

RESEARCH ARTICLE

Cutaneous sensory feedback from paw pads affects lateral balance control during split-belt locomotion in the cat

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ABSTRACT

Cutaneous sensory feedback from the paw pads plays an important role in regulating body balance, especially in challenging environments like ladder or slope walking. Here, we investigated the contribution of cutaneous sensory feedback from the paw pads to balance control in cats stepping on a split-belt treadmill. Forepaws and hindpaws were anesthetized unilaterally using lidocaine injections. We evaluated body balance in intact and compromised cutaneous feedback conditions during split-belt locomotion with belt-speed ratios of 0.5, 1.0, 1.5 and 2.0. Measures of body balance included step width, relative duration of limb support phases, lateral bias of center of mass (CoM) and margins of static and dynamic stability. In the intact condition, static and dynamic balance declined with increasing belt-speed ratio as a result of a lateral shift of the CoM toward the borders of support on the slower moving belt. Anesthesia of the ipsilateral paws improved locomotor balance with increasing belt-speed ratios by reversing the CoM shift, decreasing the relative duration of the two-limb support phase, increasing the duration of four- or three-limb support phases, and increasing the hindlimb step width and static stability. We observed no changes in most balance measures in anesthetized conditions during tied-belt locomotion at 0.4 m s⁻¹. CoM lateral displacements closely resembled those of the inverted pendulum and of human walking. We propose that unilaterally compromised cutaneous feedback from the paw pads is compensated for by improving lateral balance and by shifting the body toward the anesthetized paws to increase tactile sensation during the stance phase.

KEY WORDS: Center of mass, Inverted pendulum, Tactile sensation, Dynamic stability, Quadruped

INTRODUCTION

Legged animals must control their balance in various locomotor conditions, including changes in speed and external environment. Body balance during locomotion and standing is regulated by a complex system of sensory pathways and reflexes, originating in the visual, vestibular and somatosensory systems (Horak and

Macpherson, 1996). The fastest responses to postural perturbations are mediated by monosynaptic stretch reflexes evoked by muscle spindle primary afferents and by oligosynaptic and polysynaptic reflex pathways, especially those of cutaneous afferents of the foot (Bolton and Misiaszek, 2009; Honeycutt et al., 2012; Honeycutt and Nichols, 2010; Hurteau and Frigon, 2018; Hurteau et al., 2018; Stapley et al., 2002). It has been suggested that a major functional role of cutaneous reflexes from the foot is to maintain balance and postural stability during locomotion (Zehr and Stein, 1999). Loss of cutaneous feedback from the lower limbs as a result of neuropathy, peripheral nerve injury or limb amputation decreases balance and stability and severely impairs the control of locomotion, especially in challenging conditions, such as ladder or slope walking or with external perturbations (Bolton and Misiaszek, 2009; Bouyer and Rossignol, 2003; Hof et al., 2007; Nardone et al., 2014).

In undemanding locomotor conditions when sensory feedback is intact, animals may lessen balance demands to enhance the efficiency of locomotion. To reduce effort and energy expenditure during walking, bipedal and quadrupedal animals use gravity and the inverted pendulum mechanism to destabilize body balance in the direction of propulsion (Alexander, 1976; Cavagna et al., 1977) and in the lateral direction (Griffin and Kram, 2000; Hof et al., 2007; Townsend, 1985). This destabilization causes the forward–sideward–downward acceleration of the center of mass (CoM) during a single limb support phase in human walking (Townsend, 1985; Winter, 1995) and during the diagonal two-limb support phase by the forelimbs and hindlimbs in cat walking (Farrell et al., 2014; Prilutsky et al., 2005). In these support phases, the CoM is unstable – it moves beyond the area of support, or dynamic stability margins (Hof et al., 2005) and the animal can fall if body balance is not recovered by placement of the swinging limb in front of the moving CoM.

In more demanding locomotor conditions, such as ladder or slope locomotion, or locomotion with compromised sensory feedback, the animal changes its locomotor pattern to increase its margins of balance stability by decreasing locomotor speed, increasing step width and area of support and lowering CoM height (Farrell et al., 2015; Gálvez-López et al., 2011; Nardone et al., 2014; Schmidt and Fischer, 2010). In another example, cats stepping on a treadmill change their normal diagonal trotting gait to a gait closer to pacing, which was suggested to improve balance (Błaszczuk and Loeb, 1993). Split-belt locomotion, in which the left and right treadmill belts are moving at different speeds, may pose an even greater challenge to balance control for cats. For example, the margins of dynamic stability in the frontal (Buurke et al., 2018) and sagittal planes (Darter et al., 2018) appear to drive adaptations to split-belt walking in humans. Although the control of dynamic stability in quadrupedal and bipedal split-belt locomotion may be different (Kuczynski et al., 2017; Torres-Oviedo et al., 2011), even ordinary treadmill locomotion appears to complicate balance control in

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locomoting cats (Blaszczyk and Loeb, 1993). Therefore, we expect split-belt locomotion to evoke strong balance-related responses in cats, especially when sensory feedback is perturbed.

The goal of this study was to determine the margins of static and dynamic stability and the contribution of cutaneous sensory feedback from the paw pads to balance and stability margins during tied-belt and split-belt treadmill locomotion in the cat. Although it may seem that cats are always statically stable during locomotion, this is true only for the sagittal plane, whereas cats may be statically unstable in the frontal plane during the ipsilateral two-limb support phase (Farrell et al., 2014). We tested the hypothesis that increasing the difficulty of locomotor tasks with asymmetric belt speeds and/or compromised cutaneous feedback would change the motor strategy to improve balance by increasing the margins of static and dynamic stability.

MATERIALS AND METHODS

All surgical and experimental procedures were conducted in agreement with the Principles of Laboratory Animal Care (NIH publication no.86-23, revised 1985) and approved by the Georgia Tech Institutional Animal Care and Use Committee.

Locomotor training

Four adult female cats, *Felis catus* (Linnaeus 1758) (mass 2.55–4.10 kg), were trained for 3–4 weeks to step on an instrumented split-belt treadmill (Bertec Corporation, Columbus, OH, USA) and to wear 28 reflective markers using food reward. During training and subsequent data collection, the animal was constrained on each side by transparent Plexiglas walls that formed a locomotor area of $0.3 \times 1.5 \text{ m}^2$. Each animal was required to locomote while placing the left and right limbs on the corresponding belt (Fig. 1A). Four speed

