Frontal plane dynamics of the centre of mass during quadrupedal locomotion on a split-belt treadmill

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1. Introduction

Quadrupedal animals must coordinate the motion of limbs in order to maintain balance. Balance is controlled by keeping the position of the centre of mass (COM) between the weight-bearing limbs; e.g. [2]. Animals are said to be statically stable when the COM projection is within the edges of support [2,3]. While this may seem trivial for a quadruped standing at rest [4], it becomes more complicated when the animal begins to move. Animals are said to be dynamically stable when the extrapolated centre of mass (xCOM) projection is within the edges of support [3]. During walking, quadrupedal animals must continuously maintain balance in both the lateral and longitudinal directions. For example, walking cats are statically unstable laterally and dynamically unstable longitudinally during ipsilateral and diagonal double-support phases, respectively [5].

The lateral control of balance is particularly important in bipedal locomotion, e.g. in walking ducks [6], penguins [7], non-human primates [8] and humans [9,10], where the moving animal is only supported by a single limb for most of the walking cycle. During phases of single-limb support, the body may be modelled as an inverted pendulum [11]. According to this model, lateral balance is maintained by timely placing the swing limb on the ground to stop the body, falling under the action of the gravitational moment, and changing the pivot point of the inverted pendulum and thus the direction of the gravitational moment with each step [11,12]. To plan the timing and position of limb placement, the balance control system must have knowledge of the mechanical state of the walker, i.e. the COM position and velocity with respect to the boundaries of support [3,13]. This information is probably obtained from the integration of visual, vestibular, proprioceptive and cutaneous
afferent signals [14], although the contribution of individual sensory modalities to the integrated sensory input is still uncertain. Though derived in the context of bipedal locomotion, the inverted pendulum principles could potentially be extended and applied to quadrupedal walking. For example, the kinetic and potential energies of the body in the sagittal plane show out-of-phase changes in the walking cycle of dogs, macaques and rams, resembling the behaviour of an inverted pendulum [15,16]. Frontal plane COM motion resembles that of bipeds in long-legged quadrupeds: dogs [17], camels [18], giraffes [19] and alpacas [20], who use a pace-like walking gait, in which the phase difference between the ipsilateral hindlimb and forelimb footfalls approaches zero [21]. During pace walking, the animal body is supported mostly by either pair of ipsilateral limbs. Nevertheless, the majority of quadrupedal animals during medium-speed walking use a lateral sequence of limbs to support the body with either two or three feet on the ground at all times. For example, in cats walking overground to support the body with either two or three feet on the ground, the ipsilateral limb footfalls approaches zero [21]. During cat treadmill walking, on the other hand, this phase difference is much smaller ≤0.15 [22,24], so the COM frontal plane dynamics of cats walking on a treadmill could be similar to those of bipeds and inverted pendulum.

Indeed, we have demonstrated in cats walking on a treadmill [1] that lateral displacements of the COM and xCOM [3], with respect to the borders of support (centre of pressure, COP) are strikingly similar to those of humans [12,25] and thus could potentially be explained by the dynamics of an inverted pendulum. The results of our previous study have also suggested that cats regulate lateral balance by controlling the timing of the ipsilateral double-support phase onset (or the timing of swing onset of the contralateral forelimb). However, the extent to which frontal plane dynamics of the cat walking on a treadmill can be explained by the inverted pendulum model has not been rigorously investigated.

The goal of this study was to investigate if an inverted pendulum-based model can reproduce major features of the frontal plane COM dynamics of cats walking on a treadmill. The second goal was to use this model to interpret the effects of experimental perturbations of lateral stability. We used two types of perturbations: (i) different speed ratios of the left and right treadmill belts during split-belt locomotion; and (ii) unilateral paw pad anaesthesia. Increasing beltd speed asymmetry during split-belt treadmill locomotion leads to the reduction of the lateral margins of dynamic stability on the slower side in both humans [26,27] and cats [1]. Cutaneous feedback from the feet has been implicated in the regulation of lateral balance in cats [28,29] and humans [30,31]. Therefore, we expected that compromising cutaneous feedback from paw pads by anaesthesia unilaterally would impact lateral balance dynamics. By modelling the cat COM lateral dynamics in the range of these experimental perturbations, we hoped to understand better the mechanisms of balance control in the frontal plane and, in particular, contributions of cutaneous feedback in this control.

2. Methods

2.1. Experimental data collection

All experimental procedures were consistent with the Principles of Laboratory Animal Care (publication of the National Research Council of the National Academies, 8th edition, 2011) and approved by the Georgia Tech Institutional Animal Care and Use Committee (protocol numbers A100012D and A100011U).

