

## COUPLING BETWEEN THE HEART AND SUCKING STOMACH DURING INGESTION IN A TARANTULA

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### Summary

Electrocardiograms (ECGs) and electromyograms (EMGs) from the dorsal musculature of the sucking stomach of tarantulas (*Grammastola cala*) were recorded simultaneously from unrestrained animals during ingestion. Resting heart rates averaged  $33.6 \pm 1.9$  beats  $\text{min}^{-1}$ , which increased significantly to an average of  $51.6 \pm 3.8$  beats  $\text{min}^{-1}$  during ingestion. This is not significantly different from the average sucking stomach rate of  $53.6 \pm 3.9$  cycles  $\text{min}^{-1}$ . Activity of the sucking stomach constrictor muscles started with a phase shift of  $0.64 \pm 0.007$  cycles relative to dilator activity. In some cases the stomach dilators were active almost in synchrony with heart systole (phase shift of  $0.10 \pm 0.009$  relative to ECG), and the constrictors were active later in the cycle, during diastole, with a phase shift of  $0.71 \pm 0.007$  relative to the ECG. These data suggest that, during ingestion, fluid flows in the anterior aorta and midgut are negatively coupled as the fluids traverse the pedicel. Although such coupling was observed in about half the traces, other results were obtained that showed no evidence of coupling. Possible mechanisms for coupling and the sequence of events in the pedicel during ingestion are discussed.

### Introduction

The pedicel of spiders is a narrow constriction between the prosoma and opisthosoma (Fig. 1). Its function has not been explained adequately, but it is thought that it increases opisthosomal mobility, e.g. for laying down silk. The circulatory, digestive and nervous systems all traverse this confined space in close proximity, surrounded by a complex musculature.

The tubular heart runs dorsally in the opisthosoma suspended on ligaments in the pericardium (Wilson, 1967) (Fig. 1). Blood enters the heart during diastole through a series of laterally placed, valve-like ostia. The heart is regulated by pacemaker activity in the cardiac ganglion (Wilson, 1967; Sherman and Pax, 1968), which runs along the dorsal surface of the heart and extends down onto the aorta

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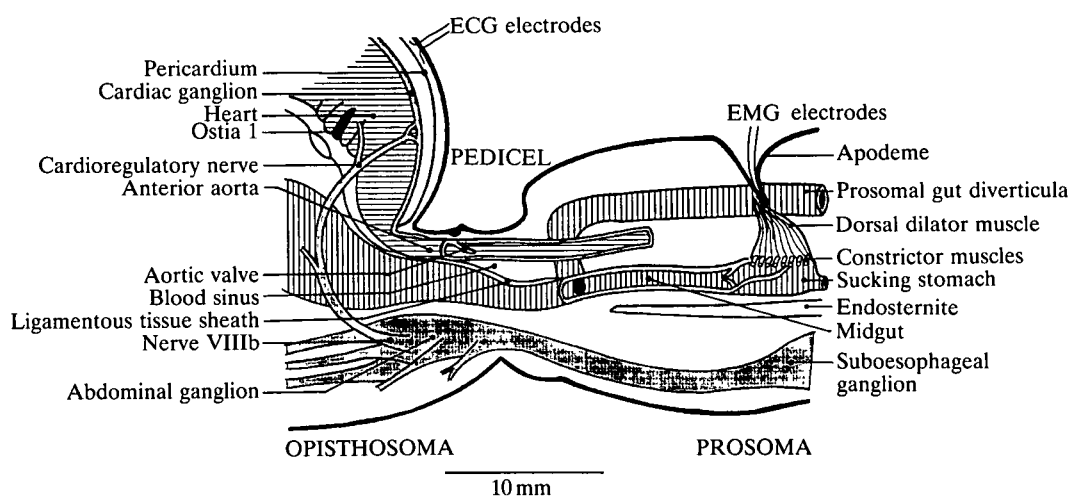


Fig. 1. Schematic section of the pedicel and midgut region of a tarantula (after Firstman, 1954; Wilson, 1965; Meyer, 1981; Gonzalez-Fernandez and Sherman, 1984; Sherman, 1985). Additional material from *Rhescostica seemani*. Sites of the recording electrodes are shown.

