The jumping behavior of jumping spiders: a review (Araneae: Salticidae)[1]

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Information related to the jumping behavior of salticid spiders is scattered across a number of different publications. Popular books sometimes cite their ability to jump *more than 20 times* their body length (Dalton 2008) or much further, without any reference to the direction of those jumps. Anyone who has observed these spiders knows that they frequently jump to reach sighted objectives, or to capture prey. Different species vary in their reliance on jumping as a means of locomotion, and they can jump in different ways. This review has been written to collect and to review information about this jumping behavior, to make it readily accessible from a critical perspective. For more detailed information you should read the original papers.

Targeting. Salticids target both nearby positions on plants, or their prey, with accurate jumps. For *Phidippus* and other salticids, distance and direction relative to gravity (inclination of a direction) represent important infomation with respect to both detoured pursuit and targeted jumps. The feasibility of a jump is evaluated by jumping spiders based on not only its distance, but also the inclination of its direction (Hill 1978, 1979, 2007, 2010a). Within limits both the magnitude and direction of take-off velocity can be calibrated to attain the required range of a jump. Thus a salticid will jump further above and at a greater velocity to reach a target at either a greater distance or a greater inclination (higher) with respect to gravity. They can also jump from many different starting positions, to include horizontal jumps from a horizontal platform, sideways jumps from a vertical platform, upside down jumps, or any intermediate position. Jumps are generally initiated with backward pitch (anterior end rotates up and toward the rear), but may also include a component of sideways roll to return the spider to a horizontal (dorsum up) orientation when jumping off of a vertical surface (Hill 2006, 2010b). Some salticids including *Colonus* can even flip around the end of a leaf to capture prey hidden beneath it, and their jumps can accurately target specific features of the anatomy of their prey (Hill 2012, 2018). Salticids can jump from the top of a one leaf up to the bottom of another leaf, they can jump backwards if startled, and they can make a free-fall jump without a dragline to escape predators. The kinematics of most of these behaviors have not been studied.

Function of the legs. The jumping kinematics of only a few species of salticids have been studied and we still have much to learn (Table 1). Salticids extend their legs III and/or IV against a surface to exert the ground force required to generate the *equal but opposite* ground reaction force that propels their ballistic flight The relative length of salticid legs varies considerably between genera and this provides a major clue with respect to their function. In general salticids with longer legs IV, including *Colonus*, *Phidippus* and *Sitticus*, power their jumps primarily by flexing legs IV in a parasagittal plane and then extending these. Ground-dwelling salticids with longer legs III, including *Habronattus* in North America and *Maratus* in Australia, rely mostly on flexing legs III in a more transverse plane prior to their extension.

Male spiders of both genera also display legs III during courtship (Otto & Hill 2012). Spiders from some genera, like *Jotus*, power their jumps with both pairs of hind legs, III and IV, which are of approximately the same length. They rely more on legs IV for horizontal jumps and more on legs III, more directly under the center of gravity, for vertical jumps (Otto & Hill 2016). *Phidippus*, relying almost exclusively on legs IV for power, can position the feet of these legs, when flexed, directly under the center of gravity to support a vertical jump off of a surface (Hill 2010b).

Salticids in general form an attachment disk for their dragline and raise their legs I and II prior to a jump. For species that power jumps with legs IV, legs III serve as a fulcrum during take-off (Hill 2010b). Species that power jumps with legs III can rock forward with legs IV to position the direction of acceleration as legs III are subsequently extended (Otto & Hill 2013).

There are published statements suggesting that both *Phidippus regius* (Nabawy et al. 2018) and *Salticus scenicus* (Parry & Brown 1959b) power their jumps with both leg pairs, III and IV. These are based on the observation that legs IV may leave a surface before legs III. I recently measured the kinematics of a horizontal *S. scenicus* jump recorded with high speed video and found that virtually all acceleration of this spider took place before legs III began to extend, and was thus the result of extension of legs IV as in many other spiders (Table 1). However the kinematics of jumps using both pairs of legs by *Jotus* are well-documented (Otto & Hill 2016).

