

RESEARCH ARTICLE

Hydraulic leg extension is not necessarily the main drive in large spiders

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SUMMARY

Unlike most other arthropods, spiders have no extensor muscles in major leg joints. Therefore, hydraulic pressure generated in the prosoma provides leg extension. For decades, this mechanism was held responsible for the generation of the majority of the ground reaction forces, particularly in the hind legs. During propulsion, the front leg pairs must shorten whereas the hind legs have to be extended. Assuming that hind legs are essentially driven by hydraulics, their force vectors must pass the leg joints ventrally. However, at least in accelerated escape manoeuvres, we show here for the large cursorial spider species *Ancylometes concolor* that these force vectors, when projected into the leg plane, pass all leg joints dorsally. This indicates a reduced impact of the hydraulic mechanism on the generation of ground reaction forces. Although hydraulic leg extension still modulates their direction, the observed steep force vectors at the hind legs indicate a strong activity of flexors in the proximal joint complex that push the legs against the substrate. Consequently, the muscular mechanisms are dominant at least in the hind legs of large spiders.

Key words: locomotion, hunting spider, hydraulics, arthropod.

INTRODUCTION

Spiders have a unique hybrid propulsive system. The femur–patella and tibia–metatarsus joints exhibit hinge axes that interconnect the respective segments at their dorsal rims (Fig. 1). Because muscles can pass these joint axes only ventrally, a muscle-driven extension is not possible. Consequently, previous research has found no extensor muscles (e.g. Ellis, 1944; Parry and Brown, 1959a; Whitehead and Rempel, 1959; Ruhland and Rathmayer, 1978). Active muscles traversing these joints induce flexion. The leg extension is achieved by hydraulic pressure generated in the prosoma (Parry and Brown, 1959a; Wilson, 1970; Anderson and Prestwich, 1975). This pressure induces a hemolymph flow into the legs. It is transmitted from the prosoma to the respective joints *via* lacunae, which are hemolymph-filled spaces between all soft tissues inside a leg. Consequently, the volume of these joints increases, which leads to leg extension (Blickhan and Barth, 1985).

In contrast to the more distal joints, the joints of the proximal joint complex, i.e. the functional hip, are flexed and extended by muscles (see Palmgren, 1978; Clarke, 1986). This joint complex consists of the coxa–body joint, the coxa–trochanter joint and the trochanter–femur joint. All of these joints are located closely together and thus it was not possible to resolve them kinematically. Nevertheless, the proximal joint complex as a functional unit is important for the power generation during locomotion.

In the late 1950s, Parry and Brown demonstrated that leg extension in spiders can be fully achieved by hydraulic pressure and that salticid jumping spiders are able to reach relatively large jumping distances solely by the use of their hind limbs (Parry and Brown, 1959a; Parry and Brown, 1959b). From their kinematic data, they concluded that hydraulics is likely to be the dominating mechanism of these spiders' jumps. Furthermore, it is known that active spiders increase internal pressure globally (Stewart and Martin, 1970; Anderson and Prestwich, 1975). Thus, for the last

decades hydraulic extension of spider legs was thought to be a major mechanism for the generation of ground reaction forces in all spiders during all kinds of locomotive behaviour. The extent of internal pressure depends on the level of activity (Anderson and Prestwich, 1975). Indicators of high internal pressure in spiders are erectile leg spines, which rise immediately prior to sudden movements such as jumps and fast starts initiating escape runs (Parry and Brown, 1959b; Rovner, 1980; Weihmann et al., 2010).

Spider legs are positioned in a roughly radial pattern. During straight level locomotion, the front legs and the second legs are directed anteriorly during the whole stride and flex in order to contribute to the animals' propulsion. The third legs start their ground contact anterior to the centre of mass and take off somewhat behind it. Thus, during ground contact, the third legs flex and extend little. They mainly rotate in the proximal joint complex to provide sufficient step lengths (Ehlers, 1939; Reinhardt and Weihmann, 2010). Only the hind legs are directed rearward throughout the entire contact phase, and extend exclusively. They extend by increasing the ventral joint angles of the femur–patella and the tibia–metatarsus joints as well as by depression of the femur towards the substrate (Weihmann et al., 2010). Consequently, it is only in the extending hind legs that hydraulic torques can generate accelerating ground reaction forces at all.