(Gonzalez-Fernandez and Sherman, 1984). This ganglion is innervated by the cardioregulatory nerve, which is a branch of the paired nerve VIIIb. The heart can pump haemolymph both forwards and backwards through anterior and posterior aortas (Foelix, 1981; Paul *et al.* 1989). The anterior aorta runs dorsally through the pedicel in a chitinous tunnel composed of two hinged lora. The aorta has a valve in the pedicel region to prevent backflow. Anterior to this valve the aorta appears to be mechanically isolated from the midgut immediately below it by a ligamentous sheet and a blood sinus (Wilson, 1965). This isolation appears to break down posterior to the valve, where the aorta and midgut run adjacent to each other. The aorta continues into the prosoma, where it bifurcates and branches into the peripheral arterial system (Foelix, 1981). Haemolymph returns from the prosoma to the lateral sacs of the opisthosoma through the lateral sinuses of the pedicel.

The sucking stomach lies deep in the prosoma within the endosternite, a collagenous internal skeleton, and below the dorsal apodeme (Foelix, 1981). The stomach is valved at both its entry and exit (Legendre, 1961) and in the resting state exhibits the so called 'collapsed square' shape. Dilation is caused by the activation of lateral muscles and a large dorsal dilator muscle that connects to the apodeme (Firstman, 1954; Meyer, 1981), while constriction is caused by a series of constrictor muscles that encircle the stomach. The stomach's function is to draw in liquefied food from the mouthparts and pump it posteriorly. The prosoal diverticula branch from the midgut but it is not clear from the literature whether ingested material enters these diverticula prior to passing through the pedicel.

Very little research has been done on the pedicel in spiders. Parry and Brown (1959) suggested that the prosoal and opisthosomal blood systems may be

separated by some form of valve in the pedicel. Wilson (1965) looked for, but failed to find, a means of hydrostatically separating the circulation in the prosoma from that in the opisthosoma. On the basis of this finding, the hydraulic collapse theory was proposed (Wilson and Bullock, 1973). This suggested that during activity (e.g. walking) haemolymph supply to the prosoma is inhibited by the high pressures generated there, and that the pressure gradient will force prosomal haemolymph through the pedicel into the opisthosoma. Since certain spider leg joints rely on hydraulic extension, this loss of haemolymph would, according to the theory, reduce the haemolymph available for leg extension and so limit the duration of activity. However, this theory has been criticised (Stewart and Martin, 1974; Prestwich, 1988; Paul *et al.* 1989) because prosomal pressure changes during activity were found not to be transmitted to the whole of the opisthosoma. Paul *et al.* (1989) proposed that there is a separate anterior and posterior circulation in spiders, separated by a physiological ligature which is not the pedicel, but must be between the two book-lung pairs in the region of the lateral sacs of the opisthosoma. Any role for the pedicel in circulatory partitioning remains unclear but unlikely.

Arthropod blood vessels are elastic (Hill and Wyse, 1989) and when haemolymph is pumped through them by the heart they presumably distend. This effect must be particularly apparent in the anterior aorta through which the haemolymph is expelled during systole (Carrel, 1987). A similar argument can be made for the midgut, through which the sucking stomach pumps pre-digested food posteriorly in a peristaltic wave (Collatz, 1987), with reflux prevented by valves and the action of the constrictor muscles (Legendre, 1961). Where the aorta and midgut are adjacent to each other in the posterior region of the pedicel, distension of one will press against the other, thus constricting its lumen and reducing flow. If fluid is pumped through both vessels simultaneously the interaction may reduce the efficiency of fluid transmission.

The aim of this investigation was to consider whether there is some form of physiological coupling between the activities of the heart and sucking stomach, which, during ingestion, pump material in opposite directions in the pedicel, through the adjacent aorta and midgut, respectively. The hypothesis under investigation is that heart and stomach contractions may be negatively coupled, thus pumping haemolymph and food through the pedicel out of phase with each other. To test for coupling, the electrical activities of the musculature of the heart and the sucking stomach have been recorded simultaneously, in freely moving animals during feeding and drinking.