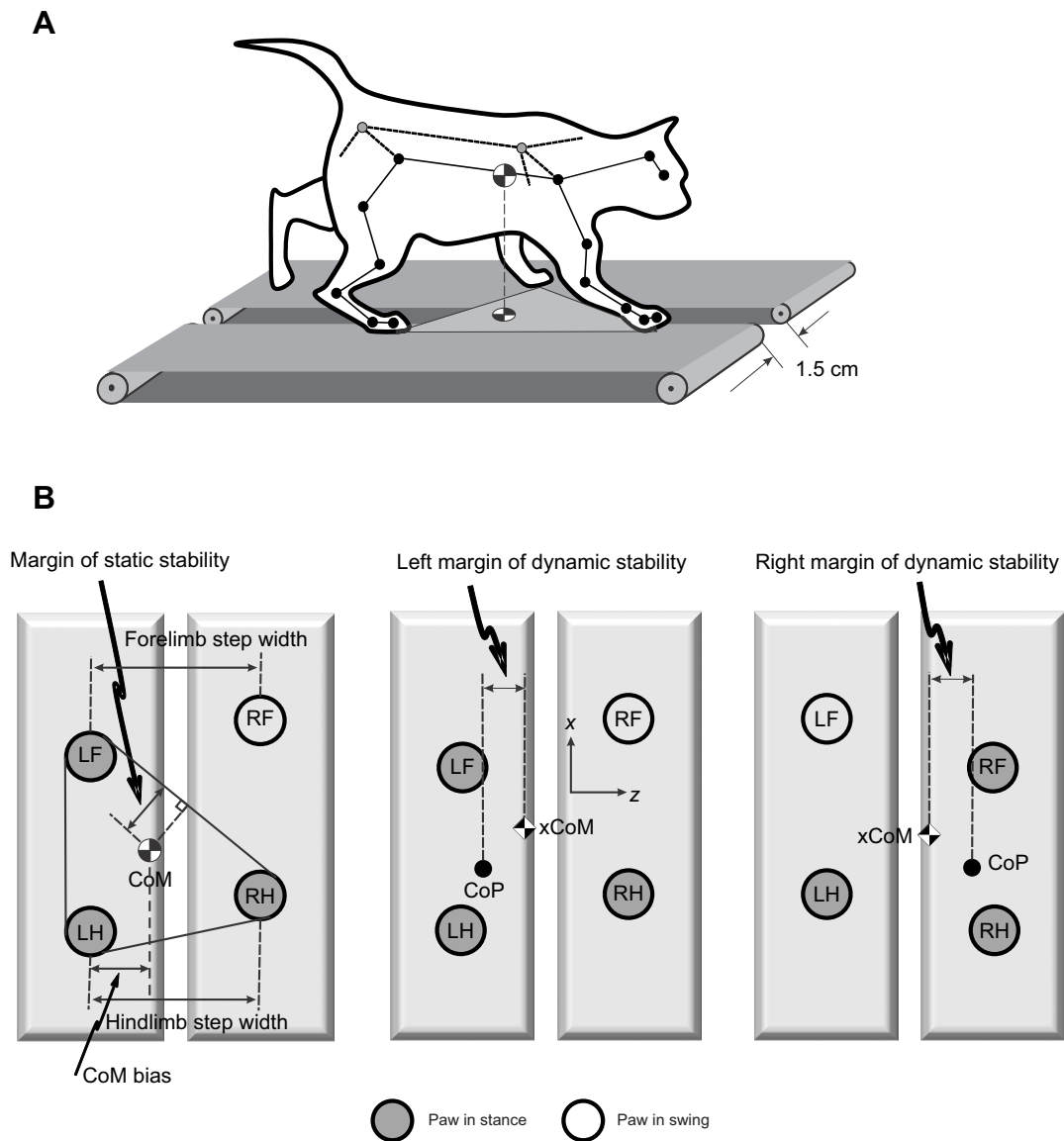


Fig. 1. Experimental setup and definitions of balance stability parameters in the cat. (A) A cat model with reflective markers for calculation of the center of mass (CoM) projection on the treadmill surface. The gray triangle indicates the area of support at a given time instant. (B) Definitions of balance stability parameters. In all panels, two treadmill belts (left and right) are shown with circles indicating paws of the right hindlimb (RH), right forelimb (RF), left hindlimb (LH) and left forelimb (LF). Darker gray circles indicate paws on the ground. The left panel defines the hindlimb and forelimb step width, CoM bias and the margin of static stability. The middle and right panels define the left and right margins of dynamic stability, respectively. xCoM, extrapolated center of mass (see Eqn 2 in Materials and Methods).

combinations of the right and left treadmill belts (and the corresponding speed ratios) were used for training and data collection: 0.4:0.8 m s⁻¹ (speed ratio 0.5); 0.4:0.4 m s⁻¹ (speed ratio 1.0), 0.6:0.4 m s⁻¹ (speed ratio 1.5) and 0.8:0.4 m s⁻¹ (speed ratio 2.0). Note that at speed ratios 0.5 and 2.0, the slower and faster belts moved at the same speeds of 0.4 and 0.8 m s⁻¹. The difference between these split-belt conditions was that the right belt moved slower at ratio 0.5 and the left belt moved slower at ratio 2.0.

Experimental procedures

Prior to and after completing training, each animal was sedated (dexmedetomidine, 40–60 µg kg⁻¹ i.m.) and skin areas around bony landmarks for reflective marker placement were shaved. Prior to each experimental session, double-sided adhesive tape was used to attach 28 reflective markers to major joints of each limb, on the left and right iliac crest and scapulae, as well as on lateral aspects of the head (Fig. 1A). The exact locations of the markers on the body have been described previously (Farrell et al., 2014; Prilutsky et al., 2005).

Each animal was tested at all belt-speed ratios either with intact or anesthetized paws (see below) in a single experimental session, except for one animal, which was not tested at speed ratio 0.5. We recorded at each belt-speed ratio starting with the tied-belt condition (0.4:0.4 m s⁻¹) for 15 s. We then changed the speed of the right or left belt to the desired ratio within ~1 s. The resulting speed ratio was maintained for 60 s, after which we returned the right or left belt speed to the tied-belt condition at 0.4 m s⁻¹ within ~1 s for an additional 15 s. The order of speed ratios within each experimental session was randomized. The animal received food and rested for ~1 min between tested speed ratios.

We repeated recordings at all speed ratios with the different paw-pad anesthesia conditions on a separate day. The order of testing the intact and anesthesia conditions was randomized across animals. Prior to paw anesthesia, the animal was sedated with dexmedetomidine (40–60 µg kg⁻¹ i.m.). The four digital pads and three parts of the metacarpal (metatarsal) pad of the right forepaw and right hindpaw were injected with 1 ml of 1% lidocaine solution. The animal was immediately awoken by injection of antipamezole (40–60 µg kg⁻¹ i.m.). The reflective markers were placed on the animal, and locomotor recordings with the same belt-speed ratios proceeded as described above. We tested the effectiveness of anesthesia using pinpricks to evoke limb withdrawal or by attaching a small piece of adhesive tape to evoke paw shake. Paw-pad anesthesia was typically effective for at least 30 min, which was sufficient to complete the experimental session.

We recorded the 3D positions of the reflective body markers with a 6-camera high-speed motion-capture system (Vicon Motion Systems, Oxford, UK) with a sampling rate of 250 Hz. The vertical component of the ground reaction force (GRF) from each treadmill belt was recorded with a sampling rate of 600 Hz in one animal.

Evaluation of locomotor balance and stability margins

Locomotion analysis was performed for all steady-state cycles recorded during 60 s of stepping at a given belt-speed ratio, except for the first 10 cycles after the change of speed from the tied-belt condition to ensure a steady locomotion pattern. The steady-state cycles selected for analysis were defined as cycles with a duration within 2 s.d. of the mean duration determined across all cycles of a given condition except the first 10 cycles. Recorded marker coordinates were low-pass filtered by a 4th order, zero-lag Butterworth filter with a cut-off frequency of 15 Hz. Filtered coordinates were used to calculate parameters of locomotor balance and stability, including step width, relative duration of limb support

phases, lateral CoM bias, as well as margins of static and dynamic lateral stability.

The step width of the forelimbs and hindlimbs was defined as the lateral distance between the centers of the left and right forepaws (or hindpaws) in each step (Fig. 1B). The step width is a simple kinematic measure of adaptive locomotor responses to threatened balance (see Introduction) and was calculated to enable us to compare our results with other studies. We computed the center position of each paw from lateral positions of the metacarpophalangeal and metatarsophalangeal markers subtracting (adding) half of the paw width and marker diameter.

Stance and swing phases of each limb were identified using the maximum anterior limb angle from the vertical (stance onset) and the maximum posterior limb angle (swing onset) (Pantall et al., 2012). The stride cycle was defined as the period between two consecutive stance onsets by the right hindlimb (RH). Each limb support phase was defined by the limbs in contact with the ground at each time instant of the stride cycle. During quadrupedal locomotion, eight limb support phases are normally identified: 4 limbs×2 (stance and swing) phases. The number of limbs on the ground at a given instant during walking is between 2 and 4, depending on locomotor task and speed (Gray, 1968; Hildebrand, 1989). Several distinct limb support phases were analyzed in this study: (1) diagonal 2-limb support phase formed by the right hindlimb and left forelimb (RH–LF); (2) diagonal 2-limb support phase formed by the left hindlimb and right forelimb (LH–RF); (3) ipsilateral 2-limb support phase formed by the right hindlimb and right forelimb (RH–RF); (4) ipsilateral 2-limb support phase formed by the left hindlimb and left forelimb (LH–LF); (5) 2-limb support phase computed as the sum of the above 2-limb support phases; (6) 3-limb support phase formed by either two forelimbs and one hindlimb or one forelimb and two hindlimbs; and (7) 4-limb support phase. The number of limbs on the ground determines the area of support and thus the margin of static stability (Fig. 1B). A decrease and increase in the relative duration of 2-limb and 3–4-limb support phases, respectively, are expected when animal balance is threatened by an increased speed ratio or reduced paw sensation.

The lateral CoM position (bias) with respect to lateral positions of the left and right hindpaws in stance of each stride cycle (CoM_{bias}) was computed as:

$$\text{CoM}_{\text{bias}} = \frac{|\text{LH}_z - \text{CoM}_z|}{|\text{LH}_z - \text{RH}_z|}, \quad (1)$$

where CoM_{bias}, LH_z and RH_z are lateral positions of the CoM and left and right hindpaws on the ground, respectively, averaged over each cycle. It follows from Eqn 1 that when the CoM is between LH and RH, 0 < CoM_{bias} < 1; if CoM_{bias} = 1 or CoM_{bias} = 0, the CoM lateral position coincides with that of the right or left hindpaw, respectively; if CoM_{bias} = 0.5, the CoM lateral position is exactly between the left and right hindpaws (Fig. 1B). The CoM_{bias} together with the margin of static stability (see below) provides a more complete assessment of the response to balance perturbations. CoM_{bias} indicates the direction in the frontal plane in which the body is more prone to losing balance.

The margin of static stability during a locomotor cycle was defined as the shortest distance between the CoM and the border of limb support area averaged across all time frames within the cycle, if the CoM was located inside the limb support area (Fig. 1B). If the CoM was located outside the limb support area, the same calculation was used and the obtained value was multiplied by –1. The lateral CoM location was computed as the weighted sum of the CoM

positions of each segment, considering the mass of each segment divided by the body mass (Farrell et al., 2014). The location of the CoM of each segment and segment mass were computed from the measured cat mass and segment length using regression equations from Hoy and Zernicke (1985).

