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The Fluid Pressure Pumps of Spiders (Chelicerata, Araneae)

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Summary. The identity of the fluid pressure pumps in spiders was investigated in *Filistata hibernalis* through measurements of the activity of certain muscle groups, leg movements, and changes in fluid pressure within the leg. Our results indicate the cephalothorax is the site of the pressure pump responsible for leg extension and the *musculi laterales* are the major muscles involved in the operation of this pump. Fluid pressures in the legs averaged 5100 $N \cdot m^{-2}$ in resting spiders, ranged from 4000 to 6700 $N \cdot m^{-2}$ in walking spiders and reached as high as 61000 $N \cdot m^{-2}$ in startled spiders. Intra-abdominal fluid pressures were also measured and found to be much lower, ranging from 1000 to 4000 $N \cdot m^{-2}$. These pressures are the result of activity of at least two sets of abdominal muscles, the sub-cuticular muscle sheet and the paired series of dorso-ventral muscles. We suggest the abdominal fluid pressure and the rigidity of the book-lungs attenuate pooling of the hemolymph in the abdomen when the spider is active. Finally we hypothesize that evolution of the hydrostatic skeleton in spiders has allowed a greater mass of flexor muscles to be incorporated into the legs and this in turn is an adaptation to the spider in prey capture.

A. Introduction

The observation of Petrunkevitch (1909) showing spiders lacked extensor muscles at certain leg joints prompted attempts to explain how these animals could extend their legs. Petrunkevitch (1909, 1916) himself suggested extension could be accomplished by elasticity of interarticular membranes. Ellis (1944) refuted this idea and claimed the force responsible for leg extension involved increases in fluid pressure within the appendage. Manton (1958) reviewed the subject and concluded that since the data available indicated arthropods generated low fluid pressures, hydraulic mechanisms could account for leg extension only after the tip of the leg was raised and not in contact with the ground. Parry and Brown (1959a, b), however, were able to conclusively confirm the hypothesis that leg extension was indeed the result of extraordinarily high transient pressure changes within the leg (up to 60000 $N \cdot m^{-2} \approx$ 450 mm Hg). They were also able to demonstrate the existence of pressures ranging from 5000 to 14000 $N \cdot m^{-2}$ in the legs of alert but inactive spiders; these pressures were termed resting pressures. The existence of these pressure levels in spiders has been recently confirmed by Stewart and Martin (1974).

The mechanism by which such pressures are produced has not been verified. Based on anatomical evidence, Ellis (1944) suggested a valve-like arrangement of the femur-patellar joint. He postulated that it operated by diverting hemolymph into blood vessels associated with the articular membrane at this joint, resulting in a localized rise in pressure. Parry (1957) dismissed this idea on a number of grounds. It could not explain extension at the tibia-basitarsal joint where no such arrangement exists; the muscles operating this valve would by nature of their multiple insertions also produce flexion of the joint; and finally, these muscles would compress the major nerve innervating the leg. Parry and Brown (1959a, b) proposed the high pressures recorded in the legs during extension resulted from contraction of the prosomal musculature producing compression of the contents of the cephalothorax. In addition, they tentatively suggested that the pumping of the heart was involved in the maintenance of the resting pressures recorded in the cephalothorax.

Wilson (1970) has provided the most recent discussion of the hydraulic mechanisms in spiders. In work primarily devoted to the anatomy of the musculature potentially involved in pressure generation, he confirmed the existence of a set of prosomal muscles, the *musculi laterales*, in a series of spiders. These muscles were first described in spiders by Brown (1939); they originate along the lateral margins of the carapace or dorsal shield of the cephalothorax and insert on the flexible arthrodial membrane just dorsal to the coxae of the walking legs. Wilson (1970) stated that contraction of these muscles would depress the carapace, causing a reduction in volume of the prosoma, and hence could explain the transient pressure increases involved in locomotion. Since their insertion is independent of the coxae, contraction would not interfere with normal coxal movements. Wilson was able to observe downward movements of the carapace in a stimulated spider. He also suggested that certain abdominal muscles, a sub-cuticular sheet and the paired dorso-ventral muscles are involved in the generation of pressure.

The basic aim of this study was to evaluate Wilson's hypotheses as to the identity of the pressure pumps in spiders. We felt this could be accomplished by establishing the relationships between pressure changes in the legs and abdomen with the activities of the various muscle groups responsible for movements of the carapace and abdominal wall.

B. Methods and Materials

Experimental Animals. Adult females of the species *Filistata hibernalis* (Hentz) were used for all observations and experiments. This species is locally abundant and proved to be a fortunate choice for a number of reasons. They were remarkably insensitive to the various procedures utilized in this study; they did not bite when handled; and, perhaps most important, their relatively slow rates of the reactions under study permitted more effective resolution of the time course of events.

Most of the experiments involved attempts to establish the causal relationship between generation of the pressures involved in leg extension and contraction of certain muscle groups, thus immobilization of the experimental animals was required to record such activities. For this purpose a mounting platform was constructed as follows: a flattened strip of balsa wood was inserted into the open end of a glass tube and glued in place. Smaller pieces of wood were glued onto the wooden strip in positions approximating the sternum and abdominal venter of a particular specimen. Attachment of a spider required it be anesthetized with carbon dioxide and then glued to the small wooden strips at the sternum and abdominal venter being careful not to block the spiracles of the book-lungs. The completely constructed platform with attached spider could then be arranged for various experiments by clamping the glass rod to a ring stand.

