reference Froude numbers having a biomechanical meaning are: $Fr = 0.5$ (walk-to-run transition speed) and $Fr = 1$ (upper speed limit at which the body takes off from the ground and thus walking is no longer feasible). The pendulum mechanism has been demonstrated not only in humans but also in a wide variety of animals that differ in body size, shape, mass, leg number, posture, or skeleton type, including birds, monkeys, kangaroos, elephants, dogs, lizards, frogs, crabs, and cockroaches, and it was even applied to estimate how fast dinosaurs were moving or the size of a dinosaur from the size of its footprint (Alexander 1989; Dickinson et al. 2000).

Multi-segment harmonic mechanical oscillators

Despite the fact that locomotion may differ widely in mammals, common principles of kinematic control can be observed. Such principles reflect similar mechanical and neural constraints. It is known that multi-segment motion of mammals locomotion is controlled by a network of coupled neural oscillators (CPGs, see Grillner 1981). Flexible combination of unit oscillators gives rise to different forms of locomotion. Inter-oscillator coupling can be modified by changing the synaptic strength (or polarity) of the relative spinal connections. As a result, unit oscillators can be coupled in phase, out of phase, or with a variable phase, giving rise to different

behaviours, such as speed increments or reversal of gait direction (from forward to backward). It has been also hypothesized that the control of locomotion may emerge from the coupling of neural oscillators between each other and with limb mechanical oscillators. Muscle contraction intervenes at variable times to re-excite the intrinsic oscillations of the system when energy is lost (Lacquaniti, Ivanenko, and Zago 2002).

Using the mathematical model constructed by Barliya et al. 2009, will be considered a model of coupled mechanical oscillators based on using first-order harmonics which approximate the behaviour of the elevation angles of the corresponding limb segments.

The law of inter-segmental coordination is a kinematic law that describes the coordination pattern between the elevation angles of the limb segments during locomotion.

During human walking, the temporal patterns of the elevation angles of the lower limb segments covary along an attractor plane common to both the stance and swing phases. When plotted with respect to each other, these angles form a ‘tear-drop’ shaped loop. The three variables θ_1, θ_2 and θ_3 , which represent motion of the major segments of the limb are considered. Ivanenko et al. 2002 have shown that the elevation angle waveforms tend to become progressively closer to sinusoids as the speed increases, as was evident from the increase of percent variance (PV) of the first harmonic. It is possible to fit the time course of each of the elevation angles using three harmonics:

$$\theta_i(t) = a_{0i} + \sum_{k=1}^{\infty} a_{ki} \cos(k\nu_i t) + b_{ki} \sin(k\nu_i t) \quad i = 1, 2, 3. \quad (1)$$

The Fourier series truncated at the first order will be considered because it has been demonstrated that it provides a good approximation of the original data.

Using the identity

$$a \cos(x) + b \sin(x) = A \sin(x + \phi)$$

where $A = \sqrt{a^2 + b^2}$ and $\phi = \arctan(\frac{a}{b})$ into (1), and obtain

$$\theta_i(t) = a_{0i} + A_{1i} \sin(\nu_i t + \phi_{1i}) + A_{2i} \sin(2\nu_i t + \phi_{2i}) + A_{3i} \sin(3\nu_i t + \phi_{3i}) \quad (2)$$

In this way, it has been written the time representation of the elevation angles in terms of amplitudes and phases of the relevant harmonics.

Let $X(t), Y(t)$ and $Z(t)$ be sinusoids with fundamental frequencies ν_1, ν_2 , and ν_3 , and corresponding phase shifts ϕ_1, ϕ_2 , and ϕ_3 , respectively; let x_0, y_0 and z_0 be

translations and the amplitudes be denoted by x_1, y_1 and z_1 . Thus

$$\begin{cases} X(t) &= x_0 + x_1 \sin(\nu_1 t + \phi_1) \\ Y(t) &= y_0 + y_1 \sin(\nu_2 t + \phi_2) \\ Z(t) &= z_0 + z_1 \sin(\nu_3 t + \phi_3) \end{cases} \quad (3)$$

From this equation we see that, in the general case, there are really 12 parameters. Barliya et al. 2009 have shown that under opportune conditions, planar intersegmental constraints were achieved. The conditions they have found are explained in the following text. They suggest to start with the simplest case of all sinusoids with equal frequency, assuming no inter-sinusoidal phase shifts.