Left and right margins of dynamic stability were determined as the lateral distance between the corresponding peaks of the center of pressure (CoP) and the extrapolated center of mass (xCoM) (Hof et al., 2005, 2007) (see Fig. 1B). The lateral xCoM position was defined as the position of the vertical projection of the CoM on the support surface plus a distance that depends on CoM velocity in the lateral direction (v_{CoM}) and the eigen frequency of the pendulum ($\sqrt{g l^{-1}}$) with length l :

$$\text{xCoM} = \text{CoM} + v_{\text{CoM}} \left(\sqrt{g l^{-1}} \right)^{-1}, \quad (2)$$

where g is the gravitational constant and pendulum length is defined as the mean of the maximum height of the proximal joints (hip or shoulder) of all limbs in a stride cycle. The CoP is the point of application in the frontal plane of the resultant vector of all GRFs acting on the paws in contact with the ground. The CoP was computed based on the lateral positions of the paws on the ground and the measured or calculated (see below) magnitude of the vertical GRF under the left and right belts:

$$\text{CoP} = (z_L F_L + z_R F_R) (F_L + F_R)^{-1}, \quad (3)$$

where z_L and z_R are the means of the lateral positions of the left forepaw and hindpaw and the right forepaw and hindpaw, respectively, in contact with the left and right belts; F_L and F_R are the vertical component of the GRF vector measured under the left and

right belts, respectively. Note that Eqn 3 neglects the effects of the lateral force component on the CoP. We excluded this force component because of its small magnitude during cat walking, i.e. over 10 times smaller than the vertical component (Farrell et al., 2015), and a low recorded signal-to-noise ratio. In three animals, the vertical GRF under each belt was calculated. The vertical force was calculated by the linear interpolation between the weight of the body during the ipsilateral 2-limb support and zero force value during the contralateral 2-limb support, taking the CoM bias into account (Fig. 2).

Statistics

We performed a mixed linear model analysis (SPSS 24, IBM SPSS, Chicago, IL, USA) to determine the significance of two within-animal independent factors – cutaneous feedback (intact and compromised) and belt-speed ratio (0.5, 1.0, 1.5 and 2.0) – on dependent variables. The animals and cycles were random factors. Dependent variables included the forelimb step width and hindlimb step width, the relative duration of the 2-limb ipsilateral, 2-limb diagonal, 3-limb and 4-limb support phases, the CoM bias, the static stability margin and the left and right dynamic stability margins. For each dependent variable, the main effect of independent factors and their interactions were determined. If the effects were significant, a *post hoc* paired comparison with Bonferroni adjustments was performed. The significance level was set at 0.05.

RESULTS

Step width

Examples of lateral paw positions with respect to the CoM during locomotion with different belt-speed ratios are shown in Fig. 3.

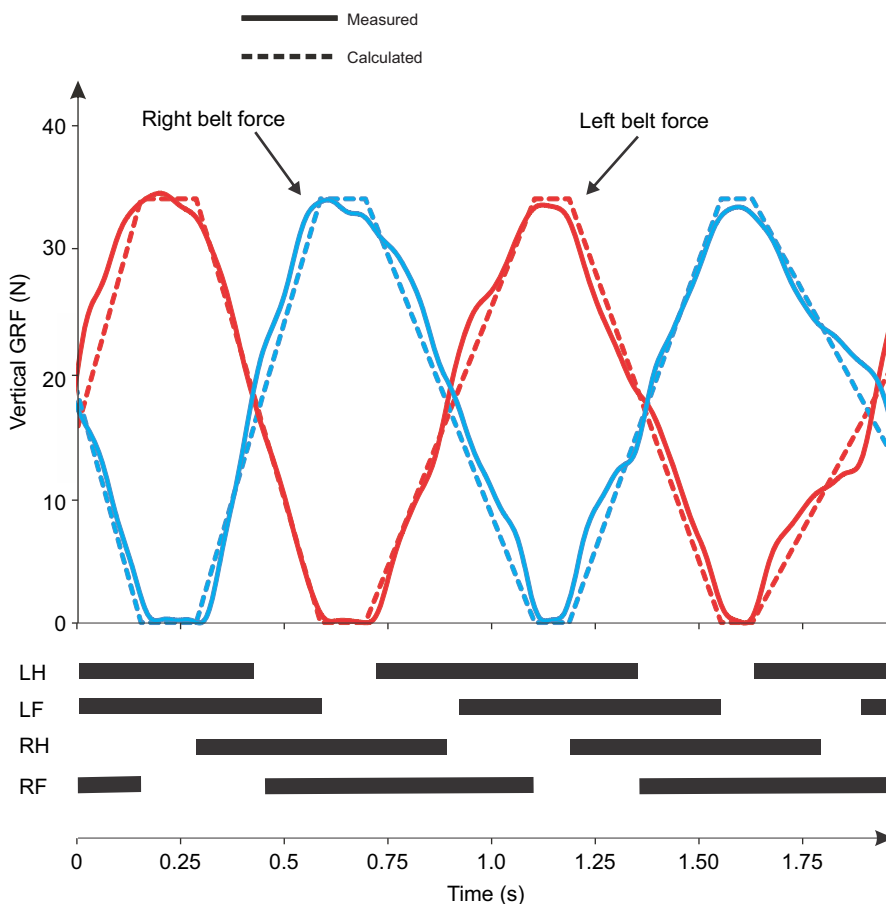


Fig. 2. Measured and calculated vertical ground reaction forces (GRFs) under left and right belts during locomotion at speed ratio 1.0. Horizontal thick lines indicate stance periods of the LH, LF, RH and RF. Cat TO.

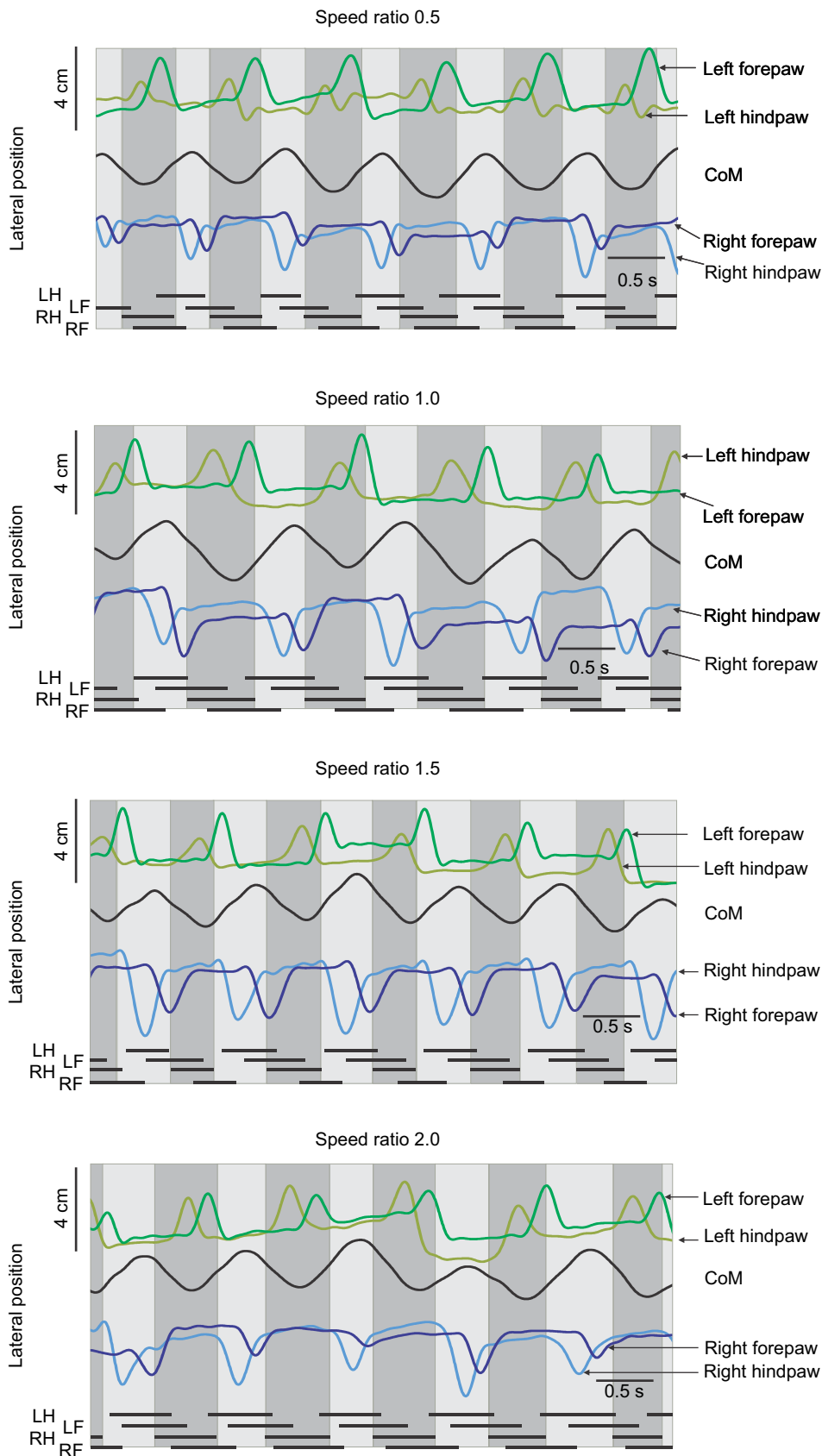


Fig. 3. Lateral displacement of the CoM, left and right forepaws and hindpaws as a function of time at different belt-speed ratios. Horizontal lines at the bottom of each panel indicate stance periods of each limb. Cat MO.

We observed that lateral paw positions of the ipsilateral forelimbs and hindlimbs during stance were essentially the same and that all four paws moved laterally by 2–3 cm during swing. The CoM

oscillated in the medial–lateral direction and reached the left and right peak positions once in each cycle. Each CoM lateral position peak occurred when both contralateral limbs were in swing (or

ipsilateral limbs were in stance), irrespective of the belt-speed ratio (Fig. 3).

