

Jumping kinematics in the wandering spider *Cupiennius salei*

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Received: 13 October 2009 / Revised: 23 March 2010 / Accepted: 31 March 2010 / Published online: 20 April 2010
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Abstract Spiders use hemolymph pressure to extend their legs. This mechanism should be challenged when required to rapidly generate forces during jumping, particularly in large spiders. However, effective use of leg muscles could facilitate rapid jumping. To quantify the contributions of different legs and leg joints, we investigated jumping kinematics by high-speed video recording. We observed two different types of jumps following a disturbance: prepared and unprepared jumps. In unprepared jumps, the animals could jump in any direction away from the disturbance. The remarkable directional flexibility was achieved by flexing the legs on the leading side and extending them on the trailing side. This behaviour is only possible for approximately radial-symmetric leg postures, where each leg can fulfil similar functions. In prepared jumps, the spiders showed characteristic leg positioning and the jumps were directed anteriorly. Immediately after a preliminary countermovement in which the centre of mass was moved backwards and downwards, the jump was executed by extending first the fourth and then the second leg pair. This sequence provided effective acceleration to the centre of mass. At least in the fourth legs, the hydraulic and the muscular mechanism seem to interact to generate ground reaction forces.

Keywords Jumping · Kinematics · Locomotion · Hunting spider · Ctenidae

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Introduction

Studies of rapid arthropod locomotion not only are of interest to biologists searching for rules governing animal function and behaviour, but also help to construct multi-legged walking machines (Blickhan 1992; Full 1993; Cham et al. 2002; Spenko et al. 2008; Daltorio et al. 2009). Spiders are particularly interesting for this purpose because of their hydraulic leg extension mechanism (Parry and Brown 1959a; Blickhan and Barth 1985; Shultz 1987; Sensenig and Shultz 2003; cp. Fig. 1d). First prototypes of technical devices have been designed after the model of the spider leg mechanism (Bohmann and Blickhan 1998; Schwörer et al. 1998; Menon and Lira 2006). But still, little is known about how spiders use hydraulic mechanisms in different locomotory activities.

The terrestrial locomotor behaviour of spiders was studied by several authors (Ehlers 1939; Wilson 1967; Land 1972; Rovner 1980; Ferdinand 1981; Ward and Humphreys 1981; Shultz 1987; Schneider and Stanek 1990), but only a few data sets are available on the kinematics of rapid movements, where limitations of the mechanical systems become most obvious. To obtain suitable information on spider locomotory systems during high-performance activity, we studied the kinematics of escape behaviour in the Central American hunting spider *Cupiennius salei*. This spider is well investigated and known for its ability to perform rapid and well-controlled movements (Melchers 1967). Along with prey capture, escape reactions are very time critical. In *C. salei*, jumping is the most spectacular, and probably also the fastest type of escape reaction (Barth 2002). Hence, we will focus on escape reactions, because we hypothesise that these reactions are close to maximum performance.

For a better understanding of the jumping mechanism, it is important to have information on the role of different legs

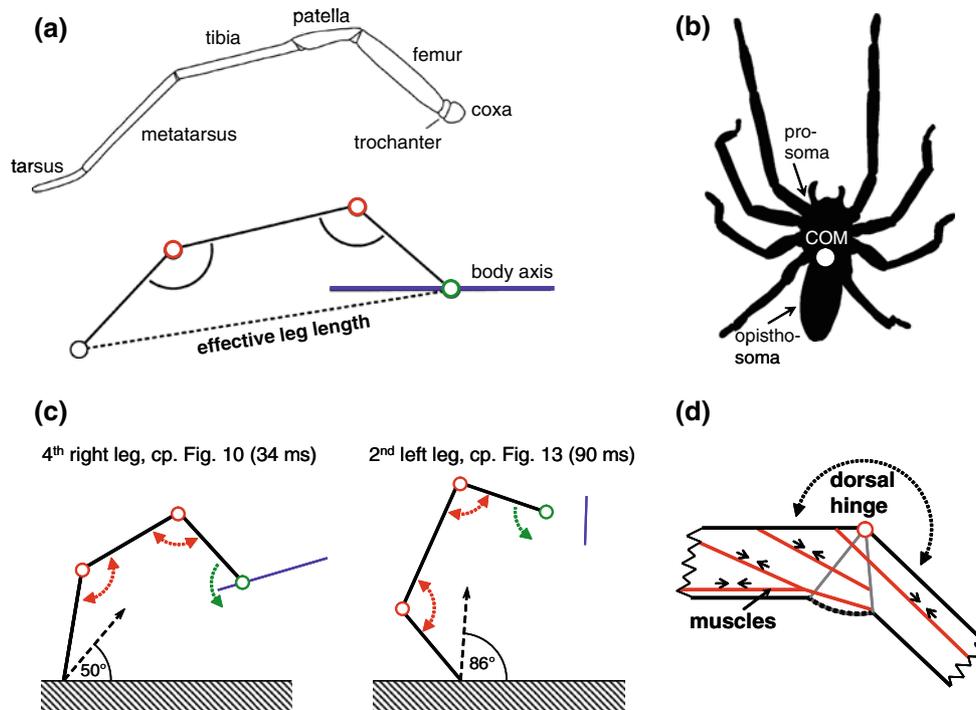


Fig. 1 **a** Joint angles and effective leg length. In the kinematic analyses, the legs were reduced to three functional segments. The circles in the schematized leg represent the digitised points (from right to left): coxal joint complex, femur–patella joint, tibia–metatarsus joint and metatarsus–tarsus joint, respectively. Red circles represent hydraulically extended joints and the green circle represents the muscle-driven proximal joint complex. **b** Leg placement immediately before the acceleration phase of a prepared jump. Differing from the resting position, the first legs were lifted while the other legs are more or less flexed. The centre of mass (COM) is close to the petiolus, the connection

between pro- and opisthosoma. **c** Schematic of a fourth (sagittal view) and a second (hind view) leg at defined instants. Red circles indicate hydraulically extended joints and green circles muscular extended joints. The blue line represents the body axis. Dotted arrows show the movements in the joints, whereas dashed arrows show the direction of ground reaction forces if hydraulic and muscular torques would cancel each other. **d** Sketch of a tibia–metatarsus joint of *C. salei* with major muscle paths: These joints are hinge joints with their pivot on the dorsal edge of the leg. Thus, muscle-driven extension is not possible (colour figure online)

and leg joints. In an early study, Parry and Brown (1959a) analysed the jumping kinematics of the salticid spider *Sitticus pubescens* using photographic equipment at time resolutions of 167 and 143 Hz. 2-D joint angles of the hind legs were estimated by projecting the legs to the sagittal plane. Melchers (1967) observed the movements of *C. salei* during prey capture by filming individuals at 1,000 Hz. This study mainly consists of extensive verbal descriptions of four experimental events and provides only a few quantitative data sets on movements of the tarsi based on projections to the horizontal plane. With a similar level of description, Rovner (1980) examined the hunting behaviour of the ecologically similar genus *Lycosa*. He described movements, but presented no quantitative data on speed or joint movements. Although kinematic data alone are not sufficient to calculate joint torques, they allow for the formulation of hypotheses on the role of different legs during jumping. Thus, in our study, we strive to increase the knowledge of the jumping behaviour in large labidognath spiders. That presumably will allow us to assess the importance and role of the hydraulic mechanism during fast leg

extension in a large spider species and may point out limitations.

We investigated leg and body kinematics during provoked jumps using high-speed video and 3-D motion-analysis. This allowed us both to examine the global kinematics of the body and to analyse the specific kinematics of individual legs during very fast movements.

Materials and methods

Animals

We used 42 healthy and completely intact specimens of the Central American hunting spider, *C. salei*, from the laboratories of F.G. Barth (Vienna) and E.A. Seyfarth (Frankfurt am Main). Spiders of different instars were examined, ranging from juveniles of about 1 cm body length and 0.11 g to specimens of 1.26 g body weight. In addition, we analysed some jumps of sub-adult spiders with body masses of about 3 g (see Fig. 2a). However, it was quite difficult to provoke

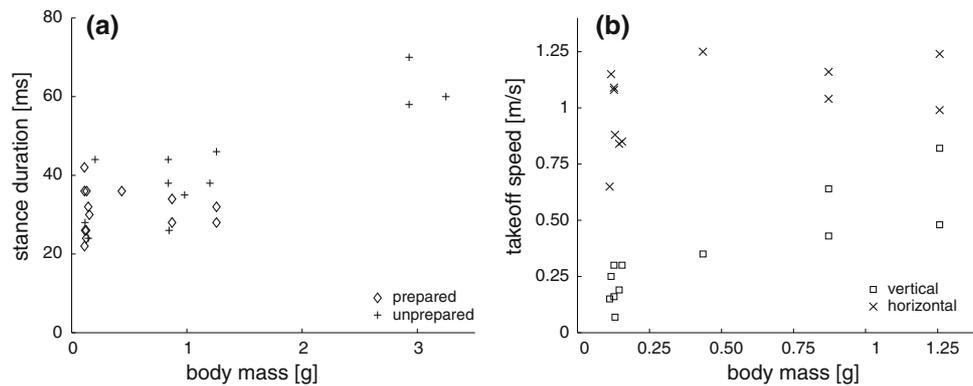


Fig. 2 **a** Duration of the acceleration phase versus body mass in prepared (diamonds) and unprepared (crosses) jumps. Prepared jumps showed little correlation of body mass and acceleration phase duration ($r = -0.0058$, $P > 0.2$). The duration of the acceleration phase in unprepared jumps increased significantly with body mass ($r = 0.87$,

$P < 0.01$). **b** Maximum horizontal (crosses) and vertical (squares) takeoff speed versus body mass in prepared jumps. We observed no significant correlation of body mass and maximum horizontal velocity ($r = 0.44$, $P > 0.05$). Body mass and maximum vertical velocity showed significant correlations ($r = 0.87$, $P < 0.01$)

these large animals to jump. The spiders were kept at room temperature (21–23°C) and fed on crickets of appropriate size. Water was given ad libitum.

