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Blood Pressure in the Tarantula, *Dugesiella hentzi**

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Summary. 1. Heart rates in intact spiders at rest were 35/min and after 3 min exercise 77/min. Recovery to the initial rate required $^1/_2$ hr. In cannulated animals heart rates ranged from 44/min at rest to 116/min after a struggle. Heart rate was relatively independent of internal pressure.

2. Variations in heart rate and amplitude occurred spontaneously and in response to various stimuli (Fig. 6).

3. Systole averages 68% of total beat duration through a range of heart rates from 21–116 min (Fig. 4).

4. Intraventricular pressures 10 min after cannulating averaged 22/13 mm Hg, but fell to 12/8 mm Hg after 10 min in the dark (Fig. 5). A maximum pressure of 102 mm Hg was measured in one animal. The pressure recorded in the heart is generated in part by the heart and in part reflects abdominal tension.

5. Resting pressures in any 2 legs were always identical and were above that in the prosoma.

6. Resting pressures in the prosoma and lateral sacs are intermediate to heart systolic and diastolic pressures which in a relaxed animal were 12/8 mm Hg (Fig. 11).

7. At rest a gradient of only a few mm Hg propels the blood through the lung books from the lateral sacs to the pulmonary veins; a gradient of 1–2 mm Hg exists between the pulmonary vein and the heart in diastole.

8. General abdominal pressure is above pulmonary vein pressure suggesting a need for a mechanism to maintain patency of these vessels.

9. During a struggle a maximum pressure of 480 mm Hg was measured in the prosoma.

10. High pressures were recorded in the lateral sacs which communicate freely with the prosoma but were not transmitted to the heart.

11. Pressures of 40–60 mm Hg were measured in the prosoma and legs during wialking (Fig. 18) and delivery of blood through the pedal arteries probably continues at this level.

12. Withdrawal of blood causes an immediate decrease in heart pressure. Within min some recovery occurs presumably because of muscular adjustments (Fig. 19).

Introduction

Apart from its interest *per se*, a special concern with the blood pressure of spiders has resulted from the observation that extensor muscles are lacking at the femur-patella and tibio-basitarsus joints. Petrunke-

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vitch (1909) first noted this deficiency and suggested that the elasticity of the interarticular membranes could produce extension of the joints. Ellis (1944) first suggested that a hydraulic mechanism is involved, and postulated that a local rise in pressure in the leg acts on the membranes to cause extension. Parry and Brown (1959a), finding no evidence for such a local rise in pressure, suggested that slight dorsoventral compression of the prosoma generated the pressure which was then reflected to all legs. Using an indirect method, they measured resting pressures of 40–110 mm Hg in the leg of *Tegenaria.* Stimulating the spider resulted in transient increases to 110—450 mm Hg. Since they felt these pressures would grossly distend the abdomen, they suggested that a sphincter in the pedicel must isolate the abdomen hydrostatically, allowing it to remain at atmospheric pressure. This arrangement would require rather high heart pressures to force blood into the prosoma, but they presented evidence for pressures as high as 116 mm Hg during systole. In the jumping spider, *Sitticus pubescens,* Parry and Brown (1959b) calculated that pressures of 130–1080 mm Hg would be necessary to generate the torques they measured during various jumps. They believed generation of such pressures might be possible. They noted that the leg spines, which become erect on compression of the prosoma, were elevated on all legs during a jump. Since only the 4th pair is involved in the jump, this indicates a prosomal pressure source as they had suggested earlier.

Evidence that the abdomen is not at atmospheric pressure came from a study of control of dragline spinning by Wilson (1961a, b). Indirect measurement of the intra-abdominal pressure of *Araneus* revealed levels of 31–43 mm Hg, close to the resting pressure recorded by Parry and Brown (1959a) in the leg of *Tegenaria.* Wilson suggested that intra-abdominal pressure, generated by the sub-cuticular muscle layer, is responsible for moving silk from the gland into the duct. Furthermore, he believes that in spiders lacking valves in these ducts variations in intra-abdominal pressure control the rate of flow (Wilson, 1969).

Using another approach, Wilson (1970) compared muscular development and body form of several spiders with different life habits. He confirmed the observation of Brown (1939) and Millot (1949) that muscles link the endosternite to the carapace but not to the ventral sternum. Since this rules out a bellows action of the prosoma for pressure generation, he suggested that prosomal compression is achieved by contraction of the musculi laterales which insert along the edge of the carapace and attach to narrow sclerites set in the flexible cuticle dorsal to the coxae. He found the sub-cuticular muscle sheath particularly well developed in the jumping spider, *Marpissa muscosa.* The sclerites mentioned above are also well developed in this spider. Since he had found no evidence previously for a hydrostatic separation of the abdomen and prosoma

(Wilson, 1965), he concluded that both the resting and transient high pressures penetrate throughout the body. The resting pressure could be maintained through slight tension of the musculi laterales in the prosoma and the sub-cuticular muscle sheath in the abdomen. This pressure, about 50 mm Hg, he considered adequate to extend the legs during normal locomotion and to maintain silk available for spinning. The high transient pressures might be due to a sudden twitch of these same muscles. However, in his most recent paper, Wilson has presented evidence indicating that during vigorous activity blood is shifted from the prosoma to the abdomen (Wilson and Bullock, 1973). This would appear to indicate an inability of the abdominal muscles to generate high pressures or even to withstand such pressures when generated by the prosoma.

The present study was undertaken to provide further information concerning the dynamics of the circulation in the spider and perhaps to clarify some of these matters. The tarantula, *Dugesiella hentzi*, is large enough to permit direct measurements of the blood pressure in various parts of the body, in many cases in two regions simultaneously. It is believed that such information is applicable to spiders generally.

Material and Methods

Specimens of *Dugesiella hentzi* were housed individually in one gallon jars containing a layer of sand. Water was provided *ad lib*, and food consisted of 2 crickets each week. A total of 36 female spiders weighing 11–18.6 g was used in this study. The experiments were performed during the months of February-May when temperatures in the laboratory were approximately 25° C. None of the animals used had yet undergone the yearly molt, nor was there any evidence that it was imminent.

Shafts of No. 21 syringe needles were used as cannulas. Prior to use, melted beeswax was drawn into them and then blown out, leaving a thin layer which seemed to retard clot formation. The cannulas were connected by polyethylene tubing to Statham pressure transducers. The system was filled with spider Ringer prepared as described by Parry and Brown (1959a) except that proportions of the phosphates were altered to give pH 7.4. A Gilson Model M5P recorder was used for most measurements. A few recordings were made with an Offner RS Dynograph.

The animal to be used was weighed, placed on a small board, and a piece of coarse-meshed cloth (3 threads/cm) was tacked around the spider. Each leg was pulled through an opening and placed in a position midway between close flexion and full extension. The legs could move at will, but for most recordings, except during struggles, they were in approximately the initial position. In a few experiments, the board which supported both body and legs was replaced by a narrow one on which only the body rested, leaving the legs unsupported. When held in this manner, a sudden puff of air caused a quick extension of all legs. Pressures were recorded during such extensions. In a few cases complete freedom was allowed after the cannulas were inserted so that pressures could be recorded during locomotion.

For cannulation of the heart, the bristles were scraped from the dorsal surface of the abdomen leaving the heart visible as a dark shadow along the midline. The cannula was inserted through the cuticle over the posterior end of the heart and a quick movement forward usually resulted in its placement within the heart. For recording from a leg, the needle was inserted into the distal end of the tibia and passed a short distance proximally. The cannulated leg was identified by number, e.g., R–1 refers to the first leg on the right side. In the prosoma the cannula was inserted through the cuticle of the right anterior quarter. A few recordings were made from the lateral sacs and from the lateral portion of the abdomen. Two recordings were made simultaneously from the heart and the left posterior pulmonary vein. Melted beeswax was used to seal in the cannulas and sometimes to seal the opening after the cannula was withdrawn if finger pressure failed to stop the bleeding. Prior to inserting the cannulas in the various regions, the pressure in the system was raised to the level anticipated in order to prevent entry of blood which had a tendency to clot in the cannulas. None of the commonly used anticoagulants was effective.

A very brief review of the circulatory system may facilitate understanding of the pressure relationships to be described (Millot, 1949; Petrunkevitch, 1922; Savory, 1928; Wilson, 1965, 1967). The tubular heart is suspended in a pericardium by 58 elastic ligaments. Their recoil returns the heart to its expanded state when contraction ceases. A posterior aorta and several pairs of slender lateral arteries emerge to supply the abdomen. The anterior aorta, demarcated from the heart by a valve, leads through the pedicel into the prosoma. In its passage through the pedicel it is protected above by the two lora and below by a ligamentous sheet which runs between the lower edges of the lora. In the prosoma, the aorta divides into 2 lateral vessels each of which runs anteriorly, sends a cephalic artery to the head region, and then dips ventrally to run posteriorly again. En route, 5 arteries arise on either side to enter and supply the appendages. Venous blood accumulates in sinuses, 3 in the prosoma and 3 in the abdomen. Blood from the prosoma returning through the pedicel immediately enters the lateral sacs, regions bounded by flexible cuticle. Blood from here passes between the leaves of the lung books and returns to the pericardium by way of the pulmonary veins. *Dugesiella hentzi* has 4 lung books and 4 pulmonary veins, 2 on each side. Re-entry to the heart is through 4 pairs of ostia in this species. The lips of the ostia are muscular and close when the heart contracts. The lateral suspensory ligaments are associated with the lips and open them at diastole.

Results

The Cardiac Cycle

The heart of these animals is large relative to body weight. Hearts were removed from 4 animals (12–15 g) and blotted before weighing. The wet heart weight averaged 0.261% of the total body weight.