Table 1. Published records relating to the use of legs to power the jumps of salticid spiders.

reference	summary
Parry & Brown 1959b	Jumps by *Sitticus pubescens* are powered by extension of legs IV in a parasagittal plane. Legs III and IV are both used in the jumps of *Salticus scenicus* as legs IV leave the surface after legs III.
Hill 2006, 2010b	Legs I and II of *Phidippus princeps* are raised prior to acceleration, and legs III serve as a fulcrum to guide jumps powered by extension of legs IV in a parasagittal plane. In preparation for a jump the orientation of the flexed legs IV varies according to the relative direction of a jump, with the feet positioned under the center of gravity for vertical jumps.
Hill 2012, 2018	Legs I and II of *Colonus puerperus* and *C. sylvanus* are raised prior to acceleration, and legs III serve as a fulcrum to guide jumps powered by extension of legs IV in a parasagittal plane.
Otto & Hill 2012	*Maratus* flex legs III, generally in a transverse plane, and raise legs I and II prior to a jump. Forward rotation of legs III at the coxa-trochanter-femur is required to accelerate forward rather than just upward as a result of leg III extension. Legs IV are extended at the start of a jump and may contribute some ground force. *Habronattus coecatus* power jumps with extension of their long legs III, also flexed in a primarily transverse plane.
Otto & Hill 2013	*Maratus watagansi* flex legs III and raise legs I and II prior to a jump. A male *M. watagansi* rocked forward with extension of legs IV for ~8 ms producing ~5 cm/s forward velocity before the longer legs III extended for ~8 ms resulting in an upward and forward take-off velocity of 92 cm/s.
Otto & Hill 2016	*Jotus auripes* and *J. remus* power their jumps by extension of both legs III and IV. Legs III contribute more to vertical acceleration, and legs IV more to horizontal acceleration, and both legs are of similar length. In one example (male *J. auripes*) extension of legs IV accelerated the spider to ~60 cm/s in 9 msec, followed by extension of legs III and IV to accelerate to ~70 cm/s in the next 2 msec, followed in turn by extension of only legs III to ~80 cm/s over the next 5 msec.
Nabawy et al. 2018	Legs III and IV were used by a *Phidippus regius* during jump but relative contribution could not be determined.
Hill (new information)	Legs I and II were raised prior to acceleration, and legs III served as a fulcrum to guide the horizontal jump of a female *Salticus scenicus*. Detailed high speed video analysis revealed that, although legs III and IV were extended during the take-off, all acceleration was associated with the extension of legs IV and not the subsequent extension of legs III.

***Mechanism of leg extension* (Table 2).** The three most important joints that must be flexed and then extended to accelerate a jumping spider during the take-off phase of a jump are the trochantofemoral, femoropatellar and tibiometatarsal joints (Parry & Brown 1959b; Hill 2010b). Of these three only the trochantofemoral joint is equipped with extensor muscles in spiders (Parry 1957; Weihmann et al. 2010, 2012). Elasticity at the femoropatellar and tibiometatarsal joints cannot account for extension at these joints (Ellis 1944) and this extension, in opposition to flexor muscles that are present, is driven by internal fluid pressure that increases respective joint volume within each leg (Parry & Brown 1959a; Reußenzehn 2010). Nabawy et al. (2018) suggested that muscle mass in the legs of *Phidippus regius*, perhaps augmented by fluid pressure (not viewed as necessary), could deliver the energy required for leg extension during a jump. However this model does not account for the need to generate sufficient torque at each joint of the leg in turn in order to deliver ground force through the foot, thus generating the ground reaction force required to propel a spider in the opposite direction (Parry & Brown 1959b; Hill 2010b). In the absence of internal fluid pressure the entire leg cannot extend. Extensors that insert inside the femur can only extend the leg at the trochantofemoral joint, but they cannot inflate and extend the large femuropatellar joint and the smaller tibiometarsal joint. It has been proposed that elimination of extensors at these joints in spiders and related arachnids allowed more space within each leg to be used for the flexor muscles that play a large role in the capture of prey, particularly since there are many different segments within each leg (Anderson & Prestwich 1975; McDonald 2014).

Earlier workers (Wilson 1970; Anderson & Prestwich 1975) thought that fluid pressure in the legs was driven by compression of the prosoma by means of the *musculi laterales*, but more recently this prosomal compression has been thought to be driven by the contraction of dorsal, dorsolateral and ventral endosternal suspensors (Schultz 1989, 1991, 1992, 1993; Hill 2010b). Kropft (2013) considered the identity of muscles responsible for prosomal compression to be unresolved, but in any case there is general agreement that prosomal compression does control the internal fluid pressure of the prosoma, legs, pedipalps, and inflatable macrosetae simultaneously. This includes generation of the very high transient pressures associated with activity ($\sim$60000 N/m^2; Parry & Brown 1959a; Anderson & Prestwich 1975). Other muscles not associated with extension also play an important role in the positioning of the legs prior to and during a jump, whether this involves flexion of the leg segments or movement of the entire leg between the prosoma and femur (Parry 1957).