Animal subjects and all experimental procedures and conditions were the same as in our previous study [1], so only their brief description is provided here. Four adult female cats with mass ranging from 2.55 kg to 4.10 kg took part in the experiments. After 3- to 4-week training with a food reward, each cat walked on a split-belt treadmill (Berteec Corporation, Columbus, OH, USA) at four-speed combinations of the left and right treadmill belts. In the control condition, cats walked on a treadmill with equal split-belt speeds of 0.4 m s⁻¹ (speed ratio 1:1). The speed of the right belt was increased by a factor of 1.5 to 0.6 m s⁻¹ and by two times to 0.8 m s⁻¹ for two additional split-belt speed ratios (0.4 m s⁻¹; 0.6 m s⁻¹ or 1:1.5 and 0.4 m s⁻¹: 0.8 m s⁻¹ or 2:1). In the last speed condition, the speed of the left belt was increased by two times to 0.8 m s⁻¹, while the right belt was kept at 0.4 m s⁻¹ (0.8 m s⁻¹; 0.4 m s⁻¹ or 2:1). In each split-belt condition, the cat first walked for 15 s at equal belt speeds of 0.4 m s⁻¹; subsequently, the speed ratio was changed to the desired value within 1 s, maintained for 60 s, then returned to the initial equal speed condition within 1 s and maintained for additional 15 s. The order of the tested split-belt speed conditions was randomized within each animal.

For additional perturbation of lateral balance by compromising cutaneous feedback from paw pads (see Introduction), the same split-belt speed conditions were tested with unilateral paw pad anaesthesia on a separate day. The order of testing sessions with and without anaesthesia was randomized across animals. Paw anaesthesia was administered using lidocaine injections in each pad of the right forepaw and right hindpaw. The anaesthesia caused the removal of cutaneous sensory feedback from the right paws for about 30 min, during which time the locomotion testing was performed; for details see [1].

During locomotor experiments, three-dimensional mechanical model of the cat body was used to compute the COM coordinates; for details see [23,32].

2.2. Experimental data analysis

We used computed COM and paw positions as functions of time to derive relevant parameters of the model. Specifically, we defined the period of lateral COM oscillations (P) as the duration of the cycle, the amplitude of lateral COM oscillations (ΔCOM) as half of the difference between the maximum and minimum lateral coordinate of the COM during one cycle, the lateral positions of left and right hindpaws (LH and RH) and the lateral COM position relative to the left hindpaw position normalized to the hindpaw step width (ZCOM); figure 1a. We selected for analysis contiguous 60 s motion recordings of each split-belt condition, removing the first 10 s of each recording, during which walking was less regular. This irregularity normally occurred within the first 5 s after the 1 s speed change from the initial speed ratio of 1:1. We observed no motor adaptation to asymmetric belt speeds in terms of step length, step duration and duty cycle. That was consistent with a previous report of the lack of motor adaptation to prolonged split-belt locomotion in cats [33]. Recordings were divided into stride cycles, defined by the moment of right hindpaw placement on the ground. Each parameter was determined in each cycle of each experimental condition and each animal.

Average COM position was calculated for each cycle by taking the average value of the COM coordinates across all time-points within a single cycle. The average COM position for a
subject in one condition was obtained by averaging across all cycles in a single recording. Standard error values were calculated across subjects in a single condition. The equations for the above locomotor parameters are listed below:

\[ P = \frac{T_{RH} - T'_{RH}}{2} \]  

\[ \Delta_{COM} = \frac{\max_{COM} - \min_{COM}}{2} \]  

\[ Z_{COM} = \frac{LH - COM}{LH - RH} \]

where \( P \) is the stride cycle period; \( T_{RH} \) and \( T'_{RH} \) are the times of the current and previous stance onsets of the right hindpaw, respectively; \( \Delta_{COM} \) is the COM oscillation magnitude in the lateral direction; \( \max_{COM} \) and \( \min_{COM} \) are the maximum and minimum values of the COM lateral displacement in one cycle; \( Z_{COM} \) is the average normalized lateral COM position; \( LH \) and \( RH \) are the lateral positions of the left and right hindpaws, respectively (figure 1a).

