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Gills as Possible Accessory Circulatory Pumps in *Limulus polyphemus*

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Abstract. Heart electrical activity (ECGs), gill closer muscle potentials (EMGs), and blood pressures in the heart and the branchiocardiac canals, were measured in adult horseshoe crabs (*Limulus polyphemus*) during various activities. During ventilation, hyperventilation, and swimming, large transient increases in pressures (10–35 cm H₂O) occur in the branchiocardiac canals, which carry blood from the gills to the heart. These pulses of positive pressure are related to, and apparently caused by, gill plate closing. During quiescent periods, with no ventilatory activity, there are no pressure pulses in the canals, but the pressure is still greater than zero. We found covariation of heart and ventilation rates during intermittent ventilation, hyperventilation, gill cleaning, and swimming, as well as evidence of transient periods of phasic coordination. The heart appears to be weakly entrained to the gill rhythm by phasic cardiorespiratory nerve input. The preferred phase of heartbeats, with respect to gill rhythm, was 0.5, or 180 degrees out of phase. In some animals, intra-cardiac pressures were enhanced when the heart and gill rhythms were entrained. We suggest that rhythmic movements of the gill plates enhance the flow of low pressure blood returning from the body to the heart. Thus, ventilatory appendage movements may constitute an accessory blood pumping mechanism in *Limulus*.

Introduction

Many invertebrates, including annelids, molluscs, arthropods, and echinoderms, have highly developed circulatory and respiratory systems. In many cases the morphology is well known, but the functional properties and

interactions of these convective systems during normal behavior have not been examined in detail. Evidence from research on decapod crustaceans suggests that investigations of the respiratory and circulatory systems of aquatic arthropods might yield valuable information for understanding the operating conditions and physiological role of coupling between these systems. Close coordination and coupling between circulatory and respiratory systems under a variety of environmental conditions has been reported frequently (*Homarus americanus*, *Cancer productus*, McMahon and Wilkens, 1975, 1977; Young and Coyer, 1979; *Cancer magister*, Wilkens *et al.*, 1974; *Carcinus maenus*, Young, 1973; *Cancer borealis*, *Cancer irroratus*, Coyer, 1977). Nevertheless, the physiological significance of respiratory/circulatory coupling is not fully understood.

The coordination of cardiac and ventilatory activity in *Limulus polyphemus* presents another interesting example, worthy of further investigation. Watson and Wyse (1978) reported frequency covariation (heart and ventilation rates changed together) and phasic coordination (heart beats occurred in phase with the gill plate movements) of heart and ventilatory systems under normoxic and hypoxic conditions, as well as during intermittent ventilation, hyperventilation, gill cleaning, and swimming. The frequency covariation observed in *Limulus*, as well as many other organisms, may serve primarily to adjust the volume of blood circulated to the rate of oxygen uptake. On the other hand, the adaptive significance of phasic coordination between the gills and heart is not clear. Watson and Wyse (1978) suggested that phasic coordination makes the two blood pumping systems more efficient. While the role of the gills as an accessory “heart” has been suggested previously (Patten and

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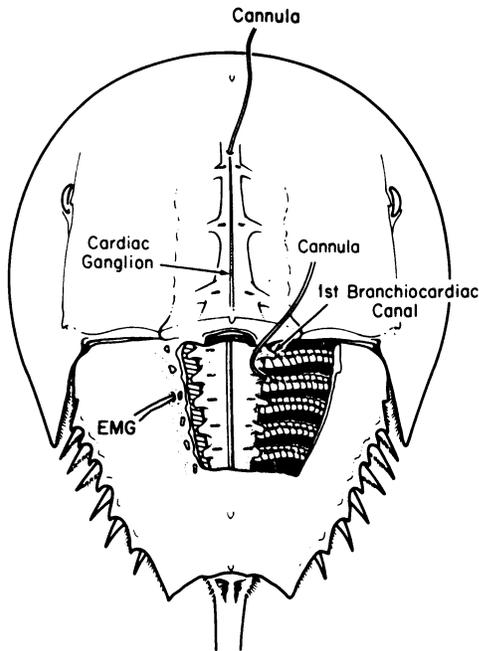


Figure 1. Dorsal cutaway illustration of *Limulus polyphemus*, illustrating the position of catheters and electrodes.

Redenbaugh, 1899; Lockhead, 1950), little physiological evidence is available to support these interpretations. The present contribution provides evidence that the gill

plates help circulate the blood in *Limulus*, and documents the hemodynamic relationships between the cardiac and ventilatory systems of intact horseshoe crabs during all of their known respiratory behaviors. In addition, we present evidence suggesting that, in some cases, phase coupling between the heart and gill rhythms enhances cardiac output.