The belt-speed ratio significantly affected forelimb and hindlimb step width during intact (control) locomotion ($F_{3,1164}=34.7$, $P<0.001$ and $F_{3,1176}=16.9$, $P<0.001$, respectively). The forelimb step width was largest at speed ratio 1.0 ($P<0.001$) and smallest at speed ratio 1.5 ($P=0.012$). The hindlimb step width was largest at speed ratios 1.0 and 2.0 ($P\leq 0.001-0.033$) and lowest at speed ratio 0.5 ($P=0.002$; Fig. 4).

Anesthesia of the right paws significantly increased the forelimb step width at speed ratio 0.5 ($F_{1,1164}=59.4$, $P<0.001$) and decreased it at speed ratio 1.0 ($F_{1,1164}=21.8$, $P<0.001$; Fig. 4A). The loss of cutaneous feedback significantly increased the hindlimb step widths at all speed ratios ($F_{1,1176}=7.2-71.5$, $P\leq 0.001-0.007$) except ratio 1.0 ($F_{1,1176}=1.4$, $P=0.237$; Fig. 4B).

Relative duration of limb support phases

In the control locomotor conditions, the relative duration of 2-, 3- and 4-limb support phases was significantly affected by the speed ratio ($F_{3,1237}=179.0$, $P<0.001$; $F_{3,1237}=119.5$, $P<0.001$; and $F_{3,1233}=5.5$, $P=0.001$, respectively). The longest duration of the 2-limb support phase occurred at speed ratios 0.5 (mean \pm s.e.m.: 39.7 \pm 2.2%) and 2.0 (34.0 \pm 2.2%) and the shortest duration at speed ratio 1.0 (18.9 \pm 2.2%; Fig. 5A). Changes in the duration of the 3-limb support phase as a function of the speed ratio were opposite to those of the 2-limb phase – the shortest 3-limb phase duration occurred at speed ratios 0.5 (46.5 \pm 3.5%) and 2.0 (56.7 \pm 3.6%) and the longest at speed ratio 1.0 (70.1 \pm 3.5%; Fig. 5B). The duration of the 4-limb support phase was relatively short, i.e. between 14.6 \pm 1.4% and 11.9 \pm 1.3% at speed ratios 0.5 and 1.0, respectively (Fig. 5C).

Anesthesia of the right forepaw and hindpaw significantly influenced the relative durations of all three support phases ($F_{1,1237}=10.3$, $P=0.001$; $F_{1,1237}=14.7$, $P<0.001$; and $F_{1,1233}=64.3$, $P<0.001$, respectively). The duration changes depended on the limb support phase and belt-speed ratio (Fig. 5). The 2-limb support duration decreased at all asymmetric belt speeds (speed ratios 0.5, 1.5 and 2.0; $P<0.001$, $P=0.026$ and $P=0.001$, respectively) and slightly but significantly increased in the tied-belt condition (speed ratio 1.0; $P=0.005$; Fig. 5A). The 3-limb support duration increased at speed ratio 0.5 ($P=0.001$), decreased at speed ratios 1.0 and 1.5 ($P<0.001$) and did not change at speed ratio 2.0 ($P=0.786$; Fig. 5B). The duration of the 4-limb support increased at all speed ratios ($P<0.001$) except the ratio 0.5 ($P=0.067$; Fig. 5C).

The decrease in the total duration of 2-limb support with anesthesia at the asymmetric speed ratios 1.5 and 2.0 (Fig. 5A) resulted mostly from the decrease in the duration of the diagonal 2-limb support phases RH-LF ($P<0.001$; Fig. 6A) and LH-RF ($P<0.001$; Fig. 6B). Note, similar durations of the support phases RH-LF and LH-RF were obtained for both the control and anesthetized conditions at speed ratios 1.5 and 2.0 and to a lesser extent at speed ratio 1.0. The RH-LF phase duration was much longer than that of the LH-RF phase at speed ratio 0.5; the latter duration was close to zero (Fig. 6A,B). The duration of the ipsilateral 2-limb support phases RH-RF and LH-LF did not change with anesthesia at speed ratios 1.5 and 2.0 ($P=0.110-0.582$ and $P=0.687-0.906$, respectively for the two phases). Note that the right belt moved twice as slow as the left belt at speed ratio 0.5 and twice as fast at speed ratio 2.0 (see Materials and Methods).

The shorter total duration of the 2-limb support with anesthesia at speed ratio 0.5 (Fig. 5A) resulted from the shortening of the ipsilateral 2-limb support phase RH-RF ($P<0.001$; Fig. 6C).

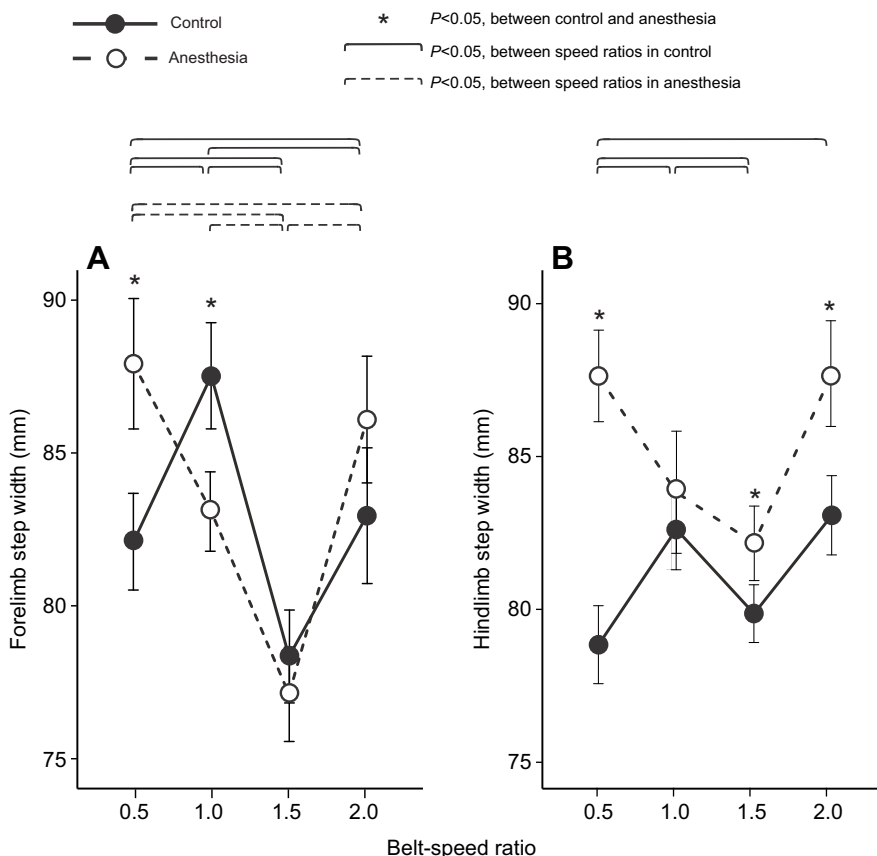


Fig. 4. Mean (\pm s.e.m.) forelimb and hindlimb step width as a function of belt-speed ratio in the control (intact) condition and with anesthesia of the right paws. (A) Forelimb; (B) hindlimb. Pooled data of all animals (total number of analyzed cycles across animals and conditions is 1186).