An intraventricular pressure record is shown in Fig. 1. The record is very similar to those obtained from vertebrate hearts, with the exception that the low point of diastolic pressure is well above zero. Thus, the initial sharp rise in pressure represents an isometric contraction; the upper rounded section represents the ejection phase following opening of the aortic valve, and at this heart rate approximately 17/25 sec after the beginning of systole, a change in slope signifies relaxation. The suspensory ligaments recoil to expand the heart, and the rapidly falling pressure indicates isometric relaxation.

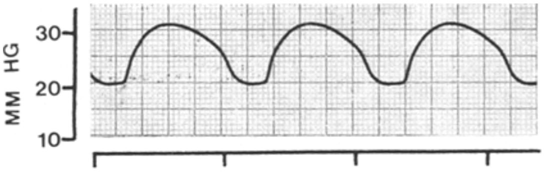

Fig. 1. Intraventricular pressure record. Time marks: 1 sec

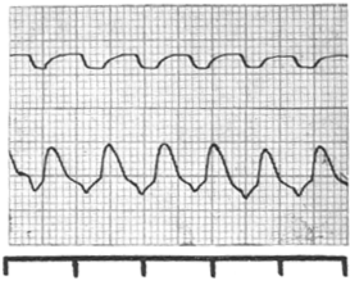

Fig. 2. Simultaneous records of pressure changes within the heart (upper record) and of cuticular movement over the heart (lower record). Time marks: 2 sec

Durations of systole and diastole in *Heteropoda* were determined by Wilson (1967) from recordings of cuticular movements over the heart. Records similar to his were obtained in *Dugesiella* by attaching a small fluidfilled plastic balloon to a pressure transducer and holding the balloon over the heart region under slight tension. The ventricle was then cannulated giving the advantage of comparison of cuticular movements with intraventricular pressures. The animal had been cooled previously so that insertion of the cannula would not cause so great an increase in rate that the cuticular changes would be obscured. It may be seen in Fig. 2 that the sharp rise in the cuticular record almost coincides with the rise in the pressure record at the beginning of systole. The slight delay in the latter may represent the time required for the ostia to close after contraction begins. The cuticular tracing falls as ejection proceeds and blood leaves the abdomen. The recoil of the elastic ligaments, indicated in the cuticular record by a sharp dip, coincides with the change in slope of the descending limb of the pressure record. The cuticle then gradually rises as blood enters to fill the ventricle.

In Fig. 3A, B are shown the recordings obtained prior to and after a period of forced walking in one animal. The time occupied by the elastic recoil of the ligaments was unaffected by heart rate. However, at the

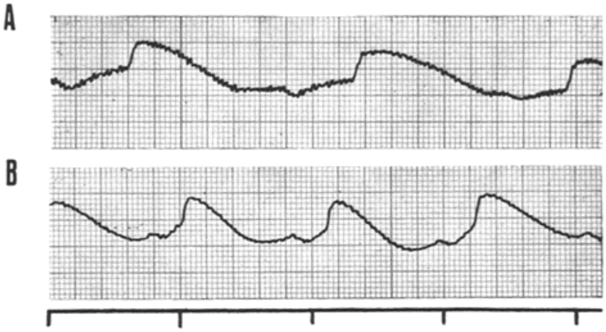

Fig. 3 A and B. Records of cuticular movement over the heart. A. Before exercise. B. After exercise. Time marks: 1 sec

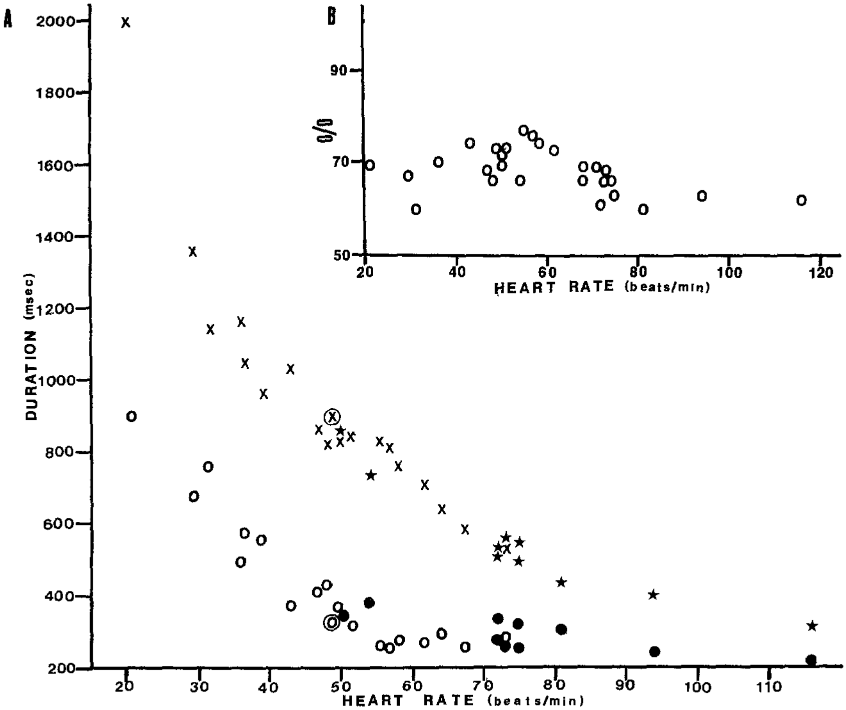

Fig. 4. A. Duration of systole (× intact animals, ★ cannulated animals, ⊗ *in vitro*) and diastole (○ intact animals, ● cannulated animals, ◎ *in vitro*) at different heart rates. B. Percentage of total beat duration represented by systole at various heart rates

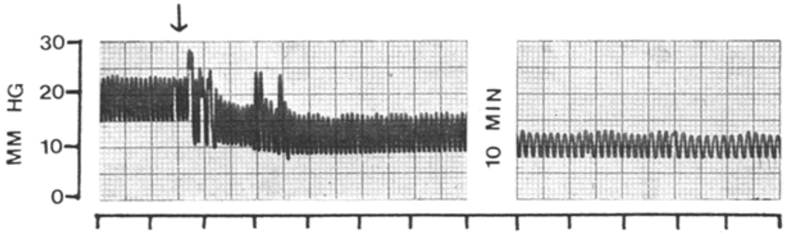

Fig. 5. Pressure record from the heart. Response to covering with a box (at arrow). Time marks: 10 sec

faster rate the interval between recoil and the ensuing systole was reduced considerably. Systole was reduced in duration also, and in this one animal the percentage of the total beat duration represented by systole increased from 70.3 to 75.9% on exercise.

From cuticular recordings in 7 intact animals, and from intraventricular recordings in 10 animals, the durations of systole and diastole were determined at various heart rates (Fig. 4A). One recording from an *in vitro* heart preparation was included. All determinations were made at room temperature, 25° C. No rates below 50/min occurred in the cannulated animals used for these determinations, but rates as low as 21/min were recorded in intact animals accustomed to being handled. In the latter group, rates above 50/min occurred only after stimulation or exercise. Over the entire range of heart rates systole occupied about 68% (range 60–76%) of the total beat duration (Fig. 4B). There appeared to be some slight decrease in percentage at the higher rates.

Heart Rate and Pressure

In order to determine the effect of a standard period of exercise on heart rate, 4 normal animals (15–17 g) were forced to run or walk for 3 min. The typical pattern of movement was a short run, then a pause, at which time they were gently prodded or stimulated to move by stamping on the floor behind them. The initial heart rate, observed through the cuticle, was 35/min (range 32–40) and immediately after the exercise the heart rate was 77/min (range 60–88). By 30 min the rates were back to the initial level.

Rates in cannulated animals were considerably higher. During the first min after cannulating the heart of 6 animals (11–18 g) the rate averaged 85/min (range 75–105). Six min later the average rate was 76/min and by 13 min it was 69/min. Covering the animals with a box resulted in further decreases in rate, suggesting that the rapid rates were due as much to general excitation as to the presence of the cannulas.

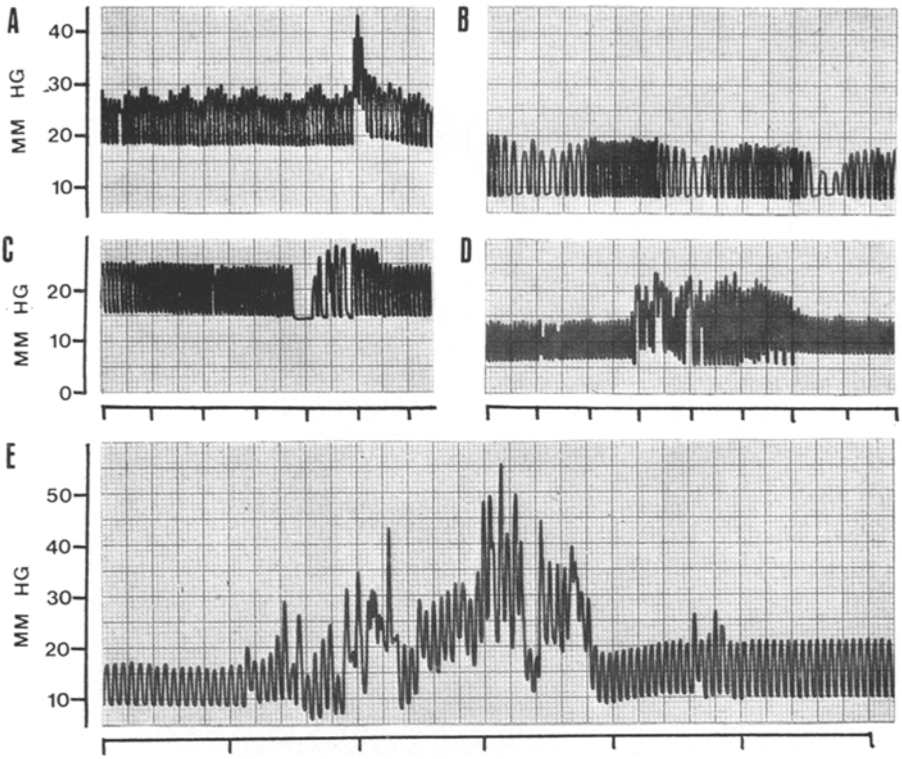

Fig. 6A—E. Pressure record from the heart. A. Periodic variation in amplitude at rest and the response to a whistle. B. Periodic variations in rate and amplitude. C. Response to touch. D. Change in amplitude during extension of a leg. E. During a struggle. Time marks: 10 sec

This response is shown in Fig. 5. The cannula had been inserted 18 min previously, and the heart rate had stabilized at 69/min at the time of covering. Ten min later the rate had decreased to 44/min.