The kinetic energy that determines the magnitude of take-off velocity is the integral of ground reaction force (equal to applied ground force in magnitude) with respect to the *distance* through which this force can be applied. The distance associated with take-off is directly related to the length of the legs that are extended. This is supported by the observation that the legs that are extended to accelerate a jumping spider tend to be longer. In the case of spiders that jump with legs III and IV, the cumulative take-off distance can also be increased by beginning a jump with one pair and subsequently completing a jump with the second pair, as has been observed in *Jotus* (Otto & Hill 2016).

Table 2. Studies related to the mechanism of spider leg extension.

reference	summary
Ellis 1944	In the absence of extensor muscles, elasticity of joint membranes cannot account for leg extension. This extension is instead closely associated with changes in hydrostatic pressure in the legs.
Parry 1957	*Tegenaria* lack femuropatellar and tibiometatarsal extensors, and these joints can be extended by the application of hydrostatic pressure to legs, but extensor muscles are associated with the trochantofemoral joints.
Parry & Brown 1959a	Hydraulic pressure in the legs of *Tegenaria* generates the torque required to extend femuropatellar and tibiometatarsal joints when loaded with weight. When stimulated transient pressures in legs ranged from 11-45 cm Hg (14665-59995 N/m^2). Pressure changes in the prosoma were transmitted to multiple legs simultaneously.
Parry & Brown 1959b	Blood pressure throughout the prosoma and appendages must increase just before acceleration as the leg spines are all erected at the same time. Estimated extension torque at femuropatellar and tibiometatarsal joints during acceleration is significant.
Wilson 1970	Study of five spider species showed that the *musculi laterales* of the prosoma and a subcuticular muscle sheet of the opisthosoma might be responsible for the hydrostatic pressures required to extend the legs. The prosoma is compressed when a spider becomes active.
Anderson & Prestwich 1975	In a study of *Filistata* it was found that the *musculi laterales* of the prosoma were responsible for changes in fluid pressure responsible for leg extension. Fluid pressure in the legs ranged from 4000-6700 N/m^2 in resting or walking spiders, and as high as 61000 N/m^2 in startled spiders. Fluid pressure in the opisthosoma was lower, from 1000-4000 N/m^2. Use of hydraulics for leg extension may allow a greater mass of flexor muscles in the legs, muscles used for prey capture.
Clark 1986	Reviewed morphology and movement at leg joints of five different spider species.
Schultz 1989, 1991, 1992, 1993	*Mastigoproctus* (Uropygi) and spiders (Araneae) lack femuropatellar and tibiometatarsal extensors and extend these joints with hydraulic pressure generated by dorsoventral compression of the prosoma by dorsal, dorsolateral and ventral endosternal suspensor muscles.
Sensenig & Schultz 2003	The tibiometatarsal and femuropatellar joints of the theraphosid spider *Aphonopelma* never extended elastically after flexion, but the metatarsotarsal joints did.
Reußenzehn 2010	In a study of *Dolomedes* legs, measured and produced predictive mathematical models that correlated leg extension with increases in joint volume.
Hill 2006, 2010b	Legs IV of *Phidippus princeps* are flexed and then extended at the trochantofemoral, femuropatellar, and tibiometatarsal joints during acceleration (take-off) to exert force against the underlying surface. Endosternal suspensors are thought to generate hydrostatic pressure required for jumps.
Weihmann et al. 2010, 2012	Kinematic analysis of leg (proximal femur to distal metatarsus) movement during forced jumps by *Cupiennius* revealed that extension at the femuropatellar joint preceded extension at the tibiometatarsal joint. At least in large spiders the basal segments (body to coxa to trochanter to femur) of each leg appear to be moved by flexors, but these are lacking in distal (femuropatellar and tibiometatarsal) joints that are extended by fluid pressure.
Kropf 2013	We still do not fully understand which prosomal and opisthosomal muscles are responsible for internal fluid pressure. The prosoma is compressed to raise this pressure. There are no extensors at the tibiometarsal joint of spiders, and each tibia is filled with flexor muscles. Articular membranes at joints are pleated to regulate torque at these joints.
McDonald 2014	With many segments per leg spiders lack space for both extensors and flexors, so they use hydrostatic pressure produced in the prosoma for extension. Hydraulic models for spiders or spider limbs that are easily constructed are also described and a related paper is linked.
Nabawy et al. 2018	By itself leg muscle mass is sufficient to deliver the power required for jumps by *Phidippus regius* but hydraulic augmentation may be present.