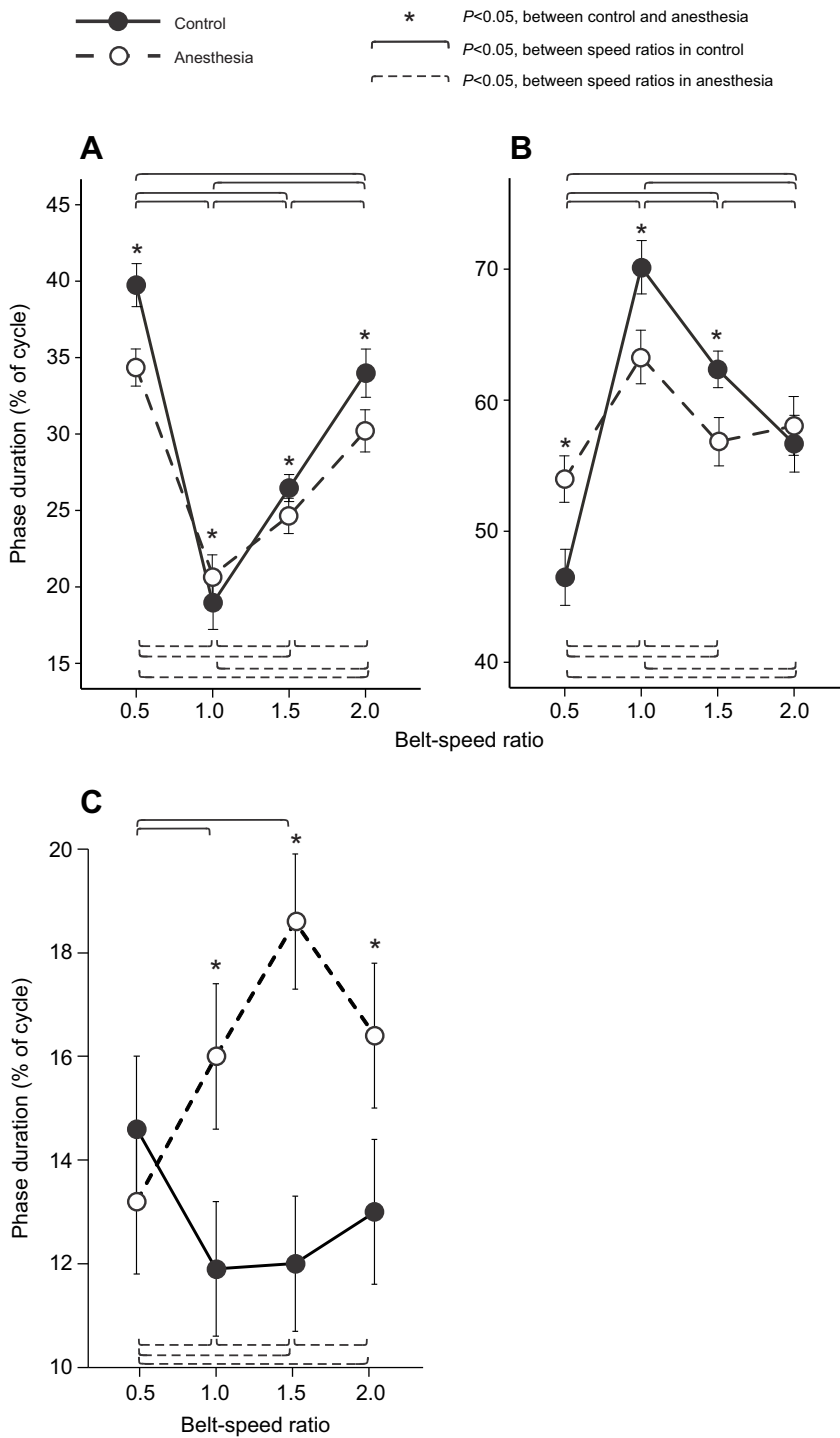


Fig. 5. Mean (\pm s.e.m.) normalized phase duration of 2-, 3- and 4-limb support as a function of belt-speed ratio in the control (intact) condition and with anesthesia of the right paws. (A) 2-limb support, (B) 3-limb support and (C) 4-limb support. Pooled data of all animals (total number of analyzed cycles across animals and conditions is 1186).

The small increase in the total duration of the 2-limb support with anesthesia in the tied-belt condition (speed ratio 1.0) reflected the corresponding duration increase of the RH–RF ($P=0.004$) and LH–LF ($P<0.001$) phases at this speed ratio (Fig. 6C,D).

CoM lateral bias and margin of static stability

We found a significant effect of belt-speed ratio, paw anesthesia and their interaction on the CoM lateral bias ($F_{3,1225}=129.3$, $P<0.001$; $F_{1,1224}=76.7$, $P<0.001$; and $F_{3,1224}=11.9$, $P<0.001$, respectively). In the control condition with intact tactile sensation of the right forepaw and hindpaw, the CoM bias was relatively close

to the midline between the two hindpaws at speed ratios 0.5 and 1.0 (the mean bias values were 0.513 ± 0.014 and 0.478 ± 0.014 , respectively). With increasing speed ratios to 1.5 and 2.0, the CoM bias significantly decreased to 0.399 ± 0.014 and 0.344 ± 0.014 , respectively ($P<0.001$; Fig. 7A), i.e. the CoM shifted toward the left hindpaw (see Eqn 1). The observed CoM bias at asymmetric belt speeds indicated that the CoM shifted toward the slower moving belt. This effect, however, was less pronounced at a speed ratio of 0.5 compared with 2.0.

The loss of cutaneous sensation with anesthesia of the right forepaw and hindpaw shifted the CoM toward the right belt

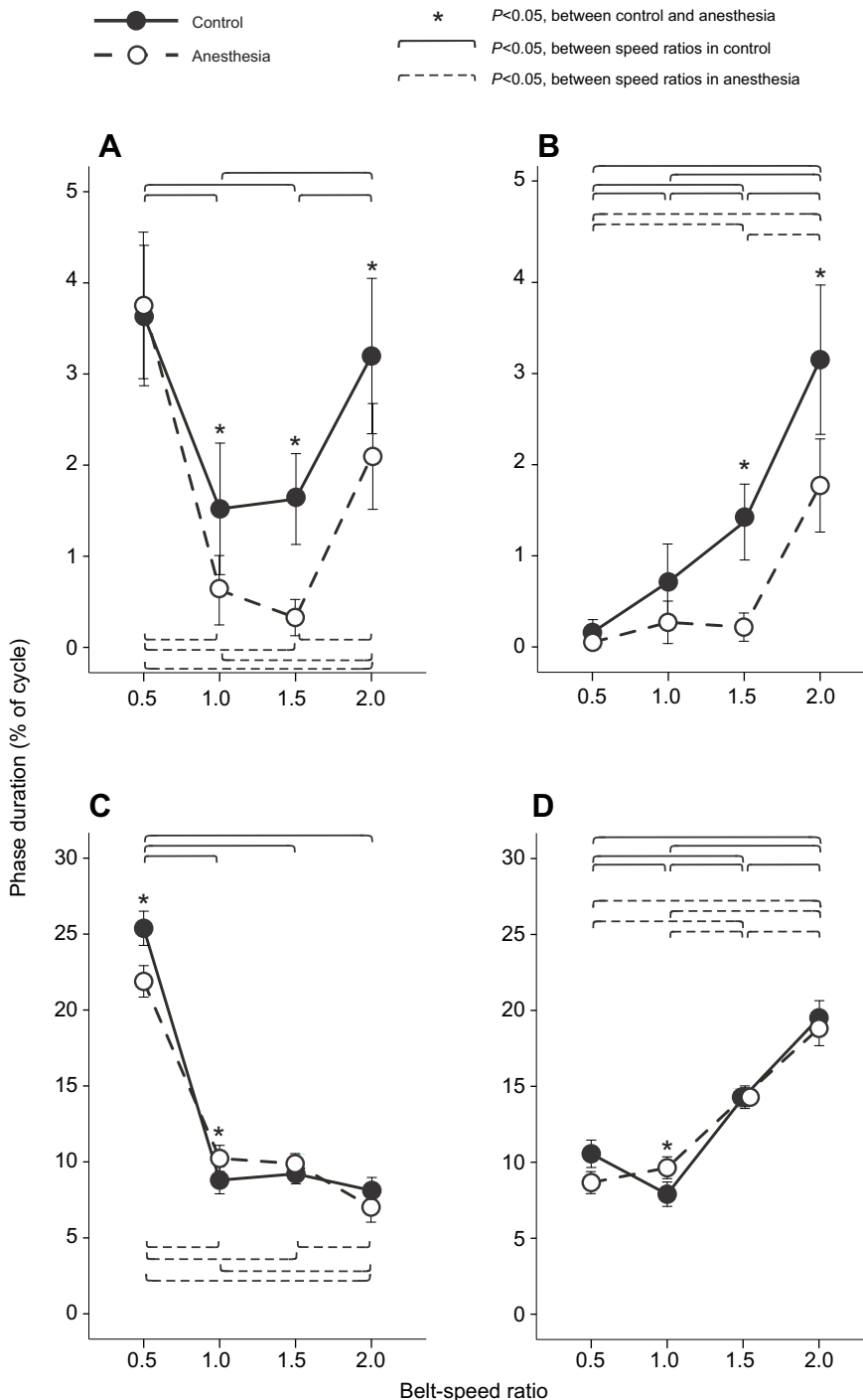


Fig. 6. Mean (\pm s.e.m.) normalized phase duration of diagonal and ipsilateral 2-limb support phases as a function of belt-speed ratio in the control (intact) condition and with anesthesia of the right paws.

(A) Diagonal RH-LF limb support. (B) Diagonal LH-RF limb support. (C) Ipsilateral RH-RF limb support. (D) Ipsilateral LH-LF limb support. Pooled data of all animals (total number of analyzed cycles across animals and conditions is 1186).

($P < 0.001$) at all speed ratios except 1.0 ($P = 0.659$; Fig. 7A). Thus, the CoM shift was toward the paws affected by the loss of cutaneous sensation at all asymmetric speeds, whether they were on the slow or fast belt.

The margin of static stability also significantly depended on the belt-speed ratio and paw anesthesia but not on their interaction ($F_{3,1226} = 191.0$, $P < 0.001$; $F_{1,1227} = 34.8$, $P < 0.001$; and $F_{3,1226} = 2.0$, $P = 0.113$, respectively). In the control condition, the largest margin of static stability occurred in the tied-belt condition (speed ratio 1.0), i.e. 22.2 ± 0.5 mm, and the smallest at a split-belt-speed ratio of 0.5, i.e. 16.3 ± 0.5 mm (Fig. 7B). The static stability margins at speed ratios 1.5 and 2.0 were between

the minimum and maximum values: 20.3 ± 0.4 and 18.1 ± 0.5 mm ($P < 0.001$).

Anesthesia of the right paws increased the margins of static stability in the asymmetric belt-speed ratios of 0.5, 1.5 and 2.0; the corresponding margins were 18.4 ± 0.5 , 21.1 ± 0.4 and 19.6 ± 0.7 mm ($P \leq 0.001$ – 0.029 ; Fig. 7B). There was no significant change in the static stability margin (22.9 ± 0.5 mm) compared with the control at speed ratio 1.0 ($P = 0.051$).

