Sagittal spine movements of small therian mammals during asymmetrical gaits

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Summary

Mammalian locomotion is characterized by the use of asymmetrical gaits associated with extensive flexions and extensions of the body axis. Although the impact of sagittal spine movements on locomotion is well known, little information is available on the kinematics of spinal motion. Intervertebral joint movements were studied in two metatherian and three eutherian species during the gallop and halfbound using high-speed cineradiography. Fast-Fourier transformation was used to filter out high frequency digitizing errors and keep the lower frequency sinusoid oscillations that characterize the intervertebral angular movements. Independent of their regional classification as thoracic or lumbar vertebrae, 7±1 presacral intervertebral joints were involved in sagittal bending movements. In only one species, no more than five intervertebral joints contributed to the resulting 'pelvic movement'. In general, the trunk region involved in sagittal bending during locomotion did not correspond to the traditional subdivisions of the vertebral column (e.g. as thoracic and lumbar or pre- and postdiaphragmatic region). Therefore, these classifications do not predict the regions involved in spinal oscillations during locomotion. Independent of the gait, maximum flexion of the spine was observed in the interval between the last third of the swing phase and touch-down. This results in a retraction of the pelvis and hindlimbs before touch-down and, we hypothesize, enhances the stability of the system. Maximum extension occurred during the first third of the swing phase (i.e. after lift-off) in all species. In general, the observed timing of dorsoventral oscillations of the spine are in accordance with that observed in other mammals and with activity data of respiratory and epaxial back muscles. Although no strict craniocaudal pattern was observable, the more cranial intervertebral joints tend to flex and extend earlier than the more caudal ones. This is in accordance with the organization and the activation of the paravertebral musculature in mammals. The amplitude of intervertebral joint movements increased caudally, reaching its highest values in the presacral joint. The more intense sagittal bending movements in the caudal intervertebral joints are reflected by the muscle fiber type composition of the back muscles involved. Despite the highly similar amplitude of 'pelvic motion', touch-down and lift-off positions of the pelvis were clearly different between the species with a long, external tail and those with no external tail.

Key words: intervertebral joints, locomotion, vertebral column, kinematic, X-ray, spinal flexion.

Introduction

The evolution of mammalian locomotion is characterized by the regular use of asymmetrical gaits (i.e. gallop, half-bound and bound) connected to extensive dorsoventral flexions of the body axis (Howell, 1944; Hildebrand, 1959; Gambaryan, 1974; Hildebrand, 1974). Mammals are the only tetrapods that show asymmetrical gaits regularly [beside young galloping crocodiles (Zug, 1974; Webb and Gans, 1982)].

According to Alexander et al., the gallop is suggested to be the most efficient mode of locomotion (Alexander et al., 1985). Sagittal spine movements are used to increase hindlimb retraction velocity but also step length, and thereby animal's speed *via* the integration of a long aerial phase and extended stance and swing phases (Howell, 1944; Hildebrand, 1959). In small therian mammals, about half of the stance length is contributed by sagittal bending movements (Fischer, 1994; Fischer and Lehmann, 1998; Schilling and Fischer, 1999; Fischer et al., 2002). Nearly half of the metabolic costs can be saved by the storage of elastic energy in the large thoracolumbar aponeurosis as well as in the paravertebral musculature itself (Cavagna et al., 1977; Taylor, 1978; Alexander et al., 1985; Alexander, 1988; Koob and Long, 2000; Fischer and Witte, 2004; Hackert, 2002). Additionally, metabolic costs can be reduced by the use of natural resonance frequencies during fast locomotion ('preferred traveling speed') (Koob and Long, 2000). Furthermore, sagittal oscillations of the body axis drive

lung ventilation in mammals during locomotion ('visceral piston model') (Bramble and Carrier, 1983; Bramble, 1989; Bramble, 1999).

The synchronous motion and the touching down of both hindlimbs at the same spot were suggested as characteristics that stabilize the locomotion of asymmetrical gaits (Howell, 1944; Goslow et al., 1973; Hildebrand, 1974; English, 1980). Furthermore, trunk movements that induce cyclic horizontal displacements of the centre of body mass (CoM) and the strength of the back movements can be interpreted as ways to adjust the optimal angle of attack of forelimbs ['CoM-shifting hypothesis' (Hackert, 2002; Hackert et al., 2006)] and thus using self stabilizing mechanisms [i.e. mechanical stability of a system without the need of sensory feedback (Wagner and Blickhan, 1999; Blickhan et al., 2003)]. Flexions of the spine are thought to decrease vertical excursions of the CoM and consequently reduce the need of compensatory limb movements (Hackert, 2002).

Despite the well-known impact of trunk movements on mammalian locomotion, only limited information is available for the kinematics of spinal movements. It is generally accepted that all spine movements are the result of small intervertebral movements that add up to what is called 'pelvic motion'. Owing to the rigid connection of the pelvis to the vertebral column, movements in the iliosacral joint are restricted. No movements were observed in this joint during locomotion in a number of small mammalian species including the species studied herein. Therefore, we can conclude that movements in the iliosacral joint have no influence on locomotion and do not contribute to pelvic displacements in the species under study (Kühnapfel, 1996; Fischer and Lehmann, 1998; Schilling and Fischer, 1999; Fischer et al., 2002). In symmetrical gaits (e.g. walk and trot), back movements are composed of lateral movements in the horizontal plane and rotational motions around the craniocaudal body axis [lateral bending and tilting, respectively (Jenkins, Jr and Camazine, 1977)]. In asymmetrical gaits, spine motion is restricted to dorsoventral flexion and extension movements in the sagittal plane.

Much information is available for back movements of walking or trotting mammals [e.g. horses (Audigie et al., 1999; Faber et al., 2001; Haussler et al., 2001; Licka et al., 2001; Robert et al., 2001); dogs (Tokuriki, 1973a; Tokuriki, 1973b; Tokuriki, 1974; Jenkins, Jr and Camazine, 1977; Ritter et al., 2001); foxes (Jenkins, Jr and Camazine, 1977); cats (Jenkins and Camazine, 1977; Carlson et al., 1979; English, 1980); raccoons (Jenkins, Jr and Camazine, 1977); skunks (van der Graaff et al., 1982); ferrets (Kafkafi and Golani, 1998); tree shrews (Jenkins, Jr, 1974; Schilling and Fischer, 1999); primates (Shapiro et al., 2001); and grey short-tailed opossums (Pridmore, 1992)]; however, little information is available for asymmetrical gaits. Most studies investigated either 'pelvic motion' (Hildebrand, 1959; Jenkins, Jr and Camazine, 1977; Fischer et al., 2002) or X-rays of manipulated cadavers to comprehend the observed 'pelvic movement' (Alexander et al., 1985; Fischer, 1994; Carlson, 1978). Some more detailed data were published only for the pika (Fischer and Lehmann, 1998).

The first study analyzing intervertebral joint movements in symmetrical and asymmetrical gaits was published for the tree shrew (Schilling and Fischer, 1999). This study exposed the restricted bending region between the eleventh thoracic and the first lumbar vertebrae, reported by Jenkins, Jr (Jenkins, Jr, 1974), as valid only during exploratory walking.

Often external skin markers or the body contours were used to evaluate spinal movements. But as intervertebral movements are hidden by movements of fur, skin and subcutaneous tissues, external marker studies are tainted with unavoidable errors. However, 3–8 skin markers along the body were used to represent vertebral column movements and analyze spinal motions in the studies named above. Especially in small to medium sized mammals, cineradiography is the only tool available to measure intervertebral movements at each segmental level (Schilling and Fischer, 1999). Only Jenkins, Jr (Jenkins, Jr, 1974), van der Graaff et al. (van der Graaff et al., 1982), Pridmore (Pridmore, 1992), Fischer and Lehmann (Fischer and Lehmann, 1998), Faber et al. (Faber et al., 2001) and Haussler et al. (Haussler et al., 2001) used either X-ray or highly invasive bone-fixed markers and were therefore able to resolve questions concerning segmental motions.

During the evolution of tetrapods, the non-regionalized vertebral column was subdivided into two anatomically and functionally different regions – thoracic and lumbar (Gadow, 1933). Sagittal spine movements are thought to be restricted to the lumbar part only, whereas the thoracic region, as a part of the rib cage, is thought to be rigid to secure respiration during locomotion and counteract loading forces transmitted to the chest wall from limbs.