Jump velocity and range. There have been many popular references to the distances attained by a salticid as it jumps, although accuracy seems to be the real priority for these spiders (Hill 2010b). The concept of *how far can a spider jump* has no meaning without reference to direction, as any animal can jump (or fall) a long way down. More meaningful concepts to be used in comparisons are *horizontal*

range (the distance that a spider can jump on a horizontal surface) and take-off velocity (both magnitude and direction or inclination in a gravitational field). Take-off velocity is a direct function of ground reaction force and take-off distance, but it can also be augmented by gravity. Acceleration during a downward jump can be greater because the force of gravity can contribute to it for ~8 msec. Thus it is significant that jumps of *Phidippus princeps* are actually *slower* when the target is in a lower position. As long as the range is sufficient these spiders do not maximize the velocity of their jumps. Instead they increase the magnitude of the velocity of their jumps, and the inclination of those jumps relative to (or above) a target to accommodate a greater distance or a greater inclination (elevation) of that target (Hill 2006, 2010b). In a recent study of jumps by *P. regius* between horizontal platforms Nabawy et al. (2018) suggested that these spiders jumped at a lower inclination (*low angle trajectory*) to minimize flight time during short jumps, and used a higher inclination (*high angle trajectory*) to minimize energy during longer jumps. However since *P. princeps* jump at a significantly lower speed to complete shorter jumps, they clearly are not minimizing flight time on these jumps. On longer jumps a take-off inclination approaching 45°, the inclination required to minimize kinetic energy required for a jump, was only observed when this inclination was required to reach a more distant target. It appears that they only jump faster and higher to reach an objective if they need to do so (Hill 2006, 2010b).

Salticids have been known to jump at 78-99 cm/s (Table 3), corresponding to a horizontal range of about 10 cm. I recently recorded a horizontal distance of ~15 cm for a 6.2 mm male *Colonus puerperus*, for a shallow jump at an inclination close to 20°. This corresponds to a take-off velocity of ~152 cm/s and a horizontal range of ~23 cm, or ~38 times the length of the spider. *Colonus* move slowly but jump very quickly to attack their spider prey (Hill 2012, 2018).

Table 3. Records pertaining to the range of jumps by salticid spiders.

reference	summary
Parry & Brown 1959b	Estimated take-off velocity of intact (no legs removed) *Sitticus pubescens* ranged from 75-78 (±8) cm/s.
Hill 2006, 2010b	The take-off velocity of *Phidippus princeps* jumping toward a stationary platform at a distance of 3-6 cm ranged from 44-92 cm/s, with significantly faster jumps when the target was at a greater distance, and significantly slower jumps when the target was below the spider rather than horizontal. These jumps were inclined from 3-35° above the target, with more distant or more horizontal jumps at a greater inclination relative to the target. Take-off velocity of jumps toward prey at an inclination of -60° ranged from 53-79 cm/s at an inclination of 3-32° above the target, with greater velocity and inclination associated with longer jumps. With prey at a fixed distance of 6 cm, jumps ranged from 53-83 cm/s at an inclination of 0-40° above the target, again with greater velocity and inclination associated with longer jumps. Jumps toward prey were significantly faster than jumps toward a stationary target at 60°, with the fastest jump recorded at 87 cm/s.
Otto & Hill 2012	A female *Habronattus coecatus* jumped with a take-off velocity of ~80 cm/s.
Otto & Hill 2013	A male *Maratus watagansi* jumped upward and forward with a take-off velocity of 92 cm/s.
Chen et al. 2013	Take-off velocity for jumps by *Hasarius adansoni* was 99±13 cm/s (N=15).
Otto & Hill 2016	Male *Jotus remus* completed horizontal jumps between platforms with a take-off velocity of ~79 cm/s and an inclination of 18.4° above horizontal. The take-off velocity of horizontal jumps by male *J. auripes* ranged from ~80-90 cm/s.
Nabawy et al. 2018	Take-off velocity of 52-97 cm/s was recorded for *Phidippus regius* jumping horizontally to a stationary platform with a near ballistic trajectory in flight
Hill (new information)	Horizontal jump distances of a fleeing 6.2 mm male *Colonus puerperus* were recorded by marking successive positions on paper. These ranged from 10.6 to 15.1 cm, corresponding to a minimum take-off velocity of 102-122 cm/s assuming an inclination of 45°. The inclination of these jumps was estimated at 20°, corresponding to a take-off velocity of 127-152 cm/s. The maximum velocity corresponds to a maximum horizontal range of ~23 cm at an inclination of 45°, or ~38 times the length of the spider.