In 10 animals (11–18 g) maximum heart pressures during the first min after cannulating averaged 44/26 mm Hg (systolic range 33–53, diastolic range 14–39). After resting undisturbed, but not covered, for 10–13 min, pressures had decreased to 22/13 mm Hg (systolic range 15–33, diastolic range 10–15). In the spider of Fig. 5, the pressure dropped immediately upon covering and decreased further to 12/8 mm Hg during the ensuing 10 min.

Direct cannulation of the heart did not interfere with ability to alter cardiac action and some of the responses observed seemed to originate in the central nervous system. In many animals allowed to sit quietly for

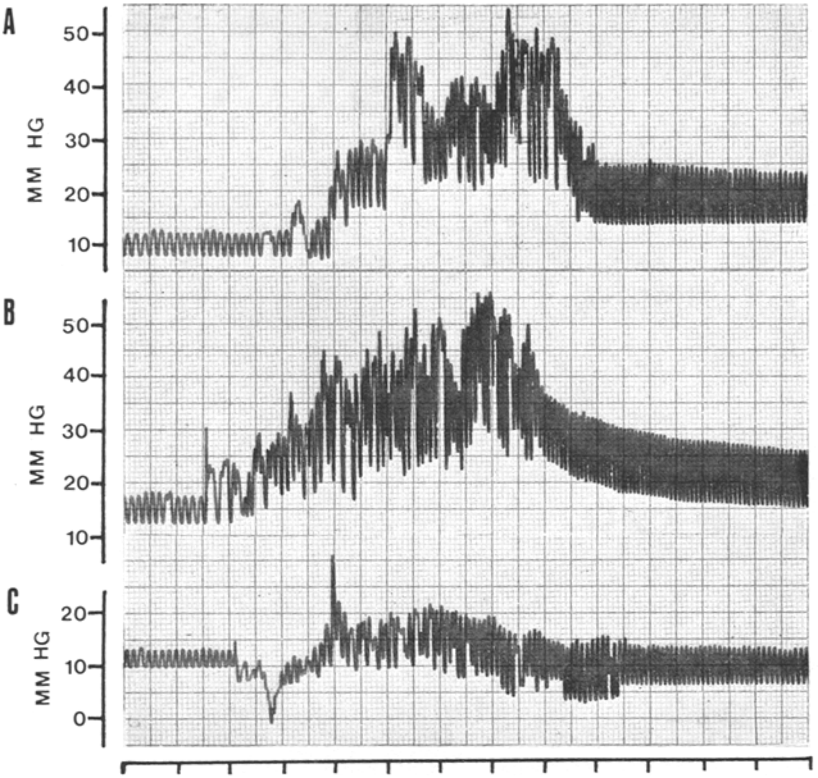

Fig. 7A—C. Pressure record from the heart. A. Effect of flexing all legs. B. 4 legs extended. C. 8 legs extended. Time intervals between records are indicated. Time marks: 10 sec

some time after cannulation, periodic variations in amplitude of beat were observed (Fig. 6A). Occasionally periodic decreases in rate along with decreases in amplitude occurred (Fig. 6B). Changes in heart activity in response to external stimulation such as a whistle (Fig. 6A) or a light touch (Fig. 6C) were also observed. When one animal voluntarily raised one of its legs, there was an increase in pulse pressure and although an initial rise in diastolic pressure occurred, it soon decreased to slightly below the level prior to the activity (Fig. 6D). In Fig. 6E is shown a recording typical of those taken during struggles. This struggle lasted 25 sec. Large fluctuations occurred in both systolic and diastolic pressure levels and the pressure rose from 16/9 mm Hg to a maxium of 55 mm Hg. Pressures as high as 102 mm Hg were recorded occasionally in other animals. The pressures were back to the initial levels by 2 min after this

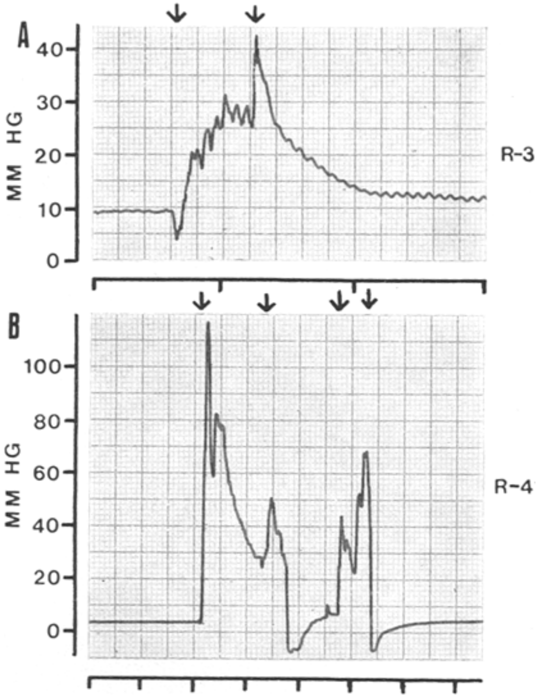

Fig. 8 A and B. Pressure records from the legs. A. Leg R-3 was extended manually (1st arrow) and then released (2nd arrow). B. Leg R-4 was flexed (1st arrow) and extended (2nd arrow). The procedure was repeated (3rd and 4th arrows). Time marks: 10 sec

struggle. The heart rate was 96/min before the struggle. During the struggle it increased and immediately afterward reached 110/min. The rate was still slightly elevated by 2 min after the struggle.

Flexion of the legs which causes a decrease in volume due to compression of the interarticular membranes was found to affect internal pressures appreciably. This was illustrated by the following experiment. The sides were removed from the box used to cover the spiders so that the legs could be manipulated with the body covered. The animal used for the experiment had been resting quietly for some time. The blood pressure was 12/8 mm Hg and the heart rate was 46/min (Fig. 7 A). Maximum manual flexion of the legs was accompanied by an immediate rise in pressure and heart rate which was due in part to stimulation of the animal. By 4 min later (beginning of record B), pressures had stabilized at 18/12 mm Hg, well above the initial levels, and the heart rate was 48/min. At this time a pencil was placed under the legs of one side and

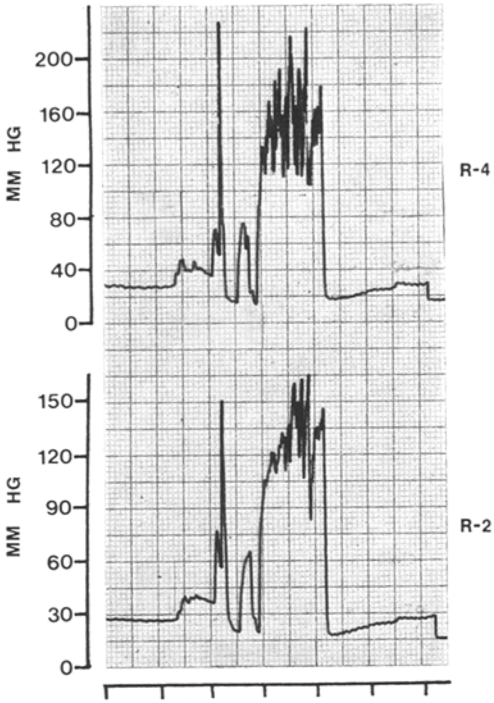

Fig. 9. Simultaneous pressure records from 2 legs during a struggle. Time marks: 10 sec

drawn outward extending them. This stimulated transient increases in pressure and rate, but by 3 min later (beginning of record C), heart rate was again 48/min and pressure was down to 13/10 mm Hg. The remaining 4 legs were then extended, resulting in a transient fall in pressure which was followed immediately by a rise in pressure of smaller magnitude than in B. In less than 2 min pressure had stabilized at 13/6.5 mm Hg, essentially the initial level, although the heart rate was still slightly elevated.

Pressure in the Legs

Movement of a leg was accompanied by marked pressure changes within that leg. In Fig. 8A is shown the effect of passively extending a leg (1st arrow). The sharp drop in pressure was due to the increase in leg volume. The subsequent rise in pressure resulted from activity of the animal. When the leg was released, the animal flexed the leg (2nd arrow), causing the sharp transient rise in pressure. Larger fluctuations occurred when a leg was manually flexed (Fig. 8B). Here the pressure rose to 117 mm Hg (1st arrow) and then fell to 24 mm Hg as blood flowed out into the prosoma. When it was extended manually (2nd arrow), after an initial transient increase the pressure fell to below 0 mm Hg. Repeating the manipulation resulted in a smaller increase, probably because of a smaller volume of blood in the leg.