In order to determine how the vertebral column is involved in sagittal spine movements, intervertebral joint movements were studied in small mammals during asymmetrical gaits using cineradiography. Adults of five distantly related therian species with different body forms (two 'tailless' and three with long tails) were investigated during treadmill locomotion. The aims of the study were (1) to determine the region of the vertebral column involved in sagittal bending, (2) to determine the amplitudes and timing of intervertebral movements, 3) to determine the contribution of different intervertebral joint movements to the resulting 'pelvic motion', and (4) to compare the pelvic displacement between tailed and 'tailless' species to examine the influence of the tail on spinal kinematics. Although kinematic data of 'pelvic movements' were published earlier (Fischer et al., 2002), new data were collected for all species in order to combine the intervertebral joint movements with the resulting 'pelvic movements'.

Materials and methods
Animals

Adults of two metatherian species [*Dasyuroides byrnei* (Spencer 1896), the kowari and *Monodelphis domestica* (Wagner 1842), the grey short-tailed opossum] and three eutherian species [Rodentia: *Galea musteloides* (Meyen 1833), the cui; Scandentia: *Tupaia glis* (Diard 1820), the tree shrew;

Lagomorpha: *Ochotona rufescens* (Gray 1842), the pika] were studied. The tree shrew, the kowari and the grey short-tailed opossum were selected because of their long, external tails. The cui and the pika are called 'tailless' in this study because their short tails do not reach beyond the body's contour. Limb kinematics of all species during different gaits was analyzed in more detail in earlier studies (Kühnapfel, 1996; Fischer and Lehmann, 1998; Schilling and Fischer, 1999; Fischer et al., 2002; Schilling, 2005b). Out of the same data pool, film sequences were selected for the current study (see below). Because no differences in the kinematic parameters were observed among the individuals of the same species in the studies cited above, data were collected only for one individual per species for the current study (tree shrew: 0,1; 151 g; kowari: 1,0; 145 g; grey short-tailed opossum: 1,0; 92 g; cui: 1,0; 207 g; pika: 1,0; 250 g). The pelvic displacements, i.e. the outcome of all additive intervertebral movements, observed in the current study matched particularly well with previously reported results. Because of the consistency of these results, we feel confident that the data presented here are representative for the species although only one individual per species has been studied. Although trunk movements have been analyzed in the tree shrew in an earlier study (Schilling and Fischer, 1999), new data were collected to guarantee the same procedure of analysis for all species.

Data collection

Animals were trained, using positive reinforcement techniques, to run on a horizontal motor-driven treadmill within a Perspex enclosure (length: 100 cm, height and width were adapted to each individual's size). Tread speed was not fixed, but held at a constant level during X-ray shots. No effort was made to film either increasing or decreasing velocity of the animals, moreover, the goal was to film the animals during steady state locomotion. Therefore, the animals ran at their preferred traveling speed, i.e. the speed at which they were able to perform for a longer period of time. Because animals prefer certain speeds to make use of natural resonance frequencies (Koob and Long, 2000), we assume that this preferred speed can be compared between the species. Intervertebral movements were recorded by high-speed cinevideography (150 frames s^{-1}) taken at the IWF Knowledge and Media gGmbH at Göttingen, Germany (Fig. 1). The X-ray system consisted of an automatic X-ray source image amplifier chain (Phillips 9807 501 800 01, Germany). Pulsed X-ray shots (57–82 kV, 200 mA) were applied. Images from running animals in lateral perspective were recorded from the image amplifier (205 mm×150 mm) using the high-speed video system Camsys® (Mikromak Service K. Brinkmann, Berlin, Germany). All experiments were approved by the Committee for Animal Protection of the State of Thuringia, Germany.

Data analysis

The analogue videotapes were converted with a video processing board ('Screen machine I', FAST Multimedia AG, Munich, Germany). The sequences analyzed were selected from our working group's data pool using the following criteria. Only trials with continuous motion and at least five successive strides were used. All landmarks had to be visible at all times. Because the trunk length of the species investigated (up to 200 mm) was almost the same as the size of the image amplifier and the X-ray equipment was fixed and could not
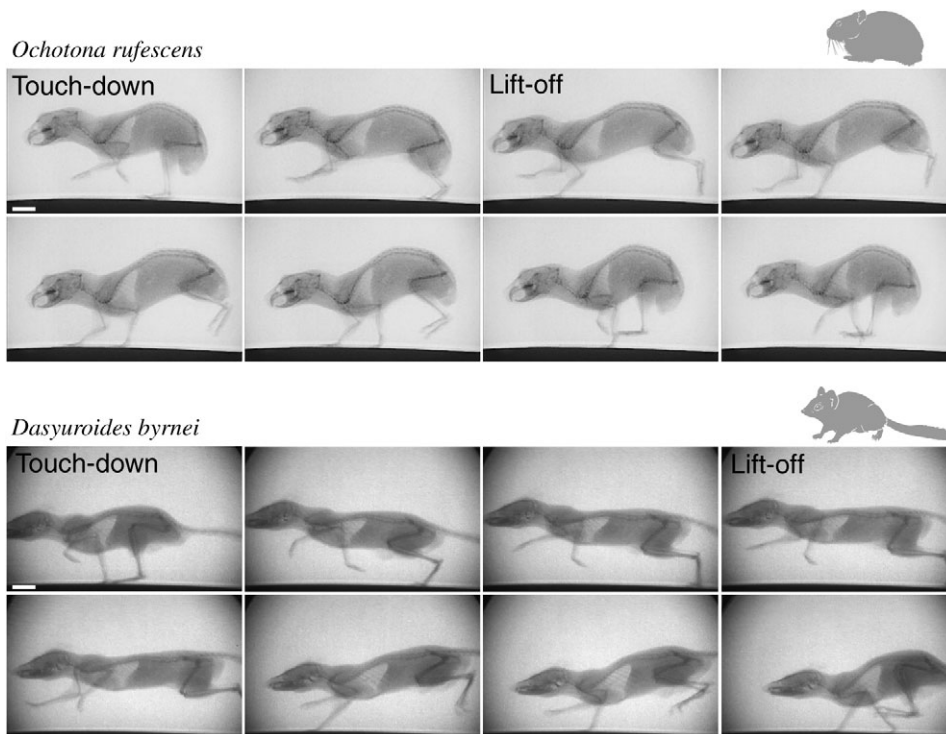

Fig. 1. X-ray sequences of the 'tailless' pika *Ochotona rufescens* during gallop (1.16 m s^{-1}) and the long-tailed kowari *Dasyuroides byrnei* during half-bound (0.92 m s^{-1}). Scale bars, 20 mm.

follow the animal's motion along the treadmill, the number of usable sequences was dramatically reduced. Finally, all strides analyzed were taken from the same film sequence and were further processed as one-motion sequences (e.g. mean curves, filtering, etc.) but presented separately according to their classification as gallop or halfbound (e.g. in the kowari and the grey short-tailed opossum).

Skeletal landmarks were manually captured at each intervertebral joint along the trunk and their *x*- and *y*-coordinates were used to define vectors for calculations of the kinematic parameters. The locations of the captured skeletal landmarks and the calculated angles of the intervertebral joints are illustrated in Fig. 2. Additionally, the position of the pelvis was determined using two landmarks on the pelvis (middle of the crista iliaca and tuber ischiadicum; Fig. 2). The pelvic angle was calculated cranially against the horizontal plane. Optical distortion due to parallax and aspect ratio were automatically corrected during frame-by-frame analysis. An orthogonal wire grid perpendicular to the projection plane of the animals provided measurement points for this correction.
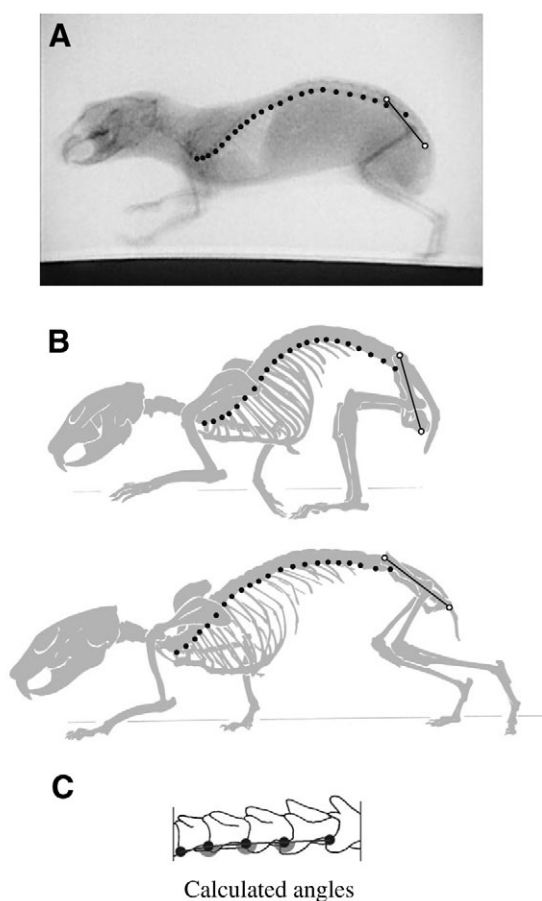

Fig. 2. Digitized skeletal landmarks in the pika *Ochotona rufescens*. (A) X-ray during stance phase. (B) Skeletal drawings at the beginning and end of stance phase [modified from (Fischer and Lehmann, 1998)]. Pelvic landmarks are indicated by open circles. (C) Calculated angles for the intervertebral joints in the tree shrew, *Tupaia glis* [modified from (Schilling and Fischer, 1999)].

