

SHORT COMMUNICATION

Postural control in the elephant

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ABSTRACT

As the largest extant legged animals, elephants arguably face the most extreme challenge for stable standing. In this study, we investigated the displacement of the centre of pressure of 12 elephants during quiet standing. We found that the average amplitude of the oscillations in the lateral and fore–aft directions was less than 1.5 cm. Such amplitudes for postural oscillation are comparable with those of dogs and other species, suggesting that some aspects of sensorimotor postural control do not scale with size.

KEY WORDS: Balance, Scaling, Multisensory interactions, Sensorimotor and inertial delay, Centre of pressure

INTRODUCTION

Many people refer to a circus act when they think how agile an elephant can be and how great their balancing skills are. Those skills are also used in the wild, to walk along narrow pathways or cross rivers on rocks, and are crucial for their survival. Indeed, elephants are the largest land mammals on Earth, weighing up to 6 tons. As a consequence, they are relatively weaker and more fragile than other mammals: the supportive tissue strength, which depends on cross-sectional area ($\propto L^2$, where L is length), increases less rapidly than the mass, which is proportional to body volume ($\propto L^3$). As a result, the area/volume ratio decreases with size (Biewener, 2005) and the consequences of a fall matter more for elephants than for smaller animals, such as dogs (McMahon and Bonner, 1984). Consequently, the ability of large animals to accurately regulate their body orientation in the gravity field may be challenging.

Standing still is an active, controlled process, mainly influenced by biomechanical considerations (such as internal or external forces) and sensorimotor signals of different origins (Horak and Macpherson, 2011). Balance is maintained by muscle contractions acting against gravity and keeping the centre of body mass (COM) vertically above the base of support (Ivanenko and Gurfinkel, 2018; Milton et al., 2018). However, the COM is not absolutely stationary as the body continually sways (Pavol, 2005), and the integration of sensory input from the proprioceptive, visual and vestibular systems guides the corrective muscular activations. These contractions change the repartition of force beneath the feet/paws, in turn changing the position of the centre of pressure (COP) that oscillates either side of the COM to keep it in a fairly constant position.

From a biomechanical viewpoint, the higher the COM ($\propto L$) the greater the postural sway for a similar angular change of the

orientation relative to the gravitational vector. Assuming geometric similarities, the moment of inertia of body segments increases with L^5 , whereas the ability of muscles to generate force depends on tissue cross-sectional area ($\propto L^2$) (Alexander et al., 1981; Biewener, 1989). Consequently, even if moment arms increase with body size and the time to complete a movement also increases with size, the steeper increase of inertia impedes the acceleration generated by muscles, delaying the corrective response ('inertial delay'; Mohamed Thangal et al., 2020) and/or requiring larger forces. In huge animals, standing still is further complicated by the scaling of their sensorimotor control (More and Donelan, 2018). For example, as a result of the scaling of nerve cross-sectional area ($\propto L^2$), a trade-off inherently occurs between the number and diameter of axons. Indeed, the axonal conduction velocity is proportional to axon diameter ($\propto L^2$), whereas the number of axons should be $\propto L^3$ to maintain an equal number of sensory receptors and motor units per unit volume (More et al., 2010). Thus, sensorimotor delay increases with size, encompassing many sources of delay such as sensing, nerve conduction, synaptic, electromechanical and force generation delays. Accordingly, one might expect that, as a consequence of both inertial and sensorimotor delays, the higher the COM location ($\propto L$), the more challenging the maintenance of balance.

The performance of postural control is usually assessed by quantifying COP-based measures of postural sway during quiet stance (Winter et al., 2003). In this study, we investigated the COP displacement and velocity of 12 elephants (mass: 3174.0 ± 947.7 kg, limb length: 160.6 ± 18.6 cm; Fig. S1A) during quiet standing. To our knowledge, there are no data on the amount of postural sway in the largest land mammals on Earth. Additionally, we compared their postural sway with that of 6 dogs and other animals' data available in the literature. While the idea of similar COP oscillations across mammals has been introduced by Ivanenko and Gurfinkel (2018), it was based only on the published data of a few mammals. Increasing the number of species investigated and including the largest terrestrial living mammal might broaden our knowledge on the effect of size on postural control.