Lemma 0.0.1. *The three equations in 3, where all sinusoids have the same frequency and phase represent the parametrization of a segment in \mathbb{R}^3*

Proposition 0.0.1. *If in 3 three sinusoids have the same frequency and two different phases, the equations in 3 define a line lying in a plane.*

Proposition 0.0.2. *The three equations in 3 where the sinusoids have the same frequency and three different phases, also lie on a plane.*

In Proposition 0.0.2, it has been shown that when $\nu_1 = \nu_2 = \nu_3 = \nu$ and $\phi_1 \neq \phi_2 \neq \phi_3$, X, Y and Z describe an ellipse in \mathbb{R}^3 , whose projections on each coordinate plane being elliptic.

Therefore, Barliya et al. 2009 have shown that the ability of three oscillators to form a planar motion in \mathbb{R}^3 is mainly determined by the fundamental frequencies (ν_i) of the three components. So they have shown that in the case in which all fundamental frequencies are equal, and in the case in which only two fundamental frequencies are equal and the corresponding phases are also equal, modulo $2k\pi$ the three oscillators parametrize a planar curve. Furthermore, it has been demonstrated that the orientation of the constraining plane is determined by the phase shifts between oscillators and their amplitudes.

According to these model, different rhythmic oscillators whose frequencies and phases determine the coupling between these different generators affect the planar inter-segmental constraint. Hence, these generators are conceptually similar to the CPGs. Although the elevation angles actually are not purely sinusoidal, Barliya et al. 2009 proposed a model based only on using first-order harmonics which approximate the behaviour of the elevation angles of the corresponding limb segments. They have also shown that the model may successfully account for the plane's main properties and for the patterns of covariation, including the shape of the loop.

Principal component analysis (PCA)

Principal component analysis (PCA) is a powerful and elegant method of data analysis aimed at obtaining low-dimensional approximation of high-dimensional processes (Glaser and Rushkin 1976). PCA is very successful in capturing data redundancies, and has been applied to human locomotion to discriminate different gaits, to determine redundancies in kinematic and electromyographic data, and to assess inter-segmental coordination.

PCA, is very successful in capturing data redundancies and has been applied in human locomotion to discriminate different kinds of gaits, determine redundancies in kinematic and electromyographic data, and assess inter-segmental coordination. To study the strategies that the CNS might use to coordinate different limb segments, it is useful to characterize the relationships between kinematic variables (e.g., joint or elevation angles). The time dependence of these variables is described mathematically by a trajectory in an M -dimensional vector space,

$$\begin{aligned} x: [0, T] &\rightarrow \mathbb{R}^M, \\ t &\mapsto \mathbf{x}(t). \end{aligned}$$

In this way we can describe the locomotion as a trajectory in an M -dimensional vector space. The locomotion has a rhythmic behaviour, so that the trajectory is a closed loop with $\mathbf{x}(0) = \mathbf{x}(T)$, where T is the period. We are interested in the relationship among the M variables characterized by the existence of an N -dimensional subspace (with $N < M$) of the vector space on which the mean subtracted trajectory lies, that is, the existence of N linearly independent M -dimensional vectors $\{\mathbf{v}_i\}_{i=1, \dots, N}$ such that

$$\mathbf{x}(t) = \mathbf{v}_0 + \sum_{i=1}^N f_i(t) \mathbf{v}_i, \quad (4)$$

where f_i are periodic scalar functions and \mathbf{v}_0 is the mean of \mathbf{x} over time. In the specific case of $M = 3$ and $N = 2$, the subspace is a plane in \mathbb{R}^3 . Suppose that an experimentally observed trajectory, called \mathbf{x} is given. We can use PCA to infer the existence of an N -dimensional subspace containing such trajectory. We should consider two cases, the first in absence of noise and the second in presence of noise.