The accuracy of capturing the skeletal landmarks was affected by both the contrast of bones and the distances between neighbored landmarks. The shorter the distances the noisier the resulting data were. As a result, the captured coordinates were tainted by a given amount of noise due to digitizing and this propagated up to angular values. We used the Fast-Fourier transformation (FFT) to filter out high-frequency digitizing errors from the lower frequency sinusoid oscillations characterizing the intervertebral angular movements. In the signal time series, digitizing errors were represented by deviations from the 'expected', real value that occurred over three consecutive frames, i.e. over a time interval of two or three sampling periods, rarely more. Digitizing errors were then included in the high frequency terms of the Fourier spectrum of the signal. At the sampling frequency of 150 Hz, errors were included in the terms corresponding to 75 Hz and 50 Hz. For a typical running frequency of four steps per second, those frequencies corresponded to oscillations which were nine times faster than the basic oscillation of the signal. In order to prepare the data for the FFT, the data series with some 210 frames, representing five locomotor cycles, were interpolated by cubic splines to become series containing a number of elements equal to a power of two. A FFT was then applied to the series. The coefficients corresponding to 75 Hz and 50 Hz were set to zero. The low frequency of the signal (up to 37.5 Hz) was preserved and transformed back using inverse FFT. The digitizing error for the pelvic landmarks was tested by repetitive digitization (five times) of five frames for each species. It ranged from 1° to 2°.

Only data of the intervertebral joints involved in sagittal bending indicated by frequencies similar to that of 'pelvic movements' were further processed. Mean touch-down and lift-off angles, effective angular movements, maximum and minimum angles during stance and swing phases, and maximum angular movements of intervertebral joint angles as well as of 'pelvic movements' were determined for trailing and leading limbs, separately, or for both hindlimbs (halfbound) and compared among the species (for definitions see Table 1). In the example of the galloping pika and the grey short-tailed opossum, mean curves of the intervertebral movements of five or six typical gait sequences were calculated in order to show the characteristics of intervertebral movements (see Fig. 4). For this, stance and swing phases were normalized to the same period using the method of linear interpolation.

Results

Anatomy

The vertebral columns of the species investigated are composed of seven cervical, 19–21 trunk, and two to four sacral vertebrae (Table 2). The species are clearly different in their numbers of caudal vertebrae. The cui and the pika have very short tails of seven and 10 caudal vertebrae, respectively. Their tails do not reach beyond the body's contour (called 'tailless'). The kowari and the grey short-tailed opossum possess 18 caudal vertebrae and, with 24 vertebrae, the tree shrew has the

Table 1. *Definitions of kinematic parameters*

Parameter	Definition
Touch-down	Hard contact of foot at the beginning of stance
Lift-off	Last moment of ground contact at the end of stance
Stride (step cycle)	From the instance of one touch-down to the next touch-down of the same foot, including one stance and one swing phase
Gallop	Both hindlimbs were clearly separable at their touch-down events
Trailing limb (T)	Hindlimb first touching the ground at the gallop
Leading limb (L)	Hindlimb second touching the ground at the gallop
Halfbound (S)	Both hindlimbs touched the ground synchronously
Effective angular movement (°)	Absolute value of the difference between touch-down and lift-off angles
Maximum angular movement (°)	Difference between maximum and minimum angles for stance and swing phase, respectively (amplitude)

Table 2. *Composition of vertebral columns of all species under study*

Species	Vertebrae							
	Cervical	Thoracic	Lumbar	Sacral	Caudal	Free ribs	Diaphragmatic	Anticline
Monodelphis domestica (gray short-tailed opossum)	7	14	6	2	18	6	T10/11	T12
Dasyuroides byrnei (kowari)	7	12	7	2	18	4	T10	T9/10
Tupaia glis (tree-shrew)	7	13	6	3	24	4	T10	T10
Galea musteloides (cui)	7	13	7	4	7	5	T13	T13
Ochotona rufescens (pika)	7	17	4	2	10	6	T11	T12

Free ribs: number of the posterior ribs that do not directly articulate with the sternum. Diaphragmatic vertebrae: vertebrae where the facet orientation changes. Anticline vertebrae: vertebrae where the orientation of the spinous processus changes.

longest tail. The pika has a relatively long thoracic region (17 vertebrae), but the shortest lumbar region (four vertebrae; defined by the occurrence or absence of ribs, respectively). The cui and the kowari are characterized by the longest lumbar regions, with seven lumbar vertebrae. Independent of the number of thoracic or lumbar vertebrae, the last 4–6 posterior ribs do not connect directly to the sternum.

In the kowari and the tree shrew, the tenth trunk vertebra is the so-called 'diaphragmatic' vertebra. At this vertebra, the orientation of the zygapophyseal facets changes from a horizontal, 'tangential' to an upright, 'radiär' orientation (Virchow, 1907). The diaphragmatic vertebra is situated more caudally in the pika and the cui (eleventh and thirteenth thoracic vertebra, respectively). The grey short-tailed opossum exhibits a diaphragmatic region, i.e. the change of the facet orientation involves more than one vertebra (Pridmore, 1992) (this study). The orientation of the spinous processus changes at the anticline vertebra, which is the tenth in the tree shrew, the twelfth in the pika and the grey short-tailed opossum, and the thirteenth in the cui. In the kowari, the ninth and the tenth thoracic vertebrae are involved in the change of the inclination of the spinous processus (Table 2).

Gaits and 'pelvic movement'

Altogether, 23–25 skeletal landmarks were captured in 862 frames for the current study. Because left and right limbs cannot be identified in cineradiography, trials were only

categorized as either gallop or half-bound without further classification (e.g. as transverse or rotatory gallop). The pika, the tree shrew and the cui presented gallops defined by clearly distinguishable trailing and leading hindlimbs. Time between the touching-down of trailing and leading limbs ranged from one to three frames (6.7 ms to 20.0 ms) in the pika and one to four frames (6.7 ms to 26.7 ms) in the tree shrew and the cui. Both metatherian species, showed transitions from gallop to half-bound back and forth within the same film sequence. In the kowari, three strides were halfbounds defined by the synchronous touching down of the hindlimbs. In the other four strides, a time lag of one frame between the touch-down of trailing and leading limbs was observed but only three of these strides retained the lag until lift-off. In one stride, the lift-off of both hindlimbs was synchronous. In the grey short-tailed opossum, six strides were half-bound and four had a duration of 6.7 ms to 13.4 ms (1–2 frames) between the touch-downs of both hindlimbs but no time between their lift-offs (except for one stride with a time lag of 13.4 ms; Fig. 3). The mean speeds for the trials analyzed were: kowari, 0.92 ± 0.06 m s^{-1}; grey short-tailed opossum, 1.15 ± 0.19 m s^{-1}; tree shrew, 1.48 ± 0.15 m s^{-1}; pika, 1.18 ± 0.05 m s^{-1}; and the cui, 1.14 ± 0.12 m s^{-1}.