Measurement of Pressure Changes. To record the pressure changes in the leg of a spider, small manometers were constructed from 10 μl disposable pipettes. These pipettes measure approximately 4.0 cm in length and have an outside diameter of 0.1 cm. One end of the pipette was sealed by melting the glass. The tube was heated for a few minutes and then immersed to cool in a beaker of saline solution. A 440 milliosmolar NaCl solution was used. This concentration was based on analysis of the hemolymph of a number of specimens. Cooling to room temperature caused the tube to partially fill with the saline. The fluid level was marked and the open end of the tube was inserted into the cut end of the femur or, in a few cases, into the cut end of the tibia of one of the legs of an anesthetized spider (see Fig. 1). The junction between the tube and leg was quickly sealed with adhesive and the level of fluid within the tube was again marked if any change occurred. After the spider recovered from the anesthesia, any change in the fluid level was marked. Since care was taken not to disturb the spider during this interval, any detected fluid movement was considered to represent resting pressure for that individual. The spider was then stimulated with puffs of air to produce leg movement and the concomitant changes in fluid movement were marked. Upon completion of the experiment, the tube was removed from the leg and estimates of the pressure changes were calculated from the distances between the various marks on the capillary manometer.

We estimated the accuracy and precision of our pressure measurements on two different sets of capillary tube manometers. In one set we marked a group of 15 tubes at varying distances and calculated the pressure change required to move the fluid to these marks using the equation $P_2 = P_1 (V_1/V_2)$ where P and V represent pressure and volume. The capillary tubes were sealed in one end of a mercury manometer and the pressure adjusted to move the fluid from its initial level to the marks upon which the calculations were based. The average deviation between the calculated values and those measured in the mercury manometer was 7.8% ± SE of 1.3. A second set of 22 capillary manometers, representing a sample of those actually used to estimate various pressures in spiders, were treated similarly. In this case, our average deviation was 12.8% ± SE of 3.3.

Capillary manometers were also used to record abdominal pressures. The capillary tubes were inserted into the posterior lateral portion of the abdomen where damage to the spider would be minimal. We were somewhat concerned about two problems which might preclude obtaining unbiased values using this technique. First, the changes in abdominal pressures associated with locomotory activity were significantly lower than those measured from the legs. Consequently, we questioned our accuracy in marking the rapid movements of fluid in the capillary tubes. To get around this problem, we were able to obtain limited use of a Sanborn Physiological Pressure Transducer, Model 267B, to measure abdominal pressures. The pressure transducer was calibrated with a mercury manometer. A second problem of concern involved the possible distortion of abdominal pressure by the inserted capillary or catheter tube. Accordingly, we also used the indirect method of estimating abdominal pressured described by Wilson (1962). We felt our estimates of abdominal pressures based on data obtained from the different techniques would be reliable enough to come to unequivocal conclusions.

The problem of an inserted capillary significantly affecting the measurement of leg pressures did not concern us since the cylindrical nature of the tube is a reasonable facsimile of a spider leg. When such a tube is attached to the leg, it acts as a substitute cylinder for the excised section of the leg.

Muscle Group Activity. We used photoelectric force transducers from the Narco Instrument Company to record movements of the carapace, the legs, and the abdominal wall. The tension generated was transmitted to a leaf spring of the transducer by means of a thread secured to the particular portion of the spider with adhesive. The output from the transducer was recorded on a Physiograph® Four-A recording system. The records were calibrated by suspending a few known weights from the transducer at the conclusion of certain experiments.

Cardiac Activity and Histological Studies. To clearly observe cardiac activity in an immobilized spider, we found it necessary to remove the surface hairs of the abdomen in the region just dorsal to the heart. We accomplished this by gluing a thread to this region, waiting for the glue to set, and then abruptly pulling on the thread. The hairs attached to the disc of adhesive were pulled from the abdomen and we could view the beating heart through the translucent cuticle.

A few specimens were dissected to compare the musculature with Wilson's (1970) descriptions and to get estimates of the size of the hemolymph channels in the pedicel. Kahle's fluid (Kaston, 1948) was used as a fixative. Measurements of the hemolymph channels were made using a Gaetner Micrometer Slide Comparator.

Finally, a few book-lungs were preserved and sectioned using the histological procedures described by Mitchell (1964). This was done to assess the effects of their morphology on hemolymph movement.

C. Experiments, Observations and Results

Effect of Removal of Abdomen on Locomotion

The first experiment consisted of determining the effect of removal of the abdomen on a spider's ability to run. If Wilson (1970) is correct about the identity of the pressure pump responsible for leg extension, spiders so treated should be able to run normally. One group of four specimens had the abdomen separated from the cephalothorax by cutting the narrow connective piece or pedicel between these structures. A ligature was applied to the pedicel prior to cutting to maintain the hydraulic integrity of the cephalothorax. As a result of this traumatic event, the spiders, *i.e.*, the cephalothoracic portion bearing the legs, began to run. If a specimen stopped moving, it was re-stimulated with puffs of air. A control group of four spiders were treated in a similar

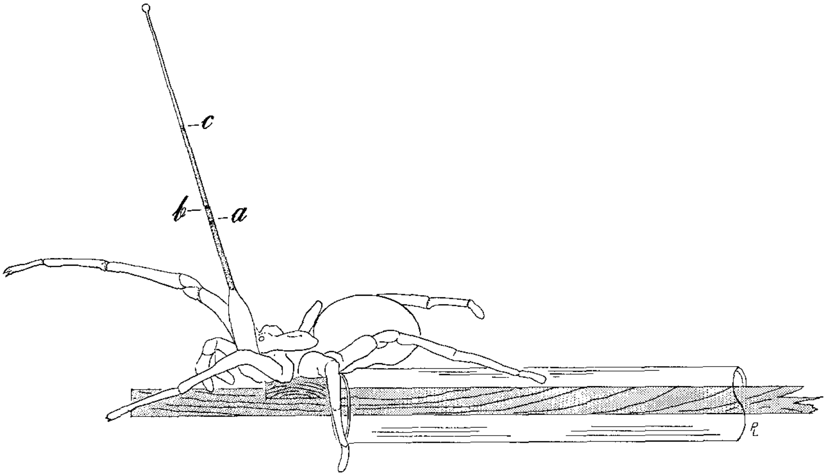

Fig. 1. Manometric measurement of leg pressures in *F. hibernalis*. The drawing shows the spider responding to stimulation with leg extension. *a* indicates the fluid level when the spider is anesthetized, equal to atmospheric pressure; *b* indicates the fluid level of an alert but inactive spider, normal pressure; *c* indicates the fluid level at peak activity, maximum pressure