The small jumping spider *Sitticus pubescens* jumps exclusively with its hind limbs whereas the more anterior leg pairs only provide an appropriate body position (Ehlers, 1939; Parry and Brown, 1959b). After they have lost contact with the ground, the spiders rotate backwards around their pitch axis until the rotation is stopped with their spinnerets on the dragline. For the species *Phidippus princeps*, Hill achieved similar results additionally for oblique jumps down from a vantage point (Hill, 2006). Because these species of jumping spiders basically use only their hind legs for jumping, the backward rotation implies that very flat force vectors pass the centre

of mass ventrally (see Parry and Brown, 1959b). In turn, such flat force vectors can only occur if the extension of the femur–patella and the tibia–metatarsus joints is caused by hydraulics.

Only two studies have focused on the jumping behaviour of non-salticid spiders. Ehlers dealt with the locomotion of several spider taxa (Ehlers, 1939). Those he could examine with respect to their jumping behaviour besides jumping spiders themselves were species of the families Oxyopidae, Sparassidae, Clubionidae and Lycosidae, for which he could show specific preparation, i.e. a specific positioning of the legs prior the effective jump. Most of the spiders, particularly the larger species, use at least two pairs of legs to accelerate themselves into jumping. Prepared jumps of juvenile *Cupiennius salei* basically follow a similar pattern; here jumps are executed by extending first the fourth and subsequently the second leg pair. However, in larger subadult and adult *C. salei*, no prepared jumps could be found (Weihmann et al., 2010). In large specimens, the kinematics of jumps and fast starting reactions differ only in the presence or absence of flight phases. In these unprepared jumps and starting reactions, all legs contribute simultaneously to the acceleration of the centre of mass. Nevertheless, escape manoeuvres such as jumps and starts are most demanding for spiders. Thus, we assumed that the animals would use all available resources in order to flee a potential threat.

Hence, also in large spider species, we could expect an extensive utilisation of hind leg extension, which is supposedly hydraulically driven. However, a recent study suggested the presence of considerable flexing activities within the proximal joint complexes during extensions of the second and the fourth legs in jumps of juvenile *C. salei* (Weihmann et al., 2010), which are rather large animals compared with the species examined so far. Moreover, by using a numerical multi-body model, Zentner simulated spider jumps with exclusive propulsion by hydraulic hind leg extension (Zentner, 2003) (see also Blickhan et al., 2005). One major finding was that large spiders with body masses above 3 g are at risk to lose ground contact at inopportune times because of ringing within the tripartite segment chain of the legs, which results in early interruptions of the jumping sequence. The ringing can be prevented by damping antagonistic muscles. However, their activity would reduce the power of leg extension and, consequently, limit ground forces available in acceleration of the animals' centre of mass. As ringing increases with size, large spiders should not be able to take off when using hydraulics only. Taking into account the fact that large spiders (in contrast to small species) do not show distinct jumps with specific preparations and activity sequences of the leg pairs (see above), these findings raised doubts about the efficiency of the hydraulic mechanism in force generation during strong accelerations, particularly in large specimens.

Here we test the propulsive mechanism by measuring kinematics and single-leg ground reaction forces of hind legs of *Ancylometes concolor*, which is a more generalist runner, in contrast to the well-investigated species *C. salei*. The reduced set of data used here does not, admittedly, permit any evaluation of the interactions between the hind legs and the other legs. Furthermore, because of possible co-activities, we are not able to evaluate the absolute amounts of hydraulically and muscularly generated forces in the single joints. Nevertheless, the applied inverse dynamics approach allows us to identify the stronger mechanism and make a precise determination of the functioning of the major hind leg joints. If flat force vectors pass by all leg joints ventrally, then the established hypothesis of almost complete hydraulically driven extension would be supported, similar to previous findings in jumping spiders. Steep force vectors, in contrast, would indicate a stronger contribution by flexor muscles.