Lateral dynamic stability

Examples of CoM, xCoM and CoP lateral positions as a function of time are shown for the control conditions at speed ratios 1.0 and

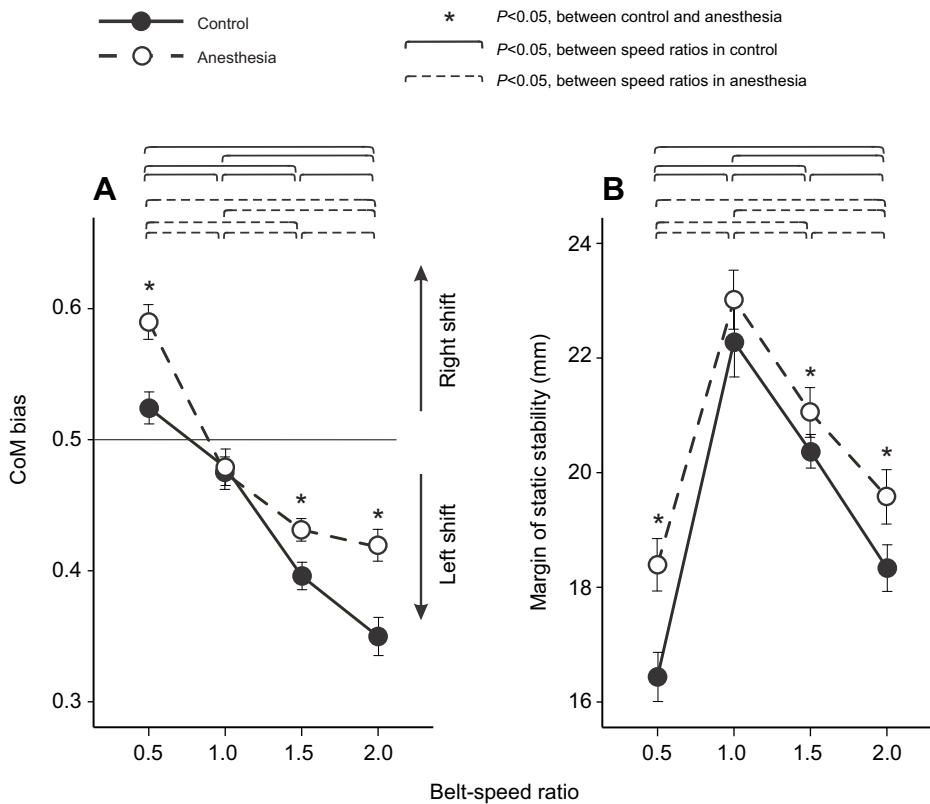


Fig. 7. Mean (\pm s.e.m.) lateral CoM bias and margin of static stability as a function of belt-speed ratio in the control (intact) condition and with anesthesia of the right paws. (A) Lateral CoM bias; (B) margin of static stability. Pooled data of all animals (total number of analyzed cycles across animals and conditions is 1186).

2.0 (Fig. 8A,B) and for the paw anesthesia condition at speed ratio 2.0 (Fig. 8C). In all cases, the left and right lateral CoM positions peaked near the time of the corresponding CoP peaks, and each peak occurred once in a cycle during ipsilateral 2-leg support phases. The xCoM peaks occurred slightly earlier in the cycle – prior to or at the offset of the 3-limb support by two ipsilateral limbs and the contralateral forelimb (Fig. 8A, phases 3 and 7). Thus, termination of the contralateral forelimb stance phase initiated the reversal of xCoM lateral displacement. The distance between the CoP left and right peaks, corresponding approximately to the step width (see Fig. 1), was greater than that of xCoM or CoM, whereas the CoM lateral displacement range was the smallest.

Left and right dynamic stability margins (defined in Fig. 8B) appeared similar during the control condition at speed ratio 1.0 (Fig. 8A). During asymmetric split-belt locomotion, the margin of the dynamic stability was smaller on the slower side (left) than on the faster one (right; Fig. 8B,C). Anesthesia of the right paws increased the range of the CoP lateral displacement (or the step width; see Fig. 4B).

Both left and right margins of dynamic stability in the control condition significantly depended on the belt-speed ratio. The left dynamic stability margin significantly decreased with increasing speed ratio from 16.3 ± 1.7 mm at speed ratio 0.5 to 9.2 ± 1.8 mm at speed ratio 2.0 ($F_{3,1237}=39.3$, $P<0.001$; Fig. 9A). The right dynamic stability margin in the control condition significantly increased with speed ratio from 9.6 ± 1.1 mm at speed ratio 0.5 to 18.2 ± 1.1 mm at speed ratio 2.0 ($F_{3,1238}=75.9$, $P<0.001$; Fig. 9B).

Anesthesia of the right paws significantly increased the left dynamic stability margin at speed ratio 0.5 ($P<0.001$) but did not change it at speed ratios 1.0, 1.5 and 2.0 ($P=0.478$, $P=0.317$ and $P=0.235$, respectively; Fig. 9A). The loss of cutaneous sensation significantly decreased the right dynamic stability margin at speed

ratio 0.5 ($P=0.004$) but did not change it at speed ratios 1.0, 1.5 and 2.0 ($P=0.274$, $P=0.118$ and $P=0.675$, respectively; Fig. 9B).

DISCUSSION

The results of this study demonstrate that split-belt locomotion and loss of cutaneous sensation from the paw pads on one side of the body significantly affects balance control, as assessed by measures of static and dynamic stability. Specifically, we found that with increasing asymmetry in speed between the left and right belts, the animal shifted the CoM toward the slower moving belt. This shift had important consequences for balance control. The shift is also consistent with the findings of Frigon et al. (2015) of greater forelimb and hindlimb extensor electromyogram (EMG) in the limbs stepping on the slow belt. Another important finding was that unilateral anesthesia of the paw pads resulted in a CoM shift toward the anesthetized side. Furthermore, we generally observed that the most pronounced changes in balance control and stability parameters with loss of cutaneous sensation occurred during split-belt locomotion. In the following, we discuss the results in light of potential biomechanical and neural control mechanisms that might participate in lateral balance control during split-belt locomotion in the cat.

Mechanisms of lateral balance control

The fact that the lateral CoM and xCoM positions peaked during and just before onset of the ipsilateral 2-limb support phase, respectively (Figs 3 and 8A, phases 4 and 8), suggests that balance in the lateral direction may be controlled by the timing of the contralateral forelimb swing onset. This swing onset initiates the ipsilateral 2-limb support phase and reversal of xCoM and CoM lateral displacement, so that they both start to move away from the closest border of support, thus increasing the margins of static and ipsilateral dynamic stability (Figs 3 and 8). It appears that

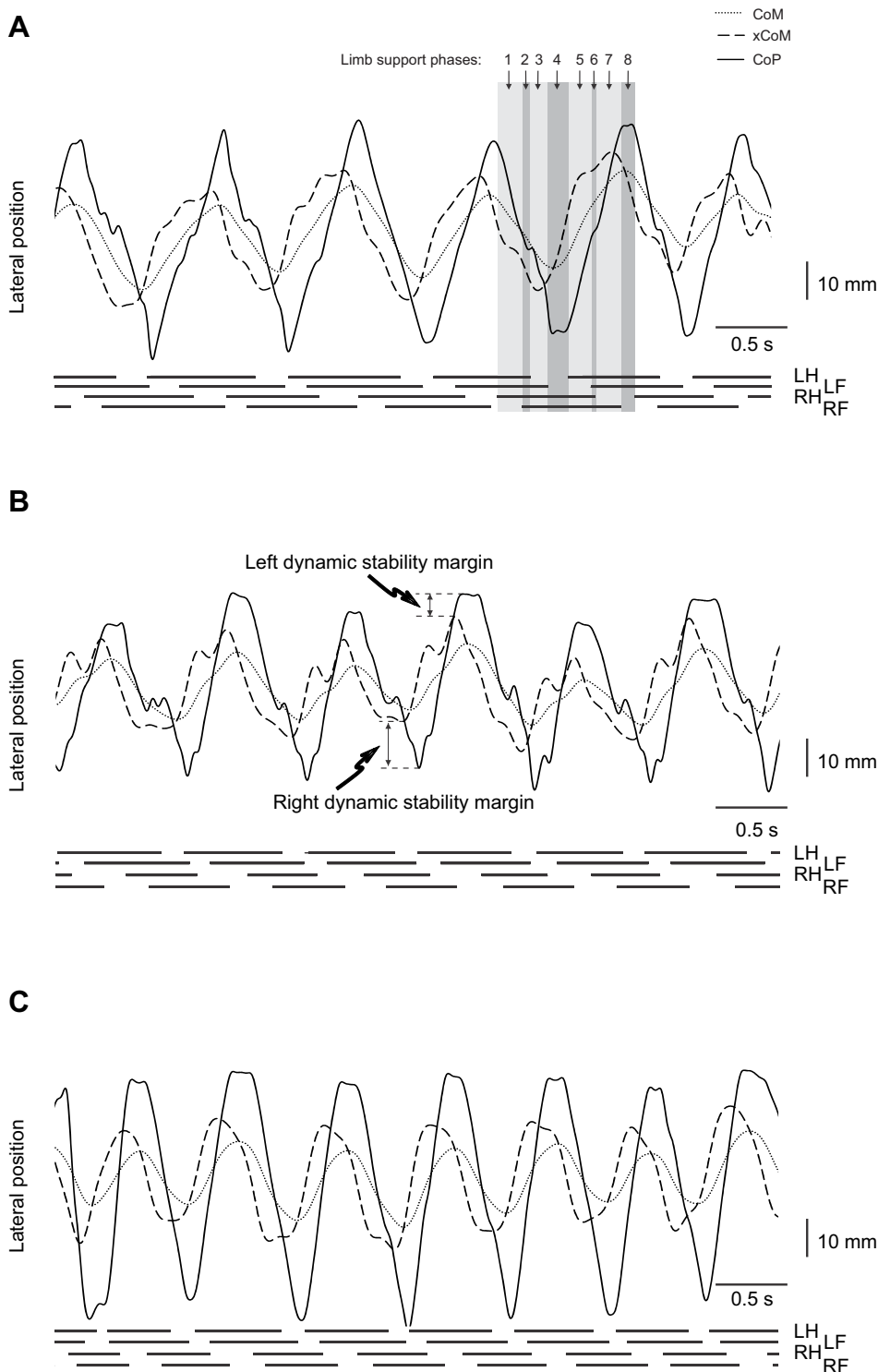


Fig. 8. Lateral displacement of the CoM, xCoM and center of pressure (CoP) as a function of time at different belt-speed ratios for the control (intact) condition and with anesthesia of the right paws.