The pelvis performs cyclic craniocaudal movements (pro- and retractions, respectively). In the protraction, the pelvis moves towards its cranial position and in the retraction, the pelvis moves caudad. All 'pelvic movements' described below
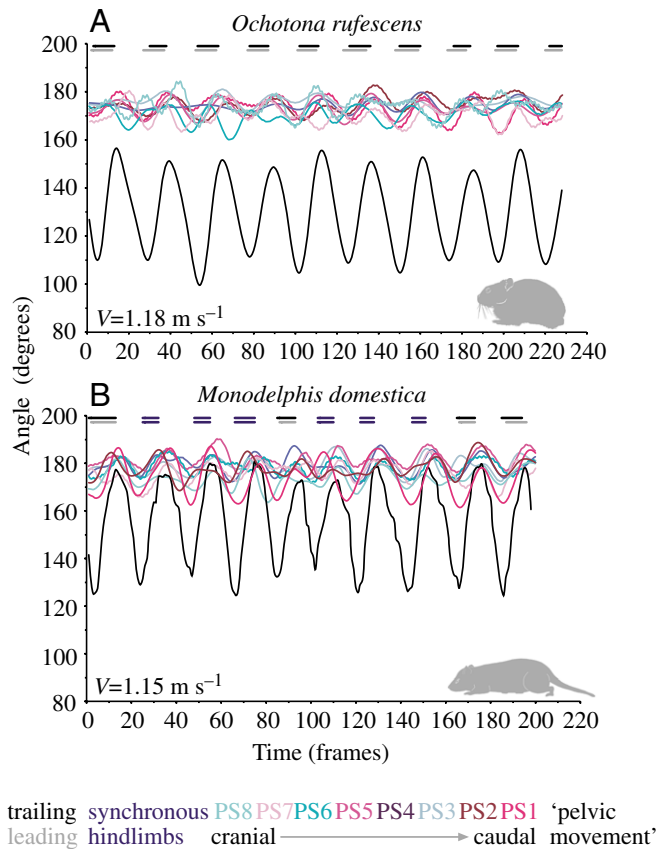
Fig. 3. Intervertebral movements of the 'tailless' pika *Ochotona rufescens* (A) and the 'long-tailed' gray short-tailed opossum *Monodelphis domestica* (B) after Fast-Fourier Transformation. The different presacral intervertebral joints (PS) are indicated by different colors. The footfall pattern of the hindlimbs is indicated by the ground contact duration (stance phase) on the top of each diagram. Note the different ranges of 'pelvic movement' of the species.

are the result of additive intervertebral movements. Former analyses of the angle resulting from digitized pelvic markers (the same as used in the recent study) and the caudal end of the sacrum showed the immobility of the iliosacral joint during locomotion for the species studied herein (Kühnapfel, 1996; Fischer and Lehmann, 1998; Schilling and Fischer, 1999; Fischer et al., 2002).

Independent of the body form (tailed or 'tailless'), effective angular movements of the pelvis during stance phase were of a comparable magnitude in all species (29° to 44°; Table 3). In the gallop, the effective 'pelvic movement' was larger in leading than in trailing limbs in all species but the cui. Effective angular movement of the pelvis in the halfbound was similar to that of the leading limbs in the gallop within the same species (kowari, gray short-tailed opossum).

In general, maximum cranial displacement of the pelvis (protraction, minimum of stride) was reached within the last quarter of swing phase (i.e. before touch-down of the trailing limb in the gallop or before touch-down of both hindlimbs in the halfbound) (Fig. 3). Thus, the pelvis was already in retraction at touch-down. Maximum caudal displacement (retraction, maximum of stride) was usually observed between lift-off of the leading hindlimb (gallop) or of both hindlimbs (halfbound) and during the first quarter of swing phase. Thus, neither maximum cranial nor caudal displacements of the 'pelvic movements' were strictly coupled with touch-down or lift-off events and both maximum pro- and retraction were observed during the swing phase. Mean amplitude of 'pelvic movement' during swing phase was comparable between all species (40° to 51°; Table 3) and independent of the existence or absence of a long, external tail.

During stance phase, maximum cranial displacement of the pelvis occurred primarily at touch-down of the trailing limbs in the cui and at the touch-down of leading limbs in the kowari and the gray short-tailed opossum. Thus, the pelvis is briefly in protraction after touch-down of the trailing limbs in the two metatherians. A comparable protraction of the pelvis but after the touch-down of the leading limbs was observed in half of the strides of the pika (Fig. 4). In all other strides, minimum value during stance phase corresponded to the touch-down of the leading limbs. In the tree shrew, maximum protraction was observed either between the touch-down of trailing and leading limbs or at the touch-down of the leading limb. Consequently, maximum protraction during stance phase is not coupled with trailing or leading limbs. Furthermore, interspecific differences were observed. Subsequently, the pelvis was retracted continuously during stance phase in all species. Owing to the continuous retraction into the swing phase, maximum caudal displacement during stance phase corresponded to lift-off angles of trailing and leading limbs, respectively. In the halfbound, minimum and maximum values of 'pelvic movement' during stance phase corresponded mostly to touch-down and lift-off angles, and therefore amplitudes were approximately the same as the effective angular movements. In all gaits, the pelvis was consecutively retracted after lift-off until the maximum caudal displacement during the swing phase was reached. The following protraction of the pelvis ended by reaching the maximum cranial displacement shortly before touch-down.

Despite comparable ranges of effective 'pelvic movements' during stance phase and amplitudes during stance and swing phases, those ranges were covered by strikingly different pelvic positions. Mean touch-down angles were particularly low in the pika with a nearly vertical pelvic position (109° for leading limb; Table 3) and were higher in all other species (127° to 135°). At lift-off, the pelvis was almost horizontal in the gray short-tailed opossum, the tree shrew and the cui (168° to 176°), slightly more inclined in the kowari (160° to 164°), but most inclined in the pika (147° and 151° for trailing and leading limbs, respectively). Thus, the pelvis of the pika was oriented vertically at the beginning of stance phase and reached a more inclined position at the end of stance phase, whereas the other species started with a less protracted pelvis and ended by a nearly horizontal position at lift-off (Figs 1 and 3).
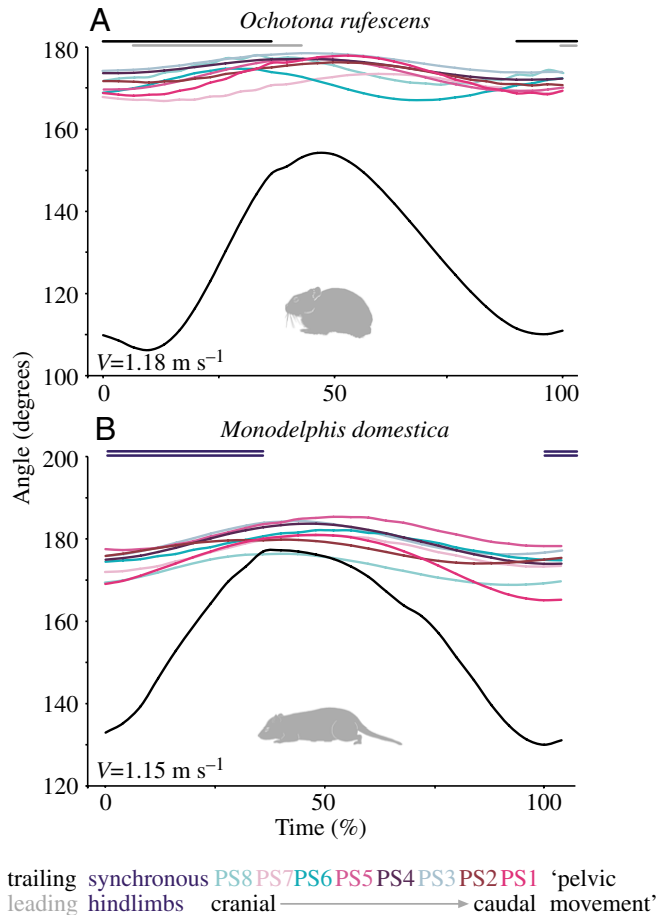
Fig. 4. Mean angular movements of intervertebral movements of the pika *Ochotona rufescens* in the gallop (A; *N*=5) and the gray short-tailed opossum *Monodelphis domestica* in the half-bound (B; *N*=6). The different presacral intervertebral joints (PS) are indicated by different colors. The footfall pattern of the hindlimbs is indicated by the ground contact duration (stance phase) on the top of each diagram.

Intervertebral movements

Independent of their regional classification as 'lumbar' or 'thoracic', six to eight presacral intervertebral joints were involved in the additive sagittal spine movements in all species but the cui (Table 3). Therefore, sagittal intervertebral joint movements were observed in the caudal thoracic and the lumbar parts of the pika (up to T14/15), the tree shrew (up to T11/12), and the gray short-tailed opossum (up to T13/14), and were restricted to the lumbar region in the kowari (up to L2/3) and the cui (up to L3/4). In general, effective angular movements of the intervertebral joints craniad from PS3 ranged between 1° to 9° in all species. Slightly higher values were often found in the second presacral joint (PS2). In the gallop, the highest effective angular movements occurred in the first presacral joint in all species (PS1: 7° to 22°). Among the species, the highest values were observed in the tree shrew and the kowari (17° to 22° for trailing and leading limbs) and the lowest values in the pika (7° and 8° for trailing and leading limbs, respectively).