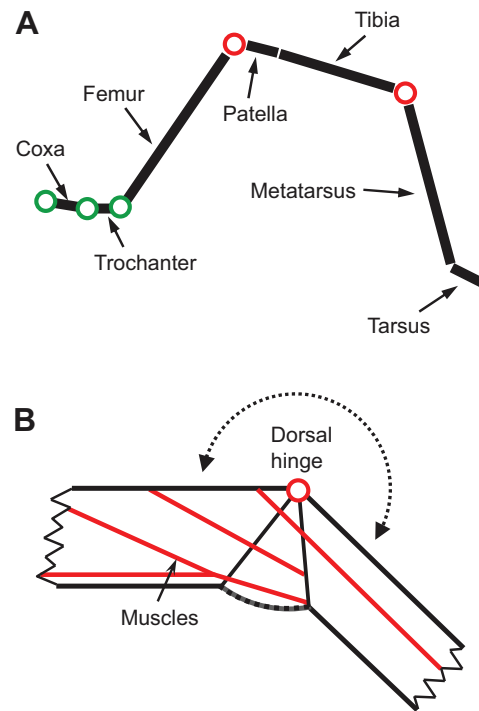


Fig. 1. (A) Sketch of a spider leg showing all segments: joints without extensor muscles are marked in red; proximal joints, which are flexed and extended directly by muscles, are marked in green. (B) Sketch of a tibia–metatarsus joint showing the major muscle paths: both the tibia–metatarsus and the femur–patella joints are hinge joints with their pivot on the dorsal edge of the leg, which precludes muscle-driven extension.

MATERIALS AND METHODS

For our experiments we recorded two-dimensional high-speed video (VDS Vosskühler HCC1000, Osnabrück, Germany) sequences of induced escape manoeuvres at 307 Hz from above and measured single-leg ground reaction forces of hind legs with a custom-made force plate at 1200 Hz. The resolution of the camera was 1024×512 pixels, so minimum tracking accuracy was approximately 0.25 mm. An accuracy of at least half that value can be assumed because the digitisation software (WINAnalyze®, Micromak Service, Berlin, Germany) that we used is able to compute sub-pixel resolutions *via* interpolating algorithms (Frischholz and Spinnler, 1993). For the experiments, we used four adult female specimens of the large South American araneomorph species *Ancylometes concolor* (Perty 1833) (mean ± s.d. body mass: 3.21±0.58 g). Because the epigynae of our specimens did not fully comply with those of the type locality, some uncertainties remain regarding their classification (see also www.ancylometes.com). Following this, the exact notation is *Ancylometes cf. concolor*.

The escape responses were initiated by waving hands, blowing air puffs or by slight touches of a soft brush onto the opisthosoma. To evoke forward directed escapes, all disturbances were exerted towards the posterior end of the spiders. Because the animals crossed the force plate in any direction, a systematic error that results in flatter or steeper force vectors can be largely ruled out. However, all errors of measurement as well as all variability in the animals' force generation are shown in the interquartile ranges shown in Fig. 2B.

We focused on accelerated straight movements such as jumps and fast starting reactions that led to escape runs. With the ground