Experimental setup

We obtained kinematic data using a manually post-triggered high-speed video system with three cameras (CAMSYS 500, mikromak®), recording a vertical and two horizontal views on the spiders. The resolution of the greyscale images was 256×256 pixels, with a time resolution of 500 frames per second. To minimise disturbance on the crepuscular animals, we restricted the illumination of the setup to three 500 W spotlights. Moreover, we did not fix markers to the legs or body to prevent sensorial distortions and possible behavioural deviations. The image sequences were saved online on hard drive and later on CD. The cameras' field of view was varied according to the individual size of the spiders to find a middle ground between sufficient magnification and the possibility of observing parts of the jumping trajectories. For calibration, we used calibration bodies made of LEGO™ blocks, which have constant dimensions of $1/10^{-3}$ inch precision according to manufacturer's information. Its modular structure facilitates the adaptation of calibration body size to the chosen field of view.

In preliminary experiments, we found that it was very difficult to elicit jumping behaviour if the spiders were placed on flat ground. To obtain an adequate number of image sequences, we designed a jumping platform consisting of a narrow piece of plastic (approx. 40×60 mm) fixed to a cardboard box. The spiders were placed to the end of the platform at a height of 16 cm (Figs. 3, 4, 5, 6). On its bottom surface, the plastic was covered with fluon™ (Sigma Aldrich) to prevent the spiders from leaving the top surface. We provoked escape reactions by short blasts of

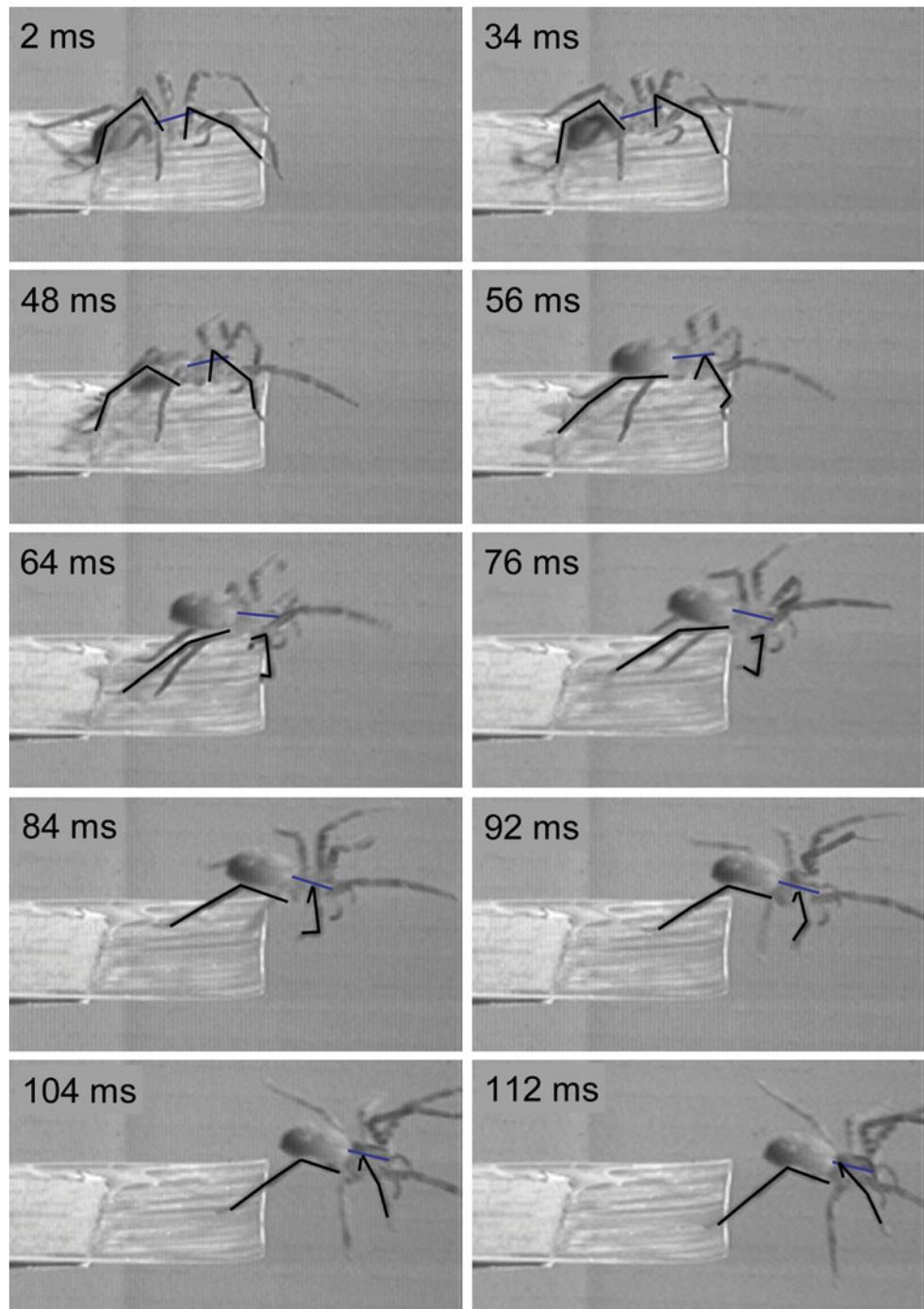
air, sudden movements of big silhouettes such as waving hands towards the animals, or by touching the spiders with a fine brush. Immediately after the experiments, the animals were weighed with a laboratory scale.

Kinematic analysis

We performed 3-D analyses using WINAnalyze 1.3 (mikromak®) software. With this software it is possible to analyse the positions of points, the lengths of lines between these points and the angles between the connecting lines. Velocities and accelerations were calculated with MATLAB 5.2 (MathWorks™). We calculated velocity data using the derivative of position data and smoothing the primary data by fitting gliding second-order polynomials to the time series including four adjacent points on both sides at each position. We estimated average peak acceleration by calculating the mean slopes of the velocity–time curve within an interval to provide the maximum velocity change.

For kinematic analysis, the legs were reduced to three functional segments: femur, patella–tibia and metatarsus (Fig. 1a). The sum of lengths of these segments is the absolute leg length. The lengths of the coxa and the tarsus were excluded. Four points had to be tracked to analyse the kinematics of the functional segments: coxa, femur–patella joint, tibia–metatarsus joint, and the metatarsus–tarsus joint. The distance between coxa and metatarsus–tarsus joint is the effective leg length. It equals the absolute leg length when the leg is fully extended and gives information about the degree of leg flexion without detailed analysis of the joint angles being necessary. In addition, we give the angular changes of the femur–patella and the tibia–metatarsus joints as well as that of the femur with respect to the platform surface. Owing to their particular importance, here, we focus on the second and fourth legs (see below).

Fig. 3 Unprepared jump with change of body axis direction: At the beginning of the jump, the body axis (*blue line*) was directed towards the background of the setup. During the acceleration phase, the body rotated to point in jumping direction at the instant of takeoff (the spider was jumping towards the right aspect of the foreground). Second and fourth right legs are accentuated by addition of stick figures (colour figure online)



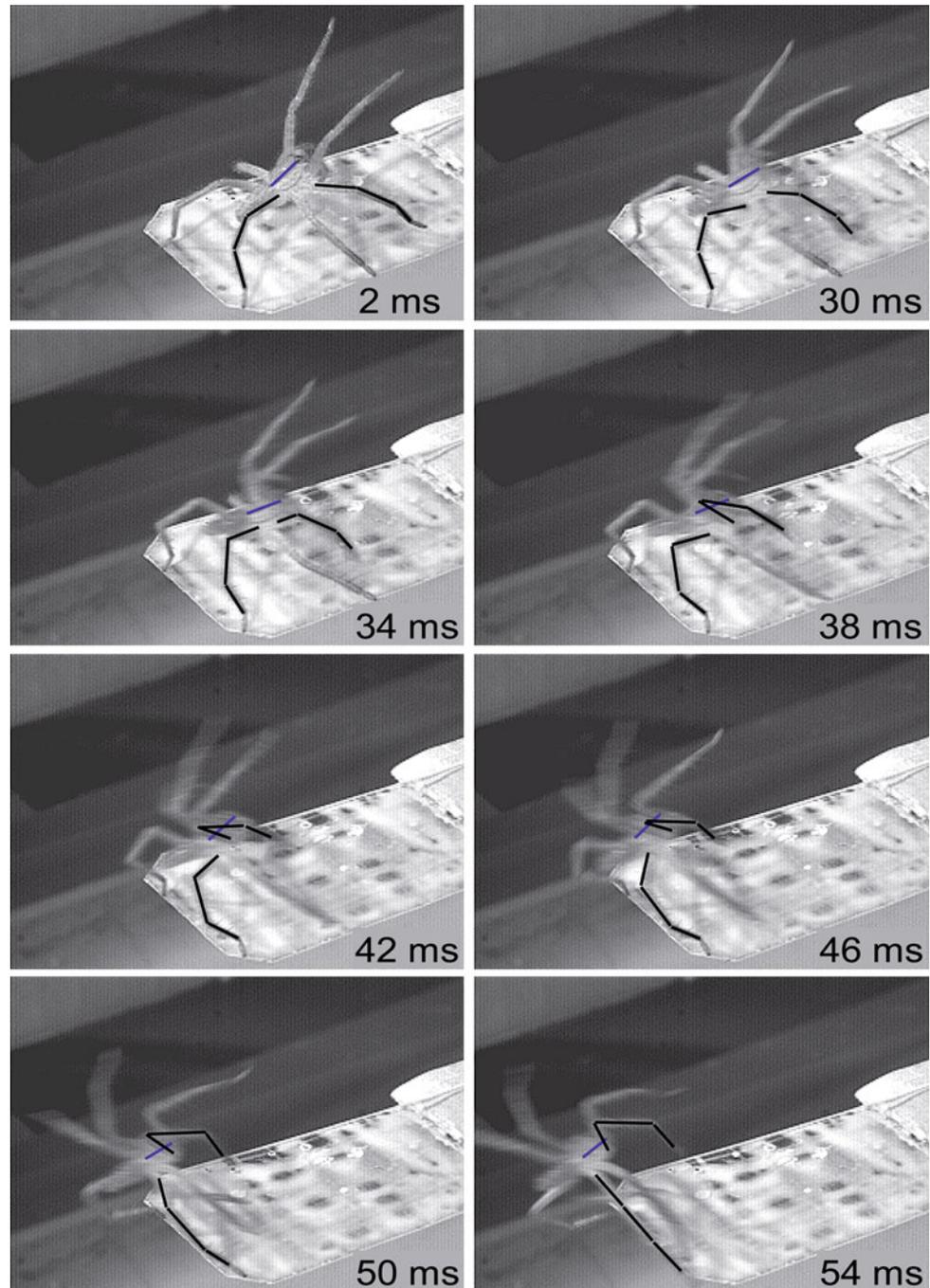
It was not possible to resolve the kinematics of the three basal leg joints: the body–coxa joint, the coxa–trochanter joint and the trochanter–femur joint. Furthermore, as the horizontal joint axes of the coxa–trochanter and the trochanter–femur joint run widely parallel, the respective joint angles could not be determined by the position of the femur with respect to the body. The longitudinal body axis was given by the line connecting the anterior end of the prosoma and the pos-

terior end of the opisthosoma. The co-ordinates of three fixed points on the jumping platform gave a fixed reference frame.