Pressures of 10 mm Hg and below were commonly recorded when the animals had been undisturbed for some time. Pressures were recorded simultaneously from various pairs of legs, and the resting pressures were always identical. In Fig. 9 are shown the pressures recorded from legs R-4 and R-2 of a struggling spider. During such struggles the legs were held closely flexed and various antero-posterior movements were made. Extensions occurred rarely despite the high pressures. Initially, the pressure in both legs was 28 mm Hg, not a resting pressure since this animal had been stimulated a few seconds previously. The struggle shown lasted 28 sec, and some of the pressure peaks are visible in both records, though not of the same magnitude. Thus, the first peak reached 230 mm Hg in R-4 while only 150 mm Hg was recorded in R-2. A pressure as high as 110 mm Hg was maintained for about 12 sec and this pressure rise was believed to result in large part from elevations of the coxae which were seen to accompany leg movements. These leg segments form much of the ventral surface of the prosoma and when raised must considerably reduce the prosomal volume. The simultaneous pressure peaks in the two legs are probably of the same origin. It may be noted that after the struggle the pressures fell transiently to below the initial level.

Pressure in the Prosoma and Leg

Resting pressures in the legs are slightly above those in the prosoma, providing the gradient for return of blood to the heart. In Fig. 10 are shown the pressure changes in the prosoma and leg R-2 during a struggle which began with a slow gradual rise in pressure in both regions. The 3 large peaks in the prosomal record are apparent, but lower, in the leg. The base level to which the pressure fell between peaks was higher in the prosoma than in the leg and this was typical of recordings from these regions. In other recordings imposed peaks were sometimes higher and more numerous in the leg than in the prosoma, suggesting that strong flexion of the particular leg had occurred. After the struggle the prosomal pressure fell quickly to the prestruggle level, while that in the leg dropped below and then gradually rose to the pre-struggle value.

Pressures in the Heart, Prosoma, and Leg

In animals at rest, prosomal pressures were intermediate to systolic and diastolic levels in the heart (Fig. 11 A). In Fig. 11 B is shown a recording taken from the prosoma during a particularly violent struggle which

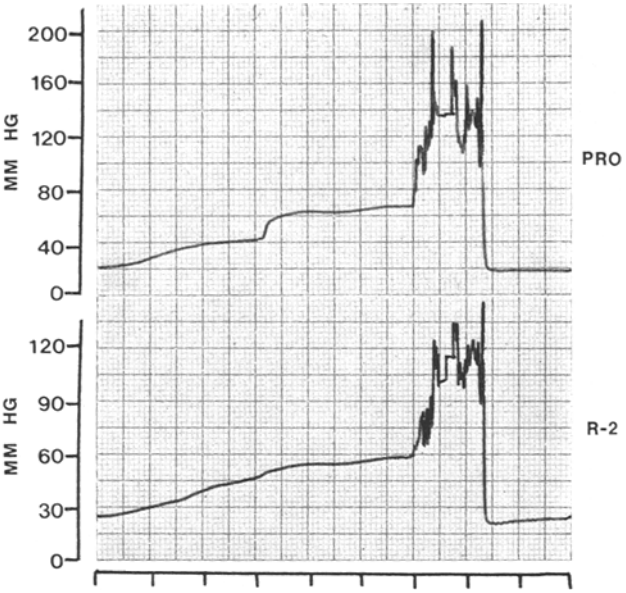

Fig. 10. Simultaneous pressure records from 2 legs during a struggle. Time marks: 10 sec

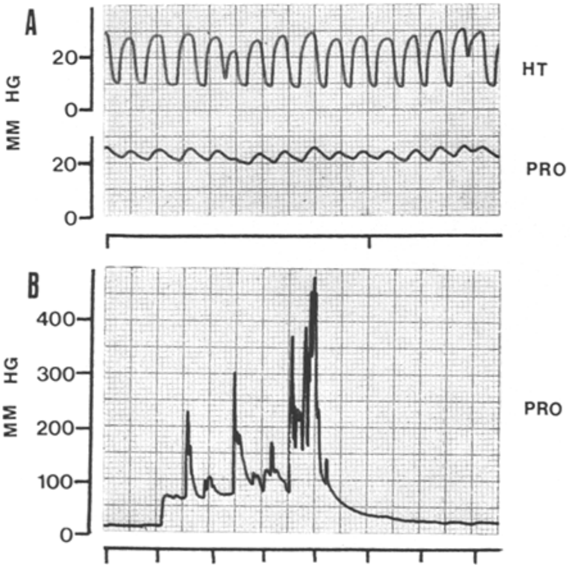

Fig. 11 A and B. A. Simultaneous pressure records from the heart and prosoma. Time marks: 10 sec. B. Pressure record from the prosoma during a struggle. Time marks: 10 sec

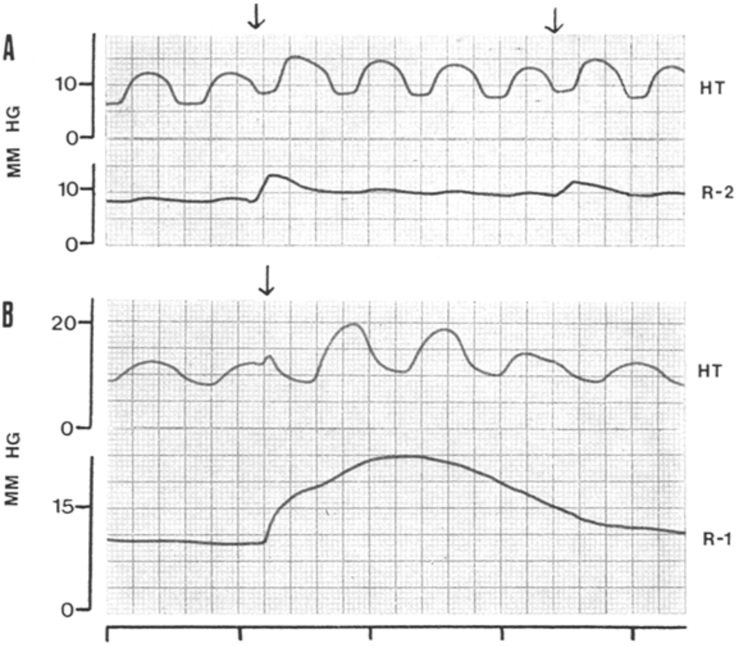

Fig. 12A and B. Simultaneous pressure records from the heart and leg. A puff of air was administered at each arrow. Time marks: 1 sec

lasted 1/2 min. During the struggle, a general rise in pressure from 10 mm Hg to over 150 mm Hg occurred, with peaks as high as 480 mm Hg. This was the highest pressure recorded in the course of this work. Since pressures higher than about 100 mm Hg were never recorded in the heart, blood flow to the legs and prosoma must cease during vigorous activity. The heart possibly delivered blood intermittently during the first 10–20 sec of this struggle. For the remainder of the struggle, blood presumably left the heart by way of the lateral arteries and posterior aorta to remain in the abdomen.

Pressures recorded within the heart during activity were quite variable. This might be expected since forces resulting from changing activity of the abdominal muscles, acting on the heart without, can add to or substract from the ventricular force. This is illustrated by the following experiment. An animal was stimulated by 2 slight puffs of air, each of which occurred at the beginning of diastole (Fig. 12A). In another animal a stronger puff of air was administered toward the end of systole (Fig. 12B). Pressures rose simultaneously in heart and leg on all three

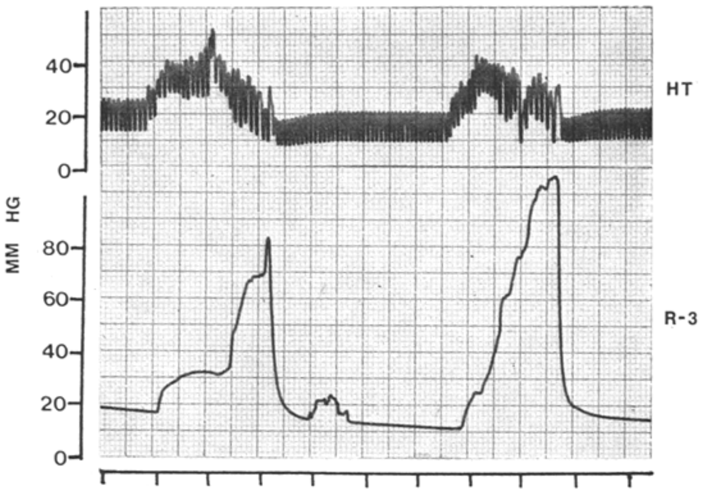

Fig. 13. Simultaneous pressure records from the heart and leg during 2 mild struggles. Time marks: 10 sec

occasions, making it unlikely that a sudden surge of blood into the abdomen from the prosoma caused the rise in heart pressures. Nor does it seem probable that these variations in amplitude represent responses to cardiac ganglion influence, although this is possible. Each puff of air (Fig. 12A) caused an elevated diastolic pressure followed by a beat of increased amplitude. It is believed that an increase in abdominal tension, occurring during systole, was responsible for the increased pulse pressures. In Fig. 12B, the pressure changes in the leg were of longer duration, and 3 beats occurred while pressure in the leg was above that in the heart. The first 2 beats of increased amplitude were probably due to an increasing tension of the abdomen during systole. The third beat which was of decreased amplitude occurred while abdominal tension was falling.