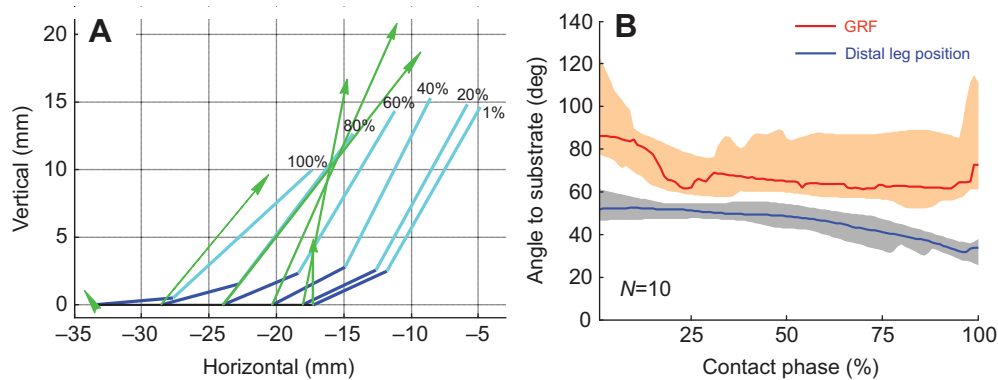


Fig. 2. (A) Ground reaction forces and kinematics of the distal hind leg of a jumping *Ancylozetes concolor*. Typical acceleration sequence of a hind limb until take-off shown in the leg plane (see Materials and methods for a definition). Albeit not shown explicitly at both axes, an interval of 10 corresponds to a force that equals the spiders body weight (mg). Reaction force vectors (green arrows) are steeper than the distal leg (cyan lines, metatarsus; blue lines, tarsus; see Fig. 3) throughout the entire acceleration phase. Percentage values at the proximal metatarsus endings denote the succession of the sequence (see Fig. 2b). The small left-most force vector pointing towards the top left corresponds to 100% stance duration and indicates gentle breaking. The x-axis originates at the centre of mass whereas the y-axis begins on the substrate surface. Increasing distances between the tarsus and the centre of mass are illustrated by a wandering tarsus. During acceleration, the spiders' centre of mass is lifted from about 6.2 mm (resting position) to 16.7 mm at maximum velocity ($0.63 \pm 0.21 \text{ m s}^{-1}$). (B) Dynamics of the hind legs in the acceleration phase of jumps and starts of *A. concolor*, showing time courses (median; $N=10$) of the angles with respect to the substrate of the ground reaction force vectors (GRF: red) and of the line from the distal tarsus tip to the proximal end of the metatarsus (distal leg position: blue). Shaded areas are inter-quartile ranges. The angle between the GRF vector and the substrate was always steeper than that between the distal leg and the substrate.

reaction forces exerted by all legs, the spiders reached accelerations of approximately $39 \pm 22 \text{ m s}^{-2}$ (mean \pm s.d.). Without discriminating between right and left legs (lateral kinematics and forces were mirrored in case of left legs), only trials of initially stationary spiders with just one hind leg on the force plate were used for the analyses. Hind legs contributed to the acceleration of the animals' centre of mass for approximately $36 \pm 6 \text{ ms}$.

To facilitate the tracking of body axis and centre of mass trajectories, we glued marker points on the anterior and posterior ends of the prosoma. The posterior marker approximately indicated the position of the centre of mass (Brüssel, 1987). All markers were digitised with WINAnalyze[®] 1.3 software. Additionally, we measured the lengths of the major functional leg segments (tarsus: $5.5 \pm 0.4 \text{ mm}$; metatarsus: $12.8 \pm 0.8 \text{ mm}$; tibia+patella: $15.5 \pm 1.0 \text{ mm}$; and femur $12.8 \pm 0.7 \text{ mm}$; see Fig. 1A) with a dissecting microscope. From these lengths plus the tip position of the corresponding tarsus and the projected segment lengths taken from the video sequences, we determined the segment angles and joint positions of the distal leg with respect to the ground. All data were processed in MATLAB 7.4.0 (The MathWorks, Natick, MA, USA). Considering the maximum angles of the distal leg of approximately 60° with respect to the ground (see Fig. 2B) and segment length as given above, digitisation errors of 1 pixel would result in maximum angular errors of only approximately 1° .

The force plate was embedded in the running track and covered by sandpaper to provide sufficient traction. Our custom-built miniature force plate allows for the measurement of three-dimensional ground reaction forces. With mean maximum vertical forces of approximately 56 mN , the signal-to-noise ratio was approximately 28:1. Similar ratios were achieved for the horizontal forces while crosstalk was even lower. The force plate was very similar to that described by Biewener and Full (Biewener and Full, 1992). It consisted of a rectangular brass frame. Thin ductile beams were milled out at all four corners such that they were arranged perpendicular to each other. The brass beams were equipped with semiconductor strain gauges, which were configured in Wheatstone half bridges and amplified by a commercial amplifier (DMCplus,

HBM, Darmstadt, Germany). The sensitive area of the force plate was approximately $18 \times 23 \text{ mm}$, enabling the measurement of single-leg ground reaction forces. Its natural frequencies were 220 Hz for the vertical and 205 Hz for both horizontal directions. To eliminate noise and ringing, we applied a 128th-order windowed linear-phase finite impulse response (FIR) low-pass filter on all force data (fir1.m from the signal processing toolbox in MATLAB). The high filter order was chosen to achieve a steep filter slope. The cut-off frequency was 120 Hz . After filtering, all ground reaction forces were normalized to body weight (mg , where m is mass and g is acceleration due to gravity). Maximum vertical forces were approximately 1.8 ± 0.29 times body weight, maximum horizontal forces in the direction of leg extension were approximately 1.1 ± 0.38 times body weight and maximum horizontal forces perpendicular to the leg plane were approximately 1.1 ± 0.39 times body weight, whereas force maxima occurred at different instants.