## Materials and methods

### *Animals*

Adult male and female Chile rose tarantulas (*Grammastola cala*, family Theraphosidae) (10–16 g) were obtained from Pro-Nature Ltd, South Humber-side, and housed individually at 20°C on a substratum of vermiculite in plastic

containers. To encourage the animals to eat promptly during experiments they were not fed during the experimental period, except when data from feeding animals were required. Water was provided *ad libitum*. All animals survived the procedure and seemed to be in good condition throughout.

#### *Preliminary investigations*

Dissections of a number of Chile rose tarantulas were performed to check that the theraphosid pedicel has a similar gross morphology to that of *Heteropoda venatoria* (family Sparassidae: Wilson, 1965). This was further checked by preparing wax sections of a specimen of a related theraphosid, *Rhecostica seemani*. No major differences were observed in either case and Wilson's diagram of the pedicel has been assumed to be an adequate representation of the pedicel in the animals used in this study (Fig. 1). Gonzalez-Fernandez and Sherman (1984) also noted no major differences in heart and pedicel anatomy between *H. venatoria* and the tarantula *Eurypelma marxi*.

#### *Experimental set-up*

Experiments were carried out at room temperature (approximately 22°C) with the animal placed inside an aquarium of approximate floor area 0.2 m × 0.15 m; this allowed the animal some degree of freedom during experiments. Observations of tarantulas feeding suggest that posture and occasional gross body movements are important during ingestion; specifically, the tarantula raises itself up on its legs and lowers its opisthosoma during the later stages of feeding. Access could be gained from above and from the front to allow the animal to be manipulated.

#### *Recording heart and sucking stomach activity*

Spiders were anaesthetised with CO<sub>2</sub> and restrained. Electromyograms (EMGs) were recorded from the dorsal dilator muscle. Ideally, to look at food transfer through the pedicel, EMGs would be recorded from the constrictor muscles of the stomach. However, since these are small and located deep within the prosoma (Fig. 1) activity of the more accessible dorsal dilator was monitored, and it was assumed that the muscle was active between constrictions. The dorsal dilator's position relative to the central apodeme of the carapace was determined using the diagrams of Firstman (1954) and Meyer (1981) and the apodeme was used as a guide for positioning the electrodes. A single hole was pierced vertically in the posterior face of the apodeme with a fine pin, and a pair of electrodes (120 μm in diameter 'Lewcasol') was inserted into the musculature, taking care that the exposed ends were not in contact with each other (Fig. 1). Electrocardiograms (ECGs) were recorded from the dorsum of the heart because of the inaccessibility of the aorta. Small holes were pierced in the cuticle on either side of the heart and an electrode was inserted into each (Sherman and Pax, 1968; Anderson and Prestwich, 1985). The electrodes did not interfere with the movements of the animal. During insertion, slight haemolymph loss was observed but no serious damage was apparent. The electrodes were sealed into place with wax and the

animal was placed in the aquarium to recover and to acclimatise for approximately 30 min. The signals from the electrodes were amplified using Grass P9B preamplifiers and recordings were made on a Gould 1602 digital oscilloscope and a Gould pen recorder.

With the electrodes in place the animal was offered live crickets which it caught in its own time. ECG and EMG activities were recorded simultaneously and continuously before, during and after feeding. If an animal refused food, it was offered water instead. While tarantulas in the wild, and at suitable humidities in captivity, drink very little, they will drink to replace fluid following blood loss (Stewart and Martin, 1970), such as that observed during electrode insertion. It was assumed that there is no difference in the ingestion mechanism used for taking in water and that used for taking in liquefied food. All results are expressed as mean  $\pm$  s.e. (number of observations or animals as specified).

Phase shifts were calculated using ECG or major EMG spikes as reference points, i.e. the phase between a prominent spike in one cycle and the same spike in the following cycle is 1.0. The phase shift of an EMG spike relative to ECG activity is the fraction of a cycle by which the EMG spike lags the ECG spike. All statistics used were standard Student's *t*-tests.

## Results

### *Heart activity*

The mean resting heart rate was  $33.6 \pm 1.9$  beats  $\text{min}^{-1}$  (8) from eight animals. Heart rates recorded during ingestion rose to a mean rate of  $51.6 \pm 3.8$  beats  $\text{min}^{-1}$  (8). The resting and ingestion rates are significantly different ( $P < 0.001$ ).