Statistics

We tested whether or not each parameter matched a normal or at least a symmetric distribution. If so, as measure for the central tendency, we present the mean

Fig. 4 Backward somersault: The first legs were lifted before the recording of the image sequence started; the second legs were lifted before the body started to move towards jumping direction. The third legs were extended during their contact phases, while the fourth legs were flexed at first and extended in the later acceleration phase. The erected leg spines are visible on the metatarsus of the right fourth legs. Second and fourth right legs are accentuated by addition of stick figures



with standard deviation; if not, or if the sample size was low, we give the median as well as the lower and upper quartiles.

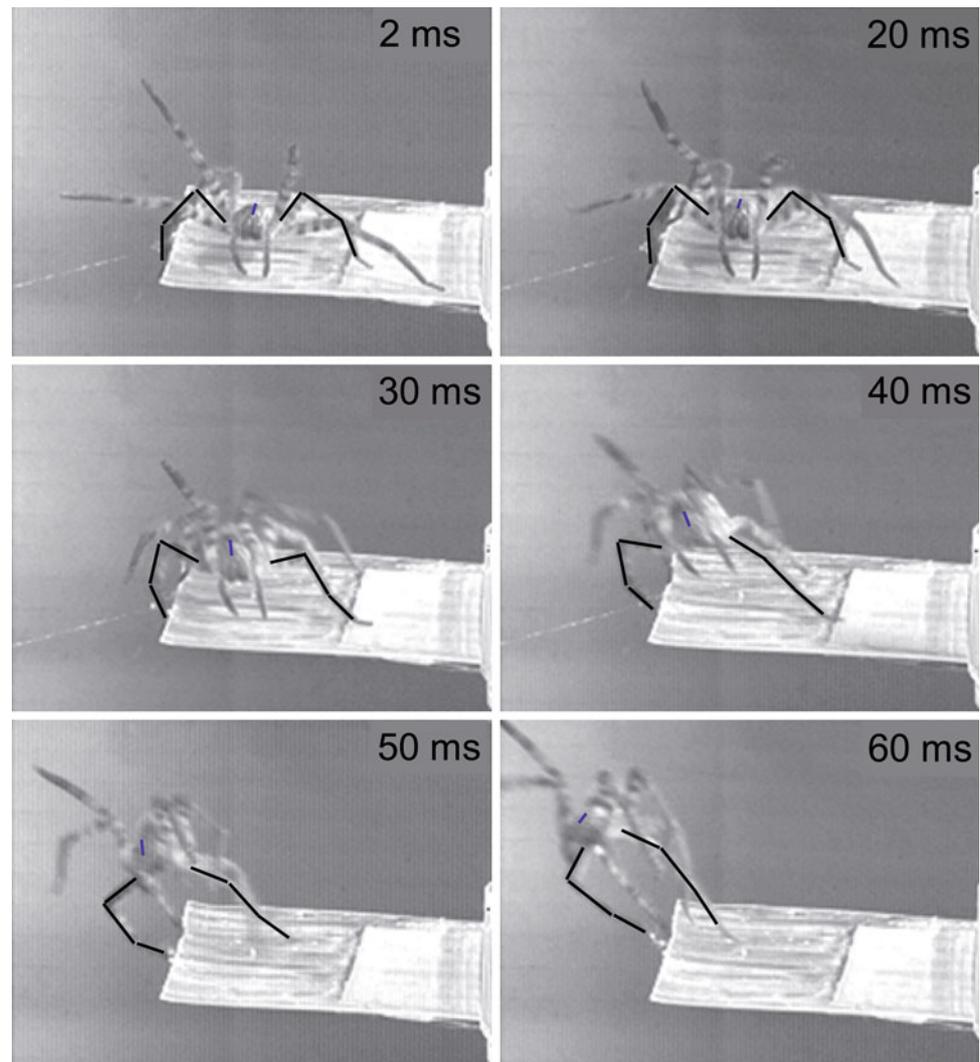
To compare two samples with normal distributions, we used t tests. If at least one sample did not follow a normal distribution, we carried out Mann–Whitney U tests. Unless specified, all tests have been done on the 5% confidence limit.

Results

Types of jumping

We observed two different types of jumping: unprepared and prepared jumps. Most of the successful trials were obtained with juvenile specimens, whereas we could record only few jumps from larger animals. We obtained recordings

Fig. 5 Sideways jump. Among the legs with ground contact, those that were directed against jumping direction extend during their contact phase, while the legs that initially point in jumping direction were first flexed and extended afterwards. Third legs are accentuated by addition of stick figures



of 21 prepared jumps; 14 of the recorded video sequences had sufficient quality for kinematic analysis. In most of our trials, the spiders quickly ran away without jumping off the platform. Frequently, they moved to the bottom of the jumping platform, with little visible effect of the fluon covering the bottom surface.

Prepared jumps

After each significant relocation, the animals connect their drag-line to the ground. During prepared jumps, the spiders show a stereotypical sequence of actions. In preparation for jumping, the animals placed their legs in a characteristic pattern. This leg placement closely resembled the patterns that were observed in salticids and other spiders immediately before jumping (Ehlers 1939; Parry and Brown 1959a; Rovner 1980). The first three leg pairs are pointing anteriorly with only the hind legs directed posteriorly (Fig. 1b). This differs from the normal resting position of the spiders, where the first two legs of each side are placed

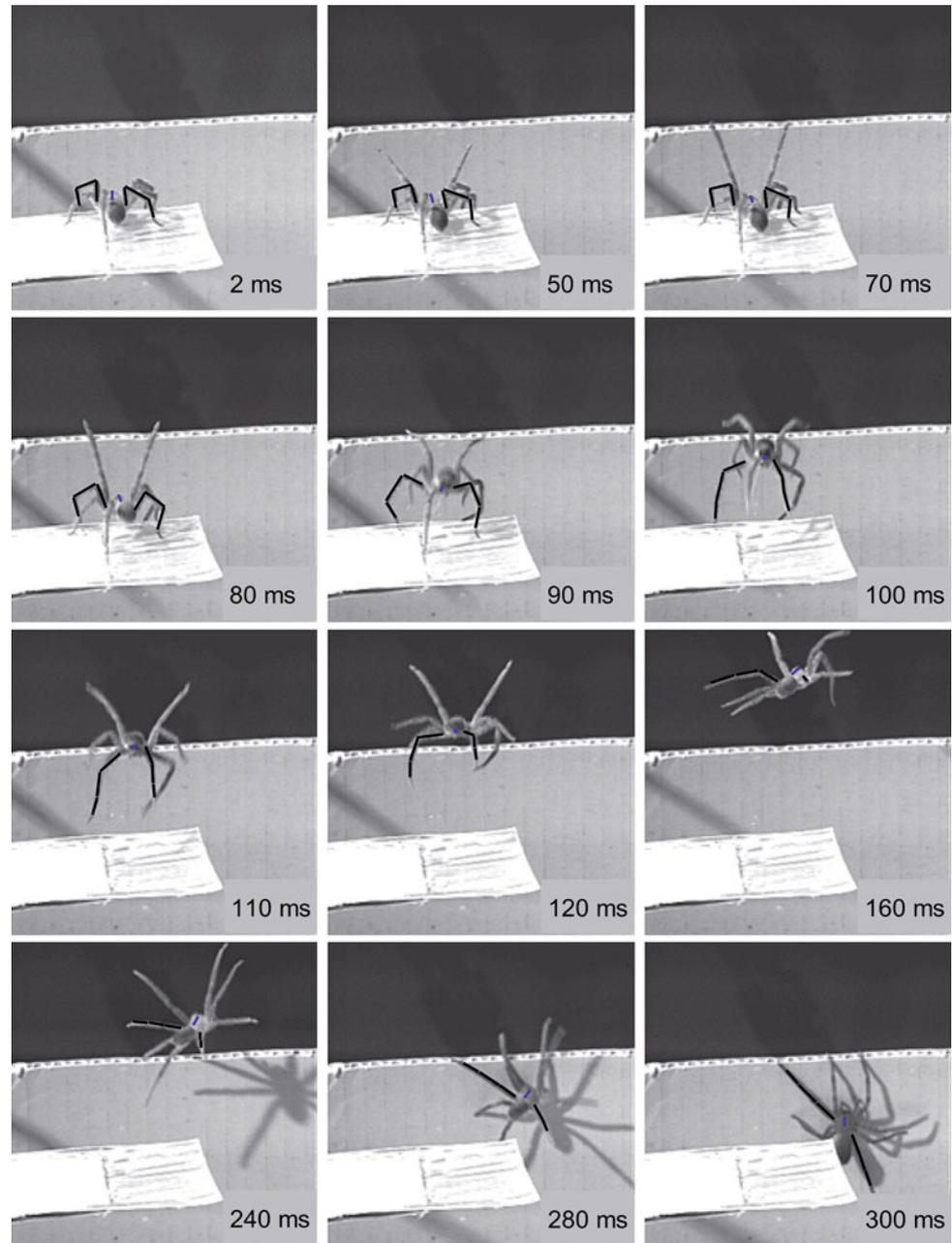
in parallel, pointing anteriorly, and the third and fourth legs also being oriented more or less parallel in posterior direction.

Sometimes, the legs were positioned only 100–200 ms before the jumping movements began. The actual jump started after leg placement. In most cases, the first legs were lifted. Then the spiders slowly flexed their third and fourth legs and moved their body backwards and downwards. During the following acceleration phase, taken as time span from the first visible body movement towards jumping direction until takeoff, the legs lost ground contact in a characteristic sequence (Fig. 7). Shortly after takeoff, all legs were bent dorsally with the spiders looking somewhat like a badminton shuttlecock during flight (cp. Fig. 6).