Another pattern of activity is evident in Fig. 13 in which are shown the pressure relationships during two relatively mild struggles initiated by the animal itself. Initially, pressure within the leg was intermediate to the systolic and diastolic levels in the heart. Heart pressures increased before any change was evident in the leg. Presumably an increase in abdominal tension was responsible and this permitted an uninterrupted delivery of blood anteriorly during the first part of each struggle. When the pressure in the leg rose above that in the heart, the entire cardiac output must have remained within the abdomen and one might expect an increased abdominal tension. In addition, an increased venous return as a result of the increased prosomal pressures should raise abdominal

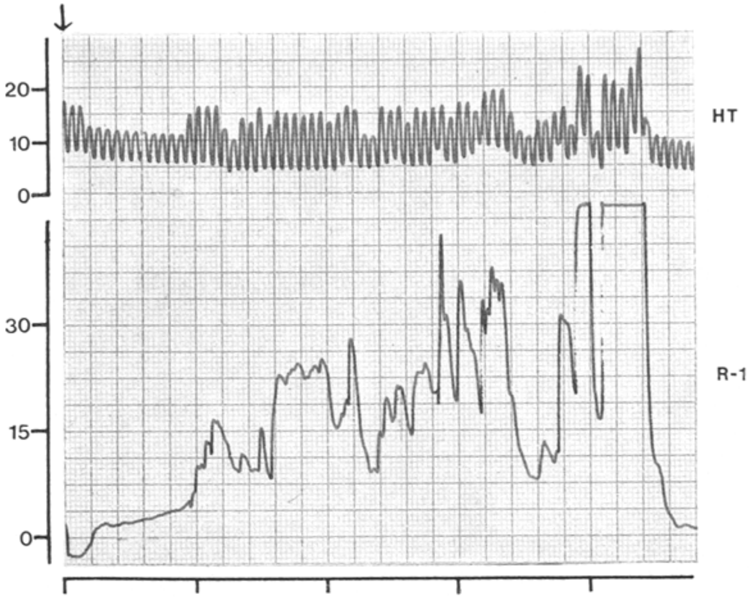

Fig. 14. Simultaneous pressure records from the heart and leg during a struggle. Time marks: 10 sec

tensions. Despite these factors, pressure levels decreased. This must have resulted from relaxation of the abdominal muscles. It is possible that the large slow beats during this time resulted from greater filling of the heart.

Recordings taken during struggles were characterized by rapid changes in pulse pressure which occurred simultaneously with sudden large shifts in prosomal pressure. A mild struggle was induced by holding the cannulated leg in the extended position so that the animal could not flex it (Fig. 14). Some of the large amplitude beats may have been induced by cardiac ganglion activity, but in most cases they occurred when an increased pressure anteriorly would have either increased the resistance to flow through the aorta or caused the aortic valve to close. The small amplitude beats occurred when pressure in the prosoma fell sufficiently to allow opening of the aortic valve. The aorta probably offers less resistance than do the abdominal arteries. Toward the end of the struggle the variations in amplitude may have been, at least in part, the result of fluctuating abdominal tensions.

Pressures Required for Extension When the Legs Are Unsupported

Whether such high pressures as may be generated in the prosoma are necessary to extend the legs was not known. The following results give an

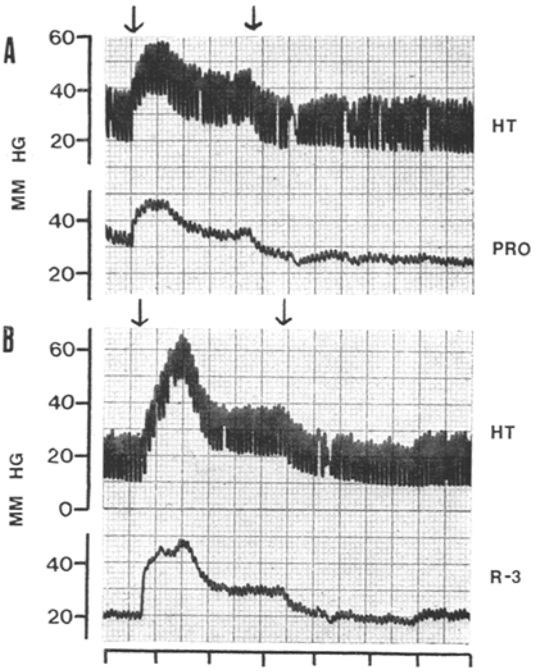

Fig. 15 A and B. Pressure records when the legs were unsupported and blasts of air were administered (between arrows). A. From heart and prosoma. B. From heart and leg. Time marks: 10 sec

indication of the pressure levels needed to extend the legs when only the body was supported leaving the legs hanging free. Pulsations of the legs occurred with each heart beat. A blast of air caused a quick elevation of the femurs and abdomen which was followed by extension of the lower joints of the legs, a hydraulic response. The femurs were then depressed, a muscular action, so that the legs were held almost straight out from the body. This extension was maintained until the air was turned off although the abdomen and legs were gradually falling. Pressures recorded simultaneously in the heart and prosoma (Fig. 15A) and in the heart and leg R-3 (Fig. 15B) rose to maximal levels when the air was turned on and then fell to 30–35 mm Hg, which levels were maintained until the air was turned off. In Fig. 16A are shown pressures recorded simultaneously in the prosoma and leg R-3 during air blasts which caused extension of all legs. Pressure in leg R-3 was maintained above that in the prosoma throughout. From the information in Figs. 15 and 16 it may be inferred that at this level of activity, an arterial pressure was

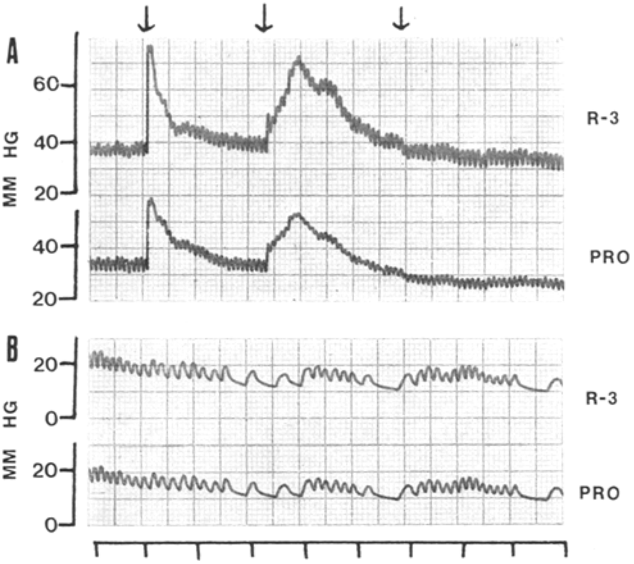

Fig. 16 A and B. Simultaneous pressure records from the leg and prosoma with the legs unsupported. A. A quick puff of air was administered (1st arrow) followed by a longer blast (between 2nd and 3rd arrows). B. Record showing erratic behavior of heart. Time marks: 10 sec

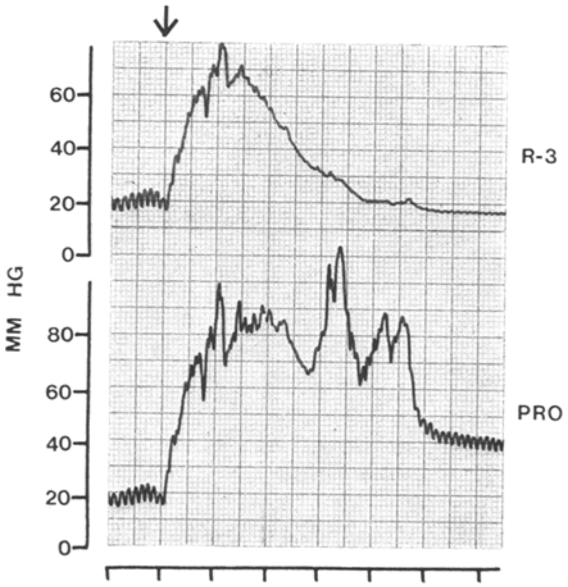

Fig. 17. Simultaneous pressure records from the leg and prosoma. A support was placed under the legs (at arrow). Time marks: 10 sec

primarily responsible for the extension. Pressures generated by the heart alone did not accomplish this result. The compression of the heart by the abdominal muscles, balanced by a simultaneous prosomal compression, established the higher base pressure from which the heart operated. Further exposures to air blasts caused lower pressure rises, and the accompanying extensions became less pronounced. After this the heart beat became somewhat slower and erratic suggesting that the unusual posture and the activity might have produced some fatigue (Fig. 16B). When a support was placed under the legs, a slight struggle ensued and the pressure in the prosoma rose well above that recorded in any of the experiments just described (Fig. 17). This suggests that the extent of prosomal compression is greater when there is a substrate for the legs to press against. The pressure in the leg rose also, but then fell to well below that in the prosoma. The pulses in the leg became much less marked after the support was placed under the legs. These phenomena suggest that the approximately 30 min interval with the legs unsupported had resulted in some abnormal condition.

That pressures of the magnitudes observed in the above experiments are adequate to extend unweighted legs was confirmed in a dead spider by injecting fluid. At 41 mm Hg all legs were extended and at 48 mm Hg all legs were raised off the substrate with R-4 and L-4 elevated the most.

Pressure Required for Walking

Extension during walking is most marked in the femur-patella joint of the 1st and 4th pairs of legs. This joint has no extensor muscles and is the primary site of the hydraulic action. In the 1st pair, directed anteriorly, the extension occurs when the leg lifts off the substrate and reaches far forward. With the 4th pair, directed posteriorly, extension occurs during the propulsive stroke after the leg tip touches the substrate. The movement in the 2nd and 3rd pairs resembles, but is less extreme than that in the 1st and 4th pairs, respectively. The abdomen is elevated while walking but is lowered occasionally so that the spinnerets touch the ground.