2.2. Model development

For the stationary cat to remain upright, the COM vertical projection must stay between the borders of support on either side. However, if the COM is moving with some lateral velocity \( v \), this could make the cat dynamically unstable. Which is to say

\[ (a) \quad \text{COM position (cm)} \]

\[ (b) \quad \text{i) Def. of COM parameters. The oscillating line corresponds to the lateral displacement of the COM during selected strides of treadmill locomotion with symmetric belt speeds (40 cm s}^{-1}; \text{cat no. 03, without anaesthesia). Positive and negative COM values correspond to displacements in the left and right directions. Square marks in the COM oscillations show the time of hindpaw lift and placement on the ground for the right hindpaw in turquoise and the left hindpaw in khaki. Positions of the top and bottom sides of each rectangle correspond to the mean lateral position of the left and right hindpaw averaged over the cycle. The height of grey and white rectangles corresponds to the mean hindpaw step width in each cycle. Horizontal thick lines at the bottom indicate the stance period of each limb; left hind (LH), left fore (LF), right hind (RH) and right fore (RF) limbs. The thickness of the rectangles is the step cycle period, \( P \), defined by timing of right hindlimb placements on the ground \( (T_{RH} \text{ and } T'_{RH}) \). The amplitude, \( \Delta_{COM} \), is half of the distance between the maximum and minimum COM points in one cycle. (b) Body oscillations. The direction of the body movement is depicted by arrows. When the left (L) paws are lifted, the body is dragged to the left by the gravitational moment. When the right (R) paws are lifted, the body is dragged to the right. (c) The inverted pendulum approximation. The inverted pendulum swings at an angle \( \theta \) from the vertical in the frontal plane. The length of the pendulum is \( l \) and the lateral displacement of the COM vertical projection is \( x \).
that $v$ must not exceed the value at which, $x_{\text{COM}}$, crosses the border of support, or the animal will not be able to suppress its lateral motion to prevent the COM from moving beyond the border of support. The $x_{\text{COM}}$ is defined as

$$x_{\text{COM}} = COM + \frac{v}{\omega},$$

where $\omega = \sqrt{g/l}$, $g$ is the acceleration due to gravity, and $l$ is the maximum height of the COM [3]; see figure 1b,c.

Presume that the cat makes balance control decisions based upon the $x_{\text{COM}}$ position in order to maintain dynamic stability. The limb lift-off times on either side would be determined by some position thresholds $p_l$ and $p_R$ of $x_{\text{COM}}$ such that $p_R$ defines the transition from the support on both sides (two-side support) to unilateral stance on the right side; $p_l$ defines the transition from the two-side support to unilateral stance on the left side. In this case, the decision-making thresholds would still be determined during the two-side support phases. During these phases, the state of dynamic stability would be defined by the inequalities $p_R < x_{\text{COM}} < p_l$. Given the definition of $x_{\text{COM}}$, we can rewrite these expressions to be $p_R < COM - q/\omega$ and $COM + q/\omega < p_l$, where $q = \sqrt{v}$ taking into account the direction of COM movement. Based on our previous study, we made an assumption that the lateral speed of the COM is roughly constant during and across intervals of support on both sides of the body, which occur during either three-limb support or diagonal two-limb support phases; see figs 1a and 8a in [1]. Because $q$ is constant, the decision-making thresholds can be formulated for COM rather than $x_{\text{COM}}$ as follows:

$$s_R < COM < s_L,$$  \hspace{1cm} (2.4)

where $s_R = p_R + q/\omega$, $s_L = p_l - q/\omega$.

Over the course of a complete stride cycle, the equations of motion that govern the lateral position of COM are determined by the decision-making thresholds $s_L$ and $s_R$. These thresholds represent the lateral coordinates of the COM at which the ipsilateral limbs transition to and from the phases of the two-side support (phases 1 and 3 in figure 2) and unilateral swing or contralateral stance (phases 2 and 4; figure 2).

During phase 1, the cat is supported by the limbs on both sides of the body, and the dynamics of the lateral COM coordinate $x$ is determined by $dx/dt = -q$ with an initial condition $x(0) = s_L$, phase 1 lasts until the COM crosses the threshold $s_R$. Because the COM travels with constant velocity $-q$, the duration of this interval can be written as $T_1 = (s_L - s_R)/q$, and its equation of motion is

$$x(t) = s_L - qt.$$  \hspace{1cm} (2.5)

Then, the cat swings the left limbs as the COM crosses the threshold $s_R$, transitioning the model into phase 2.

During phase 2, the left limbs are in the swing, and the COM accelerates in the leftward direction away from the position of unilateral support on the right side. In this phase, the dynamics of COM is determined by the inverted pendulum equation:

$$\frac{d^2x}{dt^2} = -\omega^2(x + h),$$  \hspace{1cm} (2.6)

where $-h$ is the coordinate of the right paw. When phase 2 begins, the model inherits its initial conditions from the previous phase:

$$x(T_1) = s_R, \quad x'(T_1) = -q.$$  \hspace{1cm} (2.7)

The equation of motion of the COM during phase 2 is

$$x(t) = -h + (t + s_R) \cosh (\omega(t - T_1)) - q \frac{\sinh (\omega(t - T_1))}{\omega}. \hspace{1cm} (2.8)$$