In crustaceans, there is good evidence that frequency covariation between the gills and heart is mediated by the cardiorespiratory nerves (Field and Larimer, 1975a, b; Young, 1978). In a few instances investigators recorded phasic activity in the cardiorespiratory nerves that appeared to be coupled to the ventilatory rhythm; they suggested that this type of activity would help phase-lock the heart rhythm to scaphognathite movements. In *Limulus* the cardiorespiratory nerves also appear to be important in the tonic regulation of heart rate and in the coordination between the cardiac and ventilatory rhythms (Watson, 1979). However, phase coupling between the heart and gills could also be mediated by direct pressure cues. In this study we found that phase coupling between heart and gill rhythms was associated with rhythmic bursts in the cardiorespiratory nerves. These data suggest that in *Limulus* both tonic and phasic coordination between the heart and gills is regulated by the nervous system.

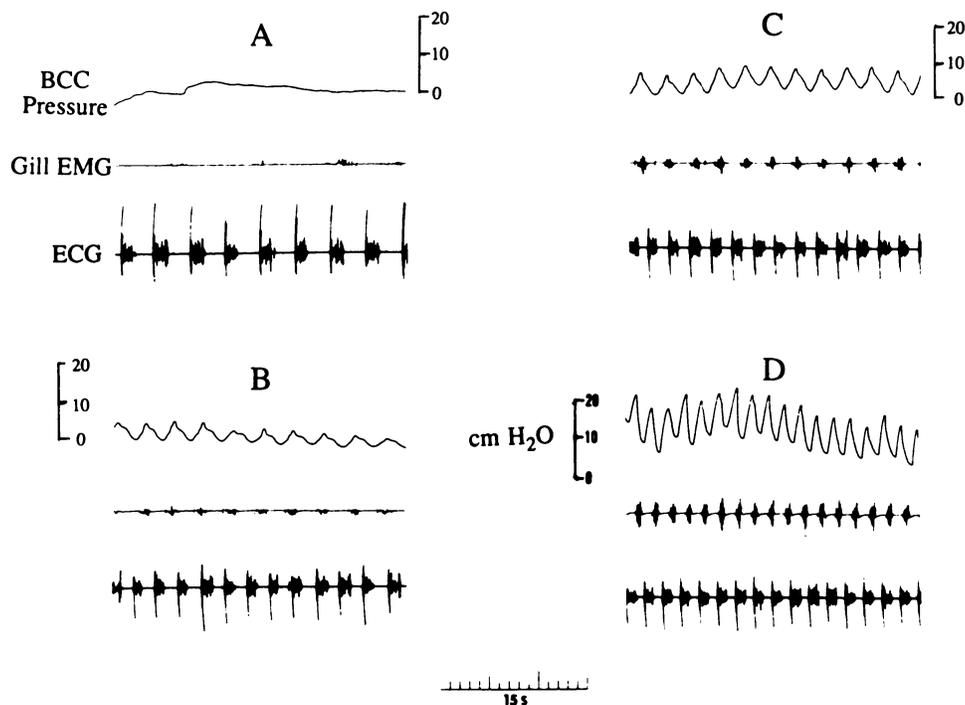


Figure 2. The relationship between pressure (cm H₂O) in a branchiocardiac canal (BCC, 2nd canal), the electromyogram (EMG) of the gill closer muscle (20) of the 2nd gill plate and heart activity (ECG) during rest (A) and increasing amplitudes of ventilation (B–D). Similar records obtained during hyperventilation and swimming are presented in a subsequent figure. Pressures are relative to ambient in the water column.

Materials and Methods

Specimens of *Limulus polyphemus* (18–25 cm carapace width) were either obtained from the Marine Biological Laboratory or collected from Buzzards Bay, Falmouth, Massachusetts. Animals were maintained in either a recirculating seawater system (University of New Hampshire, Durham, New Hampshire) or a 1200-liter tank continuously supplied with fresh seawater (MBL, Woods Hole, Massachusetts) at 13–15°C (30–33‰) and fed mussel bits every few days. Survival and health of the animals in the laboratory over several months were excellent. Twelve animals were used in our blood pressure experiments; and six were used for neurophysiology.

Electrical activity of the heart was recorded with pairs of 40- or 45-gauge stainless steel wire (annealed, epoxy coated for insulation) inserted through small holes in the dorsal midline of the opisthosoma, adjacent to the cardiac ganglia. Electrical activity of ventilatory muscles was recorded with similar wires inserted into muscle 20 (Patten and Redenbaugh, 1899) through small holes in the overlying cuticle (Fig. 1). Implants were held in place on the cuticle surface with a small amount of methylcyanoacrylic adhesive or dental wax.

Pressures in the heart and in the branchiocardiac canals (which convey blood from the gills to the pericardial cavity) were measured with polyethylene tubing (PE 100) and pressure transducers (Statham P23ID). Catheters with beveled tips were inserted into the heart or one of the branchiocardiac canals through small holes drilled in the overlying cuticle, and cemented in place with quick-drying epoxy (Fig. 1). Prebranchial blood pressure was also measured at the junction of the mesosoma and telson. Catheters were kept as short as feasible (about 18 cm), and their insertion positions were confirmed at the termination of experiments by dissection. At times, we noted reduced frequency and amplitude responses in the pressure records irrespective of the activity of the animal; this was due to clotting at the proximal end of the catheters and was alleviated by gentle flushing. Most experiments were conducted in cold seawater (13°C) to reduce the tendency of blood clotting in the catheters.