In absence of noise, the eigenvalue of the sample covariance matrix allows such an inference. For k time samples along the trajectory, the sample covariance matrix

$$\mathbf{S} = \frac{\mathbf{X}^T \mathbf{H} \mathbf{X}}{k}, \quad (5)$$

where $\mathbf{X}^T = [\mathbf{x}(t_1), \dots, \mathbf{x}(t_k)]$ is the data matrix and $\mathbf{H} = \mathbf{I} - \frac{1}{k} \mathbf{1} \mathbf{1}^T$, with $\mathbf{1}$ a column vector of M ones, is the centering matrix, has $M - N$ null eigenvalues if

the trajectory lies on an N -dimensional subspace. Thus, PCA, which consists in diagonalizing of the covariance matrix

$$\mathbf{S} = \mathbf{U}\mathbf{\Sigma}\mathbf{U}^T, \mathbf{U}\mathbf{U}^T = \mathbf{I}, \mathbf{\Sigma} = \text{diag}([\sigma_1 \dots \sigma_N 0 \dots 0]),$$

can be used, and the eigenvectors associated to the zero eigenvalues span the space orthogonal to the trajectory subspace. In simpler terms, the eigenvector matrix \mathbf{U} represents a rotation of the coordinate axes which aligns the first axis along the direction of maximum variance, σ_1 and the second to the last axes along directions with a decreasing amount of variance. For planarity of a trajectory in \mathbb{R}^3 , since variance is zero along the direction orthogonal to the plane, the eigenvector associated to the single null eigenvalue is orthogonal to the plane.

In presence of noise, assuming the noise $\boldsymbol{\varepsilon}$ has a zero mean multivariate normal distribution, $\boldsymbol{\varepsilon} \sim \mathcal{N}(\mathbf{0}, \mathbf{U}_\varepsilon \text{diag}([\sigma_\varepsilon^{\max} \dots \sigma_\varepsilon^{\min}]) \mathbf{U}_\varepsilon^T)$, we have

$$\mathbf{x}(t) = \mathbf{v}_0 + \sum_{i=1}^N f_i(t) \mathbf{v}_i + \boldsymbol{\varepsilon}(t). \quad (6)$$

If the noise amplitude is much smaller than the variance of the trajectory in the direction of smallest variability ($\max \sigma_\varepsilon \ll \sigma_N$), the smallest eigenvalues of the sample covariance matrix will not vanish but the eigenvalues associated only with noise are clearly distinguishable and thus the subspace can be identified. In practice, when a model of noise generation is not available, a heuristic criterion based on identifying a large difference between the smallest eigenvalues due to the data variability (σ_N) and the eigenvalues due to noise is used. Such a difference is usually detected on a plot of the fraction of the total variation ($V = \sum_i \sigma_i$) explained by each principal component (a ‘screen plot’). It is useful to describe clearly the relationship between subspace embedding and pathwise correlation. Consider for simplicity the planar covariation of three variables. The sample covariance, $\mathbf{S} = \mathbf{U}\mathbf{\Sigma}\mathbf{U}^T$, $\mathbf{\Sigma} = \text{diag}([\sigma_1 \sigma_2 \sigma_3])$, has two larger eigenvalues (σ_1, σ_2), due to the variability of the trajectory on the plane and noise. The correlation matrix, i.e., the covariance matrix obtained after normalizing each variable by its standard deviation (s_i)

$$\mathbf{R} = \mathbf{D}^{-1} \mathbf{S} \mathbf{D}^{-1}, \quad (7)$$

where $\mathbf{D} = \text{diag}([s_1 \dots s_M])$ is a scaling matrix, and has the three pairwise correlations as off-diagonal elements

$$\mathbf{R} = \begin{pmatrix} 1 & r_{12} & r_{13} \\ r_{12} & 1 & r_{23} \\ r_{13} & r_{23} & 1 \end{pmatrix} \quad (8)$$

These correlation values, for a given set of eigenvalues of the covariance matrix, i.e., for a given level of planarity of the trajectory, depend on the plane orientation, i.e.,

on the rotation matrix \mathbf{U} . The minimum correlation absolute value is always 0, and it is obtained when the eigenvectors of the covariance matrix are aligned with the coordinate axes. The maximum correlation value is obtained when the eigenvector associated to the largest eigenvalue (σ_1) is oriented along the bisectrix of two coordinate axes and the eigenvector associated to the second largest eigenvalue (σ_2) is aligned with the third coordinate axis. This maximum value is