Figure 2. phases of lateral COM displacement in a walking cycle. The COM position is shown as a function of time in a walking cycle. Upward and downward directions correspond to displacements to left and right, respectively. Green thick lines at 2.7 cm and -2.7 cm show the average position of left and right hindpaws, labelled as LH and RH, respectively. During phase 1, the COM moves from left to right from threshold $s_1$ to threshold $s_R$ with constant speed. At threshold $s_R$, the left paws are lifted. During phase 2, the COM continues moving right at threshold $s_R$, but changes direction in mid phase and starts moving leftwards to threshold $s_L$ owing to the action of the gravitational moment and then it crosses $s_L$ when the left paws are placed back on the ground. In phase 3, the COM moves from right to left from threshold $s_L$ to threshold $s_1$ at constant speed. At threshold $s_1$, the right paws are lifted. During phase 4, the COM first continues moving left at threshold $s_1$, but then changes direction in mid phase and starts moving rightwards to threshold $s_L$ owing to the action of the gravitational moment.

The minimum of the COM coordinate is

$$x_{\text{min}} = -h + \sqrt{(h + s_R)^2 - \frac{q^2}{\omega^2}},$$  \hspace{1cm} (2.9)

and the duration of phase 2 is

$$T_2 = \frac{\ln (h + s_R) + q}{\omega}.$$  \hspace{1cm} (2.10)

Phase 2 ends as the COM crosses threshold $s_R$, entering a phase of dual support (phase 3).

In phase 3, the cat once more has support on both the left and right sides of the body, and the dynamics is determined by the equation $dx/dt = q$, and its initial condition is $x(T_1 + T_2) = s_R$. The time it takes the COM to traverse the distance between the two decision-making thresholds is $T_3 = (s_L - s_R)/q$, and its equation of motion is

$$x(t) = s_R + q(t - T_1 - T_2).$$  \hspace{1cm} (2.11)

At the end of phase 3, the right limbs are lifted as the COM crosses the threshold $s_R$, and the model enters phase 4.

While the right limbs are in swing phase, the COM accelerates away from the position of support provided by the left limbs:

$$\frac{d^2x}{dt^2} = -\omega^2(x - h),$$  \hspace{1cm} (2.12)

where $h$ is the coordinate of the left paw. At the beginning of phase 4, the initial conditions are

$$x(T_1 + T_2 + T_3) = s_L \text{ and } x'(T_1 + T_2 + T_3) = q.$$
The equation of motion during phase 4 is
\[ x(t) = h - (h - s_l) \cos(b (a(t - T_1 - T_2 - T_3))) \]
\[ + \frac{q}{ao} \sin(b (a(t - T_1 - T_2 - T_3))), \] (2.13)

The maximum COM displacement during phase 4 is
\[ x_{max} = h - \sqrt{(h - s_l)^2 - \frac{q^2}{a^2}}, \] (2.14)

and the duration of phase 4 is
\[ T_4 = \frac{1}{\omega} \left( \frac{a(h - s_l) + q}{a(h - s_l) - q} \right). \] (2.15)

In this way, the thresholds \( s_l \) and \( s_r \) determine the position of COM at which two-side support changes to unilateral support.

Given these expressions, we can analytically compute the quantities \( A_{COM}(s_l, s_r, q) \), \( P(s_l, s_r, q) \) and \( Z_{COM}(s_l, s_r, q) \) for our model as functions of model parameters \( s_l, s_r \) and \( q \).

The amplitude of the oscillatory solution is
\[ A_{COM}(s_l, s_r, q) = \frac{x_{max} - x_{min}}{2}, \] (2.16)

and the period of the oscillatory solution is
\[ P(s_l, s_r, q) = T_1 + T_2 + T_3 + T_4. \] (2.17)

The average COM position is defined over cycle as
\[ \overline{COM} = \frac{1}{P} \int_0^P x(t) \, dt, \] (2.18)

which we normalize to the relative position in the base of support:
\[ Z_{COM}(s_l, s_r, q) = \frac{h - \overline{COM}}{2h}, \] (2.19)

where \( h \) is the distance from the midline to the support position on either side.

### 2.3. Model parameter inference

After processing the experimental data as described above, we obtained average values of the period, amplitude and normalized COM position, \( P, A, Z_{COM} \), and their standard errors \( \delta P, \delta A, \delta Z \) for each experimental condition. To find the corresponding values of model parameters, we numerically solved the system of equations for \( s_l, s_r, q \) such that the model output in terms of period, amplitude and average COM position exactly matched the experimental measurements:
\[ A_{COM}(s_l, s_r, q) = A, P(s_l, s_r, q) = P, \text{ and } Z_{COM}(s_l, s_r, q) = Z_{COM}. \]