Following surgical procedures, animals were allowed to rest for 4–5 h or overnight before measurements were made. Oxygen in the seawater of the test chamber was maintained above 90% saturation during the acclimation period and the experiments. Experiments were carried out in 80-liter Plexiglas chambers filled with seawater and arranged with a mirror underneath the test chamber for observation of the gill appendages. Wire electrodes were attached to a sliding rack above the chamber to prevent fouling of the implants. Some of the crabs were restrained in the chamber on a Plexiglas shelf with a hole situated under the animals abdomen, so the

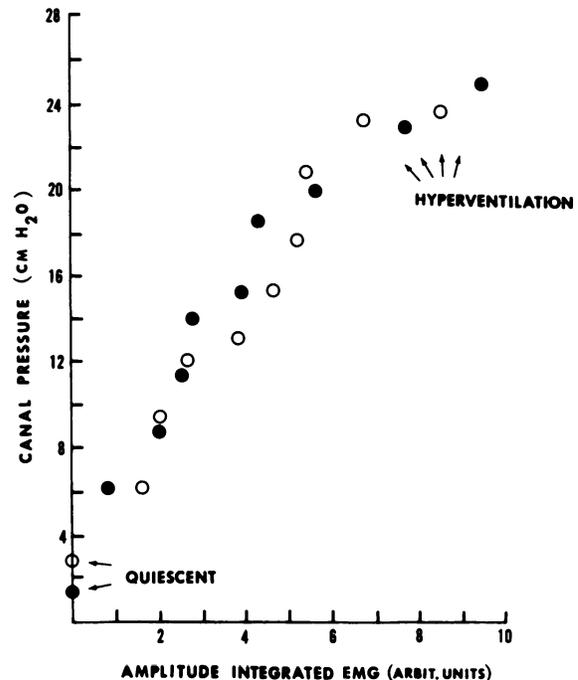


Figure 3. The relationship between strength of gill contractions and peak BCC pressure. Pressure in the 2nd branchiocardiac canal and integrated electromyogram (EMG) of a gill closer muscle were obtained during quiescent behavior, increasing ventilatory activity and hyperventilation in two different animals (open and closed circles). The pressures recorded from the BCC's were proportional to the strength of gill plate contractions.

gill appendages could ventilate freely. Others were allowed to move and swim freely about the chamber. Signals of heart and ventilatory muscle electrical activity, as well as the pressure waveforms from the heart and branchiocardiac canal catheters, were recorded individually, or simultaneously, on adjacent channels of a Grass Polygraph (Model 7D).

Cardioregulatory nerve recordings were obtained using suction electrodes from animals restrained in a Plexiglas chamber as described above. A small window was cut in the carapace to expose the cardioresgulatory nerves. All signals (EMG, ECG, and extracellular potentials) were detected with Grass P511 amplifiers, displayed on an oscilloscope, photographed with a Grass C4 camera, and recorded on magnetic tape. Recordings from isolated ventral nerve cords were carried out as described in Wyse *et al.* (1980).

Results

General respiratory behavior

During experiments lasting 7–16 h, most specimens of *Limulus polyphemus* exhibited several types of ventilatory activity: intermittent ventilation, hyperventilation, gill cleaning, and swimming. Intermittent ventilation in