The timing of intervertebral movements during galloping was highly similar among the species. In general, maximum spinal flexion was not connected to the touch-down events, furthermore, it was observed between the last third of swing phase and touch-down events. Therefore, extension of the vertebral column started in the late swing phase. More cranial parts of the vertebral column often extended earlier than more caudal ones (Figs 3 and 4), but no strict craniocaudal order between adjacent intervertebral joints was observed. However, toward the caudal end of the trunk, the described timing pattern was increasingly pronounced. At touch-down of trailing and leading limbs, all intervertebral joints were still essentially flexed in all species as indicated by intervertebral joint angles of less than 180° (Table 3, Fig. 4). Only in the cui, the first presacral intervertebral joint (PS1) was still slightly extended (181°–183°).

During stance phase, the vertebral column was extended continuously in all involved presacral intervertebral joints (Table 3). Maximum angular excursions of the first up to the sixth presacral joints were comparable to the effective angular movements, respectively, because maximum extension of this region is reached after lift-off. Therefore, maximum values of stance phase and lift-off angles often corresponded to each other. But, amplitudes of more cranial intervertebral joints (craniad from PS6) were higher than effective angular movements during stance phase due to craniocaudal progression of extension. At the moment of lift-off of trailing and leading hindlimbs, the more caudal intervertebral joints were often flexed dorsally as indicated by values above 180° (Table 3). After lift-off of leading limbs and within the first quarter of swing phase, the vertebral column was extended until maximum extension was reached. In some species, the back was clearly extended dorsally (lordosis; e.g. in the kowari, Fig. 1). Synchronously, ventral flexion started in the more cranial parts of the vertebral column. Caudal parts of the trunk were flexed in the second quarter of swing phase. In general, maximum angular excursions were higher during swing phase than during stance phase. Again, the highest values were observed in the first presacral joint in all species. The closer touch-down or lift-off events of both hindlimbs became, i.e. the more synchronously both hindlimbs moved (up to halfbound) the more stereotypic the described motion pattern became.

Discussion

Sagittal spine movements during locomotion

The use of asymmetrical gaits represents a major innovation in mammalian evolution. The most important diagnostic feature of these gaits is not the exact sequence of leg movements but the striking sagittal spine motion (Howell, 1944; Hildebrand, 1959; Gambaryan, 1974). A number of studies have shown that sagittal bending movements have a major impact on mammalian locomotion and that asymmetrical gaits are the most efficient mode of locomotion (Howell, 1944; Slijper, 1946; Hildebrand, 1959; Gambaryan, 1974;

Table 3. *Touch-down and lift-off angles, minimum and maximum values of the strides as well as maximum angular movements during stance and swing phases of all presacral joints involved in the sagittal spine movements and of the pelvis*

Species		N	Cranial PS8	PS7	PS6	PS5	PS4	PS3	PS2	PS1	Caudal pelvis
Touch-down											
Monodelphis	S	6	169±1	172±4	174±3	178±2	175±3	176±1	176±2	169±8	133±7
domestica	T	4	171±2	174±5	176±2	178±2	174±1	177±4	174±2	164±2	133±6
	L	4	171±2	175±4	175±1	178±2	175±1	179±4	174±2	164±2	131±3
Dasyuroides	S	3	–	–	173±0	177±2	180±1	180±2	172±1	160±1	131±3
byrnei	T	4	–	–	169±1	175±3	179±3	179±2	172±4	157±4	130±2
	L	4	–	–	170±1	175±3	181±2	179±2	173±4	158±4	131±2
Tupaia	T	5	175±2	171±3	166±1	175±1	176±1	177±1	174±2	174±3	132±3
glis	L	5	175±2	172±2	168±1	175±1	177±1	176±1	175±1	175±3	135±4
Galea	T	6	–	–	–	175±4	173±2	177±2	170±4	181±3	127±4
musteloides	L	6	–	–	–	176±2	173±3	176±3	174±4	183±4	133±8
Ochotona	T	9	172±4	169±3	170±3	169±2	173±2	174±2	171±3	169±4	111±5
rufescens	L	9	173±4	168±3	171±3	170±2	173±2	174±2	171±3	169±4	109±5
Lift–off											
Monodelphis	S	6	176±1	180±3	181±2	184±2	183±2	184±3	180±3	180±5	177±3
domestica	T	4	177±4	176±2	180±2	183±3	183±4	181±3	183±4	180±5	175±4
	L	4	177±4	176±2	181±1	183±4	183±4	181±2	183±4	180±5	176±4
Dasyuroides	S	3	–	–	179±3	178±1	188±1	184±1	182±3	172±2	164±3
byrnei	T	4	–	–	176±4	179±1	188±2	186±3	179±2	174±1	160±4
	L	4	–	–	176±5	178±1	188±2	187±4	180±2	175±2	163±6
Tupaia	T	5	179±2	172±3	172±2	178±3	181±1	181±1	181±1	194±5	172±3
glis	L	5	179±2	171±3	172±3	178±2	180±2	181±1	181±1	196±3	178±5
Galea	T	6	–	–	–	180±3	182±3	182±4	179±10	200±9	168±5
musteloides	L	6	–	–	–	179±3	182±4	182±4	178±10	202±8	171±2
Ochotona	T	9	176±3	172±3	174±3	177±1	176±2	178±2	176±3	176±2	147±4
rufescens	L	9	176±3	173±3	173±3	177±2	177±2	178±2	176±3	177±2	151±4
Effective angular movement stance											
Monodelphis	S	6	7±2	8±3	6±3	6±3	8±4	8±3	4±3	13±5	44±9
domestica	T	4	7±4	4±5	5±3	6±3	8±4	5±4	9±5	15±3	41±6
	L	4	6±5	3±1	6±2	6±4	8±3	4±2	9±5	16±4	44±6
Dasyuroides	S	3	–	–	6±2	2±1	7±2	4±3	9±4	12±2	32±3
byrnei	T	4	–	–	7±4	4±2	9±4	7±5	7±5	17±4	29±4
	L	4	–	–	5±4	4±2	7±4	7±5	7±5	18±5	32±7
Tupaia	T	5	4±3	4±2	6±1	3±2	5±1	4±1	7±2	20±5	40±5
glis	L	5	4±2	4±1	4±2	3±2	4±2	3±2	6±1	22±5	44±5
Galea	T	6	–	–	–	5±5	9±5	6±3	15±3	19±10	41±7
musteloides	L	6	–	–	–	4±2	9±6	7±4	11±6	19±11	38±8
Ochotona	T	9	6±4	5±4	5±3	7±3	4±3	4±3	4±2	7±3	36±5
rufescens	L	9	5±5	6±3	3±2	7±3	4±3	4±3	5±3	8±4	42±6

Table 3. Continued on next page.