We then computed standard errors for \( s_l, s_r \), and \( q \) using Bayesian inference with uniform priors. The posterior probability density function for model parameters (pdf) was therefore proportional to the likelihood function which was assumed Gaussian:
\[ p.d.f. \sim \exp \left\{ -\frac{1}{2} \left( \frac{(A - A(s_l, s_r, q))^2}{\delta A^2} + \frac{(P - P(s_l, s_r, q))^2}{\delta P^2} + \frac{(Z_{COM} - Z_{COM}(s_l, s_r, q))^2}{\delta Z^2} \right) \right\}. \] (2.20)

The computed values for \( s_r \) and \( s_l \) were used to define parameters for model interpretation for each experimental condition. The distance between thresholds (DT) was defined as the difference between \( s_l \) and \( s_r \). The threshold mean (TM) was the average of \( s_l \) and \( s_r \). The change in threshold mean with anaesthesia (ATM) was the difference between TM with and without ipsilateral paw anaesthesia in one belt speed ratio.

### 2.4. Statistics

We used a mixed linear model analysis (IBM SPSS 24, Chicago, IL, USA) to determine the significance of the effects of cutaneous feedback and belt speed ratio on \( Z_{COM}, P, \) and \( A_{COM} \). In the analysis, cutaneous feedback and belt speed ratio were within-subject independent factors. Animals and cycles were random factors. The main effect of independent factors and their interactions were determined at a significance level of 0.05. Pairwise comparisons of significant effects were performed with post hoc tests using the Bonferroni adjustment.

The significance of cutaneous feedback and belt speed ratio on model parameters was determined with \( z \)-tests. \( Z \)-scores were determined for model parameter estimates, \( s_x, s_y, \) and \( q \), as well as for other quantities used for model interpretation that depended on these parameters, \( DT, TM, \Delta TM, \). Pairwise comparisons were performed at the 0.05 significance level.

We visualized the comparison of model trajectories to experimental waveforms by superimposing the COM positions across walking cycles for all subjects in one condition. Each walking cycle of a recording was divided into 100 bins. For each bin the mean and standard error of the COM position were calculated to characterize the average waveform and its distribution for each experimental condition. Then, a chi-square test was used to evaluate goodness-of-fit of the model.

### 3. Results

#### 3.1. Model validation

Lateral COM displacements as simulated by the inverted pendulum were quantitatively similar to the mean COM displacements in different experimental conditions: belt speed ratios 1:1, 1:1.5, and 1:2 with and without unilateral paw anaesthesia (root mean square error (RMSE) < 0.01 cm; figure 3). See the electronic supplementary material, tables S1 and S2 for RMSE values and chi-squared test results for each condition.

#### 3.2. Changes in centre of mass position with belt speed ratio and unilateral anaesthesia

The COM exhibited a left-right oscillatory motion during treadmill locomotion (figures 1 and 3). Experimental COM oscillatory motion parameters, \( A_{COM}, P, \) and \( Z_{COM} \), characterized the frontal plane COM dynamics. \( Z_{COM} \), the lateral COM position averaged over the cycle shifted to the left (decreased, see equation (2.3)) as the belt speed ratio increased from 1:1 to 1:5 \((p < 0.05)\) and from 1:1.5 to 1:2 \((p < 0.05); \) figure 4a). At speed ratio 2:1 (at which the left and right belts moved at 0.8 m s\(^{-1}\) and 0.4 m s\(^{-1}\), respectively), \( Z_{COM} \) showed a significant right shift compared to speed ratio 1:1. In trials with anaesthesia applied to the right paws, \( Z_{COM} \) shifted significantly to the right (the values increased; \( p < 0.05 \)) for the belt speed ratios 1:1.5, 1:2, and 2:1, but not for 1:1 (figure 4a). See the electronic supplementary material, tables S3 and S4 for all pairwise comparisons of \( Z_{COM} \).

The amplitude of COM oscillations \( A_{COM} \) was also found to vary with the speed-belt ratio (figure 4b). \( A_{COM} \) decreased significantly as the belt speed ratio increased from 1:1 to 1:1.5, 1:2, and 2:1, as well as from 1:1.5 to 1:2 and to 2:1 \((p < 0.05)\). No significant change in amplitude of oscillations was found between speed ratios 1:2 and the 2:1 \((p = 1.00)\). \( A_{COM} \) did not change significantly in response to unilateral anaesthesia \((p = 0.990)\).
and tables S7 and S8 for all pairwise comparisons of P change in 0.082). Unilateral anaesthesia did not induce a significant in P.<ref>Figure 3. Comparison of lateral displacements of the model with the mean cat COM displacements in different experimental conditions. The model (black dashed lines) and experimental (continuous grey lines) displacements are shown for three belt speed ratios 1:1, 1:1.5 and 1:2 for intact paws (a,b,c) and unilateral paw anaesthesia (d,e,f). The experimental traces are the means computed across all cycles and cats; the thickness of the grey lines represents ± s.e. The dark grey horizontal lines are estimated lateral stability thresholds s<sub>L</sub> (top) and s<sub>R</sub> (bottom). The mean position of left and right limbs is shown in light blue. The total duration of each plot corresponds to two full cycle periods. All traces start at the onset of the unilateral right-limb support.</ref>

3.3. Changes in stability thresholds with belt speed ratio and unilateral anaesthesia

The changes in model parameters were qualitatively similar to the mean experimental COM motion parameters in different experimental conditions: belt speed ratios 1:1, 1:1.5, 1:2 and 2:1 with and without unilateral paw anaesthesia (figure 3).