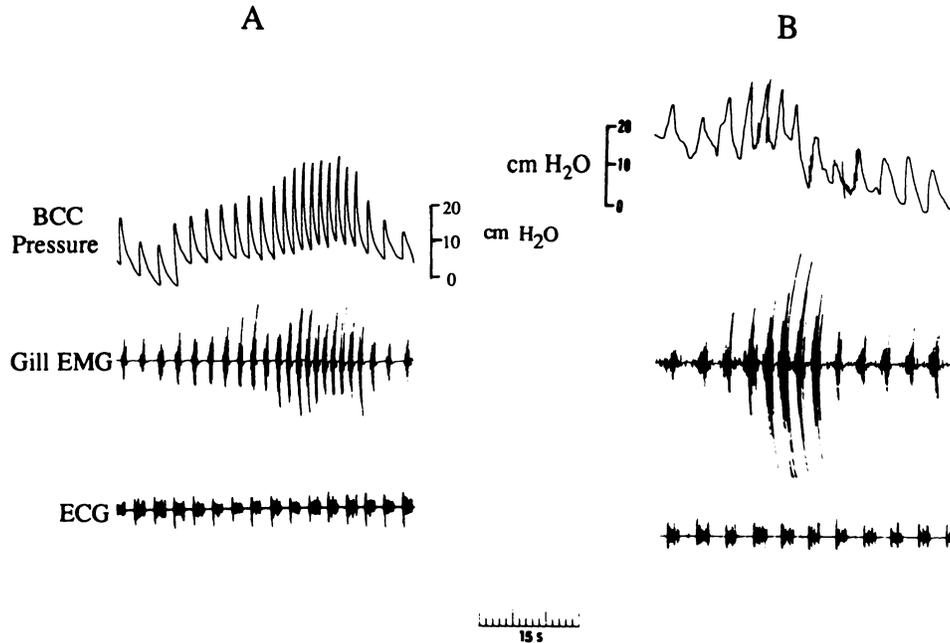


Figure 4. Pressure in one branchiocardiac canal, gill EMG and ECG during hyperventilation (A) and swimming, as indicated by the large amplitude gill EMG's (B).

Limulus occurs as alternating bouts of ventilation and apnea. Both hyperventilation and swimming are characterized by a large increase in rates of gill plate movements over that observed in shallow ventilation (Knudsen, 1973). The major difference between the two behaviors is that during swimming the legs also move in phase with the gills, while during hyperventilation leg movements are independent of gill activity. During gill cleaning, the gill plates move across the midline and flick the inner lobe of a gill plate between the book gill lamellae of the opposite side. In all the aforementioned ventilatory activities, heart rate was always positively correlated with the rate of ventilation. These respiratory and locomotor behaviors of *Limulus* have also been reported in earlier papers (Watson and Wyse, 1978; Watson, 1980a, b).

Pressures in the branchiocardiac canals during rest, ventilation, hyperventilation, and swimming

The branchiocardiac canals (BCCs), as the term implies, carry blood from the gills to the pericardial cavity and heart. Five pairs of canals correspond to the five gill appendages (Fig. 1). Blood from the venous circuit passes through an extensive gill network (Lockhead, 1950; Johansen and Petersen, 1975) before returning to the heart. We measured pressures in one canal, while simultaneously recording the electrical activity of that gill's closer muscle, during rest (*i.e.*, no ventilatory activity occurring), ventilation, hyperventilation, and swimming. During rest, no pressure pulses occur in the canal, al-

though the pressure may be greater than zero (Fig. 2A). As the amplitude of ventilation increases, pressure in the canal rises substantially (3–20 cm H₂O), as does the amplitude and frequency of the recorded EMG and the heart rate (Fig. 2B–D).

To examine more closely the relationship between the strength of gill contractions (as monitored by EMG activity) and the resulting BCC pressures, we plotted integrated EMG amplitudes *versus* the magnitude of canal pressures, during several different intensities of ventilatory activity, ranging from shallow ventilation to hyperventilation. There is a direct relationship throughout the range of pressures measured (Fig. 3). This relationship was consistent during all of our experiments, whether the animals were restrained or freely moving.

We also recorded pressures in a BCC during hyperventilation and swimming. Examples of these results are shown in Figure 4. Hyperventilation was sometimes intermittent, and with the onset of this behavior, large pressure pulses occur in the canal (Fig. 4A). During swimming, which is also periodic, the record shows essentially the same result, but the recorded pressures are more erratic (Fig. 4B). This is probably due to movement artifacts introduced to the liquid-filled pressure catheter system during swimming as the animal moved up and down in the chamber.

Prebranchial pressures (junction of soma and telson) are low during rest (1–2 cm H₂O, n = 9) and increased only slightly during ventilatory periods (2.5–3 cm H₂O). Therefore, the blood reaching the gills is at a low pres-

sure, and the rhythmic movements of the gills are likely important for circulating venous blood dorsally to the heart.

Frequency covariation between heart and gill rhythms

To assess the relationship between heart pressures and BCC pressures, we obtained simultaneous recordings of closer muscle electrical activity (EMG), BCC pressures, heart electrical activity (ECG), and intracardiac blood pressure (Fig. 5A). Throughout all of our experiments, a strong frequency coordination existed between the two rhythmic systems. When gill ventilation increased, so did the pressures in the BCC's (Figs. 2–5), and, presumably, the rate of venous return. Thus, from a hemodynamic perspective, frequency covariation between heart and gill pumps insures that the venous return is coordinated with the tonic output of the heart.

Phasic coordination between heart and gills

Most of the animals examined did not exhibit strong phase coupling between the heart and gill rhythms (see Fig. 6 for illustration of how phase coupling was determined). However, a small proportion (10–20%) of the animals examined either strongly phase coupled, or drifted in and out of the coupling mode. When phase coupling did occur, the preferred phase was usually close to 0.5 (Fig. 6), indicating that the heart beat 180° out of phase with the gills. Why is 0.5 the preferred phase? If there is some hemodynamic advantage, then the output of the heart should be maximal when the two pumps are 180° out of phase. To test this hypothesis, we recorded heart and BCC pressures for approximately 1 h, and then plotted peak cardiac pressures *versus* phase of the heart-beat with respect to the gill rhythm, on a beat-to-beat basis. We found that, in some of the animals, intra-cardiac pressure remained relatively constant regardless of ventilatory activity (Fig. 7B). In three animals, however, the cardiac pressures were greatest when the heart and ventilatory rhythms were 180° out of phase (Fig. 7A). Thus, at least in some animals, phase coupling may enhance cardiac output.