Unprepared jumps

This type of jump mostly occurred after sudden disturbances. Here, we observed no specific, previous leg placement resulting in a typical arrangement. The spiders always

Fig. 6 Prepared jump. Before the acceleration phase begins, the body was slowly moved backwards and downwards due to a slight flexion of the third and fourth legs. Then, the spider started to accelerate by extension of the fourth and second legs. After the aerial phase of the jump, the spider landed on the cardboard wall that surrounded the setup. The jumping distance was about 43 cm. Second left and fourth right legs are accentuated by addition of stick figures



jumped away from the disturbance. Sometimes the animals changed the direction of their longitudinal body axis in the horizontal plane during the acceleration phase (Fig. 3); in other cases, the spiders jumped sideways (Fig. 5) or even performed backward somersaults (Fig. 4). As in prepared jumps, spiders secured themselves by their drag-line.

We did not find a clear qualitative difference in the kinematics of unprepared jumps and fast-starting behaviour of the animals. In some cases, the animals accelerated quite similar to jumps, but simply made a start and ran off the edge of the jumping platform. The main difference with unprepared jumps was the incomplete loss of foot contact. Spiders of all sizes performed unprepared jumps. We

observed them in spiders with body masses ranging from 0.12 to 3.23 g.

Jumping distances

In two cases of prepared trials, the spiders jumped in a trajectory within the field of view of one of the video cameras. In both jumps, the spiders reached the cardboard wall that surrounded the setup at a distance of more than 35 cm. The spiders jumped down from the platform, thereby the height difference between platform and boundary was about 15 cm. One spider (Fig. 6) with a body length of about 12 mm jumped in an oblique direction. We estimated the

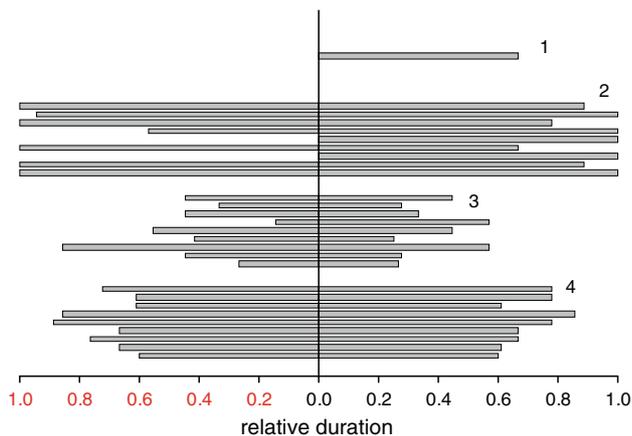


Fig. 7 Contact phase diagram for prepared jumps ($n = 9$). The stance phase durations of the legs are normalised by setting the longest duration to 1; i.e. the value 1 is valid for the leg which takes off last. The left columns mark the left legs, the right columns the right legs. The numbers (1–4) close to the right columns indicate the leg pairs (from below: lower group, fourth legs, second group: third legs, third group: second legs, single upper column: first legs). If a leg does not touch the ground during the acceleration phase, no data are shown (cp. first legs)

distance to be about 43 cm. Hence, the spider jumped a distance of about 35 times its body length. On level ground, these jumps were much shorter, but still exceeded several times the body length of the spiders when jumps coincided with steeper takeoff angles exceeding 15° .

Erection of leg spines

In *C. salei*, large spines are present on the femur and tibia of all legs. At the beginning of the acceleration phase, these spines become erect (cp. Fig. 4). In the video sequences that were analysed, the spines become completely erect within about 4.6 ± 0.9 ms ($n = 26$). Spine erection occurred always simultaneously in all segments of all legs. In prepared jumps, takeoff of the last, i.e. mostly the second (Fig. 7), leg took place 22–38 ms (median 27 ms, quartiles 24/32 ms, $n = 14$) after complete erection of the leg spines; whereas in unprepared jumps, takeoff occurred 26–64 ms (median 32, quartiles 30/56 ms, $n = 9$) after spine erection. The durations in unprepared jumps were significantly longer than that in prepared jumps ($p = 0.022$).

In both types of jumping, there seemed to be strong coupling of leg spine erection and the first visible body movements. Although in prepared jumps, spine erection took place between 10 ms before and 14 ms after the first visible jumping movements, the median value was in close temporal relation to the first movements. It occurred about 1 ms (quartiles $-1.5/4$ ms, $n = 14$) after jump initiation. During unprepared jumping, the leg spines became erect from 4 ms before to 12 ms after the first body movements (median

2 ms, quartiles 0/6 ms, $n = 9$). There was no significant difference between the two types of jumping ($p = 0.59$).

Kinematics of the body axis: orientation, speed, and acceleration

In prepared jumps, the body axis was moved in a stereotyped pattern. Otherwise, due to the variety of jumping directions, body movements varied considerably in unprepared jumps. As examples, we will only provide brief descriptions of some characteristic unprepared jumps. The higher degree of order in prepared jumps was also reflected in the duration of the acceleration phase, which was slightly, but significantly, shorter in prepared versus unprepared jumps.

Prepared jumps

During the acceleration phase of prepared jumps the body rotated forward. After the spider lost ground contact, the rotation stopped, and was reversed in most cases (Figs. 6, 8). Even among prepared jumps, velocity and acceleration of the body axis varied considerably (Fig. 9; Table 1). The maximum vertical speeds of the anterior end of the prosoma ranged from 0.04 to 0.82 ms^{-1} (0.27 ± 0.21 ms^{-1} , $n = 14$), and the horizontal speeds ranged from 0.65 to 1.25 ms^{-1} (0.96 ± 0.19 ms^{-1} , $n = 14$). The caudal tip of the opisthosoma reached vertical speeds of up to 1.24 ms^{-1} and horizontal speeds of up to 1.47 ms^{-1} . The maximum accelerations were vertical acceleration of 33.7 ms^{-2} and horizontal acceleration of 68.4 ms^{-2} for the prosoma, and vertical acceleration of 97.9 ms^{-2} and horizontal acceleration of 106.2 ms^{-2} for the opisthosoma. There was no significant correlation of body mass and maximum horizontal velocity ($r = 0.44$, $P > 0.05$; Fig. 2b). A significant correlation was found for body mass and maximum vertical velocity ($r = 0.87$, $P < 0.01$).

The orientation of the longitudinal body axis can be characterised by the change of its angle relative to the horizontal plane. In our analysis, positive angles indicate a forward rotated body axis, i.e. the tip of the opisthosoma is higher above the springboard than the anterior end of the prosoma. For some characteristic prepared jumps, the angles between the body axis and the springboard are shown in Fig. 8. Immediately before the beginning of the acceleration phase, the body performed a slight backward rotation due to the flexion of the third and fourth legs. This was accompanied by a lowering of the opisthosoma. During the acceleration phase, the longitudinal body axis rapidly rotated forward with the rotation reaching its peak value at the instant of the last leg taking off. After the legs lost ground contact, the body rotation reversed.

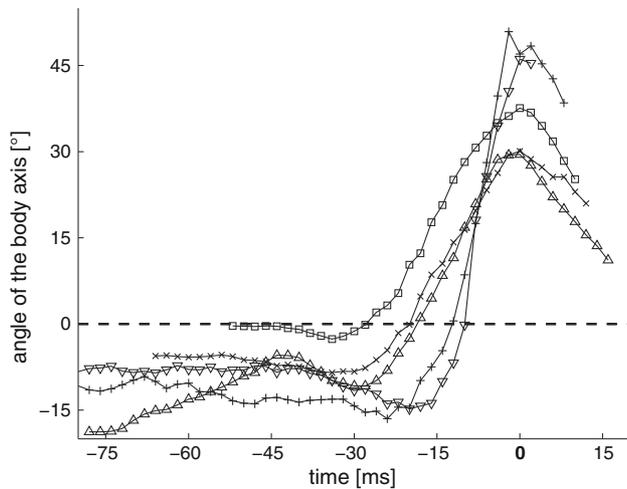


Fig. 8 Angles between the longitudinal body axis and the springboard surface versus time in some prepared jumps. Positive values indicate forward rotated postures (i.e. the tip of the opisthosoma having a higher vertical position than the tip of the prosoma). Takeoff of the last legs is adjusted to the instant of 0 ms each

Unprepared jumps

As stated earlier, the kinematics of unprepared jumps in *C. salei* was highly variable (Figs. 3, 4, 5; Table 1). Maximum vertical and horizontal components of the velocity vector of the prosoma were slightly lower or resembled the values achieved in prepared jumping, but the extreme values were close to those found for prepared jumps. Maximum vertical velocity of the prosoma ranged from 0.14 to 0.69 ms⁻¹ (0.30 ± 0.20 ms⁻¹, n = 6) and maximum horizontal velocity reached 0.68 to 1.26 ms⁻¹ (1.02 ± 0.18 ms⁻¹, n = 6). Also, the maximum acceleration of the prosoma reached values close to those found for prepared jumping (P > 0.05): vertical 8.19–53.70 ms⁻² (24.90 ±

17.6 ms⁻², n = 6); horizontal 34.13–55.10 ms⁻² (41.26 ± 7.47 ms⁻², n = 7).

Comparing small and larger spiders

Nevertheless, ignoring the type of jumping, jumping performance seemed to be different in small (0.13 ± 0.03 g, N = 12) and larger (0.92 ± 0.34 g, N = 8) spiders. Thus, maximum horizontal velocity of the prosoma was significantly higher in larger specimens (Fig. 2). It reached 1.11 ± 0.15 ms⁻¹ against 0.89 ± 0.15 ms⁻¹ in small animals. Additionally, the vertical velocities achieved by larger spiders (0.41 ± 0.26 ms⁻¹) were significantly greater than in small ones (0.2 ± 0.08 ms⁻¹). At the same time, stance durations lasted significantly longer in large spiders than in smaller ones (40.9 ± 13.3 ms; Fig. 2a). Small spiders required only 30.8 ± 7.3 ms for the acceleration phase.