$$r^{\max} = \frac{\sigma_1 - \sigma_3}{\sigma_1 + \sigma_3}. \quad (9)$$

From (9) it follows that, if two variables have a correlation r , the ratio of the third eigenvalue of the covariance matrix on the total variation, $V = \text{tr}(\mathbf{\Sigma}) = \sigma_1 + \sigma_2 + \sigma_3$, often used as an index of planarity, must satisfy

$$\frac{\sigma_3}{V} \leq \frac{\sigma_1}{V} \frac{1 - r}{1 + r} \quad (10)$$

For example, if $r = 0.9$ and $\sigma_1/V = 0.6$, then $\sigma_3/V < 0.0316$. Hence, high correlation implies high planarity. However, the converse is not true. That is, for the specific plane orientation in which the eigenvectors of the covariance matrix coincide with the coordinate axes, all correlation coefficients are zero independently of σ_3 . Thus if σ_3 is 0, planarity does not imply high correlation coefficients. Summarizing, while the eigenvalues of the covariance matrix do not depend on the plane orientation, pairwise correlations depend both on such eigenvalues and on the plane orientation. Thus correlation is not a good measure of planarity in a three dimensional space, and similarly is not a good measure of subspace embedding in higher dimensional spaces.

Experimental methods

On the whole, we recorded the walking of 17 animals (bipedal walking in 5 birds and quadrupedal walking in 12 mammals).

1. *Recurvirostra avosetta*
2. *Larus audouinii*
3. *Pavo cristatus*
4. *Rhea americana*
5. *Numida meleagris*
6. *Cervus nippon*

7. *Addax nasomaculatus*
8. *Tapirus terrestris*
9. *Camelus bactrianus*
10. *Equus gravyi*
11. *Elephas maximus*
12. *Canis lupus familiaris*
13. *Felis catus*
14. *Lemur catta*
15. *Mandrillus sphinx*
16. *Hydrochoerus hydrochaeris*
17. *Suricata suricatta*

About 30 good recordings of animal walking (one or two strides per animal) were selected for the analyses. The criteria for selection were:

- the trunk of the animal moved in the frontal plane of the videocamera (perpendicular to its optical axis);
- no other animals or objects covered the legs or any part of the animal;
- only walking was analysed (neither running nor hopping or galloping);
- no jumping or obstacle avoidance;
- only completed strides were analysed (touchdown as the onset).

Human overground walking was recorded in the laboratory conditions. Three-dimensional (3D) motion of selected body points was recorded at 100 Hz by means of the 9-TV cameras Vicon-612 system (Oxford, UK) (1 mm spatial accuracy). The positions of selected points on the body were recorded by attaching passive infrared reflective markers (diameter, 1.4 cm) to the skin overlying the following bony landmarks on both sides of the body: the tubercle of the anterosuperior iliac crest (IL), greater trochanter (GT), lateral femur epicondyle (KNEE), lateral malleolus (LM), and fifth metatarso-phalangeal joint (VM).

In addition, for the sake of comparison with animal recordings, we recorded human walking using also a videocamera (Canon ZR850, 30 Hz sampling rate)

simultaneously with Vicon recordings. The results of the kinematic analysis using the two methods have been compared.

In the bipedal model, only the movement of hindlimb landmarks were analysed:

- approximate hip joint, GT;
- approximate knee joint centre, KNEE;
- joint between the tibiotarsus and tarsometatarsus, LM;
- base of the tarsometatarsus, VM;
- end of the distal phalanx, DP;

The limb was modelled as an interconnected chain of rigid segments: GT-KNEE for the thigh, KNEE-LM for the shin, and LM-VM for the foot.

In the quadrupeds model the body landmarks were :

- for the forelimbs
 - greater tubercle, GTB;
 - elbow joint, EL;
 - lateral styloid process, LSP;
 - base of the metacarpal on the outer side, VMC;
 - end of the distal phalanx, DPF.
- for the hindlimbs
 - greater trochanter, GT;
 - knee joint, KNEE;
 - lateral malleolus, LM;
 - base of the metatarsal on the outer side, VM;
 - end of the distal phalanx, DP.

The body was modelled as an interconnected chain of rigid segments: GTB-EL for upper arm, EL-LSP for forearm, LSP-VMC for fore paw, GTB-GT for the trunk, GT-KNEE for the thigh, KNEE-LM for the shin, and LM-VM for the foot.