Cardioregulatory nerve activity during phase coupling

If the heart is entrained by the nervous system, it must receive phasic timing cues through the cardioresgulatory nerves. Furthermore, this timing information must have a fixed phase relationship to the ventilatory rhythm so it can entrain the two oscillatory systems. We recorded cardioresgulatory nerve activity from intact, immobilized animals while monitoring heart ECGs and gill plate EMGs (Fig. 8). During periods when the gill plates were making large, rapid movements, there was a phasic com-

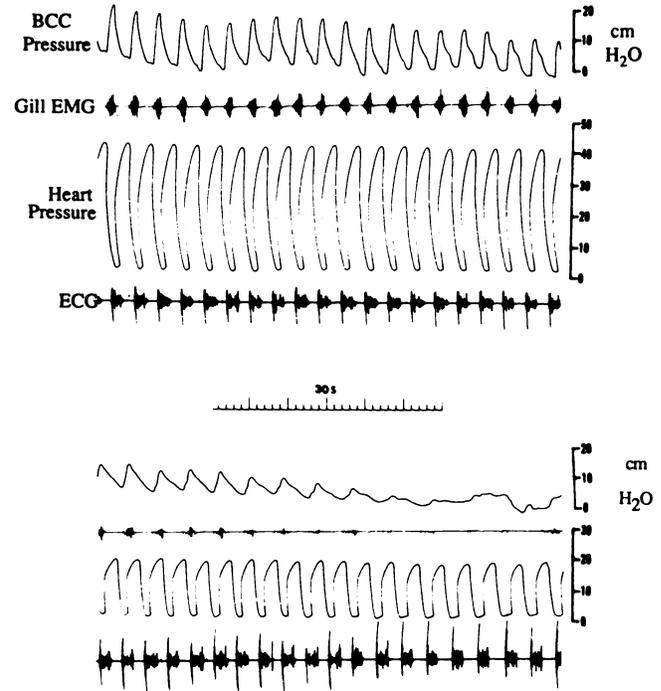
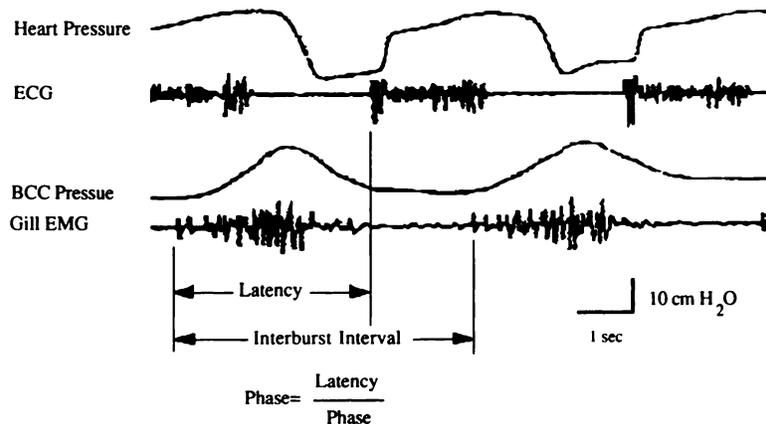


Figure 5. Pressures (cm H₂O) and electrical activity in the respiratory and circulatory systems of *Limulus*. The top four records show pressure in 1st branchiocardiac canal (BCC), EMG of the 1st gill muscle, pressure in the heart and the ECG. The bottom four traces are the same physiological processes and include a section where ventilatory activity ceased. Pressures are relative to ambient in the water column.

ponent to the cardioresgulatory nerve activity (Fig. 8A, C). Bursts comprising several different units tended to occur during and just after contractions of the gill plate closer muscle. Periods of silence followed for the remainder of the gill interburst interval. When this type of cardioresgulatory nerve activity was present the heart was phase locked to the ventilatory cycle (see top plot, Fig. 8). But when ventilation slowed and became weaker, cardioresgulatory nerves lacked phasic activity, and phase coupling did not occur (Fig. 8B, D, and top of Fig. 8).