Leg kinematics: duration of ground contact of individual legs

In prepared jumps, the total acceleration period, defined as the time from the first visible body movement towards jumping direction until takeoff of the last leg, took 22–42 ms (mean 30.9 ± 5.6 ms, n = 14). As prepared jumps were executed only by spiders with body weights less than 1.3 g, no correlation of body mass and acceleration phase duration could be observed (r = -0.0058, P > 0.2). In unprepared jumps, the duration of the acceleration phase increased significantly with body mass (r = 0.87, P < 0.01; Fig. 10a). It took 24–70 ms (mean 43.8 ± 15.5 ms, n = 12). However, if focusing on spiders with body weights below 1.3 g, the difference in stance durations between prepared and unprepared jumps was still significant (P = 0.047). These small animals required 35.9 ± 8.3 ms for the acceleration in unprepared jumps. During unprepared jumps, larger spiders

Fig. 9 Vertical (a, b) and horizontal (c, d) speed of prosoma and opisthosoma against time in two prepared jumps. Crosses: tip of prosoma, diamonds: tip of opisthosoma. The last legs’ take-off is set to the instant of 0 ms each. The opisthosoma tip reached higher vertical speeds due to the rapid forward rotation of the body during the acceleration phase

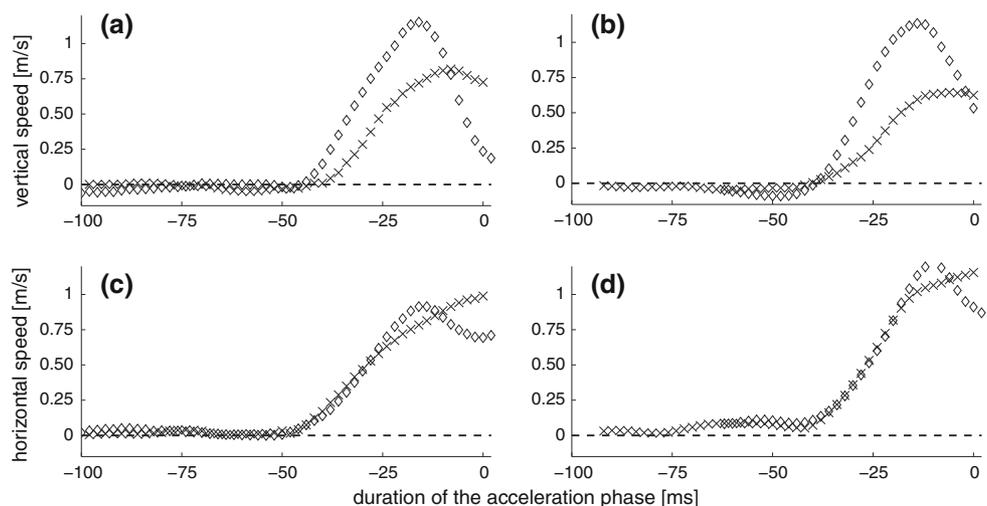


Table 1 Maximum speeds and accelerations of the anterior end of the prosoma and the caudal tip of the opisthosoma during prepared jumps

Max. speed range (ms^{-1})	Mean \pm SD (ms^{-1})	<i>n</i>
Prosoma (horizontal)		
0.65–1.25	0.96 ± 0.19	14
Prosoma (vertical)		
0.04–0.82	0.27 ± 0.21	14
Opisthosoma (horizontal)		
0.71–1.47	1.11 ± 0.23	13
Opisthosoma (vertical)		
0.44–1.24	0.87 ± 0.25	13
Max. acceleration range (ms^{-2})	Mean \pm SD (ms^{-2})	<i>n</i>
Prosoma (horizontal)		
20.5–68.4	40.8 ± 13.7	13
Prosoma (vertical)		
0.74–33.7	19.2 ± 9.5	13
Opisthosoma (horizontal)		
29.4–106.2	59.3 ± 23.7	13
Opisthosoma (vertical)		
3.7–97.9	62.3 ± 18.9	13

seem to require more time for takeoff. This increase may approximately be proportional to the increase in leg length.

Prepared jumps

During prepared jumps, the contact phase patterns of respective legs were quite regular among different trials (Fig. 7). Legs took off in a characteristic sequence. Bearing in mind that the first leg pair lost ground contact in most cases of prepared jumping just before any jumping movement occurred, the third legs were the first to lose ground contact.

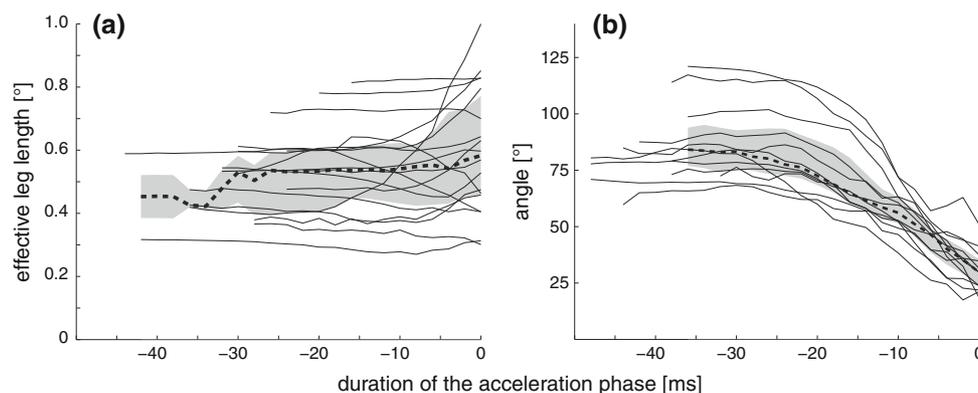


Fig. 10 **a** Normalised leg length of the third legs during prepared jumping. The instant of leg takeoff is set to 0 ms each. The **bold broken line** indicates the median and the **shaded area** indicates the interquartile range. The effective leg length of the third legs remained more or

less constant during their contact time, which was mostly short within the acceleration phase of prepared jumps. **b** Angle between the tibiae of the two hind legs during prepared jumps, seen in the *horizontal plane*. The instant of last hind-leg takeoff was set to 0 ms for each trial. They took off after 8–60% of the total acceleration phase duration at a median value of 43% (quartiles 28/44%, $n = 18$). Then, the fourth leg pair took off after 60–89% of total acceleration phase at a median value of 67% (quartiles 61/78%, $n = 18$). The last to takeoff were the second legs. They defined the total acceleration phase duration, losing ground contact after 57–100% of total duration. However, takeoff occurred predominantly at 100%; thus, the median and the value of the upper quartile was 100% each (quartiles 81/100%, $n = 18$). Values lower than 100% result from the fact that contralateral legs often takeoff at different instants. The first legs touched the ground in only two trials, where they kept ground contact during 62–69% of total acceleration phase (mean $66 \pm 4\%$, $n = 3$). Comparing ipsilateral legs, the second legs kept ground contact on the average 2.4 times as long as the third legs ($\pm 90\%$, $n = 15$), and about one-third longer than the fourth legs ($\pm 30\%$, $n = 16$).

Unprepared jumps

In unprepared jumps, leg contact durations were highly variable (Fig. 11). There was much more variability in the leg and leg joint kinematics than in prepared jumps. The legs performed a variety of movements that seemingly depended on the jumping direction. The legs that were positioned towards jumping direction were flexed during the acceleration phase and at least in sideward-directed jumps maintained ground contact much longer (Fig. 5), whereas the legs that were positioned against jumping direction extended. Since the disturbances were applied from different directions with respect to the body orientation of the spiders, we observed extremely variable behaviour of the legs.

Figure 11a shows the distribution of the contact phase durations during a ‘forward-sideward-jump’. The spider jumped in a direction about 45° to the right of the longitudi-

less constant during their contact time, which was mostly short within the acceleration phase of prepared jumps. **b** Angle between the tibiae of the two hind legs during prepared jumps, seen in the *horizontal plane*. The instant of last hind-leg takeoff was set to 0 ms for each trial

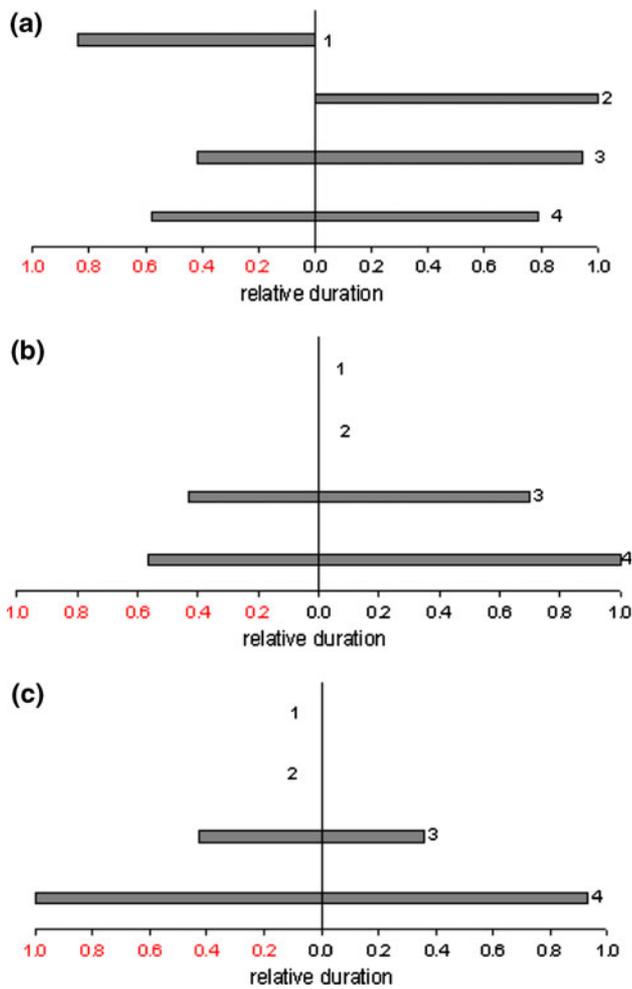


Fig. 11 Contact phase diagrams for some unprepared jumps. **a** Forward-sideward-jump towards the right side of the animal, **b** sideward jump to the right, **c** backward somersault

nal body axis (cp. Fig. 3). Most of the legs on the left side of the body lost ground contact early during the acceleration phase, whereas both the first left leg and the second to fourth legs on the right side of the body kept ground contact much longer. The first right leg was held upwards as if having sensory (i.e. antenna-like) function. Since the spider moved away from the foot positions of the left hind legs, these legs were the first to be stretched during the acceleration phase, and therefore lost ground contact quite early. However, the second left leg was lifted even before the body movement started.