The intersegmental coordination of the thigh, shin, foot (hindlimb) and upper arm, forearm and fore paw (forelimb) elevation angles in the sagittal plane was evaluated in position space using the principal component analysis. For each

eigenvector of the covariance matrix, the parameters u_{it} , u_{is} , and u_{if} correspond to the direction cosines (range: $[-1, 1]$) with the positive semi-axis of the thigh, shin, and foot angular coordinates, respectively. We specifically analysed and plotted the u_{3t} parameter to characterize the orientation of the covariance plane (Borghese, Bianchi, and Lacquaniti 1996). The planarity of the trajectories was quantified by the percentage of total variation (PV) accounted for by the first two eigenvectors of the data covariance matrix (for ideal planarity $PV = 100\%$ and the 3rd eigenvalue = 0).

Results

Since animal kinematics have been recorded using a videocamera, I first compared the results of the PCA applied to human walking recorded in the same subjects simultaneously using two techniques: VICON optoelectronic system and videocamera. The general features of the intersegmental coordination are captured similarly by the two techniques planar covariation index (PV), orientation of the covariance plane (u_{3t} parameter) and the size of the loop. These results imply a reliable analysis of gait kinematics in animals using videocamera recordings.

The animals were subdivided into the three subgroups according to their gait and anatomical features: birds (bipedal gait), ungulates (quadrupedal gait) and digitigrades (quadrupedal gait). Their results will be described accordingly.

Figure 2 summarizes the stick diagrams of walking in all recorded animals. From this illustration one can see both similar general features of limb segment orientation during walking in animals and differences between forelimbs and hindlimbs.

The rationale of this study was to investigate the rules of the inter-segmental coordination during walking in different animals. In particular, it was hypothesized that the control of locomotion may be organized in such a way that limb segment motion covary, reducing the ‘effective’ degrees of freedom. Strikingly, for all animals there was planar covariation of both hindlimb and forelimb segment elevation angles during walking (2 PCs accounted for 97.8 – 99.9 percent of the variation in the 3 angular waveforms), as it was in humans

However, there were also specific features of the inter-segmental coordination typical for different subgroups of animals. They are summarized below.

1. In birds:

- although the general orientation of the limb segments resembles that of the hindlimbs of quadrupedal animal, the hip and knee joints are hyperflexed.
- relatively small oscillations of the proximal (thigh) segment (figure 2).