To eliminate the possibility that phasic activity was due to sensory modulation, we recorded cardioresgulatory nerve activity from isolated ventral nerve cords. When there were strong bursts in the ventilatory motor nerves, we also recorded bursts in the cardioresgulatory nerves that were phase locked to the ventilatory central pattern generator (CPG) (Fig. 9). During quiet ventilation, however, only tonic firing was present. Thus, phasic cardioresgulatory nerve activity is a component of the ventilatory central pattern generator. Although these data do not prove that the phasic cardioresgulatory nerve activity is responsible for entraining the heart to the ventilatory rhythm, we suggest that phase coupling is most

A. Calculation of Phase Relationship between Heart and Gill Rhythms



B. Phase Histogram

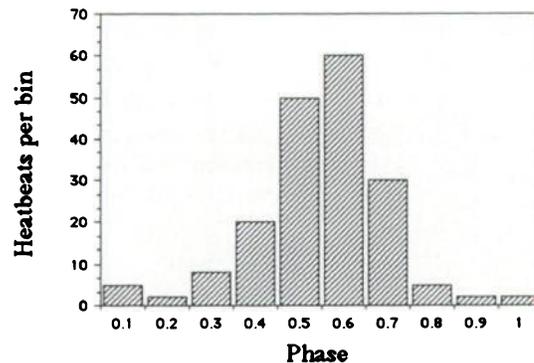


Figure 6. Phase relationships between heart and gill rhythms. A. Actual records of BCC and heart pressures, gill EMG, and ECG, showing how the phase relationship between the two rhythms was calculated. Phase is calculated by dividing the latency (time between onset of a gill muscle burst and onset of cardiac ganglion burst) by the duration of the concurrent gill interburst interval (time between the beginning of one burst and the beginning of the next burst). B. Histogram demonstrating phase preference of a cardiac ganglion burst (recorded as ECG) with respect to concurrent ventilatory event. The number of heartbeats from a particular phase were then totaled and a histogram constructed. Heartbeats per bin indicates number of events falling in each decile of phase (e.g., between 0.2 and 0.3). In this experiment, there was a very strong phase preference of 0.5 indicating the heartbeat was 180° out of phase with ventilatory activity. We did not find such strong phase preference in all animals or in any single animal at all times. But, when phase preferences existed, they were usually close to 0.5.

likely mediated by neural rather than hemodynamic mechanisms.

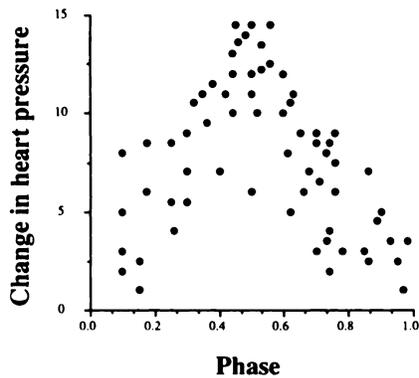
Discussion

Circulatory systems have traditionally been divided into two types: closed systems, in which the blood is always in distinct vessels separated physically from intercellular fluids; and open systems, with large, ill-defined cavities, in which the blood is not separated from the intercellular fluids. The open systems have been regarded as poorly developed and capable of generating only low

pressures and low blood flow velocities. The open circulatory system of *Limulus polyphemus* is well developed and appears to have few of the large sinuses normally found in open circulatory systems (Shuster, 1978; Redmond *et al.*, 1982). Our study indicates that high pressures occur in various portions of the circulatory system, particularly in the heart and branchiocardiac canals. Sumwalt (1933) and Abbott *et al.* (1969) also reported high pressures in the heart of *Limulus*.

Redmond *et al.* (1982) measured blood pressures in and around the heart and body of resting horseshoe crabs in water and air. They attributed the moderate variability

A. Heart Entrained to Gill Rhythm



B. Heart and Gill Rhythms Out of Phase

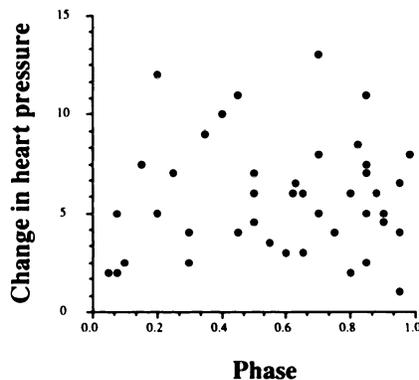


Figure 7. Influence of heart/gill phase relationship on cardiac pressures. On a beat-to-beat basis the phase relationship between the heart and the gill rhythms was calculated and plotted *versus* the amplitude of the pressure change during the subsequent heartbeat. In some animals, when the heart and gills were approximately 180° out of phase (0.5), the pressures recorded from the heart were higher (as illustrated by data from the animal plotted in A). In other animals there was no apparent influence of heart/gill phase on cardiac output (as shown by data from a different animal plotted in B).

of their data to differing activity levels. We monitored ventilatory muscles and, from previous experience (Watson and Wyse, 1978), could identify quiescent behavior, intermittent ventilation, hyperventilation, gill cleaning, and swimming. These are the most characteristic activities that involve the gill appendages (Watson and Wyse, 1978; Watson, 1980a, b). Rhythmic pressure changes in the BCCs were always associated with movements of the gills, and their amplitudes varied with the type and strength of gill movements. Thus, variability in pressures recorded in the heart and BCCs are probably due to the animal switching from one type of respiratory activity to another.