Pressures were recorded from the prosoma (two animals) and from a leg (four animals) during unrestrained walking. In all cases, pressures rose to 40–60 mm Hg when walking began and fell abruptly when the animals paused. Once the pressure has risen to these levels any limb may be extended and the pattern of movement must depend upon the nervous control of the flexor muscles. In Fig. 18A is shown a recording from an animal which at first paused after each step or two. Each pause was accompanied by a drop below the pressure level needed for extension. The last part of the recording represents a period of steady walking with a basal pressure of about 50 mm Hg. This animal was not using the can-

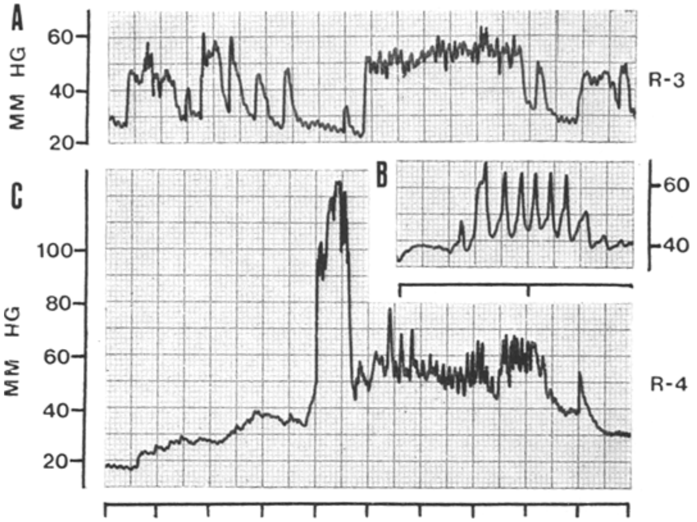

Fig. 18A—C. Pressure records during walking. A. Walking without using the cannulated leg. B. and C. Walking involving use of the cannulated leg. Time marks: 10 sec

nulated leg and under such circumstances the recordings from the leg resembled those from the prosoma. A recording made from another animal during a short period of walking is shown in Fig. 18B. This animal was using the cannulated leg (R-4) and each of the 6 large pressure peaks could be correlated visually with flexion of the leg. This appeared to be true of the second longer period of walking, also (Fig. 18C). The large peak accompanied the slight struggle which occurred in the process of stimulating the animal to move. The basal pressure levels appeared to be higher the more rapid the movement and to rise to higher levels the longer the period of movement. The heart rate in this spider increased from 60/min before the last walking session to 96/min just afterward.

The Effect of Loss of Blood

The effect of loss of blood on pressure was determined in two animals. One of these, which weighed 11.6 g, might be expected to have 2.1 ml blood (Stewart and Martin, 1970). After sitting quietly for several minutes the resting heart pressure was 21/12 mm Hg, heart rate 75/min (Fig. 19A). Removal of 1/4 ml blood resulted in an immediate fall in blood pressure to 4/—2 mm Hg, heart rate 69/min. The spider was still capable of a considerable rise in pressure and during a brief struggle it rose to 38 mm Hg (B). By 10 min after bleeding, some recovery had

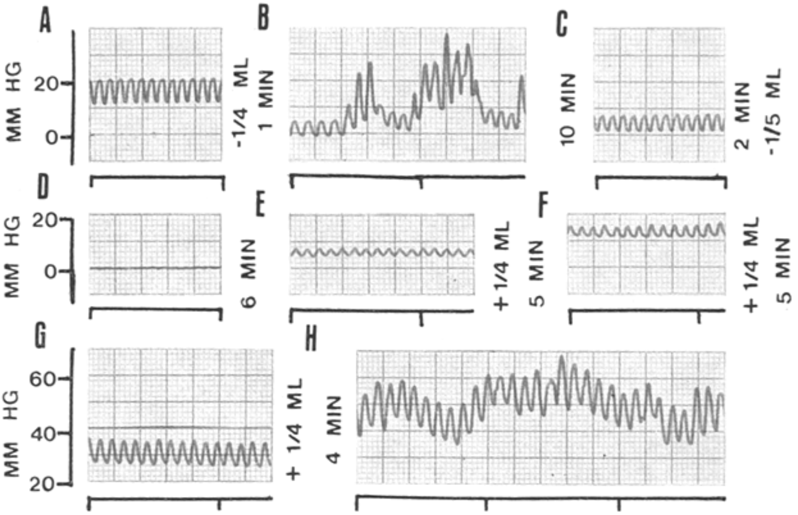

Fig. 19 A—H. Pressure records from the heart before and after removal of blood and following injections of Ringer solution. Times between successive records are indicated. Time marks: 4 sec

occurred with the pressure at 8/2 mm Hg and the heart rate 75/min (C). Two min later, at 12 min, 1/5 ml blood was withdrawn and the pressure fell to 0 mm Hg with scarcely discernable pulses at 68/min (D). Again some recovery occurred and 6 min later the pressure was 7/5 mm Hg, heart rate 74/min (E). At this time, 1/4 ml Ringer was injected and the pressure rose to 16/12 mm Hg by 5 min after the injection (F). Another 1/4 ml Ringer, which somewhat more than replaced the blood removed, was then injected, causing an initial rise, then a levelling off to 36/27 mm Hg by 5 min later (G). Another 1/4 ml was injected, causing another pressure rise, and by 4 min later pressures as high as 68/50 mm Hg were recorded, although the base level and amplitude of beat were variable (H). Heart rate was 63/min. Thus, pressure level and amplitude of beat are very dependent upon maintenance of blood volume. During the short periods allowed some compensation for loss of blood occurred. Heart rate was not greatly affected by loss of blood.

Abdominal Pressures

Blood returning from the prosoma enters the lateral sacs which are bounded by flexible cuticle. A sudden surge of blood into these spaces might only expand the cuticle and result in no very large rise in pressure. In Fig. 20 A is shown a recording from the left lateral sac. Legs R-4 and

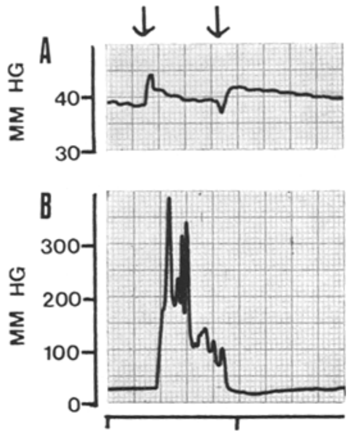

Fig. 20A and B. Pressure records from the left lateral sac. A. Leg R-1 was flexed (1st arrow) and the left pedipalp was extended (2nd arrow). B. During a struggle. Time marks: 4 sec

L-4 were held forward with tapes so that the cannula could be inserted and the high initial pressure may have been the result of this. That pressure changes from the prosomal region are freely transmitted was indicated by an immediate rise in pressure on manually flexing leg R-1 (1st arrow). Extending the left pedipalp caused an immediate fall in pressure (2nd arrow). High pressures during a struggle were also transmitted (Fig. 20B). In this spider the initial pressure was 25 mm Hg and during the 5 sec struggle the general pressure level reached 170 mm Hg with peaks to 385 mm Hg.

In several spiders the cannula was inserted dorsal to the outer end of the right posterior lung book, i.e., in the lateral part of the abdomen. Although the cannula might easily become blocked by the digestive gland, pulsations were clearly visible and the system seemed responsive to changes in pressure. In this region the pressure peaks in the recording were out of phase with those in the heart, i.e., systole resulted in a decreased pressure in the region around the heart while diastole caused a rise in pressure (Fig. 21A). Small amplitude beats in leg R-1 were accompanied by a rise in pressure in the abdomen, apparently because a larger volume of blood was retained whenever the beats were weak. Large amplitude beats in the leg were accompanied by reduced abdominal pressures. A similar relationship is shown between leg R-1 and a lateral sac (Fig. 21B) although the pressure peaks are not so completely out of phase.

In Fig. 22 is shown a recording from the lateral region of the abdomen and the heart. Except for the difference in phase, the relationship

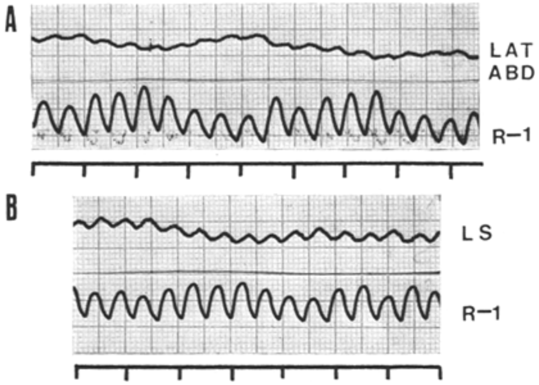

Fig. 21. A. Simultaneous pressure records from the lateral region of the abdomen and leg. Time marks: 1 sec. B. Simultaneous pressure records from the lateral sac and leg. Time marks: 1 sec

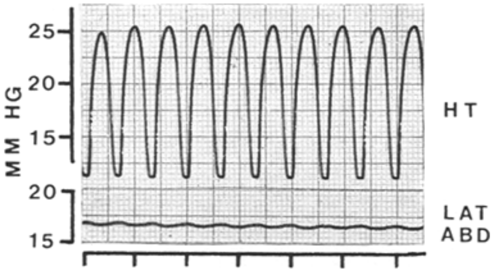

Fig. 22. Simultaneous pressure records from the heart and lateral region of the abdomen. Time marks: 1 sec

resembles that between heart and prosoma, Fig. 11A. This is not surprising since the abdomen has an arterial blood supply. Recordings from several animals suggested that there may be frequent intervals when the pressure in this part of the abdomen is above that in the prosoma. In Fig. 23 are shown several recordings from these regions. In A, a recording from an animal after resting quietly for $2^1/_2$ min, the pressures in the two regions fluctuated with the amplitude of the heart beat. When the amplitude was large, the pressure in the prosoma was very slightly above that in the abdomen at systole. It may be that the periodic increases in amplitude seen frequently in resting animals (Fig. 6A) are necessary to shift blood from the abdomen to the prosoma when an imbalance occurs. In B is shown the response to a slight puff of air (1st