fashion except no ligature was applied to the cut. Two differences were noted between the two groups. First, the spiders with the ligature were able to run for longer periods, averaging 96 sec versus an average of 71 sec for the group without the ligature. Second, the locomotion of the experimental group appeared normal in every respect with full leg extension and flexion observed, whereas the spiders lacking the ligature lost the ability to fully extend their legs within ten seconds after removal of the abdomen. This loss correlated with the appearance of appreciable amounts of fluid at the cut end of the cephalothorax. The major portion of time these spiders continued to move, they gave the appearance of an animal walking on its "knees". These results are consistent with the oft noted comment that leg extension requires an intact hydraulic system and also indicate the mechanism responsible for the acute pressure increases associated with leg extension is located in the cephalothorax.

Relationship between Carapace Movements and Leg Extension

Wilson (1970) proposed that movements of the carapace, brought about by contractions of the *musculi laterales*, caused the transient pressure increases responsible for leg extension. Accordingly, we simultaneously recorded carapace movements and leg extension in a number

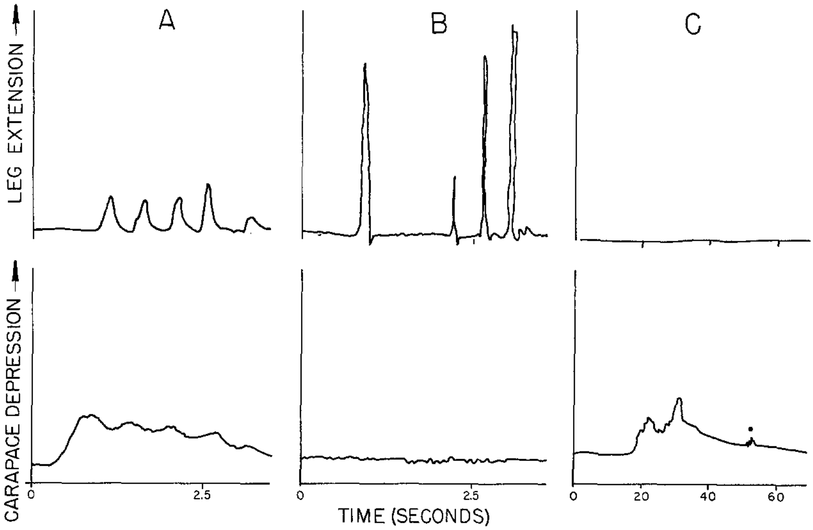

Fig. 2A—C. The relationship between carapace depression and leg extension. The more positive the graph deflection, the greater the depression of the carapace or extension of the leg. (A) illustrates the normal relationship between carapace movement and leg extension. Note the beginning of carapace depression occurs prior to leg extension. (B) shows that manipulation of the leg by the experimenter did not cause depression of the carapace. (C) illustrates that when leg extension is impossible, the carapace may still move. In each case, the time base is the same for the leg extension and carapace depression records

of specimens under a number of different experimental conditions to determine the relationship between these activities. A typical record is shown in Fig. 2A. In each case extension of a leg was accompanied by movements of the carapace. These movements consisted of a depression to a lower level followed by a series of cyclic up and down movements around this level. Each cycle of carapace movement was matched by an extension and flexion of the leg being recorded.

A question arose as to cause and effect relationship between the two recorded activities. Did carapace movement produce the conditions responsible for leg movement or vice-versa ? Fig. 2A indicates the former alternative is correct. The depression of the carapace begins prior to leg extension. Two additional experiments were carried out to test this conclusion. In the first, the legs were extended manually. The results are shown in Fig. 2B. Leg extension in this case had a very small effect on the position of the carapace. In the second, the legs were completely immobilized by the application of melted wax. The carapace retained its capacity to respond even though leg movement was absent. The results are shown in Fig. 2C. The dot over the carapace record represents the effect of manipulation at the joint between the coxa and trochanter, the only observable leg movement in this preparation.

One must consider the possibility that the carapace movement is itself caused by some antecedent activity elsewhere. Do the successive pulses of the hemolymph entering the cephalothorax as the result of cardiac activity or possibly twitches of the musculature of the abdominal wall cause the up and down movements of the carapace? This seems doubtful as spiders without abdomens could extend their legs normally if bleeding was prevented. Nevertheless, we monitored carapace movements and leg extension in a preparation where the abdomen had been removed. A ligature was applied to prevent bleeding from the cut end of the cephalothorax. Upon stimulation, these preparations produced a record essentially similar to that of the intact spider illustrated in Fig. 2A.

In short, these results support Wilson's (1970) hypothesis that a downward movement of the carapace increases the pressure within the prosoma which leads to fluid movement into the legs causing extension of these structures.

Relationship between Carapace Movement and the Generation of Pressure

We next tried to demonstrate a qualitative and quantitative relationship between carapace movements and pressure generation. Direct observation of the lateral areas of the cephalothorax was undertaken to insure that the arthrodial membrane, the flexible cuticle between the carapace and sternum, did not bulge outwards when the carapace moved downward, a situation incompatible with the generation of pressure. These observations revealed that the arthrodial membrane dorsal to the coxal bases of the legs was in fact pulled inward at the same time the carapace moved ventrally. This action would decrease the volume of the cephalothorax causing a rise in pressure. These observations are consistent with our dissections as well as those of Brown (1939), Whitehead and Rempel (1959), and Wilson (1970) relating to the origin and insertion points of the *musculi laterales.*

We then attempted to associate carapace movements with pressure change and leg extension. A capillary manometer was inserted into the cut end of the tibia in a position distal to the femur-patellar joint, the major articulation involved in leg extension. The anticipated results were obtained: any changes in the manometer fluid reflecting a change in pressure occurred only when the carapace was in motion.