Table 3. *Continued*

Species		N	Cranial PS8	PS7	PS6	PS5	PS4	PS3	PS2	PS1	Caudal pelvis
Maximum angular movement stance											
Monodelphis	S	6	8±3	8±2	7±2	7±3	8±4	8±3	5±4	13±5	44±9
domestica	T	4	8±4	7±5	6±2	6±3	8±4	6±4	10±5	16±4	47±7
	L	4	7±4	6±3	7±1	7±4	8±3	5±3	10±3	17±4	46±7
Dasyuroides	S	3	–	–	6±2	2±1	7±2	4±3	9±4	12±2	32±3
byrnei	T	4	–	–	7±4	4±2	9±4	7±4	7±5	17±4	30±4
	L	4	–	–	6±4	4±2	7±4	7±5	7±5	18±5	32±7
Tupaia	T	5	4±3	5±2	6±1	4±2	5±1	4±1	7±2	21±5	40±5
glis	L	5	5±2	5±1	4±2	3±2	4±1	3±1	6±1	22±5	44±5
Galea	T	6	–	–	–	7±5	10±4	8±4	16±5	20±10	41±7
musteloides	L	6	–	–	–	6±3	11±5	9±4	13±6	19±11	38±9
Ochotona	T	9	8±4	7±3	6±3	7±3	4±3	4±3	5±2	8±3	40±5
rufescens	L	9	7±5	7±3	5±3	7±3	4±3	4±3	6±3	9±3	43±6
Maximum angular movement swing											
Monodelphis	S	6	9±4	9±3	9±2	8±3	10±3	9±4	8±5	20±5	49±4
domestica	T	3	7±5	9±4	8±2	8±2	9±1	7±2	10±3	14±6	46±8
	L	3	7±5	9±4	9±1	9±2	10±2	7±2	10±3	14±6	47±9
Dasyuroides	S	2	–	–	13±1	8±3	10±4	8±3	11±1	25±4	50±1
byrnei	T	4	–	–	7±3	5±0	12±2	9±2	10±3	21±4	40±9
	L	4	–	–	7±3	5±0	12±2	9±2	10±3	21±4	40±9
Tupaia	T	4	6±3	5±2	7±2	5±2	6±2	4±0	8±1	25±4	50±3
glis	L	4	6±3	5±2	6±2	5±2	6±2	4±0	8±1	24±4	51±2
Galea	T	5	–	–	–	11±5	11±2	6±3	17±4	21±8	45±5
musteloides	L	5	–	–	–	10±6	9±2	7±4	16±5	21±8	45±5
Ochotona	T	9	10±5	10±3	8±3	8±3	5±3	5±3	7±3	10±3	43±4
rufescens	L	9	10±5	10±4	7±3	8±3	5±3	5±3	7±3	11±4	45±4
Minimum stride											
Monodelphis	S	6	167±2	171±2	173±1	176±2	173±1	175±1	173±2	163±1	127±2
domestica	T	3	170±1	169±6	173±2	176±1	174±0	174±1	173±1	164±2	128±4
	L	3	170±1	169±6	173±2	176±1	175±1	174±1	173±1	164±2	128±5
Dasyuroides	S	2	–	–	167±1	172±1	178±2	178±3	170±2	155±2	128±2
byrnei	T	4	–	–	169±1	173±1	176±2	178±2	170±2	154±2	128±2
	L	4	–	–	169±1	174±1	177±2	178±2	170±2	154±2	128±2
Tupaia	T	4	173±2	168±1	166±1	174±1	175±1	176±1	173±1	172±2	129±2
glis	L	4	173±2	168±1	166±1	174±1	175±1	176±1	173±1	172±2	129±2
Galea	T	5	–	–	–	169±3	171±1	174±1	164±4	179±1	123±4
musteloides	L	5	–	–	–	170±3	172±1	174±1	166±5	179±1	125±4
Ochotona	T	9	168±3	165±2	166±3	168±2	172±1	172±2	170±2	167±3	106±3
rufescens	L	9	168±3	165±2	166±3	168±2	172±1	172±2	169±2	167±4	105±4

Table 3. *Continued*

Species		N	Cranial PS8	PS7	PS6	PS5	PS4	PS3	PS2	PS1	Caudal pelvis
Maximum stride											
Monodelphis	S	6	178±3	182±2	183±1	186±3	184±3	184±3	182±3	184±3	178±3
domestica	T	3	178±4	179±2	182±1	185±2	185±2	182±2	185±3	182±4	177±4
	L	3	178±4	179±2	182±1	185±2	185±2	182±2	185±3	182±4	177±4
Dasyuroides	S	2	–	–	180±1	180±1	188±2	186±0	181±3	180±2	178±1
byrnei	T	4	–	–	177±4	180±0	189±2	189±3	181±2	178±3	169±8
	L	4	–	–	177±4	180±0	189±2	189±3	181±2	178±3	169±8
Tupaia	T	4	180±2	175±1	173±2	180±1	181±1	181±1	181±1	198±3	181±3
glis	L	4	180±2	175±1	173±2	180±1	181±1	181±1	181±1	198±3	181±3
Galea	T	5	–	–	–	182±3	183±2	183±4	184±2	203±9	171±2
musteloides	L	5	–	–	–	182±3	183±2	183±4	184±2	203±9	171±2
Ochotona	T	9	180±2	176±3	175±1	177±2	177±2	178±2	178±3	179±1	152±3
rufescens	L	9	180±2	176±3	175±1	177±2	177±2	178±2	178±3	179±1	152±3

Values (means ± s.d.) for trailing (T) and leading limbs (L) in the gallop and for hindlimbs in synchronous motion (S) in the halfbound are given separately.

N, number of strides analyzed.

PS, presacral joints.

The intervertebral joint between the last lumbar vertebra and the sacrum corresponds to PS1. Transitions of the thoracic to the lumbar vertebrae are marked by boxes. If no value is given (–), no oscillations were observed in these joints and all more craniad did not contribute to sagittal bending.

Hildebrand, 1974; Taylor, 1978; English, 1980; Pridmore, 1992; Alexander et al., 1985). According to Hildebrand, sagittal spine movements occur typically in fast carnivores, lagomorphs and rodents (Hildebrand, 1985). As this study shows, as well as previous investigations, sagittal bending is more widespread among eutherian and also metatherian mammals (Pridmore, 1992; Schilling and Fischer, 1999) (this study). This is clearly in contrast to Reilly and White (Reilly and White, 2003), who argued that some metatherians, including the gray short-tailed opossum studied herein, do not exhibit asymmetrical gaits because of their epipubic bones which are part of a kinetic linkage. This cross-couplet kinetic connection between the hindlimb and the abdominal body wall is presumed to restrict the animals to symmetrical gaits (Reilly and White, 2003). But the use of asymmetrical gaits in the gray short-tailed opossum has been reported earlier and its locomotor parameters have been analyzed quantitatively (Pridmore, 1992; Kühnapfel, 1996; Fischer et al., 2002).

However, the investigated marsupials showed both gallops and half-bounds in the recent study and they switched between these gaits within the same running trial back and forth several times. This phenomenon of changing gaits frequently has been observed earlier in a number of small- to medium-sized therian mammals in symmetrical and in asymmetrical gaits (Fischer and Lehmann, 1998; Schilling and Fischer, 1999; Fischer et al., 2002; Schilling, 2005b). That means that in the named studies the experimenters either always happened to end up at the animal's 'transition speed' (i.e. the speed at which they change gaits) or this is a characteristic inherent to smaller mammals. Since it was observed in many species and at different speeds it may be a feature of smaller therian mammals. This is supported by the observation that small mammals often use different gaits at the same velocities, which results in a large overlap between speed and used gaits (Kühnapfel, 1996; Fischer and Lehmann, 1998; Schilling and Fischer, 1999; Fischer et al., 2002). Being close to the 'transition speed' might actually be an advantage for the animal in order to make use of the gait that is to be preferred for the next strides. Because for a small animal the environment is highly irregular and structured in relation to its body size (Jenkins, Jr, 1974) adjustments in the locomotor parameters have to be made more frequently than in larger animals.

In the current study, the sagittal bending was investigated at preferred speed of the animal because animals prefer certain speeds to make use of natural resonance frequencies ['traveling speed' (Koob and Long, 2000)]. We assume that this preferred traveling speed can be compared between the species. Therefore, the analysis was performed on running sequences at whatever speed the animal chose; no effort was made to analyze either increasing or decreasing velocities or different speeds. Whereas larger mammals increase their speed by increasing step length (Heglund and Taylor, 1988), which results in a speed sensitivity of locomotor parameters such as kinematics and kinetics, small mammals accelerate by

increasing their step frequency. In particular, the species studied herein increased velocity at asymmetrical gaits by increasing their step frequency and prolonging their suspension period. Touch-down and lift-off positions of the limbs as well as stance length were independent of speed and therefore, the same kinematics can be expected at different velocities. Speed independency of limb kinematics has been shown for a tenfold range of speed in more than 300 strides for the pika (Fischer and Lehmann, 1998). In addition, speed independency of kinematic parameters was reported for the kowari and the gray short-tailed opossum (Kühnapfel, 1996), for the tree shrew (Schilling and Fischer, 1999), and for the guinea pig, a close relative of the cui (Rocha-Barbosa et al., 1996; Rocha-Barbosa et al., 2005). In particular, the detailed study on speed sensitivity of limb kinematics in the guinea pig showed that, although most joint angles were affected as speed increased, only a few angles were correlated to speed. In the hindlimb, only the flexion amplitude and the extension angular velocity of the knee joint was related to increasing speed (Rocha-Barbosa et al., 2005). Because of speed independency of limb kinematics including the pelvic motion (i.e. the outcome of all sagittal spine movements), we can expect the same trunk kinematics at different speeds for the species under study.