Pitch and braking with the dragline. Unless they are in free fall, salticids tend to brake on their dragline as they approach the end of a jump (Hill 1978, 1979, 2007, 2010a). Acceleration during each take-off launches a jumping spider onto a ballistic trajectory with a backward (front of spider moves up and to the rear) pitch that is only reversed when that spider brakes on its dragline (Hill 2006, 2010b; Chen et al. 2013; Otto & Hill 2016; Nabawy et al. 2018). *Phidippus princeps* initiated their predatory jumps with a backward pitch varying from 0.1-2.9°/msec, with significantly greater pitch associated with longer jumps up to a distance of 15 cm. The braking distance of these jumps (distance from start to initiation of braking or deceleration) ranged from 5-11 cm and also strongly correlated with the target distance (r^2=0.7084). As a result of the pitch of the flying spider the prey position was out of sight during these jumps. This braking distance, like jump velocity, must have been determined prior to the onset of each jump based on the spider's estimate of prey distance (Hill 2006, 2010b). Like the lateral and vertical turns of salticids (Land 1971; Hill 1978, 2007, 2010a; Bennett & Lewis 1979) this is a *closed-loop* (no visual feedback) performance.

When a salticid brakes at the end of a predatory jump, the legs continue to move forward to encircle and grasp the prey in a *catching basket* that can impale the prey with many spines (*macrosetae*) on the underside of the legs (Hill 2006, 2010b). Araneophagic *Colonus* jump very quickly to impale the carapace of their dangerous prey with their extended fangs, and they can also use the elastic qualities of their dragline (after braking) to recoil like a bungee jumper, pulling that prey away from a surface (Hill 2012, 2018). Similar behavior is likely in other salticids but this has not been documented.

Salticids that miss a jump can hang like a pendulum at the end of their braking distance on the dragline. Some even maintain this position as they feed on captured prey (Hill 2016). After a missed jump they can hook the dragline with one of the claws of a hind leg and climb up this dragline to recover their take-off position. As a salticid climbs up a vertical dragline, it winds this dragline up and discards it at the end of the climb. After returning to the take-off position *Phidippus* demonstrate their memory of the original direction of their prey by turning in that direction to look for it (Hill 1978, 1979, 2007, 2010a).

Jumps in the absence of gravity. Given their reliance on gravity, the question of how a salticid would behave in the absence of gravity is of considerable interest. A female *Phidippus johnsoni* on the International Space Station was observed to jump in a straight line to capture a fruit fly (*Drosophila*) at a distance of ~4 cm. This spider braked on her dragline when the prey was captured and immediately recoiled to move in a straight line in the opposite direction, not landing until she had flown several cm past her attachment disk (Hill 2016). This unique record supports the idea that many salticids, and not just the *Colonus* described previously, can recoil on their dragline at the end of a predatory jump.

Application to robotics. With the rise of robotics in recent years the mechanisms associated with salticid jumps have been the subject of considerable interest. Papers on this subject are listed in Table 4. In several papers the extension of spider legs has been analyzed and modelled with detailed mathematics to support the engineering and construction of robotic appendages that can be extended with pneumatic or hydraulic pressure. These papers should be of interest to the arachnologist since they advance the state of our modeling and understanding of the biophysics of real (not just mechanical) jumping spiders.

Table 4. Recent research relating jumping spider legs to robotic appendages.

reference	summary
Zentner et al. 2000; Zentner 2013	Developed a detailed mathematical model for the design of robot legs extended by internal fluid (hydraulic or pneumatic) pressure, based on review and mathematical modeling of the hydraulic extension of spider legs.
Luchsinger & Bräker 2010	Proposed a new kind of pneumatic actuator, based on observations related to the hydraulic extension of spider legs.
Shield et al. 2015	Developed mathematical model of a spider to show that braking on a dragline could right the pitch of a mobile robot.
Faraji et al. 2016	Developed mathematical model of a spider and robotic platform to demonstrate righting or reversal of pitch by braking on a dragline.
Landkammer et al. 2016	Comprehensive review of features of spider joints extended by internal fluid pressure, and work on biomimetic robot joints that also use internal fluid pressure following the spider model.
Abajan et al. 2017	Reviewed earlier work and future designs for robot legs extended by hydraulics after the spider model.
Spröwitz et al. 2017	Designed and successfully tested jumps by a robotic joint extended by internal flid pressure, inspired by the jumping spider model.
Zhu et al. 2018	Developed mathematical model for a six-legged robot that could jump in all directions (vertical, lateral, forward) based on the design of jumping spiders.

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