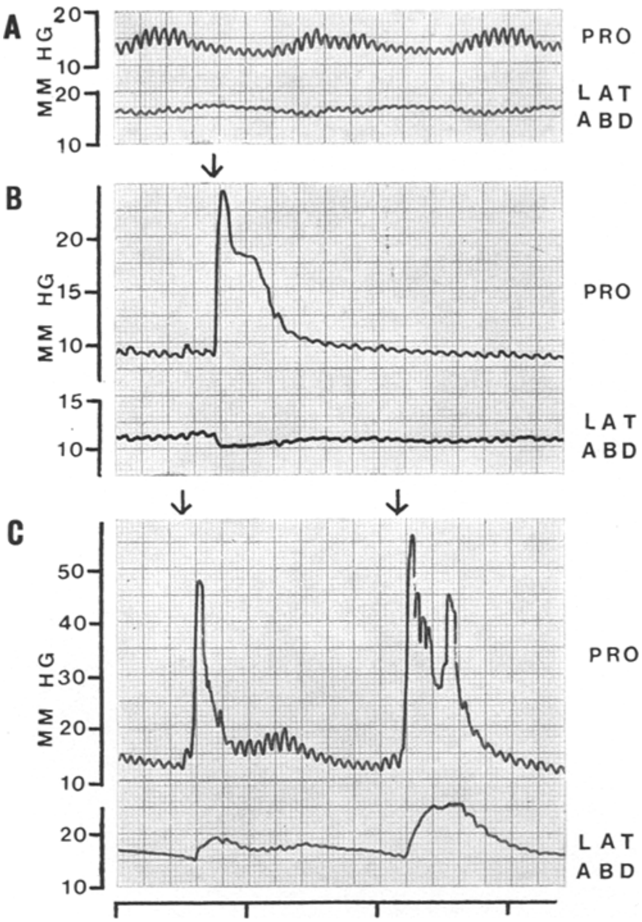

Fig. 23 A—C. Simultaneous pressure records from the prosoma and lateral region of the abdomen. A. At rest. B. Response to a slight puff of air. C. Responses to touching the legs (at arrows). Time marks: 10 sec

arrow) which caused a sharp rise in prosomal pressure but a decrease in abdominal pressure. Stronger contractions could have removed more blood from the abdomen thereby lowering the pressure, or, although it seems less likely, a relaxation of tension in the abdomen might have occurred. Stronger stimuli resulted in increases in pressure in this part of the abdomen. In C are shown responses to touching the legs (at arrows). Pressure in the prosoma rose well above that in the abdomen on each occasion. The increases in abdominal pressure, occurring simultaneously

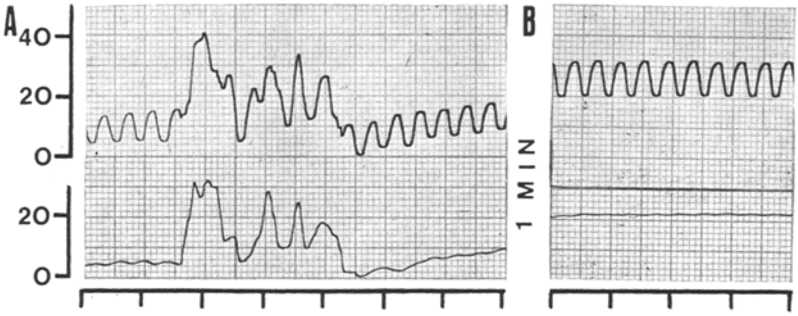

Fig. 24A and B. Simultaneous pressure records from the heart and left posterior pulmonary vein. A. Immediately after cannulating. B. 1 min later. Time marks: 2 sec

with the increases in the prosoma, must have been the result of rapid abdominal compressions occurring simultaneously with those in the anterior regions.

Pressures were recorded simultaneously in the left posterior pulmonary vein and in the heart (Fig. 24). The large fluctuations occurred as a result of inserting the cannula into the pulmonary vein and undoubtedly indicate contraction of the abdominal muscles. The pressure pulses were out of phase as would be expected. With pressures in the pulmonary veins close to heart diastolic levels, and pressure in the lateral sacs probably close to the levels in the prosoma with which it is in open communication, blood flow through the lung books should be fairly rapid. The pressure gradient between pulmonary vein and ventricle, about 1–2 mm Hg, seems narrow, but there are 8 ostia through which blood can enter the heart. It should be noted that the general abdominal pressure is well above that in the pulmonary vein and in the heart at diastole. The latter is accounted for by recoil of the elastic ligaments at diastole, but the patency of the pulmonary veins in the presence of the high abdominal pressure is not explained and presumably has a morphological basis.

Direct observation of the heart *in situ* through the subcuticular muscle sheath (with only the cuticle removed) indicated that the pericardium serves to some extent as a reservoir for blood returning during systole. On contraction a distinct space was seen to develop between heart and pericardium although it was narrower at the points of insertion of the lateral ligaments where the heart is held more closely to the pericardium. The heart probably fills through the 2 posterior pairs of ostia directly from the pericardium, while the 2 anterior pairs may conduct in part directly from the pulmonary veins which enter the pericardium close by. The lips of the ostia have been considered to open at diastole when the suspensory ligaments which attach to them recoil (Wilson, 1967). However, it has not been specified at what point in diastole opening occurs. Direct observation indicated that they are pressure-dependent valves. When a colored Ringer solution was injected into the beating heart through an ostium with the pericardium opened along the dorsal midline, no escape of fluid occurred through the ostia on recoil of the ligaments. The greater pressure within evidently prevented opening of the valves.

Discussion

Various factors have been considered to affect the heart rate in spiders. Rijlant (1933) and Wilson (1967) reported a decrease after blood loss and concluded that heart rate depends on internal pressure. Sherman and Pax (1968) noted no great difference between heart rates in intact *Geolycosa missouriensis* and in isolated hearts in which little pressure existed. In *Dugesiella* heart rates were relatively independent of pressure. Thus, a pressure of 53/39 mm Hg in one animal was accompanied by a heart rate of 77/min, close to the rate of 74/min recorded at a pressure of 7/5 mm Hg in an animal that had been bled (Fig. 19E).

Sherman and Pax (1968) found an increase in rate from 48/min before exercise to 176/min just afterward. In *Dugesiella* after a period of exercise rates averaged 88/min increasing from 35/min before. Higher rates to 116/min were observed in cannulated animals. In both *Geolycosa* and *Dugesiella* up to $^1/_2$ hr was required for recovery of the initial rate. During the struggles the heart rate in *Dugesiella* sometimes increased and sometimes decreased, but often was unchanged.

Wilson (1967) reported that the heart rate of *Heteropoda* became very slow during struggles and only increased above the normal rate after the struggle was over. He believes that high pressures generated in the prosoma are transmitted throughout the body, and suggested that the lengthened systoles during struggles were the result of back pressure on the heart. Slowing of the heart sometimes followed weak stimuli, and this he suggested resulted from nervous activity.

Larimer and Tindel (1966) have made comparable observations on crayfish. During locomotion there was usually an acceleration of heart rate but occasionally they observed a bradycardia. To better isolate the role of the nervous system they observed a resting crayfish. Thirty min after it had entered a dark chamber the rate had dropped from 120/min to 80/min and after 2 hr to 63/min. They suggested that a continuous low-level bombardment of a cardiac control center is generally facilitative with bradycardia resulting when stimulation is reduced. This may be true for *Dugesiella* also, since it is known that tarantulas have neurogenic hearts (Bursey and Sherman, 1970). When a cannulated animal was covered with a box, the heart rate decreased 36% after only 10 min, and there was an immediate drop in blood pressure. The pressure drop was most likely due to relaxation of the body musculature, but the reduction in heart rate seems more likely to be the result of an effect through the cardiac ganglion.

Relative durations of systole and diastole in *Dugesiella* differ from those reported by Wilson (1967) for *Heteropoda*. At 60 beats/min he found each phase to last about 500 msec., whereas at this heart rate in *Dugesiella* systole lasted 750 msec and diastole 250 msec. In *Heteropoda*, duration of diastole decreased almost linearly with increasing rates while that for systole decreased asymptotically. In the tarantula, durations of both phases decreased linearly between heart rates of 21/min and 55/min. The duration of systole continued to decrease, though more slowly, to a rate of 116 beats/min. Duration of diastole decreased very slowly after about 55 beats/min.

That a change in heart rate depends more closely on a changing duration of diastole than on that of systole has been considered a feature basic to all circulatory pumps (Fyhn *et al.*, 1972). This was not the case in the tarantula. At all heart rates systole occupied a fairly constant proportion of the total beat duration (60-75%). From a heart rate of 21/min to 116/min a reduction of 82% in beat duration occurred. This was accomplished by a decrease of 84% in duration of systole and 78% decrease in that of diastole. In absolute terms, since duration of systole was over twice that of diastole, it was systole which showed much greater reduction in duration. Between the two extreme rates, systole was shortened from 2000 msec to 320 msec while diastole was reduced from 900 to 200 msec. Therefore, it appears that the contraction time of these hearts can be greatly reduced.