In a selected sideward jump (Figs. 5, 11b), the first and second legs were lifted before the acceleration phase began. The spider jumped towards its right side. Accordingly, the contact phases of the right legs were considerably longer than those of the left legs. During a backward somersault (Figs. 4, 11c), the first and second legs were not touching the ground. Both third legs took off after about half of the

total acceleration phase, while the fourth legs was the reference for its duration. In this case, the leg movement showed a degree of contralateral parallelism similar to prepared jumping. Nevertheless, it is obvious that during backward jumps, the kinematics of the legs is not just mirrored as might be expected from their approximately radial-symmetric arrangement. Moreover, the variability of jumping behaviour indicates that the spiders are able to use their legs in a variety of ways. Individual legs are able to play different roles, depending on the required jumping direction.

Leg kinematics: effective leg lengths and leg joint kinematics

The kinematics of the legs during the acceleration phase of different prepared jumping trials showed a remarkable degree of similarity again, whereas no stereotypical pattern could be observed in unprepared jumps. Here, we focus on the analysis of leg movements in prepared jumps. Although the kinematics of the body and the stance phase pattern, i.e. the sequence of the legs' ground contact loss, were quite stereotypical during prepared jumps, the specific leg kinematics seemed to depend on the initial leg placement as well as on the movements of other legs. Hence, individual changes of joint angles could vary considerably.

Forelegs

As mentioned earlier, the front legs had ground contact during the acceleration phase of only two prepared jumps. Mostly they lifted before the actual jumping movements occurred and subsequently were held continuously stretched out. In many cases, we observed a slight bending of the front legs during phases of maximum acceleration of the body. This bending was mainly caused by a flexion in the femur-patella joint.

Third legs

Among those legs that have ground contact during the acceleration phase, the third legs were the first to takeoff. During their stance phase, we mostly observed a slight extension, but rarely a major increase of effective leg length (Fig. 10a). Propulsion may be supported rather by rotation of the legs within the proximal joint complex than by extension of the major leg joints. However, in two of the examined cases, one of the third legs took off even before the body started to move visibly.

Hind legs

The lengthening of the second and fourth legs contributed strongly to the jumping movements. Despite their different

positions during prepared jumps, they behaved in a rather co-ordinated manner. At the same instant as the body began to accelerate, the effective length of the hind legs, starting at about 42% (quartiles 35/49%) of the absolute length, began to increase (Fig. 12e). This occurred about 22 ms (quartiles 18/28 ms) before hind-leg took off. At this instant, the initial angle of the femur–patella joints was about 91° (quartiles 86°/102°, $n = 23$; Fig. 12f). These joints' extensions caused the effective leg lengthening at the beginning of the acceleration phase and were accompanied by a femur deflection of the same magnitude. Thereby, the femur–substrate angle decreased from 69° (quartiles 61°/72°) to a horizontal position (median -1° ; quartiles $-9^\circ/7^\circ$; cp. Fig. 12h). From 25 to 14 ms before leg takeoff, the tibia–metatarsus joint angle of about 105° did not change substantially (Fig. 12g). On the contrary, we observed a decrease in the joint angle of the hind legs' tibia–metatarsus by about 9° compared with initial conditions, whereas the femur–patella angle slightly increased. The tibia–metatarsus joint began to extend about 12 ms before leg takeoff, i.e. approximately 10 ms after the femur–patella joint. At this instant, the femur–patella angle had already increased by almost 15°. At the end of their stance phase, the hind legs were largely outstretched. At takeoff, the femur–patella angle was about 152° (quartiles 147°/165°, $n = 23$) and rather similar to the tibia–metatarsus angle of about 157° (quartiles 149°/167°, $n = 23$) that resulted in a median value of the normalised effective length of 93% (quartiles 90/97%, $n = 23$).

Unlike that observed in *Sitticus* by Parry and Brown (1959a), the hind legs of *C. salei* were not held in a plane parallel to the sagittal body plane during the acceleration phase. Prior to the beginning of the acceleration phase, the angle between the functional patella–tibia segments of the two hind legs was about 85° (quartiles 77°/94°, $n = 12$). It decreased considerably during the extension of the hind legs to reach approximately 30° (quartiles 23°/35°, $n = 12$) at takeoff (Fig. 10b), indicating a doubling of the effective leg length. Accordingly, the leg angle to the sagittal plane decreased.

Second legs

Normally, the second legs also take off after a strong extension (Figs. 6, 12a), but in some trials, even a flexion of the major leg joints occurred, and therefore a decrease of the effective leg length. Since the longitudinal body axis rotated forward during the acceleration phase, the initial movements varied depending on the initial leg placement. The first movements range from a slight leg flexion when the leg tip was positioned more anteriorly to a pure extension for a more posterior position of the leg. After these first movements, the angles of the hydraulic leg joints, starting

with 78° (quartiles 72°/98°) in the femur–patella joint and 111° (quartiles 103°/119°) in the tibia–metatarsus joint, increased. That resulted in an increase of the effective length from about 42% (quartiles 38/55%) to a more or less extended position at takeoff. However, the leg joint extension was considerably less than in the fourth legs. The normalised effective leg length at the instant of leg takeoff was about 78% (quartiles 70/86%, $n = 10$). Thereby, the femur–patella angle was significantly smaller with a median value of 115° (quartiles 113°/131°, $n = 9$; Fig. 12b). The tibia–metatarsus angle at takeoff was 150° (quartiles 134°/165°, $n = 10$; Fig. 12c). Both joint angles were extended by about 35°. Simultaneously with the extension of the femur–patella joint, the femur angle changed by some 90° relative to the substrate (median 91°, quartiles 79°/96°; Fig. 12d). This change even exceeded the one observed in the fourth legs. Since in *C. salei*, hind legs are only slightly shorter than the frontal leg pairs (Table 2), also the absolute leg extension contributing to the acceleration of centre of mass was probably smaller in the second legs. The time span from the first movement of the centre of mass until the takeoff of the second legs lasted some 8.5 ms (± 3.6 ms) longer than in the fourth legs (median 30 ms; quartiles 24.5/34.5 ms). However, the main leg extension took place only in the last 15 ms (Fig. 12a), although femur depression began about 25 ms before and the movement of the centre of mass even 30 ms before the takeoff of the second legs. Thus, their extension started considerably after that of the fourth legs and lasted for a shorter time.

Discussion

General observations

Escape jumping in *C. salei* occurs mostly when the animals are extremely disturbed. Nevertheless, citing a doctoral thesis of Brittinger (1998), Barth (2002) described that it was possible in juvenile *C. salei* to regularly elicit jumps after a fly passed close enough to be detected by the animal. Wasserthal (2001, 2009) showed that medium-sized specimens of the genus *Cupiennius* are important predators of relatively large sphingid moths. The spiders show a typical behaviour consisting of entering onto an inflorescence, waiting for a potential prey which intends to harvest nectar, and subsequently aiming a jump upon that prey. After they attack, the spiders, still secured by their drag-line, hang with the catch in their fangs. These well-aimed prey jumps are also seemingly prepared jumps, quite similar to the escape manoeuvres described here. However, large spiders are vulnerable with respect to their opisthosoma when falling from considerable heights (own experimental experience). The probability of injuries may even increase in the

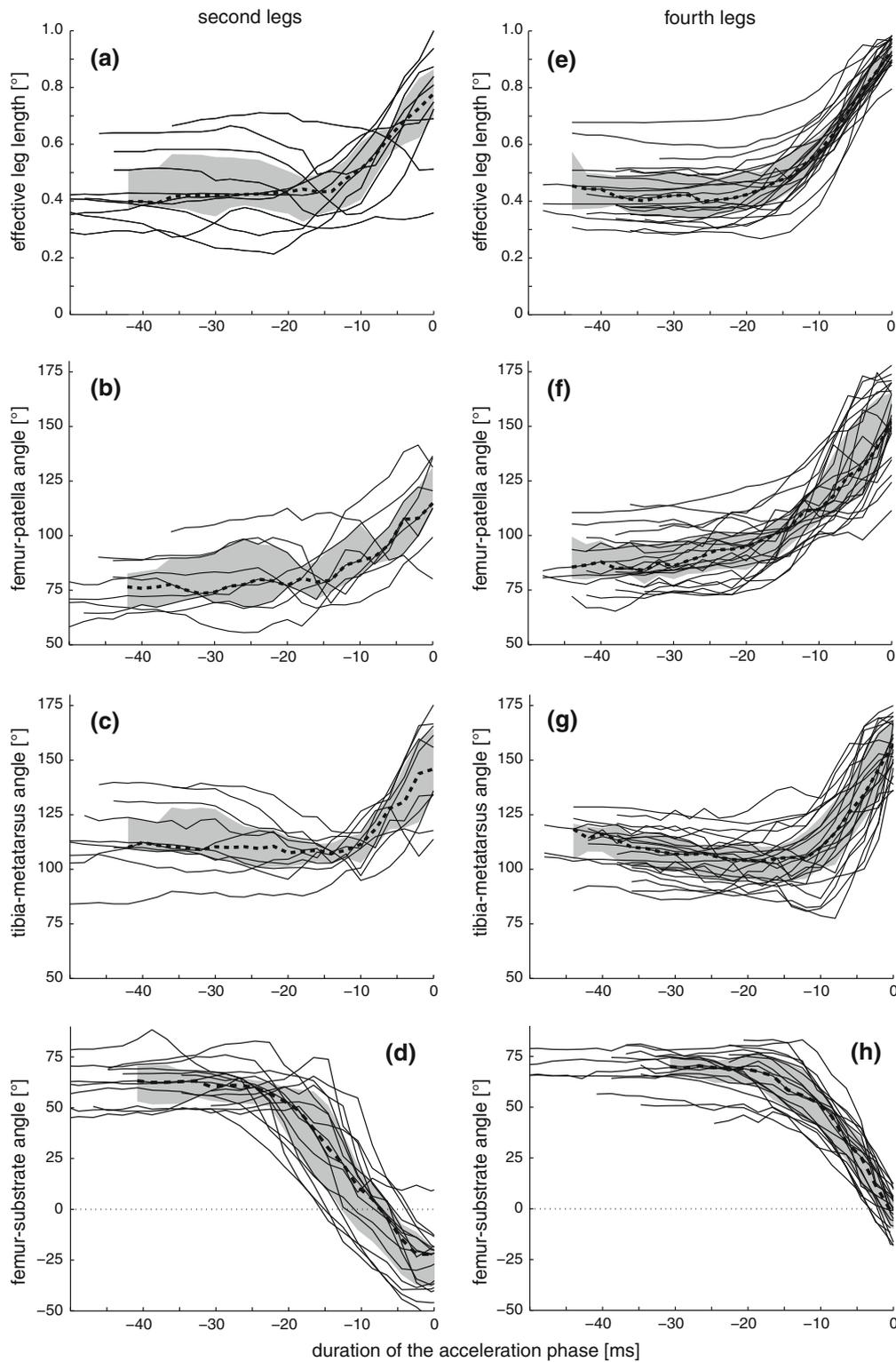


Fig. 12 Normalised effective leg lengths (a), femur–patella angles (b), tibia–metatarsus angles (c), and femur–substrate angles (d) of the second legs during prepared jumping. Like the fourth legs, also the second legs extended during the acceleration phase, but they showed a higher degree of variability. Furthermore, the pattern of joint movements resembled that of the fourth legs, but in the distal joints the degree of joint extension was lower and that of the femur–substrate