To demonstrate the quantitative relationship between carapace movement and pressure, we simultaneously recorded the tension developed

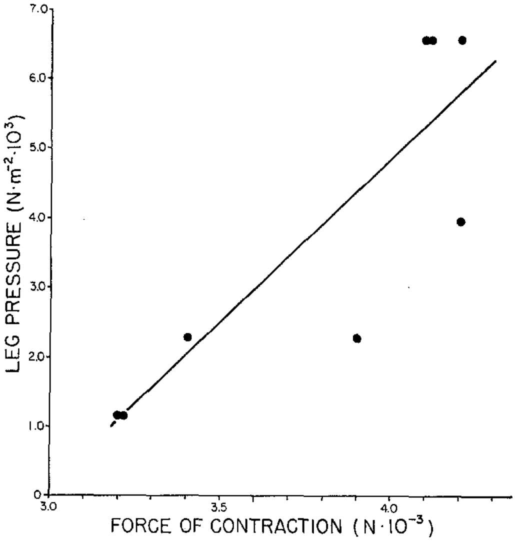

Fig. 3. The relationship between pressure in the leg and force of contraction of the carapace musculature. The correlation coefficient for the regression is 0.85

during depression of the carapace and changes in leg pressure in a series of appropriately prepared spiders. We were not always successful. The major problem involved obtaining an unbiased record of the tension generated by the *musculi laterales* by recording at only one attachment point, *i.e.*, the myograph attached by means of a thread to the dorsum of the carapace. These muscles attach to the lateral dorsal margins of the carapace and insert on the arthrodial membrane just dorsal to the coxae of the legs. When activated, these muscles depress the carapace and also pull the arthrodial membrane towards the mid-line. Consequently, not all of the force in any one preparation is transmitted to the myograph. Fig. 3 is a graph of the data on one of the more successful preparations. The correlation coefficient in this case is 0.85.

Leg Pressures in Resting and Active Spiders

We also estimated the pressures in the legs of resting and active spiders. We felt it necessary to determine whether these pressures in *F. hibernalis* are comparable to the studies of Parry and Brown (1959a, b) where the relationship between pressure change and leg extension was established. The results are shown in Table 1. All pressures are given in units of $N \cdot m^{-2}$ in accord with the International System of Units and are relative to atmospheric pressure.

Table 1. Fluid pressure in the legs of resting and active *F. hibernalis*

Pressure ($N \cdot m^{-2} \cdot 10^3$)	
Resting spiders	Active spiders
5.1	18.8
4.1	12.0
1.9	25.3
6.7	15.0
10.6	38.8
2.8	10.2
3.3	26.7
0.8	11.2
7.0	22.6
10.1	16.8
3.9	41.6
	61.3
	17.7
	31.3
	40.0
$\bar{X} = 5.1$ (*ca.* 38 mm Hg)	$\bar{X} = 26.0$ (*ca.* 195 mm Hg)
SE = 1.0	SE = 3.7
$n = 11$	$n = 15$

The resting pressures measured in *F. hibernalis* agree with those obtained by Parry and Brown (1959a) as well as those of the recent study by Stewart and Martin (1974). We agree with Wilson (1970) that the term "resting" pressure is inappropriate. This pressure is measured in an immobilized but alert spider and represents a transient state between a truly resting phase and one in which the spider is active. During the daytime when *F. hibernalis* is inactive in the tubular portion of its web, its legs are flexed against its body. This posture would not require any significant pressure in the cephalothorax. At night this spider moves to the junction of the tubular and sheet portion of the web. The body is raised above the web and the legs are slightly extended. This situation is indicative of the state where the pressure pump is active and elevates the prosomal pressures to what Wilson (1970) terms normal levels.

The peak or activity pressures of *F. hibernalis* also agree with available literature values. Parry and Brown (1959b) demonstrated pressure changes of this magnitude could account for the leaps of the jumping spider, *Sitticus pubescens* (Fabricius). They pointed out that leg extension during normal walking would not require such high pressure changes. Our peak pressures are the maximum pressure changes observed. We often observed pressure changes much lower than maximum, ranging from 4000 to 7000 $N \cdot m^{-2}$. Normal leg extension was observed at these submaximal pressure pulses. The maximal pressure changes probably represent a "startle" reaction by the spider. The speed at which a spider can move in a situation would depend on the magnitude of the maximal pressure change.

Abdominal Fluid Pressure

Wilson (1965) demonstrated there is no hydrostatic separation between the abdomen and cephalothorax in spiders. Consequently, it was necessary to measure abdominal pressures to understand the hydrostatic system in these animals. We were concerned with the relationship between the flow of hemolymph associated with locomotion and the flow of hemolymph associated with normal circulatory functions. Using three techniques, we estimated abdominal fluid pressures. The values are reported in Table 2. Comparison indicates the pressures estimated using Wilson's (1962) method are lower than those obtained from the pressure transducer and micropipette manometer. We suspect his method tends to underestimate pressures especially in active spiders. In Wilson's method, the abdominal pressure is estimated by elevating a mounted spider against a known force, in this case a glass slide, and measuring the surface area of the abdomen in contact with the slide when it is just barely lifted above its rest position. If the duration of the pressure pulse is shorter than the time required to make a measurement, only lower pressures, and not peak pressures, will be recorded. Fig. 4B was obtained with the pressure transducer and shows a tracing of abdominal fluid pressure before, during and after stimulation. If the measurement using Wilson's method was not completed during the short time the spider was active, it would show the pressure to be less than 2000 $N \cdot m^{-2}$ when in fact the maximum pressure was closer to 3000 $N \cdot m^{-2}$.