In any animal capable of compression of the body so that an external force is applied to the heart, the pressure pulses may not represent the true power of the heart, nor are the pressure levels a measure of the peripheral resistance. For example, in the experiment in which air was blown on an animal (Fig. 15), compression of the body occurred and the pressure levels rose throughout. No doubt an increased resistance to flow anteriorly resulted from prosomal compression, but a simultaneous compression of the abdomen raised heart pressures so that circulation forward continued. No noticeable increase in pulse pressure occurred other than transiently, the entire system simply began operating at a higher pressure level, permitting leg extensions to occur.

The results of earlier indirect determinations of blood pressure in the spider have been confirmed, in part, by the present study using a direct method. The maximum pressures generated in the prosoma of the house spider (Parry and Brown, 1959a) and in the tarantula are nearly identical. Wilson (1970) suggested that the pressures of 30–40 mm Hg which he measured in the abdomen of *Araneus* (1962b) and the "resting" pressure of 50 mm Hg measured by Parry and Brown (1959a) in the leg are not really resting pressures, and should rather be considered the normal pressure of an alert spider, sufficient for ordinary locomotion and for maintaining silk available for spinning. These values are remarkably close to the 40–60 mm Hg actually measured here during walking. In *Dugesiella* resting pressures may now be defined which probably will apply in other species. To obtain a gradient of pressure into the heart where the lowest normal diastolic pressure recorded in this study was 8 mm Hg (Fig. 5), all other regions must be at higher pressure levels. But the gradient does not need to be excessive, and in this instance, the highest pressure was the systolic pressure of the heart, 12 mm Hg. The average heart pressures of many cannulated spiders were 22/13 mm Hg, levels about 1/2 the values previously suggested to be resting pressures.

Parry (1960) believed that the unloaded leg could be extended by a pressure of 50 mm Hg but considered this much too little to account for results obtained previously with the loaded leg (Parry and Brown, 1959a). They had determined torques during extension of a leg, weighted with a 45 mg weight, in the horizontal plane (the body apparently was oriented vertically). They calculated that pressures up to 450 mm Hg would be needed to generate the torques and implied that these results refuted Manton's assertion that extension of the posterior legs, with the tips on the ground, is due to muscular depression of the femur (Manton, 1958). Wilson (1970) doubted that high pressures were needed for ordinary locomotion but suggested they might be part of an "escape reaction" enabling the animal to run faster or to jump. The high pressures might be maintained long enough for a jump, but it appears unlikely that very high pressures are needed for walking and running, particularly since these pressures are maintained for so short a time, perhaps 2 sec in the struggle shown in Fig. 11B. If a spider can extend its legs at a pressure level of 50 mm Hg, and can maintain the circulation during this time, it seems unlikely that pressures 5–10 times as high would be needed for rapid walking. The flexor muscles must overcome this hydraulic force in each leg with every step, and fast walking requires their rapid action. It is possible that the highest pressure recorded here, 484 mm Hg, results from the maximum possible compression of the body with all legs closely flexed.

Wilson suggested that the high pressures in the prosoma are generated by contraction of the musculi laterales only. Since numerous muscles attach the coxae to the endosternite, he felt coxal movement might be impeded if the carapace-endosternite muscles are involved too. But when air is blown on *Dugesiella* to induce extension, the elevation of the coxae is obvious, and since the coxae form much of the ventral surface of the prosoma this must affect the pressure. Wilson noted that the pressure rises when the animal gets up on its feet. The reason for this probably lies in the way the body is suspended among the legs. The coxae and the sternum are joined by flexible cuticle and with the mass of the body exerting a downward force, the distal ends of the coxae must be pressed up into the prosoma. There was some evidence that unless the legs were resting on a substrate the ability to elevate the coxae is limited. Very high pressures were never observed in animals whose legs were unsupported. This suggests that for maximum compression of the prosoma, a substrate to press against is required. When a substrate was placed under the animal of Fig. 17, prosomal pressure rose immediately. If, as Wilson believed, only the musculi laterales are involved, a support should have had no effect.

Parry and Brown (1959b) considered the segmental muscles of the abdomen inadequate to maintain significant internal pressure. Wilson (1970) agreed and suggested that the maintained abdominal pressure of 40–50 mm Hg resulted from tension in the sub-cuticular muscle sheath. However, since the pressure increases observed in the abdomen were not great, a reconsideration of the segmental muscles may be indicated. After bleeding, the ventral surface of the abdomen becomes distinctly wrinkled and this may result from contraction of the paired musculus longitudinalis intermedius (Brown, 1939) which run the length of the abdomen along its ventral surface. In addition, there are two pairs of dorso-ventral muscles which insert on the dorsal abdominal cuticle lateral to the heart. Their contraction could depress the portion of the cuticle lying over the heart, thus raising the intraventricular pressure. Their insertions are visible externally and Wilson observed a dimpling of the cuticle here during struggles. This was seen in *Dugesiella* also during violent struggles. This evidence indicates that these muscles play some part in developing abdominal pressure.

During activity the abdomen of *Dugesiella* is elevated. Wilson (1965) described no such action in *Heteropoda*. He identified only 1 pair of levator muscles whose contraction elevates the abdomen along the hinge line between the 2 lora. These are small muscles and evidence that they are given hydraulic assistance is provided by the observation that when an animal had lost much blood the abdomen was not lifted, but dragged along the ground. A possible mechanism is filling of the lateral sacs which, located somewhat ventrally, may press against the adjoining portion of the prosoma.

Probably all or most of the abdominal muscles are involved in producing the pressure increases which, though not as great as those which may occur in the prosoma, enable the heart to continue delivery of blood anteriorly during most ordinary activities. When prosomal pressures rise to high levels the blood from the heart has an exit through the abdominal arteries. The activity of the heart is not disrupted by such pressures since they do not reach this portion of the abdomen. Whenever the pressure falls anteriorly the aortic valve opens to deliver blood.

Wilson (1965) found no valve in the pedicel nor is one indicated from the work here. High pressures were recorded in the lateral sacs which are in open communication with the prosoma, yet little evidence was found for an increased return of blood to the heart during activity. For example, during the struggles shown in Fig. 13, the diastolic level first increased, but then decreased as the prosomal pressure continued to rise. High pressures were never measured within the heart, nor in the pulmonary vein. One might have predicted some isolating mechanism since otherwise high pressures acting on the heart externally would seriously disrupt its activity. Some morphological mechanism must exist to hold the pulmonary veins open in the face of higher surrounding pressures in this region of the abdomen, and it is likely that there is also some means of closing these channels when excessively high pressures are attained in the prosoma and lateral sacs. It is possible that the 1st pair of dorsoventral muscles is involved. These muscles run from the anterior region of the abdomen posteriorly under the anterior pair of pulmonary veins to insert on the dorsal cuticle close to the posterior pair of veins. Their contraction might close both pairs of pulmonary veins.

The rapid exhaustion of spiders during enforced exercise noted by Bristowe and Millot (1933) was attributed by Wilson (1970) to exhaustion of the hydraulic system. Evidence for this view was presented in a later paper (Wilson and Bullock, 1973). Using an indirect method, it was found that during struggles blood was shifted from prosoma to abdomen in *Amaurobius ferox*. The recordings indicate that the shifts between regions reach plateaus fairly quickly, about 6 sec after the beginning of a 19 sec struggle. Results obtained with *Dugesiella* do not indicate much depletion of blood from the prosoma. After struggles, pressure within the prosoma fell to only the initial resting level. It may be that the plateaus indicate that the lateral sacs have filled, and after this, outflow from the prosoma is slight. If elevation of the abdomen is hydraulic in part, it is possible that after a struggle, or during walking, the lowering of the abdomen, which is seen frequently, causes some return flow of blood to the prosoma. It is possible that some depletion of blood from the legs occurs during walking or in struggles. The frequent pauses seen in locomotion may be necessary for re-charging the legs with blood. Wilson and Bullock (1973) have suggested that oxygen lack due to interuption of blood flow is also a factor in the long recovery period needed. During ordinary activity, such as walking, it is unlikely that blood flow anteriorly ceases, and even in struggles, the pressures in the prosoma fall intermittently to allow opening of the aortic valve. The long recovery time after exercise is more likely necessary to recover from an oxygen debt. Cloudsley-Thompson's report (1957) that *Ciniflo* spp. can maintain maximum speeds for long periods if given oxygen supports this view.

In the resting animal the pressure gradients from one region to another are small. Rapid delivery of blood may not be needed since metabolic rate is low (Stewart and Martin, 1969). Leg pressure is slightly above prosomal pressure permitting return flow of blood during inactivity which may last for hours. The gradient from prosoma to abdomen is slight and on occasion may even be reversed. At such times amplitude of beating increases periodically to redistribute the blood. Pulmonary vein pressure is only slightly above heart diastolic pressure. However, it is well below prosomal and lateral sac pressure, giving a fairly large gradient for flow through the lung books. In activity, with the animal on its feet, pressure in the prosoma rises. When walking begins, levels of 40–60 mm Hg are adequate for leg extension. Although simultaneous recordings from the legs and prosoma during walking were not made, the general level of pressure in the prosoma may rise above that in the legs. This would increase leg pressure, either from the reduced rate of outflow or from an actual entry of blood from the prosoma, depending on the magnitude of the gradient. Flexion of a particular leg would expel blood into the prosoma. Delivery of oxygenated blood through the pedal arteries probably continues unless the pressure rises above perhaps 100 mm Hg, although there was great variability among animals in the respect. It is believed that the very high pressures do not occur often and are simply a byproduct of violent activity.

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