### *Sucking stomach activity*

The sucking stomach rate during ingestion averaged  $53.6 \pm 3.9$  cycles  $\text{min}^{-1}$  (8 animals). The overall sucking stomach rate was not significantly different from the heart rate during ingestion ( $P > 0.1$ ). Activity on the sucking stomach trace was only seen when the animal was eating or drinking. Movement of the limbs produced large-amplitude signals on both traces, disrupting normal recording. Eating lasted for approximately an hour, depending on the size of the meal, but the sucking stomach was not active during the whole of this time. (Eating is divided between release of digestive juices, pre-oral digestion and mastication and ingestion itself.) Drinking often occurred as a series of bursts of activity (Fig. 2). Recordings with high signal:noise ratios from five feeding sessions showed two sets of peaks on the sucking stomach trace; a larger and a smaller set (Fig. 3). The larger peaks are assumed to be from the dorsal dilator muscle on the grounds that it is this larger muscle into which the electrode has been inserted. The smaller peak was assumed to indicate activity in the smaller constrictor muscles of the sucking stomach which lie in close proximity to the dilators (Fig. 1). Further evidence for this will be presented in the Discussion. The contractions of the constrictors occur with a phase shift of  $0.64 \pm 0.007$  cycles relative to the dilator (136 observations



Fig. 2. Heart and sucking stomach recordings made during drinking showing intermittent activity of the dorsal dilator muscle of the sucking stomach. Top trace, heart activity (ECG) is indicated by large-amplitude peaks. Some cross-talk from the activity of the stomach dilator was occasionally seen and is apparent in this record. Bottom trace, sucking stomach dilator activity (EMG). Note that this record shows no sign of coupling between EMG and ECG.



Fig. 3. Heart (ECG) and sucking stomach (EMG) records showing coupling. A and B show coupling at different rates in the same preparation and the double sucking stomach peaks, most evident in A. The larger response is thought to be from the dilator muscle, the smaller cross-talk from constrictor muscles.

from five preparations). No significant difference was observed in this value between preparations ( $P > 0.1$ , Student's *t*-test).

#### *Evidence supporting coupling*

Although nine records showed heart and sucking stomach activity occurring at different rates and with no apparent phase relationship (e.g. Fig. 2), six of the traces recorded during or immediately after ingestion showed coupled heart and

sucking stomach activity. Analysis of the temporal relationship of the peaks revealed that the ECG spike occurred just prior to the EMG peak, or to the major EMG peak if both types were present (Fig. 3A). This relationship remained constant as rate changed within the same preparation (Fig. 3). If the sucking stomach contractions lag dilations by 0.64 cycles, then the heart and sucking stomach are contracting out of phase.

#### *Phase relationship of coupling*

Using traces with the highest signal:noise ratio, the phase relationships between the ECG spikes and the EMG spikes of the dilator and constrictor muscles of the sucking stomach were determined. The phase shift for stomach dilation relative to the ECG averaged  $0.10 \pm 0.009$  (141 pairs of spikes from six preparations). This varied from 0.06 to 0.23 between preparations, but very little within a preparation (s.e. typically 0.025). Selection of those records with the best signal:noise ratio (showing all three peaks) gave a phase shift of  $0.71 \pm 0.007$  (105) for the constrictor muscle relative to the ECG. This is in accord with an indirect estimate (0.74) obtained by adding the dilator phase shift relative to the ECG (0.10) to the constrictor phase shift from the dilator (0.64). In several instances sucking stomach dilation preceded heart contraction (phase shift=approximately 0.9). We have no explanation for this observation, but it does not influence our major conclusions.