(A) Control condition at speed ratio 1.0.
 (B) Control condition at speed ratio 2.0. In A, 8 phases of limb support are shown with gray rectangles. In B, the definitions of the left and right dynamic stability margins are shown. Horizontal lines at the bottom of each panel indicate stance periods of each limb. Cat MO.

the reversal of xCoM and CoM displacement was due to the action of gravity and the inverse pendulum mechanism described in the Introduction. Specifically, a medial CoM position with respect to the CoP during the ipsilateral 2-limb support period creates an external moment in the frontal plane that first decelerates the lateral CoM motion toward the ipsilateral CoP, reverses the CoM direction of motion and then accelerates it in the opposite direction. This acceleration is subsequently controlled by contact of the contralateral hindlimb and immediately following

contact of the contralateral forelimb, together causing a sharp deceleration of the xCoM (Fig. 8A, limb support phases 1 and 5) followed by a reversal of xCoM and CoM lateral displacement (Fig. 8A, limb support phases 3 and 7). Thus, the position and timing of the stance onset and offset of each paw must be controlled with high precision to maintain balance. Cats actively control the hindpaw and forepaw positions in the sagittal plane at stance onset and offset during overground locomotion (Klishko et al., 2014).

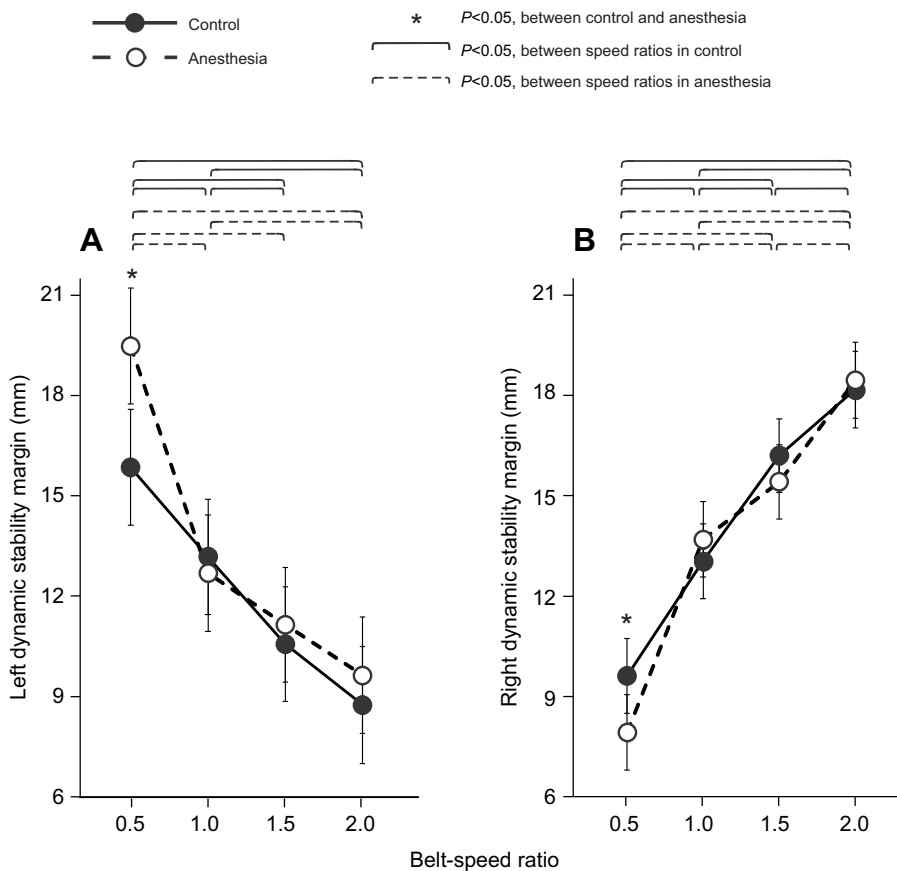


Fig. 9. Mean (\pm s.e.m.) left and right dynamic stability margins as a function of belt-speed ratio in the control (intact) condition and with anesthesia of the right paws. (A) Left; (B) right. Pooled data of all animals (total number of analyzed cycles across animals and conditions is 1186).

Studies have described a similar mechanism of lateral balance control in bipedal animals, including humans (Demes et al., 2015; Griffin and Kram, 2000; Hof et al., 2007; Roden-Reynolds et al., 2015; Townsend, 1985), but not in quadrupeds. It appears that the lateral dynamics of the CoM with respect to the left and right borders of support are strikingly similar between bipedal walking in humans and quadrupedal locomotion in cats (Fig. 10). For example, peaks of CoM (or sacrum) occur in the middle of stance by the ipsilateral foot or two paws in both cases. With the onset of this stance phase [or the onset of the contralateral limb(s) swing phase], the lateral displacement of CoM starts decelerating, reverses its movement direction in the middle of the phase and then starts accelerating in the opposite direction. The lateral dynamics of the CoM are consistent with the inverted pendulum mechanism controlled by shifting the pivot of rotation (CoP) of the pendulum between the left and right borders of support.

Paw-pad cutaneous feedback in the control of lateral balance during split-belt locomotion

The results of this study are consistent with previous reports on denervation or anesthesia of the paws in cats during locomotion. Although cats with removed cutaneous feedback from the paws can recover basic movement patterns during undemanding locomotion on a flat surface, there are substantial locomotor deficits in more challenging tasks, such as ladder or slope walking (Bouyer and Rossignol, 2003), and in response to lateral shifts of the support surface (Bolton and Misiaszek, 2009). We also observed small or no changes in balance control parameters (i.e. hindlimb step width, CoM bias, margins of static and dynamic stability) after anesthesia of the right paws during tied-belt locomotion (speed ratio 1.0). However, when the speed of the two belts became asymmetric with

split-belt locomotion, these parameters changed to increase balance stability. For example, at all asymmetric speeds, hindlimb step width increased (Fig. 4B), thus increasing the margin of static stability (Fig. 7B) and left dynamic stability at speed ratio 0.5 (Fig. 9A).

Interpreting changes in limb support phase duration in response to anesthesia of the right paws is less straightforward. First, it should be noted that the relative duration of the 3-limb support (47–70% of the cycle time) was the longest among all other support phases (Fig. 5B) with the ipsilateral 2-limb support duration being the second longest (up to 20–25%; Fig. 6C,D). Thus, the mean margin of static stability determined over the entire cycle (Fig. 7B) reflects mostly static stability during the 3-limb support, in which the CoM projection is within the area of support, as shown in our previous studies (Farrell et al., 2014, 2015). According to those studies, the margin of static stability during the 3-limb support of overground walking with speeds of 0.5–0.6 m s⁻¹ was 1–2 cm, whereas the static stability during the ipsilateral 2-limb support was between 0 and –0.5 cm (i.e. the CoM was slightly outside the base of support; see also Figs 3 and 8A, speed ratio 1.0). Thus, the mean margin of static stability over the cycle (~2.2 cm at speed ratio 1.0; Fig. 7B) is consistent with the margin of static stability during the 3-limb support phase of overground locomotion (1–2 cm; Farrell et al., 2014; 2015), especially considering that the step width during split-belt locomotion may be larger because of the gap between the belts (Fig. 1A). Second, large margins of static stability during locomotion in animals with four or more limbs may still be advantageous for balance control even though these animals may be statically stable throughout most of the locomotion cycle. For example, the static stability margin of the six-legged fruit fly appears to explain transitions from the tetrapod to tripod gait with increasing locomotion speed (Szczecinski et al., 2018).