In spite of deviations, our data support Wilson's (1970) findings. During inactivity there is a small but definite residual pressure in the fluid contents of the abdomen. When stimulated, there is a transient increase in abdominal fluid pressure.

Our next procedure involved determining the mechanism which increases the abdominal pressure above atmospheric pressure. We simultaneously monitored movements of the carapace and abdominal fluid pressure. A representative record is shown in Fig. 4. The correspondence between the abdominal pressure fluctuations and movement of the carapace indicates the involvement of the prosomatic pressure pump. Fig. 4 suggests that the abdominal musculature is also involved in the generation of pressure. In this and other records of abdominal pressures, the pressure was invariably higher than normal after movements of the

Table 2. Abdominal fluid pressures

Method	Pressure (N·m^{-2}·10^{3})	
	Normal (resting)	Active (maximum measured in stimulated spiders)
Wilson (1962)	0.2–0.4[b]	0.8
	0.3	1.5
	0.4	0.5–1.3
	0.5	1.9
	0.7	2.1
	1.3	1.7
	0.8	—
	$\bar{X}=0.6$ (5)[a]	$\bar{X}=1.5$ (11)
	SE = 0.14	SE = 0.22
Sanborn physiological pressure transducer	1.1–2.1	2.5–3.3
	0.8–2.2	2.1–4.0
	1.1–1.3	1.5–2.7
	0.3–1.3	0.8–2.7
	1.3–2.7	4.0–17.7
	1.3–2.0	2.1–3.3
	$\bar{X}=1.0$–1.9 (8–14)	$\bar{X}=2.2$–4.0 (17–30)
	SE = 0.16–0.22	SE = 0.44–0.78
Micropipette manometer	(normal pressure could not be measured by this method)	7.3
		3.1
		2.0
		2.4
		5.2
		3.3
		1.7
		2.0
		6.3
		1.1
		$\bar{X}=3.4$ (26)

[a] Figures in parentheses represent pressures in mm Hg.

[b] Two figures separated by a dash indicates the range of pressure observed in an individual over a few hours.

legs had stopped. If the abdominal musculature did not develop tension during and after activity of the prosomatic musculature, the pressure in the abdomen should have fallen precipitously to its original level.

Abdominal Musculature

Our dissections reveal at least two major sets of muscles which should affect the fluid pressure in the abdomen. A series of paired segmental muscles are found on both sides of the mid-line and run

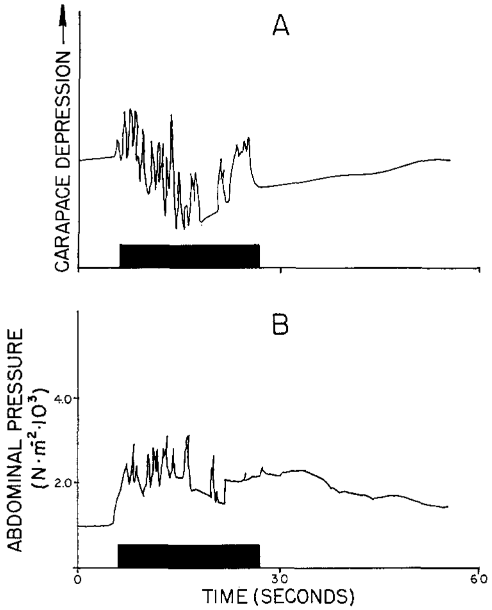

Fig. 4A and B. Simultaneous recordings of the carapace movement (A) and abdominal pressure (B), both as a function of time. Note the pressure peaks correspond approximately with carapace movement. Also note the elevated abdominal pressures after the cessation of carapace movement. The dark line on the abscissa indicates the time interval during which leg extension occurred

dorso-ventrally. Their contraction would compress the abdominal contents. The apodemes representing the attachments of these muscles to the dorsum of the abdomen are pulled ventrally when these muscles are active. Also present in this spider is a thin but well defined sub-cuticular muscular coat surrounding the major portion of the abdomen. Wilson (1970) claims this muscular sheet would, when activated, squeeze the abdominal contents and thus increase the fluid pressure in the abdomen.

In order to demonstrate activity of these muscle groups, we attached a thread from the myograph to different locations on the external abdominal wall. Investigation of the dorso-ventral muscles was accomplished by attachment of the thread along the dorsal mid-line. When these muscles were active, movements of the apodemes were also noted. This made it simple to distinguish between increases in tension caused by these muscles as versus those caused by the sub-cuticular muscle sheet. Another myograph thread was attached to the lateral wall of the abdomen to record activity of the sub-cuticular

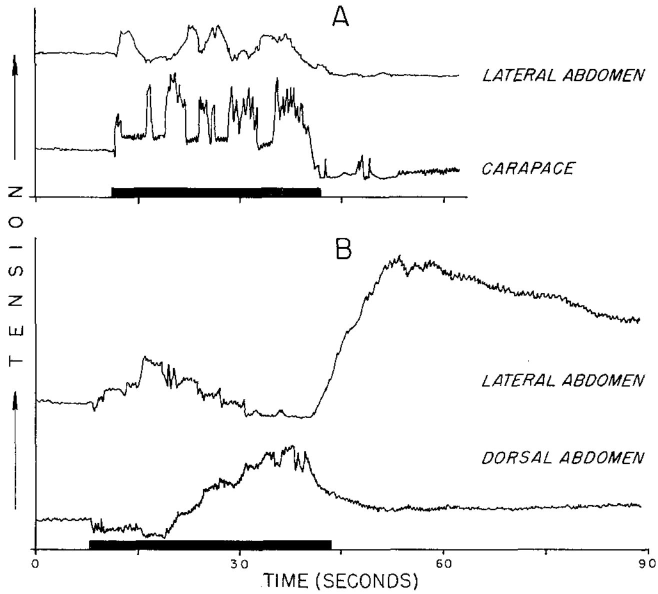

Fig. 5. (A) Simultaneous myograph recordings from the carapace and lateral abdomen. (B) Simultaneous myograph recordings from the lateral and dorsal abdomen of a spider subjected to repeated stimuli. The dark bar on the abscissa indicates the time interval during which leg extension occurred

muscle sheet. We also recorded the movements of the carapace in some of these preparations to show the temporal relationships between locomotion and activity of the abdominal muscles. The abdomen was immobilized to prevent its movements up and down or from side to side.