angle was higher. Normalised effective leg lengths (e), femur–patella angles (f), tibia–metatarsus angles (g), and femur–substrate angles (h) of the fourth legs during prepared jumping. The fourth legs extended during the acceleration phase. The femur–patella joints were extended throughout the entire contact phase, while the tibia–metatarsus joints were first slightly flexed, then rapidly extended

Table 2 Leg length of adult female (3.71 ± 0.58 g, $N = 6$) and juvenile (0.91 ± 0.15 g, $N = 3$) specimen of *C. salei*

	First legs	Second legs	Third legs	Fourth legs
<i>C. salei</i> ♀				
mm	51	50	41	48
%	125	122	100	117
<i>C. salei</i> juv.				
mm	38	37	30	35
%	127	124	100	119

Lengths are given as absolute values in mm and relative to the length of the third legs in %. Always both legs of a leg pair were measured from the proximal rim of the coxa to the distal end of the tarsus

highly structured natural habitats of *C. salei* (Barth and Seyfarth 1979). Furthermore, since *C. salei* lives on vegetation, jumps may bear the risk of large dislocations and landing in harmful environments.

The ability to escape rapidly by sudden jumps or startles might be advantageous when spiders are threatened by predators. In such cases, there may be insufficient time to optimise leg placement. This may, in turn, contribute to the finding that the acceleration phase is slightly, but significantly, longer in unprepared versus prepared jumps. Prepared jumps may occur mainly in situations of disturbance, but without the necessity to escape as fast as possible. Here, if in a position lacking alternatives, e.g. at the end of a branch, the spider can escape by controlled and directed jumping. This behaviour maximises jumping distance and control by placing the legs in an optimised pattern before takeoff. As indicated by the decreased takeoff time, the spiders are able to utilise the muscular power of their legs in a shorter period of time that may result in slightly higher accelerations.

Sens (1996) analysed fast movements of large bird spiders and found that in these species, the ‘jump’ is not driven by hydraulic leg extension, but by flexion of the anterior legs. This might be due to scaling effects. Geometrically similar spiders should be able to generate the same prosomal pressure (Parry and Brown 1959b). Ignoring fluid viscosity, the equilibrium of inertia with the driving torque and similar internal pressure should result in about the same takeoff velocity for small and large animals. Animals with more compact legs, i.e. lower slenderness (leg length divided by diameter) should have an advantage. If viscosity comes into play, the pressure at the joints needs time to build up. Thus, the advantage of the larger leg diameter that reduces the flow impedance is offset by the necessity to fill the higher joint volumes. This has been confirmed by computer simulations (Bohmann and Blickhan 1998; Zentner et al. 2000).

The initial leg placement pattern in prepared jumps of *C. salei* closely resembles patterns described for Salticidae and jumping species of some other taxa (Ehlers 1939; Parry

and Brown 1959a). For Salticidae, Ehlers (1939) describes three different types of jumping, depending on the initial leg placement pattern: (1) jumping by rotation and extension of the third legs, (2) jumping by combined use of third and fourth legs, and (3) jumping only by extension of the fourth legs. Both Ehlers (1939) and Parry and Brown (1959a) stated that *S. pubescens* jumps solely by extension of the hind legs. According to our kinematic analyses, *C. salei* seems to use mainly the fourth and second legs for prepared jumps, with the third legs playing only a marginal role. However, without ground reaction forces, any statements about the contribution of the different legs rely merely on leg kinematics and body movements and need further verification.

Leg spine erection

Several authors observed that large leg spines become erect during rapid movement of spiders. In her study on the prey capture of *C. salei*, Melchers (1967) stated that the erection of the leg spines indicates “excitement”. Parry and Brown (1959a) are interpreting the spine erection during the jumping of *S. pubescens* as being evidence for the hydraulic mechanism of leg extension. We found that during jumping, the erection of the leg spines took place just at the same time as the body started to accelerate by leg extension. The simultaneous spine extension in all leg segments is an evidence for a simultaneous increase in hemolymph pressure in all legs. This of course holds true only if the individual spines become erect at similar pressures. However, as we squeezed isolated legs with a forceps, we could observe a nearly synchronous spine erection on different leg segments. The squeezing of the legs was done very slowly so as to not affect hemolymph flow.

Several hypotheses of a possible function of the erectile leg spines have been suggested in the past few decades. Gaubert (1892) and Rovner (1980) propose a defensive role of the spines, which are according to Rovner ‘keeping the opponent safely away from the spider’s body’. Harris and Mill (1977) on the other hand state that the spines act as pressure sensors. These two functional interpretations must of course not necessarily be contradictory. However, during the feeding of the animals, we observed that the spines became erect only during rapid movements, and not while the spiders moved slower, even if the prey they held with the chelicerae was struggling to escape. If a major role of the leg spines was a defence mechanism, then spine erection should also occur in situations like this, bearing a high risk of being injured by a still active prey. A third function might be some kind of defence against lesser threats by trying to injure them with the leg spines and avoid probably more costly biting (Isbister and Hirst 2002). However, the by far most conclusive hypothesis was elaborated recently

by Spagna et al. (2007). They derive the functional role of erectile leg spines from ground conditions in the typical habitats of the relatively small animals, often characterised by lacking continuous footholds and being full of gaps. Here, the spines increase the probability of successful contact of single legs considerably.

Global kinematics

The observed forward rotation of the body axis (Fig. 8) during takeoff might be caused by the position of the centre of mass. When the opisthosoma contributes considerably to the total body mass, the centre of mass lies closer to the petiolus, i.e. the connection between prosoma and opisthosoma (cp. Fig. 1b), whereas the centre of mass is located more anteriorly when the opisthosoma is smaller (Brüssel 1987). Assuming that the hind legs play a major role in force production during jumping, the anterior position of the centre of mass with respect to the hind coxae would cause a forward rotation of the body. If the opisthosoma was larger, causing a more posterior position of the centre of mass, the rotation would decrease or even be reversed. The animals that were used in our experiments had different sizes. However, the juvenile specimen was mostly characterised by relatively small opisthosomata and thus was quite lightweight compared to the size of their prosoma. During experiments with heavier sub-adult animals, it was much more difficult or even impossible to elicit prepared jumps.

Parry and Brown (1959a) observed a backward rotation in jumps of *S. pubescens*, which was mostly reversed during the aerial phase, presumably caused by controlled tension in the drag-line. They estimated the directions of the ground reaction force vectors and calculated the resultant joint torques in the hydraulic joints and in the proximal joint complex. Although they assumed that the ground reaction forces point to the centre of mass, by demonstrating the mentioned backwards rotation of the body length axis immediately after takeoff, they could show that the reaction forces of the crucial fourth legs are very flat and pass under the spiders' centre of mass ventrally. However, if they had neglected high rotational accelerations of the body, their calculations of the joint torques might be improved. Still hydraulic torques should dominate in jumping *S. pubescens*.

Taking into account the shape of *Sitticus* projected onto the sagittal plane, the centre of mass is likely to be located in a position dorsal to the coxae. In *C. salei*, the centre of mass is located more ventrally. Hence, if the angle of the ground reaction force vector would be the same as in *Sitticus*, the tendency to backward rotation should be decreased in *C. salei*. Only slightly steeper force vectors may even result in a forward rotation. The rate of rotation should

increase with steepness and extent of the force vectors. However, the different direction of body rotation in jumps of *Sitticus* might be caused simply by the different body shape compared to *C. salei*.

Both species seem to use their drag-line to control the aerial phases of their jumps by varying the rate of silk production. Reducing the silk production may reduce a given rotational velocity of the body. If the trajectory of the silk glands is not in line with the trajectory of the centre of mass, the decelerating force that aligns the body axis along the flight direction causes a moment of rotation. Moreover, the dorsal bending of the legs seems to stabilise body orientation as well. Adopting a posture roughly imitating a badminton shuttlecock (cp. Fig. 6) is likely to stabilise its aerodynamics (Haake 1998) and may also contribute to rapid alignment along the flight trajectory. At least two prepared jumps were considerably longer than a dimensionless mass point that would have travelled with the same initial conditions (takeoff velocity and angle). As drag should rather reduce flight distances, the specific leg posture seems not only to stabilise the flight trajectory, but also to provide a certain degree of lift enhancing the flight phase. Because the behaviour of interest are jumps down from a vantage point, it is conceivable that spiders behave similar to ants (Yanoviak et al. 2005) and are able to steer during the aerial phase by influencing their trajectory using subtle adjustments of the leg posture. Furthermore, in some jumps, fast movements of the two front leg pairs were observed during flight. These movements possibly have similar effects on the body rotation as the running-like leg movements in the aerial phase of long jumping athletes and may also influence the body orientation during flight. These factors seem to be sufficient to effectively control the body orientation and trajectory, enabling the spider to execute controlled landings. Landings are secured by fast flexion of the legs as soon as the ventral part of the prosoma or the legs tarsi touches down.