To test the significance of the hydraulic mechanism during thrust generation, it was necessary to measure the direction of the ground reaction force vector with respect to the leg segments within the leg plane. A leg's plane is defined as the plane that can be spanned between the major leg segments (see Cruse and Bartling, 1995). Any leg extension occurs in this plane. In legs with more than two segments, such as the roughly three-segmented spider legs, it can be difficult to fix this plane clearly if joint axes are not parallel to each other. However, because leg extension in the hind legs of *A. concolor* occurs predominantly in the femur–patella and tibia–metatarsus joints and these joints' axes are essentially parallel to each other, the major functional leg segments (tarsus–metatarsus, tibia–patella and femur; see Fig. 1A) are all in the same plane. Consequently, the axes of the femur–patella and tibia–metatarsus joints are perpendicular to that plane. Although during pushing *A. concolor* did not hold their hind legs parallel to the sagittal body plane, as was previously observed for jumping spiders (Parry and Brown, 1959b), the hind legs were held almost perpendicular to the substrate, just as in jumping *C. salei* (see Weihmann et al., 2010). Knowing this, the three-dimensional position of the metatarsus

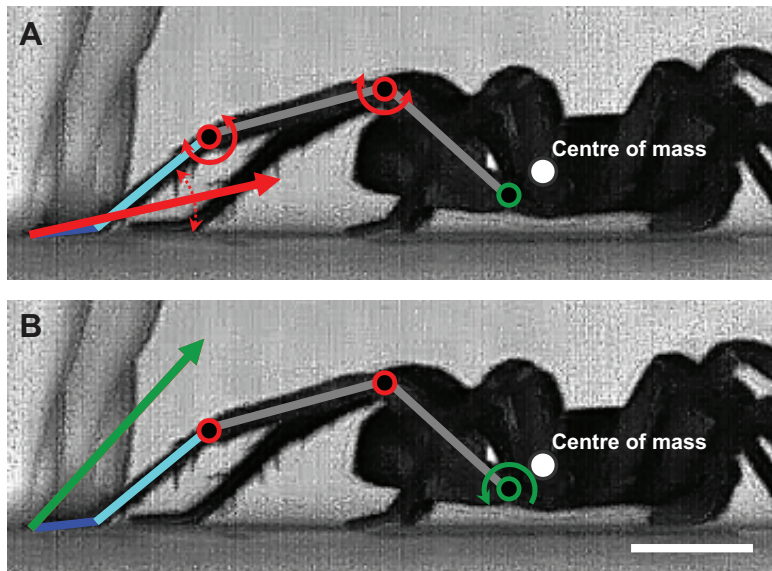


Fig. 3. Side view of the initial phase of a jump of *A. concolor* just after internal pressure has been raised (indicated by erected leg spines). (A) If power generation of the hind limbs is dominated by hydraulics, because of extension of the femur–patella and tibia–metatarsus joints (curved red arrows), flat force vectors (large red arrow) are to be expected (see Materials and methods) (see Günther et al., 2004). Green circle, muscle-driven proximal joint complex; red circles, joints without extensor muscles; cyan line, metatarsus; blue line, tarsus (see Fig. 2A). (B) If hydraulics plays no major role in the generation of the hind legs' ground reaction forces, caused by strong femur depression (green curved arrow), steep force vectors (large green arrow) that pass the hydraulically extended leg joints dorsally are to be expected. Our results (see Fig. 2) agree with this situation. Scale bar, ~10 mm.

sufficiently determines the orientation of the entire leg plane. Thus we considered the plane spanned between the line from the tarsal tip to the tibia–metatarsus joint and the vertical projection of this line onto the ground as equivalent to the leg plane. We determined the position of this plane for all instants throughout the period of thrust generation and considered only those fractions of the horizontal forces lying in this plane. The coordinates in Fig. 2A are shown in a body fixed coordinate system, i.e. increasing distances between tarsus and centre of mass caused by the extending leg and accompanied acceleration of the spiders' body are illustrated by a wandering tarsus.