Our experiments indicate both abdominal muscle groups become active when the spider is stimulated. Two observations suggest our records are not a passive reaction to pressure pulses generated in the cephalothorax. First, everytime we recorded from the dorsum of the abdomen (dorso-ventral muscles) we observed an inward puckering of the associated apodemes. Secondly, as shown in Fig. 5A, our records from the lateral abdomen show contractions of the sub-cuticular muscle sheet to be independent of the carapace; contractions occur either before, during or after carapace depression.

The activity of the dorso-ventral and sub-cuticular muscles appears qualitatively different from those operating the prosomatic pressure pump. Functionally they are similar to the tonically active smooth muscle of vertebrates. The *musculi laterales* appear phasic in action and resemble skeletal muscle of vertebrates.

The onset of tension development in the abdominal muscles is variable. Most of our records indicate that tension developed at about the same time as that in the prosomatic musculature. In some instances, as stated earlier, tension in the abdominal muscles developed prior to that in the prosoma. The durations of activity in the abdominal muscles were longer than those of the muscles moving the carapace which explains the elevated abdominal pressure occurring after cessation of activity of the prosomatic musculature.

Factor Affecting Hemolymph Distribution

A number of workers (Parry and Brown, 1959a; Wilson, 1970; Wilson and Bullock, 1973; Stewart and Martin, 1974) have focused attention on the potential and/or actual problems resulting from the presence of three independent pressure pumps. These problems involve conflicts of hemolymph distribution relative to its functions of respiratory gas transport and as the medium to exert pressure in locomotory activities. As such we felt it necessary to estimate the magnitude of those variables affecting fluid movement. The data reported in Tables 1 and 2 provide for estimates of the pressure gradients between the cephalothorax and abdomen. The well known sensitivity of flow rate to tube dimension required consideration of the size relationships of the circulatory channels between the cephalothorax and abdomen. The pedicel which connects these tagmata contains a single median anterior aorta which conveys hemolymph anteriorly from the heart into the cephalothorax. Two lateral channels representing the venous return to the abdomen are also present. The mean radius ± SE of the anterior aorta of nine specimens is 0.137 mm ± 0.003. Comparable values for each of the venous channels are 0.152 mm ± 0.011.

D. Discussion

Our observations confirm the hypothesis of Wilson (1970) that increases in fluid pressure responsible for leg extension are generated by contraction of the *musculi laterales* in the cephalothorax. These muscles attach at one end to the dorsolateral margins of the carapace. The other attachment is to the flexible cuticular membrane which connects the carapace and sternum; attachment here is just dorsal to the coxae of the legs. Contraction of the *musculi laterales* both depresses the carapace and also pulls the cuticular membrane medially. This compresses the prosomal contents and creates a rise in hydrostatic pressure.

Whitehead and Rempel (1959) argue that contractions of any muscles connecting the carapace to the appendages would contribute to an increase in pressure. Stewart and Martin (1974) presented some observations to support the claim that other muscles are also involved in generating pressure. They showed that leg extension in stimulated spiders was accompanied by elevation of the coxae. Presumably all of the legs reacted in this fashion simultaneously. Such action would compress the contents of the prosoma and thus would contribute to the increase in fluid pressure.

While we observed indications of muscle activity in addition to that of the *musculi laterales,* we feel their effects are of relatively minor importance in normal walking and running. For example, we occasionally observed puckering of the cuticular membrane between the coxae of the legs in stimulated spiders. These areas on the cuticle are far removed from the insertion of the *musculi laterales.* We suggest that activities of these other muscle groups would be important only in "startle" reactions where such movements, by virtue of their simultaneous nature, cause compression. In any case, it is unlikely that any muscles attached to the segments of the legs would be important in locomotory pressure generation since simultaneous contraction of these muscles could limit the freedom of motion of the legs (Wilson, 1970). In normal walking, on the other hand, antagonism of compression and expansion effects on fluid pressure would result from the alternation of movement amongst the eight legs of the animals.

The involvement of muscles other than the *musculi laterales* in maintaining prosomatic pressure above ambient when a spider is not moving cannot be discounted. Tonically active muscles in the prosoma associated with maintaining posture may well influence fluid pressure. Tonic pressure does not appear to be due to elastic tension of the body wall since anesthetized spiders do not have elevated pressures. The identity of the muscles causing resting pressures is not known. Without dismissing the possibility that the *musculi laterales* may contribute to the resting pressure by maintaining tonus, our records indicate that during activity these muscles behave in a phasic fashion, *i.e.*, they reach peak contraction rapidly (in about 50 msec at 23–25° C) and generate relatively high degrees of tension (see Fig. 2A).

For the purpose of comparing leg pressures measured in this study with those available in the literature, it is important to recognize the various physiological states of the spiders which correspond to different pressure levels. Pressures obtained from alert but non-moving spiders have been termed resting pressures (Parry and Brown, 1959a; Stewart and Martin, 1974). We agree with Wilson's (1970) argument that this name is a misnomer: pressures obtained from spiders in this condition should be termed normal pressures. Spiders at rest have their bodies in contact with the substratum and, as such, fluid pressure would be zero. On the other hand, the fluid pressure of an alert but non-moving spider should be elevated above ambient levels. Observations on spiders recovering from the effects of the CO_2 anesthesia support this interpretation. The legs of an anesthetized spider are flaccid and are haphazardly arranged. As the spider recovers, there are a few low amplitude movements of the carapace accompanied by a small but definite rise in pressure and repositioning of the legs in a pattern characteristic of an alert spider. The legs now exhibit turgor and their slightly extended position reflects the effects of activity in the intrinsic flexor muscles balanced against a small pressure head produced in the prosoma.