### **Discussion**

#### *Heart and stomach activity*

The average resting heart rate of  $33.6 \text{ beats min}^{-1}$  is comparable to previously recorded rates for tarantulas:  $30 \text{ beats min}^{-1}$  in *Eurypelma marxi* (Sherman and Pax, 1970),  $35 \text{ beats min}^{-1}$  in *Dugesiella hentzi* (Stewart and Martin, 1974),  $18 \text{ beats min}^{-1}$  in *Brachypelma smithi* (Anderson and Prestwich, 1985) and  $21 \text{ beats min}^{-1}$  in *Eurypelma californicum* (Paul *et al.* 1989). The increased heart rate ( $51.6 \text{ beats min}^{-1}$ ) early in ingestion may be, in part, a response to increased activity of the foregut and locomotor muscles. Recorded heart rates in active tarantulas include  $60\text{--}88 \text{ beats min}^{-1}$  (Stewart and Martin, 1974),  $58 \text{ beats min}^{-1}$  (Anderson and Prestwich, 1985) and  $53\text{--}67 \text{ beats min}^{-1}$  (Paul *et al.* 1989). After activity, heart rate recovers to its resting rate as a logarithmic function of the magnitude of the increase in rate (Paul *et al.* 1989); e.g. for an increase in rate of  $20 \text{ beats min}^{-1}$ , recovery to rest would take approximately 3 min in *E. californicum*. The heart rates in the current investigation may reflect recovery from locomotory activity or disturbance, as well as an increased rate associated with ingestion. Some traces did suggest that heart rate decreased with time during ingestion, but this was not observed consistently.

The sucking stomach acts as a pump, dilating to draw in liquefied food and then contracting to force it posteriorly. The sucking stomach musculature consists of slow (Type I) fibres allowing long periods of ingestion to be sustained without

fatigue (Meyer, 1981). This is claimed to be an efficient process leading to rapid ingestion (Foelix, 1981), but there appears to be no information in the literature on the actual timing of these muscular events. The muscle potentials recorded in this investigation suggest that the constrictors of the stomach contract with a phase shift of 0.64 relative to the dilators. Wilson (1967) produced a pulse waveform of sucking stomach activity of *H. venatoria* by recording deflections of the prosomal cuticle above the stomach (Wilson, 1967; his Fig. 3, trace D). A single small peak occurs between each larger peak, with a consistent phase shift of 0.63. He does not state which features of the waveform correspond to which phase of stomach activity. However, if the large peaks are assumed to be caused by the larger dilator and the small peaks by contraction of the small constrictors, then the results are consistent with the 0.64 relationship found in the present investigation.

#### *Evidence and possible mechanisms for coupling*

This investigation strongly suggests that heart and sucking stomach activities often become synchronised during ingestion. The heart and stomach activity occurred at the same rate under these conditions, and the phase relationship remained constant for long periods in some observations. Furthermore, the rates of activity in the two systems changed in synchrony within a single preparation. The record from Wilson (1967, Fig. 3) suggests decoupled activity, as we observed on many occasions.

The timing of the electrical events cannot be related to the mechanical events in the pedicel with any degree of certainty. Paul *et al.* (1989) questioned whether there can be a shift in the pacemaker site in arachnid hearts. ECGs in this study were recorded from the dorsum; how this relates to mechanical contraction close to the aorta is uncertain. Bromhall (1987) recorded activity in the posterior aorta of a smaller spider (*Dysdera* sp.) in antiphase with that of the heart and this raises the question of the phase shift in the anterior aorta relative to the dorsum. Bromhall's (1987) data suggest that the phase shift may be as great as 0.5. Furthermore, the sucking stomach is situated up to 10 mm anterior to the pedicel in the species we used. We have no information about the speed of passage in the midgut; hence the time interval between contraction and the movement of a pulse of material through the pedicel is unknown. A detailed model of events must await more mechanical information.

A neuronal mechanism is more likely than any other to be responsible for the observed coupling. The hearts of spiders and other arachnids are under neurogenic control (Sherman and Pax, 1968). This is mediated by the cardiac ganglion (Wilson, 1967), which is supplied by cardioregulatory nerves from the paired nerves VIIIb (Gonzalez-Fernandez and Sherman, 1984) (see also Fig. 1). Coupling of the pumping actions of the heart and sucking stomach may be mediated by neural processes from a common pattern generator, which could lie in the suboesophageal ganglion. Nerve VIIIb arises from the abdominal ganglion some distance behind the sucking stomach (Sherman, 1985) and no connection between the sucking stomach musculature and either this nerve or the ganglion has yet been



demonstrated. Babu (1985) does not indicate any nerves arising from the brain to innervate the sucking stomach, and he notes that only the optic nerves come from the supraoesophageal ganglion (cf. protocerebrum), which would suggest that the stomach musculature is controlled by the suboesophageal ganglion, from which the abdominal nerve bundle, and hence the cardioregulatory nerves, also arises.