Accounting for the specific morphology of spider legs, we strive to evaluate our data by means of an inverse dynamics approach according to a model suggested by Günther et al. that allows for analyses of arbitrary configurations of multi-segmented legs acting in a two-dimensional plane (Günther et al., 2004). If, in the leg plane, a ground reaction force vector passes a certain joint axis ventrally, then an extensor torque acts in the respective joint and, *vice versa*, a flexor torque acts for a ground reaction force vector passing dorsally [see fig. 1 and corresponding figure legend in Günther et al. (Günther et al., 2004)]. This is valid as long as all leg segments are in static equilibrium. It is still valid as an approximation if all inertial forces and torques of the leg segments can be neglected compared with the ground reaction force and joint torques, respectively. The mechanical calculations of Günther et al. are generally applicable for open chains of rigid bodies such as spiders' legs, irrespective of ground reaction forces exerted by other legs (Günther et al., 2004) (see also Günther et al., 2003). Following their reasoning, the ground reaction force vector is transmitted unchanged to the proximally adjacent segment (action=reaction) if we assume static force equilibrium. Thus, the perpendicular distance of the joint position to the leg force vector multiplied by the absolute value of the latter is the corresponding joint torque. The side on which the vector passes by the joint determines the sign of the torque (flexion/extension). Consequently, the ratios of the perpendicular joint distances to the leg force vector mirror the corresponding ratios of the joint torques. Therefore, according to the specific anatomy of the spider's legs, we can conclude decisively that an extension torque in any joint means that hydraulic torque contributions exceed those of the (flexor) muscles crossing this joint.

RESULTS

In contrast to jumping spiders, we found that the body axis of *A. concolor* rotates forward during flight (see also Weihmann and Blickhan, 2006). Accordingly, this requires force vectors to pass the spiders' centre of mass dorsally. However, both dominating hydraulics and forward rotation could be found in the case of the force vectors passing dorsally to the centre of mass but ventrally to the joints examined (Fig. 3A). The observation of body rotation alone is obviously not sufficient to determine whether hydraulics play a major role in the power generation of the hind legs of *A. concolor*, particularly if allowing for the other legs to exert ground reaction forces simultaneously.

For our analysis it was necessary to determine the point of force application of the hind limbs throughout the whole acceleration phase. The joint angle between the distal segments tarsus and metatarsus was almost constant (140.3 ± 1.8 deg), and the distal end of the metatarsus rarely touched the substrate (Fig. 2A). Therefore, forces were always applied at the tip of the tarsae. Consequently, it was sufficient to compare the force vector acting at the tip of the tarsae with the line from the very tip to the tibia–metatarsus joint (see Fig. 2).

However, as hind legs are maximally flexed in the initial acceleration phase, the maximum angle of the distal leg with respect to substrate can be found at this instant. The minimum angle of the ground reaction force with respect to the ground occurs later. Thus, in our experiments the force vectors exerted by the hind limbs were consistently steeper than the distal leg segments (Fig. 2B, Fig. 3B). For the 10 trials analysed, no overlap of the interquartile ranges of both measures could be determined.

DISCUSSION

Such steep force vectors are only possible if a potential muscular contribution within the femur–patella and the tibia–metatarsus joints exceeds the hydraulic torque contribution within each joint. As the ground reaction force vectors pass all joints on the dorsal side at all instants during thrust generation, all net joint torques must be flexor torques [see Results and Günther et al. (Günther et al., 2004)]. Therefore, for spiders' bow-shaped legs with force vectors steeper than the line from the tarsal tip to the tibia–metatarsus joint (Fig. 2), we can state that the more proximal a joint the higher the joint torque.

Thus, in the hind legs of *A. concolor*, muscular (flexor) torque contributions exceed hydraulic (extensor) torque contributions in any joint throughout the entire period of force application. However, if the animals did not use hydraulics at all, force vectors would be even steeper. Thus, apparently, large spiders still use hydraulic torques. Although hydraulics are globally active during accelerated locomotion like in starts and jumps, large spiders apparently do not use it primarily for propulsion.

It remains to be determined why the hydraulic mechanism has evolved in spiders at all. Regardless of whether spider ancestors were small or rather larger animals, the reduction of extensor muscles in the distal limb segments provides considerable space inside the exoskeleton suitable for flexor muscles (Anderson and Prestwich, 1975). Thus, the generation of strong flexion forces seems to be one of the main advantages of reduced extensor muscles. These flexions can be used to both overwhelm large prey and generate propulsive forces in the frontal leg pairs.