Pressures obtained from active spiders have been termed transient pressures by Parry and Brown (1959a). We suggest that such pressures be termed maximum pressures. Experimentally such pressures are measured in animals subjected to various stimuli. In our experience, the pressures recorded are those corresponding to simultaneous extension of all the legs: this reaction represents a "startle" response. Pressures so obtained represent the maximum response of the prosomal pump. In the hydraulic extension system the velocity of leg extension and hence movement depends directly on the speed with which the hemolymph can be moved into the extensible articulations in the leg. The velocity of fluid movement in turn is directly proportional to the driving pressure. Therefore, maximum pressures have functional significance as an index of the speed of reaction which could be obtained by the spider.

Finally, we must mention the pressure level required for leg extension in normal walking. There is a consensus among the various investigators that maximum pressures generated in the prosoma are greatly in excess of that required for leg extension in normal walking. The exceptions are situations where extension of the fourth pair of legs provide the propulsive force for the jump in certain salticid spiders (Parry and Brown, 1959a, b). Table 3 is provided to compare these different pressure levels obtained in published studies.

The only apparent difference is in the normal pressure levels. This difference is slight and probably reflects differences in the criteria used by the different investigators in determining when a spider is alert but inactive. Consequently, we consider the correspondence of the various pressure levels striking especially when one considers the differences in the techniques employed to obtain such data. This similarity and widespread taxonomic diversity represented by the animals in question strengthens the concept of general applicability of hydraulic phenomena in spiders.

Our results also indicate at least two sets of abdominal muscles are involved in the generation of fluid pressures in spiders. We were able to demonstrate active responses in the series of paired dorso-ventral muscles and in the sub-cuticular muscle sheet which invests the ab-

Table 3. Comparison of various leg pressures in spiders

Species	Pressures ($N \cdot m^{-2} \cdot 10^3$)			Source
	Normal	Maximum	Pressures recorded during normal walking	
Tegenaria sp. (Agelenidae)	6.7 (50)[a]	59.9 (450)	—	Parry and Brown (1959a)
Dugiesiella hentzi (Girard) (Theraphosidae)	1.3 (10)	63.8 (480)	5.3–8.0 (40–60)	Stewart and Martin (1974)
Filistata hibernalis (Hentz) (Filistatidae)	5.1 (38)	61.2 (460)	4.0–6.7 (30–50)	this study

[a] Figures in parentheses represent pressures in mm Hg.

domen. These findings support Wilson's (1970) contention, based on anatomical evidence, as to the activity of the sub-cuticular muscle sheet as well as the claim of Stewart and Martin (1974) pertaining to the dorso-ventral muscles. We agree with the latter workers that other groups of abdominal muscles may be involved in pressure generation in these animals.

The temporal relationships of activity of the abdominal musculature relative to the activity of the prosomatic pressure pump support Wilson's (1970) suggestion that the abdominal musculature attenuates the pooling of blood in the abdomen when a spider is active. Our experiments (Fig. 5) indicate the abdominal musculature, the paired dorso-ventral muscles and the sub-cuticular muscular sheet, are partially responsible for the increase in abdominal pressure during activity. In some cases, especially those where a spider was subjected to repeated stimulation, the activity in these muscle groups persisted long after leg movement had ceased. In these situations, the increased fluid pressure in the abdomen would aid return of accumulated hemolymph to the prosoma.

The significance of these results can be more clearly seen in a discussion of the dual role of the hemolymph as the medium for transport of respiratory gases and as a mechanism for exerting pressure. A number of workers (Wilson, 1970; Wilson and Bullock, 1973; Stewart and Martin, 1974) have focused attention on the potential problems resulting from the dual role of the hemolymph in these animals. In a resting spider the heart in the abdomen pumps oxygenated hemolymph across the pedicel into the cephalothorax via a single medially located anterior aorta. This hemolymph provides for respiratory gas exchange for the organs located in this tagma, particularly the large masses of muscles contained therein. The hemolymph also provides the medium for exertion of pressure. The venous return pathway consists of two channels located laterally in the pedicel. These channels lead to the book-lungs in the abdomen where external respiratory gas exchange occurs. From here the hemolymph is transported to the heart for recirculation. Stewart and Martin (1974) demonstrated that a gradient of pressure exists to provide the motive force for this circulation of fluid in quiet animals. However, the picture becomes complicated during vigorous activity: the variables affecting the flow of hemolymph change in such a way as to promote the net accumulation of hemolymph in the abdomen (Wilson and Bullock, 1973). This itself limits further locomotory activity in a number of ways. First, an adequate supply of oxygenated hemolymph is not transported and unless the muscles involved have an anaerobic capacity this would lead to a cessation of their activity. Second, there is not a sufficient volume of fluid for effective operation of the prosomatic pressure pump for if the volume of fluid in the cephalothorax decreased, the resting length of the muscles would decrease thus attenuating the tension these muscles could develop.