MATERIALS AND METHODS

Elephants

Elephant data were collected at the same time as in the study of Genin et al. (2010) in 2006 at the Thai Elephant Conservation Centre near Lampang (Northern Thailand). The study was approved by the ethics committee of the Faculty of Medicine of UCLouvain and the Forest and Industry Organization (FIO) in Thailand. Sixteen elephants were recorded while they stood motionless without visual movement of the head and neck. The distance from the ground to the top of the scapula was measured, except for three of the elephants, which were considered to be too dangerous to be approached by an experimenter. Four elephants were removed from the analysis because of step initiation during data acquisition. The mass of the 12 remaining elephants ranged from 1.2 to 4.0 tons (Fig. S1A).

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Additional data

We compared elephant data with data from other animals. Those data included the recording of 6 dogs using a similar experimental setup (same force plates) and other data from the literature. Six dogs (body mass ranging from 5.7 to 30.0 kg) were recorded in the Laboratory of Physiology and Locomotion at Louvain-la-Neuve (Belgium). The protocol used was approved by the SPW Agriculture ressources naturelles environnement and by the Ethics Committee for Animal Experimentation of UCLouvain. As for the elephants, the dogs had to stand still. The distance from the ground to the top of the scapula was measured using an anthropometers. At least six recordings were performed for each dog. A digital camera was positioned on the lateral side of the dog to allow qualitative screening of the trials. Because of step initiation, 15 recordings were suppressed and a total of 21 quiet standing trials were analysed (Fig. S1A). The data from the literature included centre of pressure digitised traces, redrawn and analysed from Funato et al. (2017) (rat), MacPherson and Horak (2012) (cat), Chang and Ting (2017) (flamingo), Ivanenko et al. (1999) (human) and Clayton and Nauwelaerts (2014) (horse).

Data analysis for both elephants and dogs

All trials were screened and periods suitable for analysis were selected based on the body axes (aligned visually with the force plate coordinate system) and on the absence of stepping movements (four elephants and one dog were removed from the analysis). One session was recorded for each elephant, whereas at least three trials were recorded for the dogs (see details in Fig. S1A).

The forces exerted by the ground on the feet/paws of an animal during standing were measured by means of 1×1 m force platforms mounted at ground level. For the elephant recordings, 16 platforms were used, placed to form a 2×8 m track (Fig. 1). For the dog recordings, the same platforms were used, but two (1×2 m) were

sufficient. Forelimbs and hindlimbs were always placed on different force plates so that we could also estimate body mass partition (Fig. S2A) and the COP (Fig. S2B) separately for forelimbs and hindlimbs. Each plate was composed of a steel frame, four 3-axis force transducers and an aluminium plate surface. The force transducers consisted of strain-gage instrumented spring blades. Each force plate weighed 270 kg. The plates had a natural frequency of around 300 Hz. Cross-talk between the three axes was less than 1% of the applied force, independent of the point of application of the force. Each plate contained its own data acquisition system. The transducer signals were amplified, low-pass filtered (4-pole Bessel filter with a -3 dB cut-off frequency of 200 Hz) and digitised by a 16-bit analog-to-digital converter at 50 Hz. The gain of the amplifiers was set so that the resolution was maximal. For elephants, the effective resolution was 1.91 N in the vertical direction and 0.43 N in the horizontal and lateral directions. For dogs, the resolution was 0.075 N in the vertical direction and 0.15 N in the horizontal and lateral directions. As a consequence, the relative resolution (i.e. resolution divided by body weight) was better for elephants. However, matching the relative resolution of elephants and dogs (to 0.13% of body weight) does not affect our results (Fig. S3A). The plates were connected to a PC via TCP/IP over the ethernet. The amplifier gain, analog-to-digital converter data acquisition, zero-offset and ethernet interface were all controlled by an embedded micro-controller (Rabbit Semiconductor, Davis, CA, USA). The signals from the plates with vertical forces above 2% of body weight were summed digitally on the PC in order to obtain the vertical (F_z), forward (F_y) and lateral (F_x) components of the ground reaction force (GRF).