It is likely that the rhythmic movements of the gill appendages of *Limulus* serve to enhance gas exchange and to pump oxygenated venous blood to the pericardial cav-

ity. It has been reported that blood moves from the large ventral sinuses through the gill lamellae and BCCs to the pericardial cavity (Patten and Redenbaugh, 1899; Lockhead, 1950; Redmond *et al.*, 1982). We have also observed blood moving in this manner in juvenile horseshoe crabs. In this study we recorded large pressure pulses in the branchiocardiac canals during normal ventilation, hyperventilation, and swimming—all important components of the daily activities of horseshoe crabs. These changes in pressure always occur during contraction of the gill closer muscles, and their amplitudes are proportional to the magnitude of the gill plate movements. We never detected pressure surges in the branchiocardiac canals during quiescent behavior, when the gill plates were not moving, but the heart was still beating. Thus, it is likely that venous return to the heart is assisted by the gill appendages, which may serve as an accessory heart in *Limulus*.

Although pressure pulses recorded from the BCCs are likely caused by movements of the gill appendages and result in the flow of blood from the gills to the pericardial cavity, additional studies will be required to prove this hypothesis. In particular, it is important to determine if valves are present in the BCCs to rectify flow, and to continuously monitor the dynamics of blood flow in the canals.

Apparently, enhanced blood flow from ventilatory movements in horseshoe crabs is established in early life stages. We had the opportunity to observe blood flow in young specimens of *Limulus* (5 mm carapace width) under a dissecting microscope, because animals this small are quite transparent. With each ventilatory movement and during swimming activity, blood rapidly pulses into the pericardial cavity and heart. We also observed covariation of heart and ventilatory rates.

Occasionally, horseshoe crabs exhibit phase coupling between the heart and gill rhythms. Our analyses suggest that, in some animals, this coupling may increase cardiac output. It may also allow the animal to do the same amount of circulatory work more efficiently, but we have no data to support this hypothesis at present. The preferred phase of almost all animals that demonstrated phase coupling was approximately 0.5, or 180° out of phase. Why would this relationship between two systems lead to enhanced blood flow? When the gill plates close, due to the contraction of gill muscle 20, oxygenated blood is forced dorsally through the BCCs to the pericardial cavity. If the heart and gills are 180° out of phase, then the heart will be relaxing as blood enters the pericardial cavity (see Fig. 6). When the heart relaxes, blood enters the heart through the ostia. Thus, maximal blood is available to the heart during the filling phase of its contraction-relaxation cycle. This appears to increase the

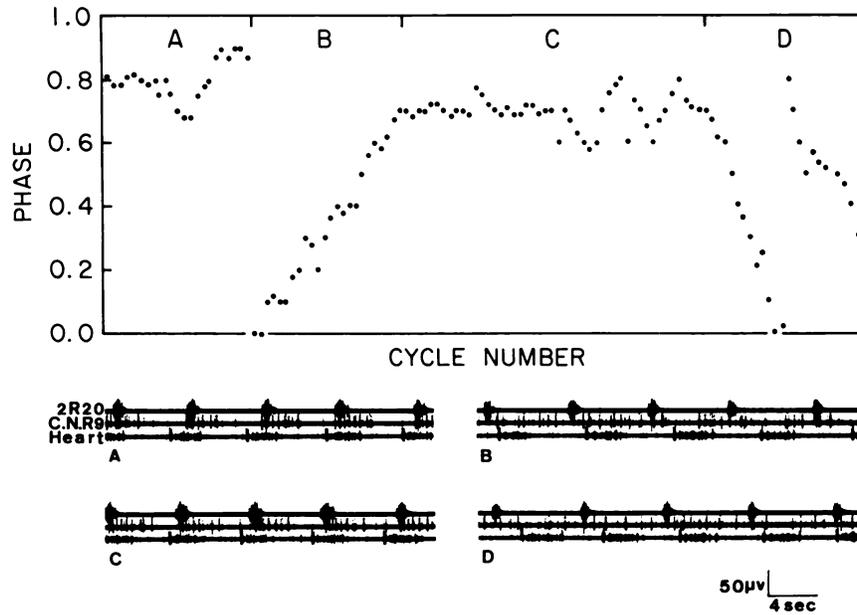


Figure 8. The relationship between bursting in the cardiac nerves and the degree of coupling between the heart and gill rhythms. The top graph shows a sequential phase plot of heartbeats with respect to the concurrent gill interburst intervals (Phase = heart latency/duration of the gill burst interval). In this particular experiment, there was good coupling between the heart and gill rhythms during segments A and C, and drifting, or no phase coordination during B and D. Representative segments of records from these periods are shown below (A–D). During periods of coupling (A and C) there was discrete bursting in cardiac nerve 9, while during periods of drifting (B and D), the cardiac nerve activity was more weakly phasic. This suggests that coupling may be related to the degree of phasic activity in the cardiac nerves.

force of the next heartbeat (Fig. 7) and, as a consequence, may lead to an increase in cardiac output.