We observed a significant left shift of the estimated threshold for initiation of the left ipsilateral support, s<sub>L</sub>, with changing the belt speed ratio from 1:1 to 1:2, from 1:1.5 to 1:2, and from 2:1 to 1:1, to 1:1.5 and to 1:2 for the unanaesthetized conditions (p < 0.05; figure 5a). The threshold for initiation of the right ipsilateral support, s<sub>R</sub>, also shifted to the left with a change in speed ratio from 1:1 to 1:1.5 and to 1:2, from 1:1.5 to 1:2, and from 2:1 to 1:1.5 and to 1:2 (p < 0.05; figure 5a). There was also a much greater change of threshold s<sub>R</sub> than s<sub>L</sub> between speed ratios 1:1 through to 1:2, i.e. from −0.835 cm to 0.017 cm for s<sub>R</sub> and from 0.931 cm to 1.266 cm for s<sub>L</sub>. Anaesthesia of the right paws caused a significant right shift of threshold s<sub>L</sub> at speed ratios 1:1.5 and 1:2, and of threshold s<sub>R</sub> at speed ratios 1:2 and 2:1 (p < 0.05; figure 5d).

We did not detect significant changes in the model velocity parameter q with changes in speed ratio or paw anaesthesia conditions (p > 0.05; figure 5b).

Because s<sub>L</sub> and s<sub>R</sub> depended differently on changes in the belt speed ratio, we quantified the net change in the COM dynamics by the threshold mean—the average of s<sub>L</sub> and s<sub>R</sub> at a given belt speed ratio and by the distance between thresholds—the difference of s<sub>L</sub> and s<sub>R</sub> at a given belt speed ratio (figure 6). The threshold mean significantly increased—indicating a shift to the left side—with a change in belt speed ratio when comparing 1:1 to 1:1.5 and to 1:2 belt speed ratios, as well as in the 1:1.5 to 1:2 and 2:1 belt speed ratio comparison (p < 0.05; figure 6a). The threshold mean significantly decreased with a change in belt speed ratio when comparing the 1:2 to the reverse 2:1 belt speed ratio (p < 0.05). The application of an anaesthesia to right-side paws significantly decreased the threshold mean at the 1:2 belt speed ratio, indicating a shift in the threshold mean towards the right side of the cat. However, when we considered the change in threshold mean in response to anaesthesia application across different speed ratios, we did not find significant differences among 2:1, 1:1.5 and 1:2 ratios (p > 0.05; figure 6b). The distance...
One of such factors could be energy expenditure, see for example [5,23,34,35]. However, both humans and cats prefer shifting their support leg to the faster moving side of the treadmill to satisfy task demands [26]. In particular, the stability margins have been reported for human split-belt walking [26] (see their fig. 2). The authors have demonstrated (see also [12]) that these results are expected from the dynamics of an inverted pendulum model. In particular, the model predicts an inverse relationship between the duration of the unilateral support phase and the margin of stability on that side. Assuming that the unilateral support phase on the faster moving side is much greater than the decrease of the stability margins on the slower side (figure 5a). Thus, the swing phase duration of the COM is greater on the faster moving side. We found that the change in the two thresholds owing to anaesthesia ($\Delta s_l$ and $\Delta s_R$) was found to increase in magnitude with changes in belt speed ratio from 1:1 to 1:2 and 2:1 ($p < 0.05$). Additionally, the unilateral application of anaesthesia to the right side shifted the COM towards the anaesthetized side regardless of the speed-belt ratio of 1:2 or 2:1 (figure 7). There was no significant difference between changes in the thresholds for the two speed ratios ($p > 0.05$).

### 3.2. Effect of anaesthesia is independent of the sign of speed difference

We found that the change in threshold mean owing to anaesthesia in terms of its magnitude and direction was not statistically different across speed ratios of 2:1, 1:1.5 and 2:1 (figure 6b). To explore this further, we compared the changes in both thresholds $s_l$ and $s_R$ owing to right-side paw anaesthesia for speed ratios 2:1 and 1:2.