Calculations and data processing were performed using custom software (LABVIEW 14, National Instruments, Austin, TX, USA). Data were sampled at a frequency of 250 Hz. Filtering of GRF (dual-pass 2nd order 20 Hz low-pass Butterworth) was applied.

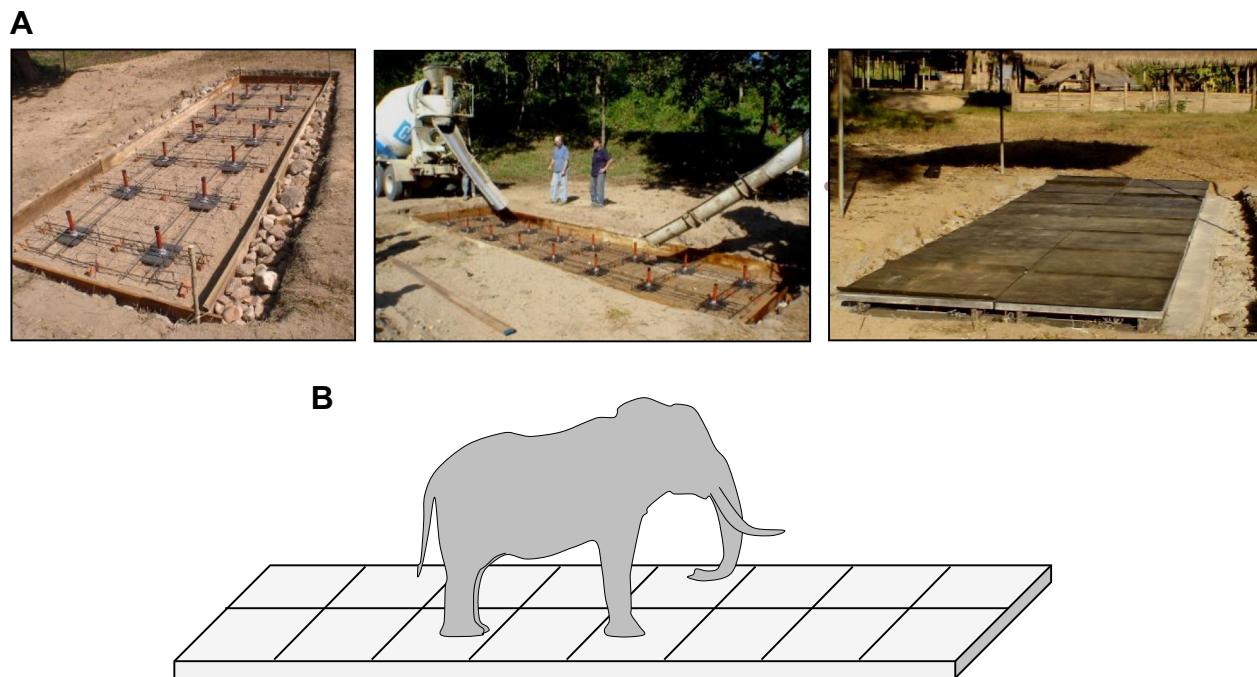


Fig. 1. Experimental set-up for elephant recordings. (A) A $3 \times 9 \times 0.6$ m hole was dug, reinforcement frames were placed as indicated, and the hole was filled with concrete. (B) Once the concrete layer was levelled and dry, the force platforms were installed, composed of 16 individual 1×1 m plates. The set of plates had to be aligned, flat and at floor level. Once all the platforms were mounted, a small wall of brick was built all around to provide a continuum between the ground and the platform.

Note that changing the low-pass cut-off frequency does not change the outcome of the study (Fig. S3B). Data were recorded during a period of 4.4 s for elephants and 5–10.1 s for dogs (see Fig. S1A). Because of the short duration, only simple parameters have been computed. Longer data collection is difficult to achieve in animals that are not trained to stand still, particularly with curious elephants. To make comparisons between elephants and dogs, the duration of the trials was standardised to 4.4 s. The modification of the duration of the recordings does not affect the results in dogs (Fig. S3C). However, this limiting factor must be considered and the results should not be compared with those of other species recorded over much longer sampling durations.