Hydraulic pressure acting simultaneously with active flexor muscles, i.e. as a kind of co-contraction, may increase the stiffness of the tibia–metatarsus joints. Using a numerical multi-body model to simulate a spider's jump generated by extension of the hind legs only, Zentner demonstrated that large animals, with body masses above 3 g, should not be able to take off using hydraulics alone (Zentner, 2003) (see also Blickhan et al., 2005). This is partly because antagonistic muscles must be activated to damp segmental oscillations. Without this muscular damping, ground contact is lost early (see Introduction). Joint stiffness and dampening were found to be crucial for a coordinated leg extension and effective acceleration of the body.

The hydraulic mechanism obviously provides sufficiently strong torques for substantial propulsive contributions of the hind legs in small spiders (Parry and Brown, 1959b). In large spiders such as *A. concolor*, the advantage of strong leg flexion remains valid. Here, during jumps and starts, the net propulsive power is shifted more to their front legs. In contrast to jumping spiders, the ground reaction forces of the frontal legs and the second legs are as strong as those exerted by the hind legs. The ground reaction forces of these leg pairs are directed mostly parallel to the substrate (Weihmann and Blickhan, 2006). They propel the spiders' centre of mass almost completely in the direction of motion. The hind legs generate strong vertical forces that lift the centre of mass off the substrate. Yet, the propulsive power of the hind legs is not fully eliminated because the force vector is still always directed frontally. It seems that depending on the spider's body size both hydraulics and muscular leg flexion contribute, to variable degrees, to the propulsion of the hind legs. Accordingly, we suppose that the distribution of flexor muscle activity across all legs and leg joints might vary with body size and the number of active leg pairs in order to optimise jumping distance, control (such as to prevent excessive rotation during flight) and the degree of target orientation.

In all small, fast-running animals, the time span that muscles need to reach appropriate tension succeeding an excitatory action potential and the time span these muscles need to relax are relatively long compared with stepping frequency. This way, a typical stance phase in cockroaches running at approximately 0.2 m s^{-1} lasts for approximately 60 ms. The time from the onset of the stimulation until the contraction has ceased back to 10% of its peak force is at least 50 ms (Ahn and Full, 2002). Hence, the locomotor system of cockroaches must be delicately tuned in order to avoid synchronous activity of antagonistic muscles and, therefore, wasting of physiological energy, particularly at higher running speeds. It has been shown that at least some spider leg muscles have relatively

low contraction speeds (Siebert et al., 2010), thus in spiders the problem could be even more critical. One way to avoid such unfavourable interactions is to replace one of the antagonists by a passive structure, and indeed several arachnid orders, such as those that include harvestmen, solpugids and whip scorpions (Sensenig and Shultz, 2003), have such structures. In various major leg joints, each of these groups reuses mechanical energy for leg extension, which was originally generated by muscles during leg flexion and stored temporarily in elastic transarticular sclerites. In spiders, the function of the elastic sclerites seems to be transferred to the hydraulic mechanism. Here, the tonic and therefore very efficient musculature of the hydraulic pressure pump in the prosoma generates adequate extensor torques in all femur–patella and tibia–metatarsus joints simultaneously. Thus it permits the extension of a certain leg whenever counter forces are low, irrespective of whether the forces are internal or external. Hydraulics are obviously needed for sufficiently fast extension of the frontal leg pairs during swing. This task is crucial for continuous running but needs only weak joint torques, whereas strong hydraulic torques could strongly impede the flexion of the frontal legs during their stance phases. Thus, in regularly running spider species or in species that jump with all legs synchronously, strong hydraulic joint torques might be obstructive for strong accelerating forces of the frontal leg pairs. In contrast, the insignificance of the frontal legs' flexion for the acceleration of the centre of mass in jumping spiders makes strong hind leg extension necessary, but also enables strong hydraulic hind leg extension without hampering the other legs. Still, according to our results, *A. concolor* is able to execute occasional escape jumps adequately with only small hydraulic contribution.

Our experiments are the first to examine the use of hydraulics in a physiologically relevant motion scheme by relating direct measurement of ground reaction forces and corresponding kinematics. To find appropriate strategies for the use of hydraulics in spiders, we focused on fast, accelerated movements as those are the most demanding for the animals. Further examinations considering the scaling principles of the semi-hydraulic locomotive apparatus in spiders may help to better localise its limits, understand its design criteria and support convergence of the design of small hydraulically driven walking machines and other robots to the degree of sophistication found in biological examples.

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