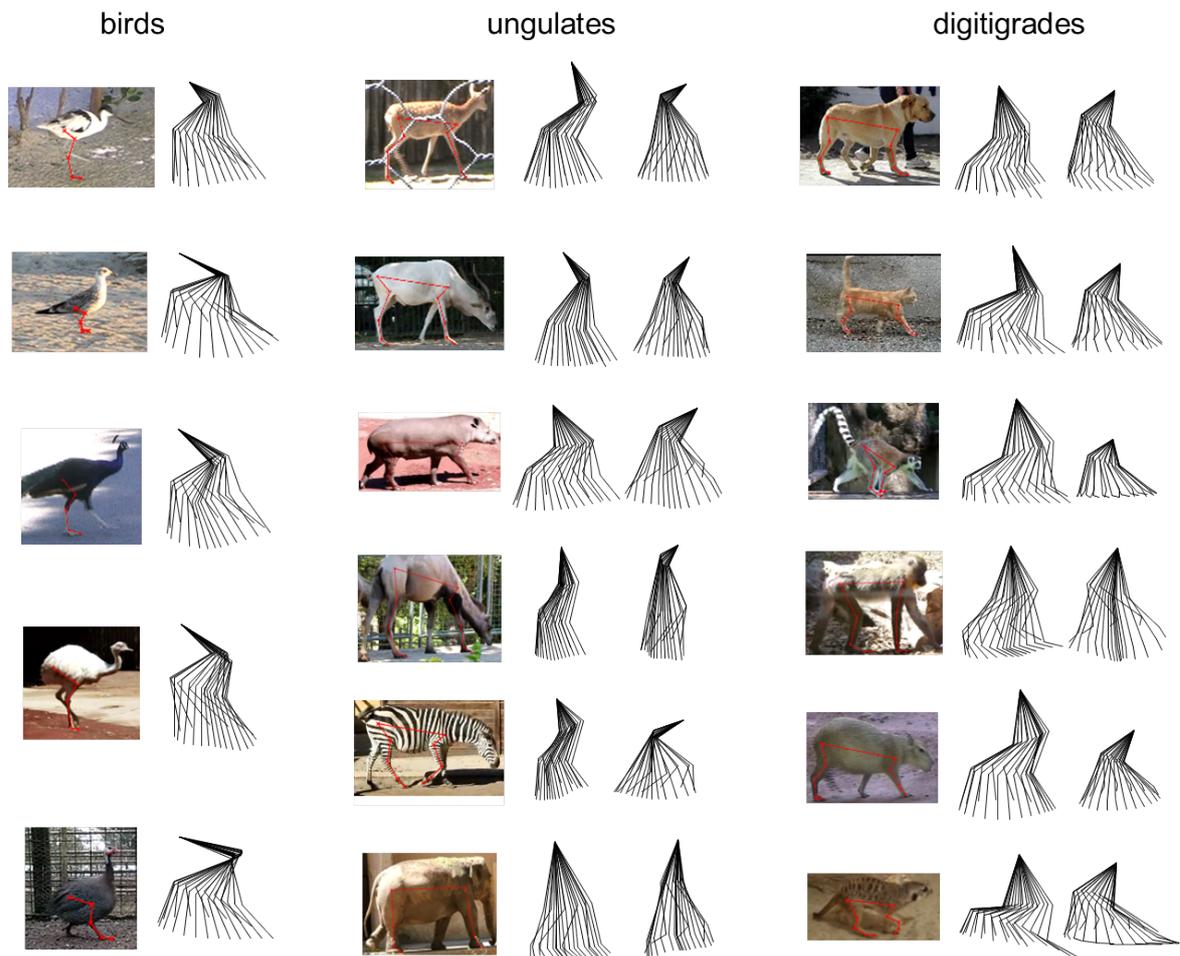


Figure 2: General features of walking in different animals.

- the orientation of the covariance plane (figure 3, left panels) tended to be aligned with the thigh axis (u_{3t} parameter was generally close to one
2. In quadrupedal animals:
- as a general rule, the orientation of limb segments during walking is different for the forelimb and hindlimb (figure 2). In particular, the orientation of the proximal (upper arm and thigh) limb segments relative to the vertical is basically opposite (mirrored) for the forelimb and hindlimb.
 - the orientation of the distal segments (foot, fore paw) is constantly changing throughout the gait cycle. However, at any given whole limb