From the GRF, the lateral (COP_x) and fore–aft (COP_y) position of the centre of pressure was computed as follows:

$$COP_x = \frac{-M_y - hF_x}{F_z}, \quad (1)$$

$$COP_y = \frac{M_x - hF_y}{F_z}, \quad (2)$$

where M_x and M_y are the moment components in the force transducer coordinate system, and h is the vertical distance between the force transducers and the tread surface (Dewolf et al., 2018). Classic stabilographic variables were then calculated. The amplitudes of COP_x and COP_y were determined as four standard deviations (± 2 s.d.) of the time series. The 2D COP excursion area was evaluated as the 95% COP confidence ellipse (Ivanenko et al.,

1999). The mean 2D COP velocity was determined from the average absolute value of the time derivatives of the 2D COP displacements.

Statistical analysis

In order to assess the difference between dogs and elephants on postural sway, independent sample t -tests were performed to compare dogs and elephants with an α -threshold of 0.05 (PASW Statistics 19, SPSS, IBM, Armonk, NY, USA). Each variable was normally distributed within each of the two populations (checked using the Kolmogorov–Smirnov test). If the assumption of homogeneity of variance was not met (checked using Levene's test), adjusted t -tests were used. The statistical results (P -value) are presented in Fig. S1C and D.

RESULTS AND DISCUSSION

COP oscillations in the elephant

While foot pressure distributions have already been examined during locomotion in elephants (Panagiotopoulou et al., 2012, 2016), this study reports for the first time the displacement of the COP during quiet standing, computed from the forces exerted by the ground on the animals' feet. Our results show that the average amplitude of oscillations in the lateral and fore–aft directions was 1.13 ± 0.9 and 1.16 ± 0.6 cm, respectively (Fig. 2). Both COP_x and COP_y oscillation range was less than 1% of leg length (Fig. S1A). In addition, the mean 2D COP velocity of elephants was equal to 3.48 ± 1.0 cm s⁻¹.

Maintaining balance during posture is an important task of legged animals living on the land. Given the graver consequences of falls in