Timing of the sagittal spine movements

Hildebrand suggested that spinal flexions and extensions are coupled in their timing to the trailing limb (Hildebrand, 1959). This is in contrast to the results of the current study. In all species, maximum dorsal or ventral flexions were usually observed in the swing phase and they were not coupled with touch-down or lift-off events. Hildebrand's observation on the cheetah (Hildebrand, 1959) was drawn from a Walt Disney video (60 Hz). Therefore, the observed coupling of spinal motions to the trailing limb could be the result of the low temporal resolution. Our results confirm Gambaryan's observations (Gambaryan, 1974), who reported the maximal flexion of the spine before touch-down and the maximal extension shortly after lift-off of the hindlimbs. In the galloping cat, a marked flexion of the spine was observed during E1-phase of the step (=first extension phase of the knee-joint, i.e. second half of swing phase) and the following extension continued during E3 (i.e. second half of stance phase) and into the following F epoch (=flexion, i.e. first half of swing phase) (English, 1980). The timing in the galloping cat is therefore similar to the timing found in smaller mammals.

Although for none of the species investigated in the recent study airflow measurements exist, our observations of the timing of the vertebral column movements are in accordance with airflow measurements in galloping mammals. Surprisingly, these descriptions of the timing of the ventilatory cycle were based on the timing of forelimb's support, although it is well known that lung ventilation is driven by oscillations of inner organs and thus by those of the spine (e.g. Bramble, 1989; Bramble and Jenkins, Jr, 1993; Simons, 1999). However, expiration was generally observed during stance phase and inspiration during swing phase of the forelimbs in several

galloping mammals (Attenburrow, 1982; Bramble and Carrier, 1983; Bramble, 1989; Young et al., 1992; Simons, 1999). Inhalation began after lift-off of the leading forelimb (Bramble, 1989) and thus shortly before the touch-down of the hindlimbs. At the same time, maximum flexion of the spine was reached and the extension of the vertebral column started (Fig. 1). Exhalation onset was observed shortly after the impact of the trailing forelimbs [hard contact (Bramble, 1989)]. Synchronously, hindlimbs were at lift-off or within the first quarter of swing phase and the maximum extension of the spine was reached, i.e. flexion movements just started (Fig. 1). Thus, the timing of maximum flexion and extension of the back corresponds to that of the ventilator cycle in mammals and supports the 'visceral piston model' (Bramble and Carrier, 1983).

Spinal extensions started before touch-down, resulting in a retraction of both hindlimbs prior to ground contact. Retraction of fore- and hindlimbs prior to touch-down was shown by several studies to be a common feature of mammalian locomotion (Fischer, 1994; Fischer and Lehmann, 1998; Schilling and Fischer, 1999; Schmidt and Fischer, 2000; Fischer et al., 2002; Schmidt, 2005) and was observable in different gaits and even during the first postnatal steps (Schilling, 2005b). Using a conservative spring-mass model as well as a biomechanical model for fast, quadrupedal locomotion, studies have examined the effect of the limb's retraction in order to test its influence on running stability (Herr et al., 2002; Seyfarth et al., 2003). In all models, pre-stance leg retraction enhanced stability significantly. Therefore, the spinal extension prior ground contact of either trailing and leading limbs at the gallop or both hindlimbs at the halfbound can be interpreted as a feature that stabilizes the motion.

Sagittal bending and regionalization of the trunk

It is generally accepted that spinal movements are the result of small additive movements between adjacent intervertebral joints. Due to the less flexible thoracic (rib-bearing) region in comparison to the lumbar (ribless) region (Rockwell et al., 1938), dorsoventral flexions and extensions of the vertebral column are generally thought to be restricted to the lumbar region of the vertebral column (Slijper, 1946; English, 1980; Hildebrand, 1985; Fischer and Lehmann, 1998). The thoracic region is assumed not to be involved in sagittal spine movements in order to allow the respiratory function of the thorax. However, the current study showed that the caudal thoracic intervertebral joints were involved in sagittal bending movements in at least some species.

Independent of their regional classification as lumbar or thoracic, 7±1 presacral intervertebral joints contributed to sagittal spine movements in the therian mammals under study (except the cui). Whereas in the kowari and the cui, sagittal spine movements were restricted to the lumbar region (up to L2/3 and L3/4, respectively), the last caudal thoracic intervertebral joints were involved in sagittal bending movements in the gray short-tailed opossum (up to T13/14), the tree shrew (up to T11/12) and the pika (up to T14/15). Thus,

the number of intervertebral joints taking part in sagittal bending was not correlated with the transition of the thoracic to the lumbar region in the species under study. Furthermore, the comparison of the number of thoracic intervertebral joints to the number of free ribs occurring in the caudal thoracic region in the different species, does not point to a simple relationship between the morphology of the skeleton and the observed sagittal bending.

Although the trunk vertebrae of mammals are usually classified into thoracic and lumbar groups, they can also be divided according to their orientation of the zygapophyseal facets into pre- and postdiaphragmatic vertebrae. Additionally, the vertebral column has been divided according to the inclination and width of the spinous processus into a region anterior and a region posterior to the anticline vertebra (Virchow, 1907; Fick, 1911; Rockwell et al., 1938; Slijper, 1946; Gambaryan, 1974; Boszczyk et al., 2001). According to Slijper (Slijper, 1946), the diaphragmatic vertebra or the diaphragmatic region (i.e. when the change of the facet orientation involves more than one vertebra) is of major importance for the axes of motion along the vertebral column. In the anterior, prediaphragmatic region, the vertebrae possess more or less horizontally oriented zygapophyseal facets ['tangential' after (Virchow, 1907)], whereas in the postdiaphragmatic part, the facets are more upright and lie in an approximately parasagittal plane ['radiär' after (Virchow, 1907)]. Virchow referred to a 'Wechselwirbel' that points to the junction of fore- and hindlimbs' impact on the vertebral column (Virchow, 1907). However, several authors have pointed out that the horizontal orientation of the facets in the anterior trunk allows for lateral bending and tilting movements but restricts sagittal bending, whereas the parasagittal orientation of the facets in the postdiaphragmatic region permits sagittal bending but restricts lateral bending or tilting (Rockwell et al., 1938; Slijper, 1946; Washburn and Buettner-Janusch, 1952). According to Fick, the size of the zygapophyseal articular surface points to the amount of intervertebral joint movements (Fick, 1911).

If the zygapophyseal orientation influences the trunk bending, sagittal bending should only be observed in the postdiaphragmatic region. In all species, sagittal spine movements clearly occurred in the postdiaphragmatic region, but in none of the species was there a simple relation to the zygapophyseal facetation. The diaphragmatic, as well as the anticline vertebra is situated clearly more anterior than the intervertebral joints involved in sagittal spine movements. That means, neither the change of the facet orientation nor the change in the spinous process orientation were related to the region of the vertebral column used for sagittal bending. Although Pridmore (Pridmore, 1992) did not analyze the trunk movements in the gray short-tailed opossum quantitatively, he pointed out that trunk bending during locomotion cannot be related simply to the zygapophyseal facetation.

Our observation that sagittal bending can involve caudal thoracic parts is in contrast to Fischer and Lehmann (Fischer and Lehmann, 1998), who reported a restriction of sagittal bending in the lumbar region in the pika. However, they used only five skeletal landmarks along the vertebral column to analyze its motion and did not therefore investigate intervertebral movements. A restricted region of sagittal flexions and extensions between Th11 and L1 was reported for the tree shrew (Jenkins, Jr, 1974) and has been validated for exploration walks only (Schilling and Fischer, 1999). The observation that also the caudal thoracic part of the vertebral column is involved in sagittal bending movements was reported earlier for the tree shrew (Schilling and Fischer, 1999) and was confirmed by the current results. Furthermore, it was demonstrated for other therian species as well by the recent study.

The amplitude of intervertebral joint movements varied slightly between the joints, the species, and between gaits, but the highest values were always observed in the last presacral joint. The highest mobility was also found in the presacral joint during manipulation of the anesthetized cat (Carlson, 1978) and the rock hyrax (Fischer, 1998). Despite the different directions of movements at symmetrical gaits in comparison to asymmetrical gaits (tilting and lateral bending *versus* sagittal bending), the largest motion was also measured at the lumbosacral junction in horses (Haussler et al., 2001).