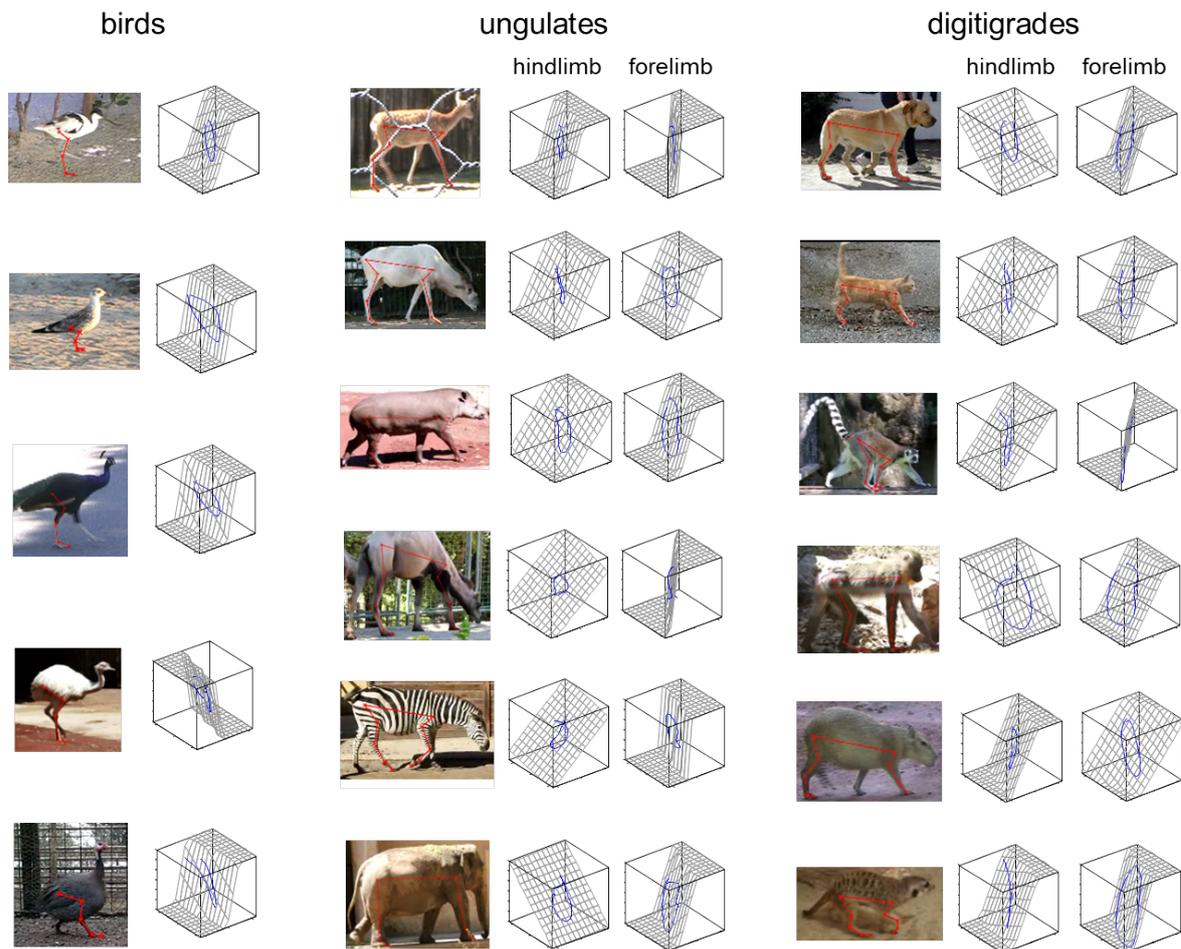


Figure 3: Planar covariation of limb segment elevation angles during walking in different animals.

orientation relative to the gravity, it is similar during stance and swing for the hindlimb but opposite for the forelimb (figure 2).

- as a consequence of different distal segment behaviour, the orientation of the covariance plane is generally different for the hindlimb and forelimb (figure 3).
- even though planar covariation of segment elevation angles has been found in all animals, the orientation of the covariance plane (figure 3) and phase relationships between segment angular motion are generally different and animal specific.

Concluding remarks

As a general conclusion, this study represents the first attempt to look at the rules of the inter-segmental coordination in different animals using the principal component analysis of limb segment motion. These data is available in the literature only for human (Borghese, Bianchi, and Lacquaniti 1996, Grasso, Bianchi, and Lacquaniti 1998, Ivanenko et al. 2008) and monkey (Courtine et al. 2005) locomotion. Strikingly, it has been found in this study that the planar covariation of limb segment motion holds also for walking kinematics of a variety of different animals with quite different anatomy, body weight, biomechanics, cycle duration (from 0.65s to 3.2s) and repertoire of motor behaviour: from small animals (birds) to very big animals (elephants), from herbivores to predators, from ungulates to digitigrades and domestic animals.

The results of this study revealed that there were large differences across animals in phase shifts between segment angular motion. The modelling of the inter-segmental coordination using harmonic mechanical oscillators approach showed that the orientation of the covariance plane is highly determined by these phase shifts, in addition to changes in the amplitude of angular movements. As a result, even though planar covariation of segment elevation angles has been found in all animals, the orientation of the covariance plane is generally different and animal specific.

This functional difference is consistent with high specialization of the musculoskeletal apparatus of the forelimbs and hindlimbs and body anatomy to animal gait. For instance, it has been previously shown for humans that the orientation of the covariation plane may correlate with the energetics of walking (Bianchi, Angelini, and Lacquaniti 1998a). Further experiments are needed to understand how differences in the phase relationships and planar covariation of limb segment motion are related to performance of locomotion (energetics, speed, etc.) or specialization of different animals for specific gaits (endurance walking in humans or an ability to perform extremely fast movements in gepard). In addition, such studies may be to the construction of biologically inspired robots or clinical studies (Grasso et al. 2004). In fact, such comparative and evolutionary related studies using mathematical frameworks and tools for analysing or controlling multiple degrees of freedom in animal motion represent a fascinating area of research.

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