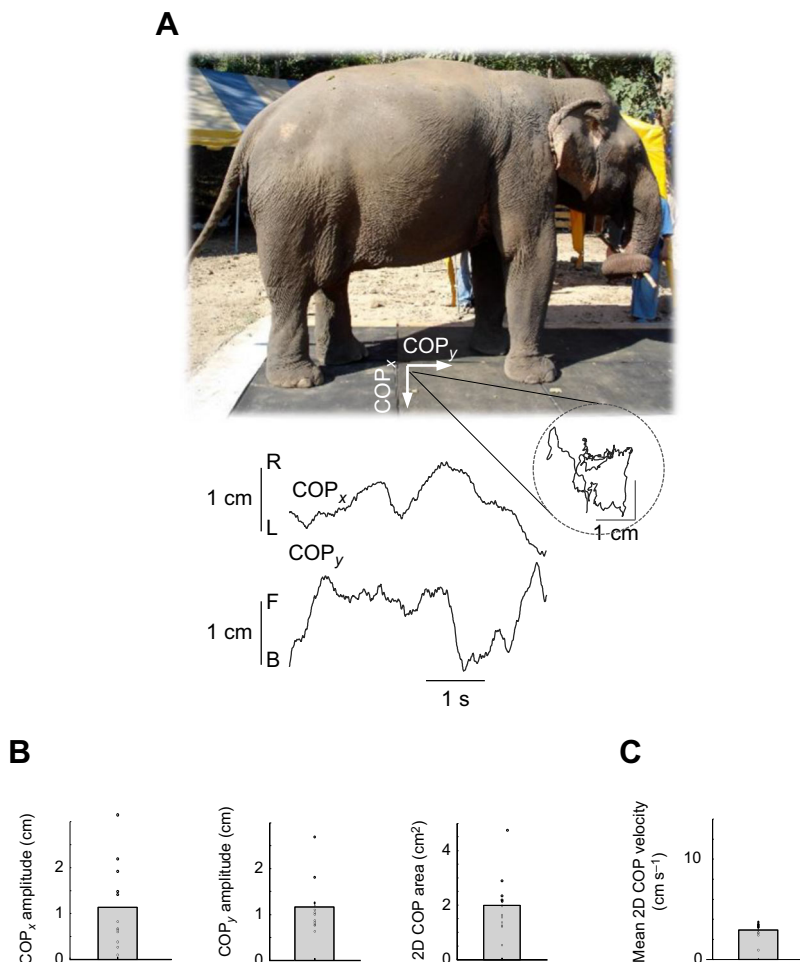


Fig. 2. Centre of pressure displacement fluctuations during quiet standing in elephants ($n=12$). (A) As the standing posture is a quasi-static situation, the centre of pressure (COP) approximately reflects the movements of the centre of mass (COM) in a transverse plane. The figure illustrates one example of the lateral (COP_x) and fore–aft (COP_y) centre of pressure traces versus time. The insets represent the corresponding xy oscillations of the COP displacement around the mean position. R, right; L, left; F, forward; B, backward. (B,C) Mean COP_x and COP_y amplitude and 2D COP area (B) and mean 2D COP velocity (C) in elephants. Each dot corresponds to individual data.

large animals, gravity monitoring appears to be more crucial for large animals (Hooper, 2012), but simple feedback control is less effective when time delays are longer (More and Donelan, 2018). Because of their longer and heavier body segments, elephants are faced with longer nerve conduction delays and longer inertial delay to the completion of corrective movements. While these longer delays are partially offset by their longer movement durations, during a postural task, the available movement time does not increase as sharply as the delays, changing only with the square root of limb length (Mohamed Thangal et al., 2020). Consequently, the inertial and nerve conduction delay relative to movement duration is respectively about 5 and 3 times longer in an elephant than in a dog. Because of the time-delayed feedback and potentially greater sensory dead zones (range of sensory input for which no corrective actions are taken; Eurich and Milton, 1996), the ability of elephants to accurately regulate their body orientation in the gravity field may be more challenging than for smaller animals. In the following paragraphs, we will compare the postural sway of elephants with the

COP displacement of other animals, and discuss potential scaling interpretations for sensorimotor postural control.

Comparison of postural control in animals

Using a comparable experimental setup, we observed similar COP_x and COP_y range of oscillations in dogs and elephants (Fig. 3B; Fig. S1B). Relative to leg length, COP displacement was greater in dogs (COP_x : $1.59 \pm 0.3\%$; COP_y : $2.1 \pm 0.2\%$) than in elephants (COP_x : $0.7 \pm 0.6\%$; COP_y : $0.7 \pm 0.3\%$). Similar amplitudes of postural sway have also been observed in horses (Clayton and Nauwelaerts, 2014), rats standing bipedally (Funato et al., 2017), cats, flamingos (Chang and Ting, 2017) and humans (Ivanenko and Gurfinkel, 2018). Examples of COP oscillation and qualitative comparison of postural sway are presented in Fig. 3B. Intriguingly, postural sway during standing is comparable despite the difference in the species considered with respect to size, morphology and phylogenetic relatedness. Indeed, one may have expected different postural oscillations due to differences in the size.