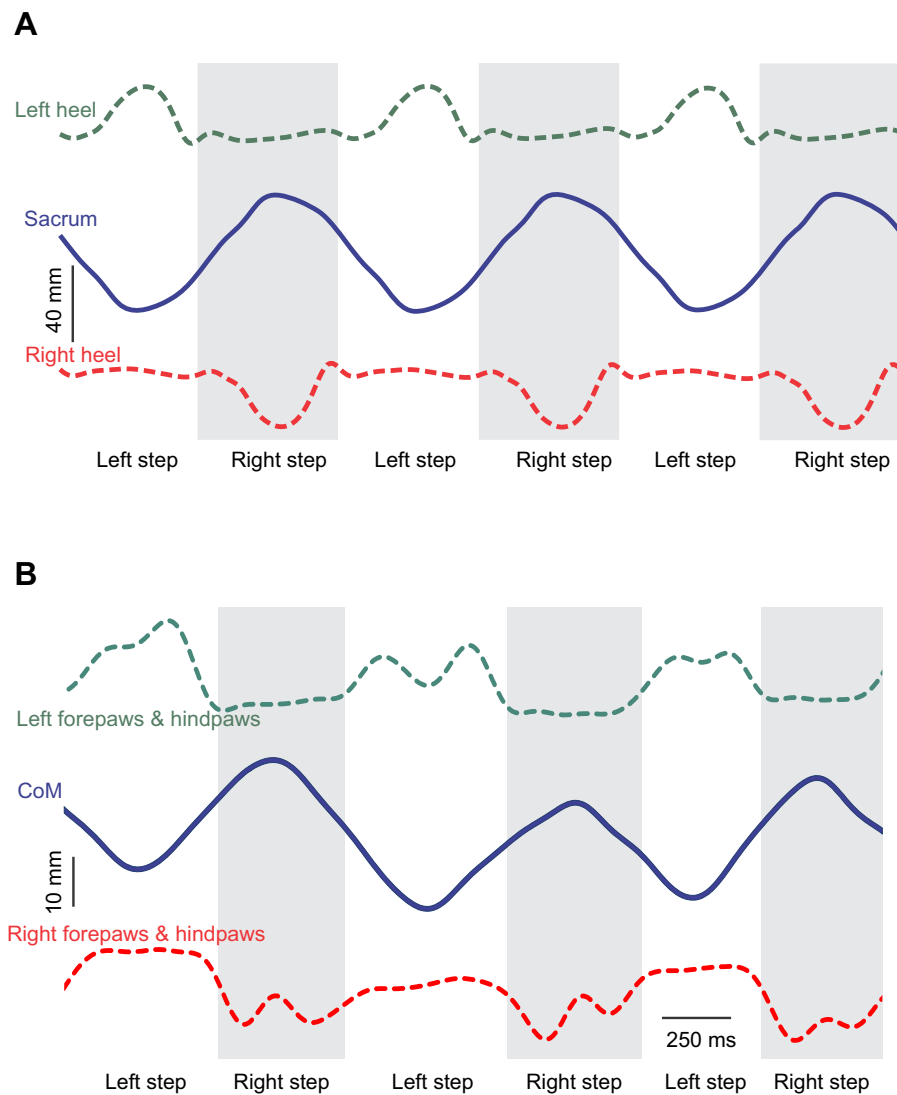


Fig. 10. Lateral displacement of the CoM with respect to the left and right feet during human and cat walking. (A) Average lateral displacement of the sacrum, and left and right heels as a function of time during level walking of human subjects (modified from fig. 4 of Roden-Reynolds et al., 2015, with permission). (B) Lateral displacement of the cat CoM, and left and right paws as a function of time during walking in the intact condition with speed ratio 1.0. Cat MO. Lateral displacement of the ipsilateral paws was computed as the mean of the ipsilateral forepaw and hindpaw positions (see Fig. 3, speed ratio 1.0).

Shortening the duration of the diagonal 2-limb support phases at speed ratios 1.0 to 2.0 after anesthesia (Fig. 6A,B) improves balance stability because, during this phase, the dynamic stability in the frontal and sagittal planes is reduced (Farrell et al., 2014). The shortening of the diagonal 2-limb support phase leads to a gait approaching pacing (more synchronous movements of the ipsilateral limbs; Hildebrand, 1989) and to the occurrence or increase in the duration of 4-limb support (compare limb support periods at speed ratios 1.0–2.0 in Figs 5C and 6A). Similar changes in the limb support phases during locomotion on a treadmill compared with overground locomotion (Błaszczuk and Loeb, 1993) are thus related to improved balance stability in the forward and lateral directions.

As discussed above, the loss of cutaneous sensation unilaterally increased the time the four limbs contacted the surface at speed ratios 1.0–2.0 to maximize balance stability (Fig. 7B), but not at ratio 0.5 (Fig. 5C). At speed ratio 0.5, the 4-limb support duration did not change while the 3-limb support became longer with removal of cutaneous sensation of the right paws (Fig. 5B,C). This result could be related to the fact that at this speed ratio the anesthetized paws were stepping on the slower belt and that this condition required greater loading of the anesthetized right limbs to manage the rightward shift of the CoM (Fig. 7A), which could not be achieved in the 4-limb support (see below).

Indeed, cats tended to shift their CoM, and thus body weight, onto the anesthetized paws (Fig. 7A). This finding resembles reports on grip force when holding an object between the fingers and thumb in human subjects – when tactile sensation of the fingers and thumb was reduced by anesthesia, the subjects increased grip force (Monzee et al., 2003; Westling and Johansson, 1984). Increasing pressure on the anesthetized fingers and thumb by humans and on the paws by cats may improve tactile sensation to accomplish the task.

The lateral shift of the CoM toward the anesthetized paws at asymmetric speeds was opposite to or coincided with the CoM shift in the control condition at speed ratios 1.5 and 2.0 or 0.5, respectively (Fig. 7A). The reason for the CoM shift toward the slower moving belt in the control condition is not clear. It could be related to the fact that energy expenditure for locomotion increases with locomotion speed (Taylor et al., 1982) and thus the CoM shift toward the slower belt could reduce energy expenditure. In contrast, the body shift toward the slower belt reduces margins of static (Fig. 7B) and lateral dynamic stability on that side (Fig. 9).

Curiously, the unilateral removal of paw sensation affected the margins of dynamic stability only at speed ratio 0.5 and the margin changes were opposite for the left and right sides (Fig. 9). These results appear consistent with the patterns of the CoM shifts due to the speed ratio and paw-pad anesthesia (Fig. 7A). The CoM shifted

to the slower moving belt with normal paw sensation and toward the anesthetized side at all speed ratios except 1.0. Thus, at speed ratios 1.5 and 2.0, the speed ratio-dependent shift of the CoM to the left, slow-moving belt is compensated by the anesthesia-related CoM shift to the right side, which may partially explain the lack of a significant effect of anesthesia on dynamic stability at these speed ratios. There was no CoM shift due to the speed ratio or anesthesia at speed ratio 1.0; this might partially explain the absence of change in dynamic stability with anesthesia at that speed ratio. At speed ratio 0.5, the speed ratio-related CoM shift to the slower, right belt coincided in direction with the anesthesia-related CoM shift toward the anesthetized right side; these changes appear to increase the left margins of dynamic stability and decrease the right margins (Fig. 9).

The same speed difference between the slow and fast belts but the opposite slow-moving belt at speed ratios 0.5 and 2.0 could also explain the V- or inverse V-shaped relationships between the speed ratio and the step width (Fig. 4), the limb phase durations (Figs 5 and 6) and the static stability margin (Fig. 7B).

One limitation of the study was that we could not distinguish directly the effects of locomotion speed and the speed ratio on the measures of stability because we did not obtain those measures in tied-belt conditions at all tested speeds. However, this limitation should not affect our conclusions about the role of paw sensations in balance control because we compared the effects of paw-pad anesthesia at the same speed ratios. Nonetheless, we could speculate based on the data from this and other studies that it is likely that the speed ratio and not locomotion speed is responsible for the observed locomotion changes. First, during tied-belt locomotion with intact paw sensation, the left and right margins of stability and the CoM shift are expected to be symmetric (Figs 3, 7 and 8; speed ratio 1.0). Second, the EMG magnitude of extensor muscles is higher on the side of the slower moving belt and the EMG difference between the slow and fast sides increases with the difference in belt speed (Frigon et al., 2015), suggesting a COM shift toward the slower belt. Third, at speed ratios 0.5 and 2.0, which correspond to the same speed of the slow and fast belts (i.e. 0.4 and 0.8 m s⁻¹), the CoM shifts toward the slower belt in both cases (Fig. 7A).

Conclusions

The CoM lateral displacement with respect to the CoP position during locomotion in the cat closely resembled that of the inverted pendulum and of human walking. This suggests that the locomotor CoM dynamics in the frontal plane is similar between cats and humans. Thus, the cat may be an appropriate model system to investigate certain aspects of lateral balance control in humans. We also found that during split-belt locomotion, cats shift the CoM toward the slower moving belt, which reduces balance and stability margins on that side. Removal of cutaneous sensations from the paws unilaterally shifts the CoM toward the anesthetized limbs and improves balance by increasing the step width, the relative duration of the 4-limb support phase, the margin of static stability and the margin of dynamic stability on the contralateral side when it moves faster.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: H.P., Y.I.M., S.P.D., B.I.P.; Methodology: H.P., A.N.K., B.I.P.; Software: H.P., B.I.P.; Validation: B.I.P.; Formal analysis: H.P., A.N.K., B.I.P.; Investigation: H.P., E.M.L., Y.I.M., A.N.K., A.F., S.P.D., B.I.P.; Resources: S.P.D.,

B.I.P.; Data curation: H.P., E.M.L., A.N.K.; Writing - original draft: H.P., B.I.P.; Writing - review & editing: H.P., E.M.L., Y.I.M., A.N.K., A.F., S.P.D., B.I.P.; Visualization: H.P., B.I.P.; Supervision: S.P.D., B.I.P.; Project administration: B.I.P.; Funding acquisition: B.I.P.

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