The change in the two thresholds owing to anaesthesia ($\Delta s_l$ and $\Delta s_R$) was found to increase in magnitude with changes in belt speed ratio from 1:1 to 1:2 and 2:1 ($p < 0.05$). Additionally, the unilateral application of anaesthesia to the right side shifted the COM towards the anaesthetized side regardless of the speed-belt ratio of 1:2 or 2:1 (figure 7). There was no significant difference between changes in the thresholds for the two speed ratios ($p > 0.05$).

### 4. Discussion

The inverted pendulum-based model closely reproduced the experimentally measured COM lateral oscillations of cats walking on a split-belt treadmill with different belt speed ratios and with intact and unilaterally anaesthetized paws (figure 3). These results support the hypothesis that COM frontal plane dynamics of cats walking on a treadmill can be described by an inverted pendulum model.

We also tested the effect of varying belt speed ratios on COM lateral position and on lateral stability margins. As demonstrated in this (figures 3, 4a and 5a) and other recent studies in cats [1] and humans [26,27], the COM and xCOM shift towards the slower moving split-belt. We found that with a progressive change in belt speed ratio, the increase of the lateral stability margins on the faster moving side is much greater than the decrease of the stability margins on the slower side (figure 5a). Thus, the swing phase duration affected the lateral stability margins on the faster and slower sides asymmetrically. The same asymmetric changes in margins of stability have been reported for human split-belt walking [26] (see their fig. 2a). The authors have demonstrated (see also [12]) that these results are expected from the dynamics of an inverted pendulum model. In particular, the model predicts an inverse relationship between the duration of the unilateral support phase and the margin of stability on that side. Assuming that the unilateral support phase on the faster moving side of the treadmill is shorter, and therefore the stability margin is greater, the cycle-averaged xCOM should shift away from the faster moving leg. On the other hand, humans and presumably cats can voluntarily increase or decrease margins of stability by, for example, walking with a wide or narrow step width to minimize the risk of falling in an unstable environment or to satisfy task demands [5,23,34,35]. However, both humans and cats prefer shifting xCOM towards a slower belt. It is likely, therefore, that other factors besides the model parameters. 

One of such factors could be energy expenditure, see for example [5,23,34,35].
shown for split-belt speed ratios 2 : 1, 1 : 1, 1 : 1.5 and 1 : 2. Dark grey bars show results for intact paws; light grey bars show results for anaesthetized right paws.

Asterisks depict significant effects of the speed ratios (**p<0.01); hashtags (#) depict significant effects of the unilateral anaesthesia (#p<0.05, ##p<0.01).

Figure 5. Estimated thresholds for initiation of ipsilateral double-support phases, sL and sR, and model velocity parameter q as function of belt speed ratio and anaesthesia. (a) Mean thresholds sL (upper sides of bars) and sR (lower sides of bars). The average (±s.e.) of the two thresholds is shown in the middle of each bar. (b) Model velocity parameter q. Means (±s.e.) were computed using Bayesian inference for each experimental condition. In each panel, a model parameter is shown for split-belt speed ratios 2 : 1, 1 : 1, 1 : 1.5 and 1 : 2. Dark grey bars show results for intact paws; light grey bars show results for anaesthetized right paws.

Specifically, the potential role of the nervous system in setting the lateral stability thresholds during locomotion.

It is possible to derive the relationship between the relative COM shift during unilateral paw anaesthesia and the shift in the perception threshold. Let us assume that a reduced cutaneous feedback from ipsilateral paws shifts a perceived COM location in the lateral direction. A compensatory shift to restore the pre-anaesthesia pressure distribution among the paws should be equal and opposite to the perceived COM shift. Thus, we can use the experimentally measured anaesthesia-evoked COM shift to define the extent of the cutaneous feedback reduction by anaesthesia of the ipsilateral paw pads. The relationship between the perceived COM shift and the cutaneous feedback reduction can be derived as described below.

If we neglect relatively small vertical accelerations of the body caused by limb extensions during walking in the cat, i.e. approximately 2 m s⁻² (approx. 20% of acceleration of gravity; see fig. 3 in [42]), the sum of the vertical forces applied to the left and right paws from the ground is equal and opposite to mg:

\[ F_L + F_R = mg, \]

where \( m \) is the cat’s mass and \( g \) is the gravitational acceleration. Because the net rotation of the cat in the frontal plane during the whole walking cycle is zero, the net resultant moment of all forces acting on the cat in the frontal plane with respect to the COM must be zero in accordance with conservation of angular momentum. Then, assuming negligibly small ground reaction forces in the medial-lateral direction [5], the resultant moment with respect to the COM in the frontal plane is

\[ 0 = F_L(x + h) + F_R(x - h). \]