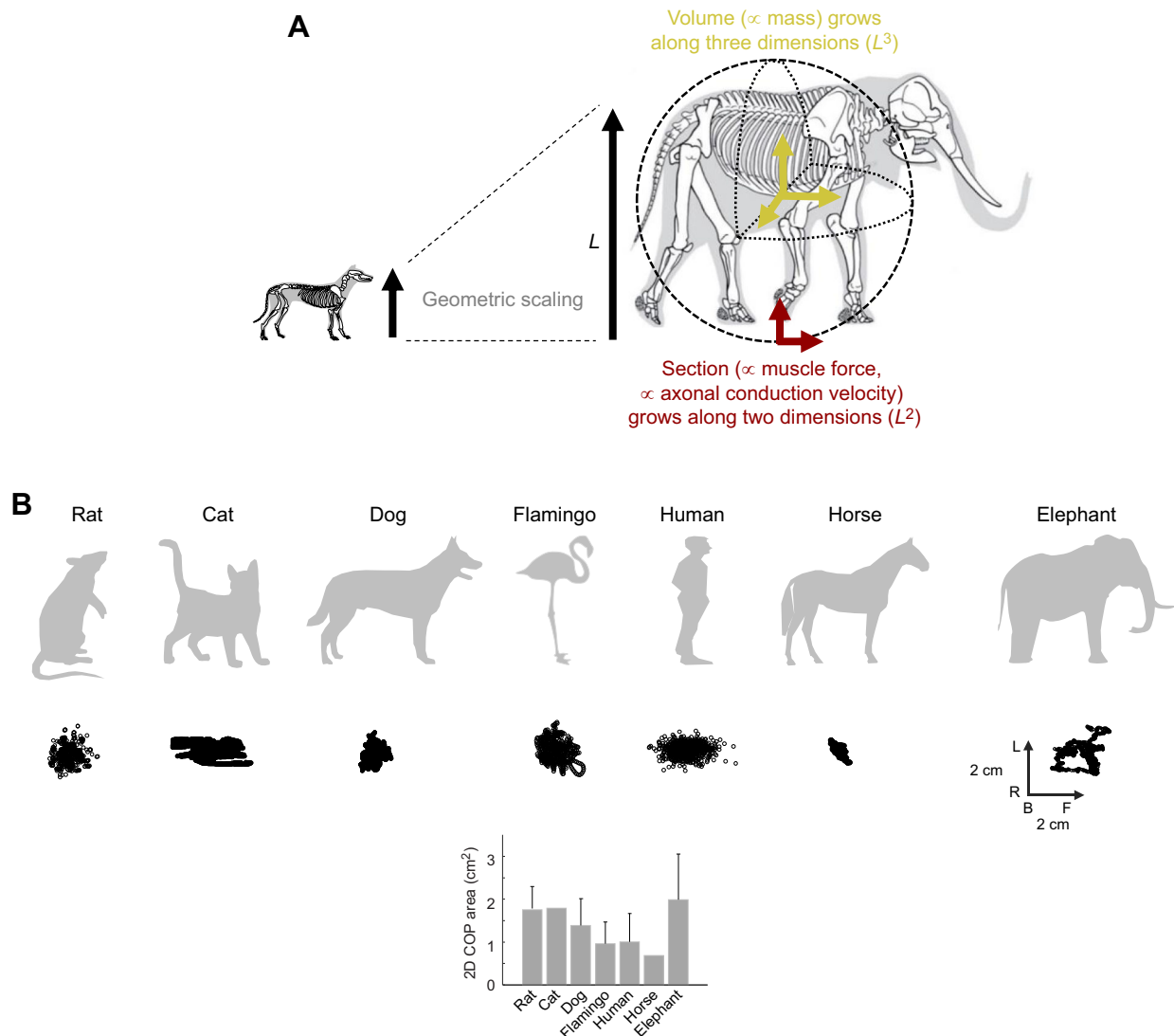


Fig. 3. Scaling of postural control in terrestrial mammals. (A) Differences imposed by scaling between dogs and elephants. L , length. (B) COP excursion area during quiet standing is similar across species of different sizes. Example COP traces were digitized and redrawn from Funato et al. (2017) (rat), MacPherson and Horak (2012) (cat), Chang and Ting (2017) (flamingo), Ivanenko et al. (1999) (human) and Clayton and Nauwelaerts (2014) (horse). The COP excursion areas were also computed when raw data were available. If not (for cats and horses), the COP excursion areas were estimated based on the reported COP displacement (Clayton and Nauwelaerts, 2014; MacPherson and Horak, 2012).

Furthermore, foot morphology also differs considerably, elephants having a plantigrade foot posture due to a compliant fat pad (Panagiotopoulou et al., 2012), whereas dogs have a digitigrade foot posture (Carrier and Cunningham, 2017). It can be assumed that, as in humans, the foot posture may modify the ability to apply ankle joint torque (Carrier and Cunningham, 2017) and foot/paw deformation can appreciably influence postural oscillations (Gurfinkel et al., 1994). For instance, a compliant fat pad is expected to increase the absolute COP displacement (Gurfinkel et al., 1994). Other factors may also contribute to postural body sway such as a greater base of support in elephants. However, it is unlikely that the base of support plays a major role for defining the postural margin of stability and the control of the amplitude of COP oscillations for the following reasons. First, the base of support (its sagittal component) in elephants and dogs is similar when normalised by limb length ($P=0.102$; Fig. S1, right panel). Second, postural COP oscillations are much smaller than the actual base of support and would probably provide stability even if they were larger (although the larger oscillations would require much larger muscle forces to compensate for the COM displacement).