Prepared jumps

Although we observed a quite stereotypical movement pattern during prepared jumping (Figs. 7, 12), the kinematics of individual legs varied. The second and fourth legs and leg joint kinematics seemingly play a major role for the production of propulsive forces in prepared jumps. The kinematics of the leg joints of these two legs are rather similar, but leg extension in the second legs was delayed. The contact phase of the second legs ended about 8 ms after the fourth legs took off. Since leg extension lasted only some 15 ms, more than half of the second legs' extension occurred in this time span. Hence, the second legs provided a strong contribution to the acceleration of the centre of mass particularly in the late acceleration phase (cp. Fig. 6).

Therefore, the jumping movements can be roughly divided into two phases. In the first phase, the fourth legs are strongly extended while the effective lengths of the second legs remain nearly constant although their femora already have flexed. Thus, the body was pushed by the hind legs over the stiff second leg pair. During this phase, the longitudinal body axis was rotated forwards while the body moved upwards and forwards (Figs. 8, 9). When the body has moved far enough, so that the foot positions of the second legs were located posteriorly with respect to the centre of mass, the extension of the second legs began, causing further acceleration towards jumping. However, the impulse necessary for the centre of mass acceleration was divided between the fourth and the second leg pairs. Owing to the sequential activity, the overall force generation took longer and maximum forces may be kept smaller. In this way, it is possible to achieve considerable jumps with unspecialised, force-limited legs exhibiting relatively slow muscular responses (Siebert et al. 2009).

The horizontal distance from tarsus to coxa of the fourth legs exceeds that of the second (Fig. 1c). Their leg planes are largely parallel to the sagittal plane, whereas the second legs act more or less in the transversal plane. On the one hand, for optimal acceleration, ground reaction forces should point towards the centre of mass. On the other hand, least total muscle force could enable jumping might be produced with the least total muscle force by directing the ground reaction forces of the legs close to the joint centres (Alexander 1977, Full et al. 1991; Günther et al. 2004). In either case, lesser-inclined force vectors should be preferred more in the fourth legs than in the second legs (Fig. 1c). To generate such force vectors, hydraulic extension is required for both the femur–patella and the tibia–metatarsus joint.

In the following, we examine the influence of the supposed direction of the ground reaction forces on the spider legs if they are assumed to be massless. Static joint torques can be calculated as the product of the reaction force vector and its perpendicular distance to the corresponding joint centres. In the second and fourth legs, the static joint torques of the distal joints and the one of the proximal joint complex would have about the same absolute values at different ground reaction force angles (cp. Fig. 1c). Owing to the steeper position during jump, in the second legs the hypothetical force vector is also relatively steep with respect to the ground (about 86° for the chosen example), whereas in the fourth legs, this angle is about 50° . In both cases, the force vectors are assumed to pass the femur–patella joints slightly ventrally. If force vectors are steeper, the proximal muscular torque dominates. With flatter force vectors, the hydraulic torques outweigh the muscular torques. The observed forward rotation of the body axis during the acceleration phase of prepared jumps provides direct evidence that the ground reaction force vectors of the fourth legs pass

the centre of mass dorsally and therefore the coxae as well (Fig. 1c).

Acting primarily in the transversal plane the steepness of the ground reaction force vectors of the second legs depend on the extent to which the contra-lateral legs push against each other. In running cockroaches, this contra-lateral pushing is significant among the legs of the tripod with ground contact, and causes the ground reaction forces in the transversal plane to point toward the centre of mass (Full et al. 1991; Dickinson et al. 2000). If in *C. salei* second legs' forces, generated during prepared jumping, should also point more or less to the centre of mass, effective leg torques would be largely produced hydraulically.

The tibia–metatarsus joints of the hind legs performed a slight flexion in a phase when the body already was accelerating, i.e. when the femur–patella joints began their fast, continuous extension (Fig. 12f, g) and the deflection of the femora already took place. Assuming a vector of the ground reaction force as depicted in Fig. 1c, the effective lever arm and therefore the torque in the tibia–metatarsus joint is clearly larger than that in the femur–patella joint. However, the imbalance seems to be one reason for the initial bending of the tibia–metatarsus joint. Moreover, a simplified dynamic simulation (for tarantula hind legs) that considers hydraulic actuators only allow for the reproduction of the observed initial bending of the tibia–metatarsus joint (Bohmann and Blickhan 1998; Fig. 13). As mentioned previously, the simultaneous leg spine erection of all legs at the beginning of the acceleration phase indicates an overall pressure increase. The joint torque generation by hydraulic pressure is determined by both the legs' anatomy and fluid dynamics. On the one hand, especially in a bent leg, the diameters of the lacunae providing space for the transport of hemolymph to the joint regions have only small diameters (Blickhan and Barth 1985; Sens 1996). During dynamic situations, the drag of the fluid within the lacunae results in a pressure drop between leg segments (Bohmann and Blickhan 1998). Thus, there is a delay in the development of torque between the distal and the proximal hydraulic leg joint. On the other hand, the effective cross-section area of the tibia–metatarsus joint is considerably smaller than that in the femur–patella joint (Parry and Brown 1959b; Karner 1999). The faster rising and stronger extending force at the femur–patella joint, thus, may facilitate or even cause an initial passive flexion of the tibia–metatarsus joint. Such reaction had not been observed in the second legs. This may point towards a more balanced action of both hydraulically extended joints, which would require more centrally oriented ground reaction forces, increasing the hydraulic contribution.

The countermovement prior to the actual jump led to an increased flexion of the fourth legs and a more anterior placement of the second legs' tarsi with respect to the cen-

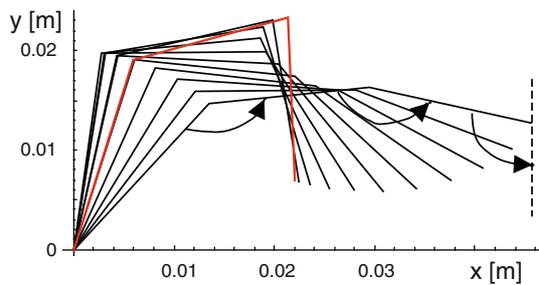


Fig. 13 Numerically modelled extension of a spider's hind leg. Starting in a rather flexed position (red) leg extension is initially provided by the extension of the femur–patella joint while the tibia–metatarsus joint is passively flexed. The latter contributes only in the late acceleration phase to the leg's extension (adapted from Zentner et al. 2000). The passive flexion of the tibia–metatarsus joint, obviously smaller in *C. salei* (cp. Fig. 12g), is probably caused by differences in the directions of the ground reaction forces (Weihmann and Blickhan 2006) that are assumed to point to the centre of mass by Zentner (colour figure online)

tre of mass. That, in turn, obviously increased the distance available for the fourth legs' elongation, i.e. acceleration, and the efficiency of the second legs acting as struts to vault over. This is even facilitated by the relatively long legs of *C. salei*. Possibly, also the effective mechanical advantage of respective muscles gets optimised compared to the situation with more extended legs (Alexander 1995). Furthermore, if flexors of the proximal joint complex are notably involved in the force generation of the fourth legs, the countermovement could have quite similar effects to human countermovement jumps, using force enhancement due to stretch of active muscles (Edman et al. 1978). The counter movement prior to prepared jumps cannot be motivated by exploring elastic mechanisms. Mammals use counter movements to improve power output in muscles connected to a serial elastic element. Following Blickhan (1986) and Sensenig and Shultz (2003), joint elasticity is low in the main joints of large spiders. In addition, joint elasticity acts parallel to the muscle and therefore cannot be used to alter the muscle's point of operation. Apodemes, as passive elements being in series with muscles, act as rather stiff towing ropes hardly affecting muscle length (Ker 1977; Ahn and Full 2002). However, even if apodemes are capable of elastic energy storage the very short muscles of the proximal joint complex have, if any, only very short apodemes (Palmgren 1978). The muscles in femur and tibia are larger and have longer apodemes. During the acceleration phase, these muscles should relax in order not to hamper leg extension. Arthropods that use catapult mechanisms and rely on elastic energy storage do load their springs for leg extension before the jump. However, they largely decouple the springs from leg extension (click mechanism) and therefore do not exploit initial counter movements (Gronenberg 1996; Burrows 2007; James et al. 2007).

Unprepared jumps

In unprepared jumps, the movements of the legs were not stereotypical (Fig. 11). In contrast, the leg movements were surprisingly variable and, apparently, depended on the direction of the stimulus that caused the escape reaction. This is supported by the radial leg arrangement in *Cupiennius*. Locusts cannot place their hind legs in such a lateral position and as the other legs are much shorter, the insect will hardly be able to jump sideward in a similar way. Furthermore, in *C. salei*, the different leg pairs have a rather similar anatomy, which suggests that any leg can provide similar propulsion. Principally, a backward-jump could just be generated by extension of the first and third leg pairs, i.e. by mirroring the pattern during the forward jump. However, this was not the case (Figs. 4, 11c). In our example, a backward-jump started from a position where the front legs were already lifted off the ground. The jump was generated by fast backward movement of the body bringing the prosoma caudal to the footholds of the hind legs and a subsequent extension of these legs supported by fast depression within the coxae. Thus, the different jumps require very different motor patterns. However, also the unprepared jumps seem to be biphasic. In a first phase, the centre of mass is shifted almost horizontally in the direction of the jump. In a second phase, the extension of the legs in the jumping direction provides the required momentum. The simultaneous rise in hemolymph pressure, as indicated by the leg spine erection, is the basis for the versatile jumping behaviour in which different legs can be used for the production of propulsive forces.

To summarise, depending on the direction of disturbance, wandering spiders are able to perform unprepared jumps in all directions with respect to their body axis. In these actions, the individual legs fulfil very different tasks. In forward-directed prepared jumps, the legs follow a distinct activity sequence. *C. salei* seems to leapfrog with the hind limbs over the second leg pair. Thereby, the kinematics of the hind legs is in agreement with simulations based on hydraulic extension. Further measurements are necessary to clarify the role of hemolymph pressure and musculature as well as the influence of the highly variable mass distribution.

Acknowledgments We would like to thank F.G. Barth (Vienna) and E.A. Seyfarth (Frankfurt am Main) for providing animals for our experiments and M. Günther (Tübingen) for valuable suggestions concerning torque generation in the spider legs. The work was supported by the Deutsche Forschungsgemeinschaft (PE 693/1-1, BI 236/9-1).

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