After solving for \( x \), i.e. the COM position between the left \( (h) \) and right \( (-h) \) paws, we obtain

\[ x = \frac{F_R - F_L}{F_L + F_R} h. \]
We define $F_0R$ as the perceived load on ipsilateral paws after anaesthesia, where

$$F_0R = FR\left(1/C_0d\right).$$

(4.3)

Here, $\delta$ is a parameter that ranges from 0 to 1 and which represents the per cent reduction in load perception. The perceived COM position is defined as $x'$:

$$x' = \frac{F_k - \hat{F}_k}{\hat{F}_L + \hat{F}_R} h = \frac{F_k(1 - \delta) - \hat{F}_L}{\hat{F}_L + F_k(1 - \delta)} h.$$

(4.4)

Therefore, for small $\delta$, the difference between the perceived and actual COM positions $\Delta x = x' - x$ can be approximately found as $\Delta x \approx -h\delta/2$. This bias in perception will lead to the apparent shift of the stability thresholds in the opposite direction: $\Delta s = -\Delta x \approx h\delta/2$. Thus, the contribution of cutaneous receptors to the load perception can be estimated as

$$\delta \approx 2\Delta s/h.$$ 

(4.5)

Based on our inferences, the stability thresholds were shifted by anaesthesia by approximately 0.2 cm (figures 6b and 7) with the half distance between the paws of approximately 2.5 cm (figure 3), which suggests that cutaneous anaesthesia reduced the perception of the force by approximately 16%. This value appears rather small considering that paw pad anaesthesia completely eliminated withdrawal response to pinpricks in our experiments [1]. The relatively small reduction in perception of limb load after elimination of touch and pain sensation in paw pads suggests a substantial contribution to load perception from other load sensitive mechanoreceptors located throughout the limb including those responsible for osseoperception [43].

We found that the effect of anaesthesia may depend on the magnitude of speed ratio as the shift of the relative COM position and of lateral stability thresholds with anaesthesia perturbation was not significant in the 1:1 belt speed condition, but reached significance at higher belt speed ratios (figure 5a). The stronger effect of paw anaesthesia with increasing belt speed asymmetry is consistent with previous reports.

**Figure 6.** Estimated mean of thresholds $s_L$ and $s_R$ (± s.e.), the change in threshold mean with anaesthesia, and the distance between thresholds as functions of belt speed ratio. (a) The threshold mean (the average of thresholds $s_L$ and $s_R$). (b) The change in the threshold mean with the application of anaesthesia. (c) The distance between thresholds $s_L$ and $s_R$. Means (± s.e.) were computed using Bayesian inference for each experimental condition. In each panel, a model parameter is shown for split-belt speed ratios 2 : 1, 1 : 1, 1 : 1.5 and 1 : 2. Dark grey bars show results for intact paws; light grey bars show results for anaesthetized right paws. Asterisks depict significant effects of the speed ratio (*$p < 0.05$, **$p < 0.01$); hashtags (#) depict significant effects of the unilateral anaesthesia (#$p < 0.05$).

**Figure 7.** Effect of anaesthesia is independent of the sign of speed difference. The change in thresholds $s_L$ and $s_R$ owing to cutaneous anaesthesia applied to right paws for opposite split-belt speed ratios. Comparison shows no significant difference between the changes in thresholds $s_L$ and $s_R$ ($p > 0.05$) owing to anaesthesia for 1:2 and 2:1 speed ratios.
that bilateral removal of cutaneous feedback from cat hindpaws causes greater locomotor deficits in more demanding tasks (i.e. slope and horizontal treadmill walking) than in normal overground or tied-belt treadmill walking [29,44]. A possible interpretation of our results is that the balance control system’s reliance on cutaneous feedback from the paws increases in unusual circumstances and more demanding tasks such as a large belt speed difference. Still, during normal cat walking, bilateral removal of hindpaw cutaneous feedback leads to modest effects of other sensory inputs on dynamic stability in the frontal and sagittal planes in walking cats.

**Ethics.** All experimental procedures were consistent with the Principles of Laboratory Animal Care (publication of the National Research Council of the National Academies, 8th edition, 2011) and approved by the Georgia Tech Institutional Animal Care and Use Committee.

**Data accessibility.** Original experimental data are available as the electronic supplementary material online at rsf.igshare.com.

**Authors’ contributions.** E.M.L. wrote the code to analyse experimental data; E.M.L. and W.H.B. processed data and conducted statistical analysis; H.P., A.N.K. and B.I.P. collected data; E.M.L., Y.I.M., H.P. and B.I.P. developed the study concept and experimental design; E.M.L., W.H.B. and Y.I.M. developed the model; E.M.L., W.H.B., B.I.P. and Y.I.M. wrote the original draft; all authors participated in writing the final draft.

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**References**


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