Sagittal spine movements and its engine – the paravertebral musculature

The mammalian paravertebral musculature is organized in long muscle tracts that enable the high mobility of the vertebral column especially in the horizontal and sagittal planes. Particularly, the longissimus and the iliocostalis tracts were strengthened and gained importance in axial motion in mammals. Neither epaxial nor hypaxial muscles are restricted exclusively to the thoracic or the lumbar region of the vertebral column, furthermore they form long, fused muscle tracts that extend between the head and the pelvis. Long back muscles dorsal to the vertebrae, such as the sacrospinalis muscle (mm. longissimus lumborum et iliocostalis), are responsible for extensions of the vertebral column, whereas longitudinal muscles ventral to the vertebral column, such as the psoas muscles and the rectus abdominis muscle, are involved in flexions of the back (Slijper, 1946; English, 1980; Alexander, 1988).

The sacrospinalis muscle originates *via* the large thoracolumbar fascia from the spinous processus, the sacrum and the pelvis. It inserts onto the caudal, free ribs and the transverse processus of the vertebral column (Slijper, 1946; Cooper and Schiller, 1975; Alexander, 1988; Schilling, 2005a). Thus, it spans over the complete lumbar region to the caudal thoracic portion of the vertebral column. Therefore, it is not surprising that the observed sagittal spine movements were not obligatorily restricted to the lumbar region of the vertebral column but rather involve 7±1 intervertebral joints independent of their classification as thoracic or lumbar vertebrae.

The long, multisegmental muscle tracts found in amniotes fused from the ancestral, segmental organization of the paravertebral musculature in basal vertebrates, e.g. fishes and

amphibians, but the plesiomorph segmental organization is still recognizable by the innervation of the muscle tracts in mammals (Schilling et al., 2005). Therefore, a tendency of craniocaudal progression of dorsoventral flexions of the vertebral column was observed in the current study but because of the fusion of the muscle fibers no strict craniocaudal sequence of consecutive intervertebral joints was found. This supports the observation of English, who recorded the activity along the m. longissimus dorsi in galloping cats at four different lumbar vertebrae levels (L1, L3, L5, L7) (English, 1980). Although the muscle activity at more cranial levels was slightly ahead of more caudal levels (English, 1980) (Fig. 4), there was not a significant difference in timing.

Independent of the gait, the timing of sagittal extension in the small mammals of the current study was similar. Extension of the back normally started around touch-down of the trailing or leading hindlimb and lasted into the first third of swing phase, i.e. after lift-off of both hindlimbs. These results are in accordance with the muscle activation pattern of the major extensor muscles of the trunk. In the galloping cat, the multifidus, the longissimus, and the iliocostalis muscles were activated around the touch-down event of the hindlimbs and clearly turned off after lift-off within the first 20% to 35% of the swing phase (English, 1980).

Although the amplitudes of intervertebral joint movements varied slightly among the species, maximum angular excursions seemed to be dependent on the craniocaudal position along the vertebral column. Towards the caudal direction, amplitudes of intervertebral movements increased and the highest angular excursion was observed in the last presacral joint in all species. This increase in the amplitude (i.e. the intensity of sagittal bending movements) towards the caudal direction is supported by the proportion of various muscle fiber types within the paravertebral musculature. In the pika, the cui and the tree shrew, the percentage of oxidative fibers decreased in the caudal direction while the percentage of glycolytic fibers increased (Schilling, 2005a) (personal observations). Since metabolic profiles of muscles relate to their function (Burke, 1981; Fischer, 1999; Scholle et al., 2001), the craniocaudal gradient in fiber type distribution suggests a functional transition along the longitudinal body axis. Because of its higher percentage of glycolytic fibers, the more caudal part of the back is best suited to be more involved in the more extensive, fast, and forceful sagittal bending movements than more cranial regions of the back.

The resulting 'pelvic movements'

A decisive difference between tailed and 'tailless' species in touch-down and lift-off positions of the pelvis, but the same amplitude of 'pelvic movement' was described in a previous study (Fischer et al., 2002) and confirmed by the current results. Whereas 'tailless' species showed a nearly vertical touch-down (100° to 111° for trailing and leading limbs) and a more protracted lift-off position of the pelvis (131° to 151° for both hindlimbs), the tailed species presented a more retracted touch-down (127° to 142° for both hindlimbs) and an almost horizontal lift-off position of the pelvis (160° to 178° for both hindlimbs). Only the 'tailless' cui behaved more like the tailed species in its pelvic course (Fischer et al., 2002) (this study). Despite this, for its close relative the guinea pig, comparable values of touch-down and lift-off positions, as with the other 'tailless' species investigated here, were reported (Rocha-Barbosa et al., 1996). However, of the species under study, the cui's asymmetrical gaits were the most difficult to record. It seemed to avoid the use of gallop or halfbound, which may be related to its natural subterranean habitat (Koch, 1978; Künkele and Hoeck, 1987).

We hypothesize that the more retracted touch-down and a more or less horizontal lift-off position of the pelvis is ancestral for therian mammals. Fossils of the mammalian stem lineage were of a comparable body size to the species investigated here and possessed long tails (Jenkins, Jr and Schaff, 1988; Krebs, 1991; Luo et al., 2001; Vasquez-Molinero et al., 2001; Ji et al., 2002). In order to prevent a ground contact of the tails during touch-down, we suppose that they used a similar range of pelvic movements during asymmetrical gaits as described here for tailed species. Owing to their lack of a long tail, 'tailless' species such as the pika (Fischer and Lehmann, 1998) (this study) as well as the rock hyrax (Fischer et al., 2002) were able to shift their range of 'pelvic motions' craniad. In this position, displacements of the pelvis result in relatively higher contributions to step length than in the more retracted 'pelvic motion' described for tailed species.

Despite the different touch-down and lift-off positions of the pelvis, the amplitude of 'pelvic movements' during stance phase was comparable amongst all species under study (29° to 44° for trailing and leading hindlimbs) and similar to species of comparable body size [Shaw's jird, 28° for trailing and 23° for leading limbs (Gasc, 1993); guinea pig, approx. 35°; taken from fig. 9 (Rocha-Barbosa et al., 1996)]. It is slightly higher in medium-sized mammals like the rock hyrax [49° for trailing and 46° for leading limbs (Fischer, 1994; Fischer et al., 2002)] and clearly higher in larger, fast running mammals [dog, 50° (Alexander et al., 1980); cheetah, 65° (Hildebrand, 1959)] than in small mammals. In relatively dorsostabile mammalian species, 'pelvic movements' are reduced [horse, 20° (Hildebrand, 1959)].

Sagittal bending

Sagittal bending is more widespread in therian mammals than suggested by earlier studies and did not correspond to the traditional subdivisions of the trunk vertebrae such as the possession or lack of ribs (thoracic *versus* lumbar region), the number of free ribs, or the position of the anticline or the diaphragmatic vertebra (pre- *versus* postdiaphragmatic region) in the species under study. Therefore, no prediction for the trunk region involved in sagittal bending can be made from these skeletal characters. Furthermore, other morphological characters such as the insertion or origin of the major flexors or extensors of the back did not coincide with the region of the vertebral column oscillating during locomotion. Thus, the skeletomuscular characters cannot be simply related to the

particular part of the trunk that contributes to sagittal spine movements during asymmetrical gaits in small mammals.

Thus, other variables than locomotory demands must have had an impact on the evolution of sagittal mobility in therian mammals. Rewcastle (Rewcastle, 1981) pointed out that the ability to gallop may be closely related to the faculty of sagittal vertebral flexion–extension. Reconstructions from the fossil record suggest that sagittal bending abilities may have evolved in the stem lineage of therian mammals (Vasquez-Molinero et al., 2001; Ji et al., 2002) and were added to the plesiomorph abilities of lateral bending and long-axis torsion (Pridmore, 1992). Ancestral therian mammals were of a similar body size as the species under study (Jenkins, Jr and Parrington, 1976). Fischer speculated that sagittal mobility has evolved in the context of homoeothermy (Fischer, 1998). Necessities like rolling up, and thereby reducing the exposed body surface but also self-grooming in order to clean the fur from parasites and maintain its insulatory function are highly probable circumstances for the development of a highly mobile spine. On the other hand, other non-locomotor activities such as high accelerations while evading predators or jumping performances may additionally have had a major impact on morphological characters of the skeletomuscular apparatus. Therefore, we suggest that these non-locomotory conditions have the same impact on vertebral characters than locomotory ones. It follows that, predictions on trunk bending during locomotion concluded only from morphological characters may be misleading and non-locomotory functions of the spine have to be taken into account.

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