We cannot estimate the quantitative contribution of blood flow to the heart from ventilatory movements of the gill appendages, or cardiac output from our data because we did not measure blood flow. Measurements of cardiac output in *Limulus* at rest, calculated from the Fick equation, are reasonably high (Mangum *et al.*, 1975) and we expect the values to increase during activity. The use of microcatheter tip flow probes should al-

low measurements of cardiac output; then the possibility that phase coupling in *Limulus* leads to enhanced cardiac output can be more rigorously tested.

Phase coupling between *Limulus* heart and gills appears to be mediated by the cardioregulatory nerves. Bursts of action potentials, which are phase locked to the ventilatory CPG, can be recorded from the cardioregulatory nerves in intact animals and in isolated preparations (Figs. 8, 9). When bursts are present in some animals, the heart is coupled to the gill rhythm; when the bursts are

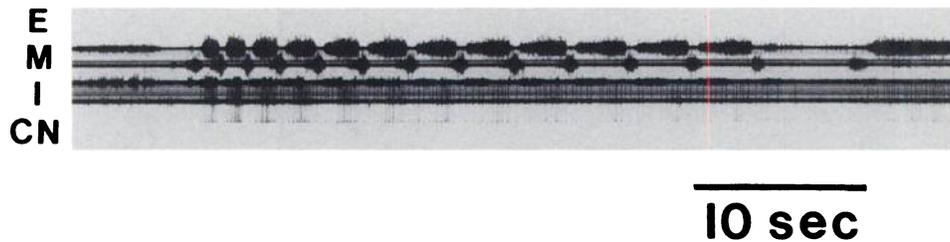


Figure 9. Rhythmic bursts recorded from cardioresgulatory nerves in isolated ventral nerve cords. It is possible to monitor motor patterns which represent ventilation by recording from the External (E), Medial (M) and Internal (I) branchial nerves in the isolated nerve cord. Strong ventilatory motor patterns produced by the isolated ventral nerve cord are accompanied by rhythmic bursts in cardioresgulatory nerve #10 (CN), which emanates from the 2nd abdominal ganglion. This indicates that the ventilatory central pattern generator may also provide timing information to the cardioresgulatory nerves, and thus to the heart.

not present, the two pattern generators run independently. But the heart may also be receiving timing input from the blood pressure pulses in the BCCs. To separate these two influences and to determine which is the controlling factor, we used a motor to move all the gill plates at a frequency that was slightly different from the output of the ventilatory CPG. We monitored the output of the ventilatory CPG by recording EMGs in the gill muscles. We found that the heart was phase coupled to the ventilatory CPG, but not to the imposed gill movements. In other words, the heart was entrained by some type of neural input that was phase locked to the ventilatory CPG, but was out of phase with pressure pulses from the BCCs (unpub. data). Thus, we conclude that phase coupling between the heart and gills in *Limulus* is mediated by the cardioregulatory nerves.

The coordination between cardiac and ventilatory rhythms in *Limulus* is very similar to that in decapod crustaceans. Decapods also exhibit frequency and phase coordination between the two systems (Wilkens *et al.*, 1974; McMahan and Wilkens, 1975; Wilkens, 1976; Field and Larimer, 1975a, b; Young and Coyer, 1979). The frequency coupling in decapods is not as tight as in *Limulus*, but the phase coupling is very similar. It only occurs in a small percentage of the animals studied and ranges from strong coupling to a drift and lock mode, to nonexistent. In decapods, cardioregulatory nerves also appear to mediate phase coupling. Young (1978) showed that cardioinhibitory units, and perhaps cardioacceleratory units as well, occasionally fired in bursts that were phase locked to the scaphognathite rhythm. In *Limulus*, the inhibitory and excitatory units in the cardioregulatory nerves have not yet been identified. Nevertheless, in both decapods and *Limulus*, phase coupling appears to be mediated by cardioregulatory nerves that transmit information from ventilatory CPGs in the CNS to the cardiac ganglion. Further experiments are necessary to demonstrate which units are involved and to examine why coupling strength is so variable.

The movement of fluids in circulatory systems of invertebrates is accomplished by a variety of mechanisms, including tubular "hearts," sac-like hearts, chambered hearts, contracting blood vessels, several types of accessory pumps and body movements (Schmidt-Nielsen, 1983). In general, locomotion and associated body movements are important in blood flow in many small and large animals, coupling metabolic needs with delivery of nutrients and oxygen to the tissues. This strategy appears to be an important facet of hemodynamics. The horseshoe crab provides yet another example of the efficiency of this organization. The rapid movements of the gill plates that are associated with swimming also serve to ventilate the book gill lamellae and pump the oxygenated blood to the pericardial canal.

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