The fact that dilations and contractions of the sucking stomach are coordinated (Foelix, 1981) suggests that there is probably some neural coupling associated with the stomach itself, and this may extend to the cardiac ganglion, moderating heart activity and effecting coupling of this system too. Wilson (1967) claimed that the central nervous system could have both an excitatory and an inhibitory effect on the heart, and Gonzalez-Fernandez and Sherman (1979) demonstrated the presence of cardioregulatory neurones in the CNS of a spider. As a result of this Gonzalez-Fernandez and Sherman (1984) isolated the abdominal ganglion from the rest of the CNS when investigating cardiac ganglion physiology; this was done to remove the possibility of any centrally mediated reflexes being transmitted to the heart.

We have no conclusive explanation for the lack of coupling observed in some experiments. It is possible that electrode insertion may have caused damage in some cases and this may have disrupted coupling. Another factor may be stress in the animal. The heart can change from pumping anteriorly to pumping posteriorly (R. Paul, personal communication) and coupling need only occur when the heart is pumping forwards, since posterior flow of haemolymph will not affect the passage of food in the midgut. The heart is presumably a more powerful pump than the stomach by virtue of its size, and its activity may mechanically 'override' that in the stomach and midgut. Because of this, coupling may not increase the efficiency of haemolymph supply during ingestion but may increase the speed and efficiency with which food can be taken into the body (by preventing it from coming up against antagonistic haemolymph flow in the pedicel).

#### *Coupling in relation to pedicel morphology*

During activity, haemolymph pressure increases in the prosoma (Stewart and Martin, 1974). Feeding involves prosomal muscular activity (e.g. Legendre, 1961; Collatz, 1987), occasional gross body movements and perhaps an elevated heart rate, all of which may elevate prosomal pressure. It is generally accepted that high prosomal pressures inhibit further supply of haemolymph to the prosoma by the anterior aorta (Paul *et al.* 1989). This inhibition is presumably not so great as to prevent further haemolymph supply completely, otherwise coupling would be unnecessary. This high pressure, and perhaps also the muscular activity in the prosoma, may squeeze the prosomal arteries. The haemolymph in the arterial system may move either towards the periphery or back towards the heart, where it will be trapped by the aortic valve (see Fig. 1). This could be the cause of the inhibition of further haemolymph supply and may also cause distension of the aorta anterior to this valve.

Coupling may prevent interference due to distension of the midgut and aorta

posterior to the valve. However, anterior to the valve, any distension due to prosomal pressure would probably be independent of the two pumping systems and cannot be compensated for by coupling. The way, therefore, to prevent backflow distensions anterior to the valve from interfering with the passage of food in the midgut would be to isolate the midgut mechanically from the aorta.

In the absence of detailed information about fluid flow in tarantulas, any model is speculative, but the following argument suggests what may be occurring in the pedicel during ingestion. Systolic contraction of the heart, cited as lasting some 75% of the cardiac cycle in *D. hentzi* (Stewart and Martin, 1974), pumps haemolymph through the pedicel in the anterior aorta. About 10% of the way through the cardiac cycle the dilators of the sucking stomach contract, increasing stomach lumen volume and setting up a suction pressure. Haemolymph presumably begins to move into the prosoma, passing the aortic valve as it does so. The mechanical isolation here may reduce any effect on the midgut, which should be empty anyway. Liquefied food or water is drawn into the expanded sucking stomach from the oesophagus. Haemolymph is prevented from re-entering the heart through the aorta by the aortic valve. The sucking stomach contracts about 70% of the way through the cardiac cycle. Valves at the entry to the stomach prevent fluid escaping to the oesophagus. Fluid is forced in a posterior direction through a further set of valves and moves towards the pedicel. The heart should now enter diastole and begin to refill. The fluid in the midgut passes through the pedicel, where the mechanical isolation may ensure little or no impact on the presumably quiescent aorta. Posterior to the aortic valve, fluid passage may squeeze the aorta slightly as it enters the midgut diverticula. Here it no longer affects, or is affected by, the circulation. The heart has refilled ready for the next cycle to begin.

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