We also found that the mean and root mean square of COP velocity time series was higher in dogs than in elephants (Fig. S1C). While the parameters related to the magnitude of COP displacement are considered to be related to the effectiveness of the postural control system, the parameters related to COP velocity have been claimed to represent the amount of activity required to maintain stability (Cieślińska-Świder and Błaszczuk, 2019). Reducing the velocity of the COM movements could moderate in direct proportion the inertial delay (Mohamed Thangal et al., 2020). Large animals may thus partly cope with the longer delays by moving slowly. Similarly, large animals demonstrate a maximum speed of locomotion lower than that predicted based on the scaling of movement duration (Alexander, 2005; More and Donelan, 2018; Iriarte-Díaz, 2002; Ren et al., 2010). In addition, COP velocity is highly correlated with COM acceleration (Masani et al., 2014) and high accelerations and decelerations would require large forces, which may be restricted by other physiological limitations, including the scaling of muscle strength (Biewener, 1989).

Potential interpretation of the effect of size on postural control

How mammals of different sizes, such as dogs and elephants, display similar amplitudes of COP oscillations (Fig. 3A) remains an open question. The similar sway amplitudes may suggest the existence of a common multi-modal sensory threshold for the control of posture. Similar proprioceptive thresholds across animals are consistent with the existence of a potential common sensory threshold for COP control and suggest that not all aspects of sensorimotor postural control scale with size.

The question arises as to what kind of sensorimotor postural margin our results may reflect. Among a range of possible explanations, the similar COP oscillations (Fig. 3) may come not from assuming the control of similar body sway relative to the vertical but from assuming similar muscle force efficiency instead. Long-lasting maintenance of postural muscle activity (minutes or even hours) is associated with low energy cost and probably must be optimised. To control similar angular body sway, oscillations in the gravitational postural torque ($mg \cdot \Delta x$, where m is mass, g is acceleration due to gravity and Δx is the amplitude of COM oscillations) would be proportional to L^4 (as $m \propto L^3$ and $\Delta x \propto L$), while the compensating counterbalancing postural muscle torque

($F_{\text{muscle}} \cdot l$, where l is the muscle lever arm) increases as a function of L^3 ($F_{\text{muscle}} \propto L^2$ and $l \propto L$). Thus, controlling similar body sway for big animals would require much less economical involvement of postural muscles. In contrast, another solution that seems to be adopted would be the use of sensorimotor margins for maintaining similar (unscaled) Δx across animals and, thus, similar relative muscle force oscillations during posture. Thus, the conservation of postural sway magnitude could reflect a common neuromuscular limitation.

Whatever the exact mechanism for small relative COP oscillations in elephants may be (Fig. 3B), postural control varies significantly with body size, in which both mechanical (e.g. passive dynamics, leg geometry, muscle intrinsic properties; McMahon and Bonner, 1984) and neural factors (e.g. specific low-level muscle activity, integration of several sensory and motor areas; Mohamed Thangal et al., 2020; More and Donelan, 2018; More et al., 2010) are likely to contribute. Such a cross-species study identifies the consequences of size on the control of posture, encouraging further research on how the nervous system and biomechanics deal with body size changes across a larger cohort of species.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: A.H.D., Y.P.I.; Methodology: A.H.D., Y.P.I.; Software: A.H.D.; Validation: A.H.D., Y.P.I., P.A.W.; Formal analysis: A.H.D., Y.P.I.; Investigation: A.H.D., R.M.M., P.A.W.; Resources: P.A.W.; Data curation: A.H.D., R.M.M., P.A.W.; Writing - original draft: A.H.D., Y.P.I.; Writing - review & editing: A.H.D., Y.P.I., R.M.M., P.A.W.; Visualization: A.H.D.; Supervision: Y.P.I., P.A.W.; Project administration: P.A.W.; Funding acquisition: P.A.W.

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Data availability

All data and custom software related to this paper are available from Zenodo: doi:10.5281/zenodo.4576160

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