One of the major factors leading to the accumulation of hemolymph in the abdomen is reversed pressure gradient in the systemic circuit, *i.e.*, between the heart and prosoma. During maximum activity, the fluid pressure in the prosoma can approach 61000 $N \cdot m^{-2}$ (Table 3) while the maximum systolic pressure measured in the hearts of various spiders is approximately 13000 $N \cdot m^{-2}$ (Parry and Brown, 1959a; Stewart and Martin, 1974). Our observations, as well as those of others indicates the heart stops beating in such circumstances. Retrograde flow is prevented by a valve located at the juncture of the heart and anterior aorta at the level of the pedicel (Petrunkevitch, 1933). In short, fluid input to the prosoma is stopped when a spider is extremely active. The net loss of fluid from the prosoma during vigorous activity is also enhanced by an increased pressure gradient in the venous return circuit. Using the appropriate values in Tables 1–3, one can calculate that the pressure gradient between cephalothorax and abdomen increases from approximately 4000 at rest to 43000 $N \cdot m^{-2}$ during maximum activity. Flow through the venous return channels in the pedicel must be relatively high: there is little attenuation of the prosomatic pressure in the transit of hemolymph through the pedicel (Stewart and Martin, 1974); there are no anatomical elements which would restrict flow in these vessels, in fact they distend when a spider is active (Wilson, 1965); and finally their combined cross-sectional areas is relatively large, 0.15 mm^2 in the case of *F. hibernalis* (this study). This latter dimension represents a two and one half fold greater size than that of the major artery in this spider.

The functional role of the abdominal musculature is clearly obvious in these circumstances. By contracting when the spider is active, they

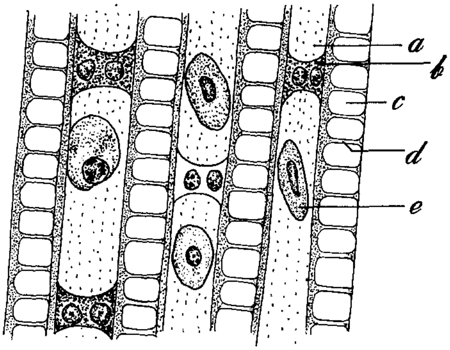

Fig. 6. A cross-section of the book-lung of *F. hibernalis*. *a* hemolymph channel; *b* pulmonary cells; *c* air space; *d* cuticular struts; *e* hematocyte

attenuate the shift of fluid from the cephalothorax to the abdomen, as well as speeding the recovery from an imbalance of fluid. Their contraction increases the fluid pressure within the abdomen, thus generating a pressure head promoting flow to the prosoma.

The use of the hemolymph as a medium to generate pressure as well as in the transport of respiratory gases points to the significance of the morphology of the book-lungs in relation to fluid dynamics. The book-lungs are the major structures located in the ventral anterior portion of the abdomen. Each lung consists of a number of flattened, triangular shaped, air-filled cuticular pockets which invaginate a hemolymph sinus. The hemolymph returning from the prosoma passes between these air pockets and returns by way of paired pulmonary veins to the heart for recirculation. These alternating air pockets and hemolymph channels (numbering approximately 95 per lung for an adult *F. hibernalis*) are arranged in parallel. Consequently, resistance to flow is lower than would be the case if arranged in series (Burton, 1965). This is significant since only a very small gradient of pressure is involved in transporting hemolymph through the book-lungs under resting conditions (Stewart and Martin, 1974). When a spider is active, however, these workers have demonstrated a large pressure drop occurs during transit of hemolymph through the book-lungs. They concluded flow must be very rapid in the book-lungs. This would be true if hydraulic resistance remained constant as the driving pressure increased. In biological systems, normally, modification of resistance involves changes in the dimensions of a fluid channel. Channel widths are decreased in size due to active "myogenic" elements or distend in response to an increase in pressure of the fluid volume (Burton, 1965). Our examination of the structure of the book-lungs indicate the air spaces and hemolymph channels are incapable of any appreciable change in size. Fig. 6

represents a highly magnified view of the cross-section of the lung of *F. hibernalis*. The air spaces, representing a total surface area of 101 mm^2, have a width of about 5 micra. This width is maintained by a large number of cuticular struts which interconnect the two cuticular surfaces lining the air space. This orientation resists compression. Expansion of the hemolymph space, about 13 micra in width, at the expense of the air space would also be resisted by these structures. In addition there are some cellular elements which bridge across the hemolymph space. Whether these cellular formations function as active components which modify fluid resistance can only be conjectured. These details of book-lung structure are, according to the descriptions given by Millot (1949), not unique to *F. hibernalis*. Based on this analysis, we support Stewart and Martin's (1974) contention that hemolymph flow is rapid in these structures when the spider is active. Functionally the rigidity of the book-lungs precludes pooling of the hemolymph in these structures, an occurrence which would otherwise intensify the problems of fluid imbalance.

A final comment is in order concerned with the limitations, real or potential, associated with a hydrostatic skeleton in spiders. Hydrostatic skeletons, at least to the extent developed in spiders, are commonly associated with organisms living in the aquatic environment (Chapman, 1958). One would hardly expect that a group of small arthropods relying on such a system in the terrestrial environment would be as evolutionary successful as spiders apparently are. The effectiveness of this system would be seriously reduced through desiccation as well as bleeding which might result from injury during prey capture. In addition, such a system might preclude prolonged vigorous activity, a serious limitation for a predator. Yet spiders are an evolutionarily successful group of terrestrial arthropods. At least part of their success is due, as Wilson (1970) suggests, to the evolution of devices to capture prey with a minimum of risk. The use of silk to ensnare prey as well as reliance on poison effectively reduces the danger of bleeding. The evolution of a epicuticular wax layer to retard evaporative water loss and the ability to lose appendages without copious fluid loss are other characteristics of spiders which offset the limitations of a hydrostatic skeleton. We suggest there is in addition a positive advantage in using hydrostatic pressure to extend legs. Spiders as predators rely on using their legs in dealing with prey organisms. Legs are important even in those spiders which use silk to ensnare prey. The importance of these appendages to a spider is immediately obvious if one compares their relative size with that of the legs of most other arthropods. Using fluid pressure generated elsewhere for leg extension, more muscle mass associated with leg flexion can be incorporated into the legs proper. The resultant increase in power would give a spider another significant advantage in overcoming prey.

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