HEART ACTION OF THE FRESHWATER BIVALVE
ANODONTA ANATINA DURING ACTIVITY

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SUMMARY

1. Heart action of *Anodonta anatina* (L.) was investigated by recording the electrocardiogram (ECG), heart impedance, and ventricular and pericardial cavity pressure during different aspects of the normal behaviour. The contribution of mechanical and nervous mechanisms in controlling changes in heart action is discussed.

2. Pressure recordings were generally more reliable than the other methods and it is suggested that pericardial pressure pulses indicate the stroke volume output of the ventricle.

3. During spontaneous periods of prolonged shell closure there was an initial small increase in heart activity followed by a large reduction in both heart rate and systolic pressure, indicating that total heart output was considerably reduced. When the shell reopened, heart rate increased very rapidly with an initial overshoot of the normal level; systolic pressure increased more slowly with no overshoot.

4. These major changes in heart activity appear to be associated with respiratory changes and are controlled largely by the nervous regulatory system, but some minor rhythmic variations in the amplitude of heart beat are probably caused by mechanical factors.

5. Characteristic patterns of change in heart action were recorded during burrowing. These appear to result from haemodynamic changes associated with the muscular movements of the digging cycle. Control of the heart by the nervous regulatory system is apparently of much greater importance in relation to respiratory control than in relation to the haemodynamic functioning of the fluid-muscle system in locomotion.

INTRODUCTION

The extensive literature on mechanical, pharmacological and nervous aspects of the cardiac physiology of bivalve molluscs has been reviewed by Krijgsman & Divaris (1955) and more recently by Hill & Welsh (1966), Pujol (1968) and Narain (1976). It is well established that the rate and amplitude of heart beat is controlled by a diffuse myogenic pacemaker that is affected by stretch in the ventricle wall but, at the same time, cardio-regulatory nerves excite or inhibit heart action through the production of neurohumours. Heart action can therefore be affected by direct mechanical factors, such as the haemodynamic changes during body movements (Brand, 1972), or by the

nervous regulatory system as an integrated part of a physiological response. Most studies have considered single aspects of this complex control mechanism in isolation, often using isolated ventricle preparations or other techniques that involve considerable surgical disturbance to the animal, so there is very little knowledge of the way these mechanisms normally operate to control heart action in undisturbed, freely-moving animals.

The comparatively recent development of impedance techniques has provided a suitable method for recording heart action without serious damage to the animal (Hoggarth & Trueman, 1967), and this has now been used to study variations in heart rate of several bivalves in both natural and laboratory conditions (Helm & Trueman, 1967; Trueman, 1967; Trueman & Lowe, 1971; Coleman & Trueman, 1971; Colman, 1974), including studies on the effects of temperature (Lowe, 1974), feeding (Thompson & Bayne, 1972; Widdows, 1973) and mantle cavity ventilation (Walne, 1972; Lowe & Trueman, 1972). In addition, Bayne (1971) and Taylor & Brand (1975) used changes in heart impedance to derive an index of gill perfusion for studies on the mechanism of respiratory control during hypoxia. Earll (1975) has attempted to correlate changes in heart rate with different aspects of the behaviour of *Scrobicularia* and, like Colman (1974), discusses the difficulties of interpreting heart impedance recordings.

Other aspects of heart function such as diastolic and systolic pressures have only rarely been investigated (Smith & Davis, 1965; Tiffany, 1972), and there is no reliable information on changes in heart output. In a previous study (Brand, 1972), the haemo-dynamics of blood circulation of the freshwater bivalve *Anodonta anatina* were investigated using techniques which caused very little damage to the animal. The techniques of recording heart action by means of the electrocardiogram (ECG), heart impedance, and ventricular and pericardial cavity pressures have now been used in a more complete study of heart action during all aspects of the normal behaviour of *Anodonta*. This paper describes changes in heart activity and discusses the mechanism controlling and affecting heart action during normal behaviour.

MATERIALS AND METHODS

Anodonta were collected from gravel pits at Catwick, E. Yorks. and kept in tanks containing gravel substrate and water collected from the natural habitat. All experiments were carried out in the laboratory at room temperature of approximately 18 °C, using animals of 6–8 cm shell length.

The ECG and heart impedance were recorded from fine chlorided silver electrodes implanted through very small holes drilled in the shell over the heart, and sealed in place with black wax. The ECG was recorded using a Narco Biosystems condenser-coupled Hi-Gain preamplifier and the impedance across the heart by means of a Narco Impedance pneumograph; both were displayed on a multichannel pen recorder (Narco Physiograph).

Ventricular and pericardial pressures were recorded on the pen recorder using Statham P23BB and Narco Linear Core fluid pressure transducers. The cannulae were short no. 20 hypodermic needles connected to the pressure transducer by a 30 cm length of 3 mm bore rubber pressure tubing. Full details of the experimental

procedures used to record heart, pericardial cavity and pedal haemocoel pressures from animals fixed to the side of a tank, and from freely burrowing animals, are given in Brand (1972). In this paper all pressures are expressed as cm of water using the tank surface as the zero reference level.

In the recordings made from *Anodonta* fixed to the side of a tank, shell gape was generally recorded from a thread attached to the free valve, using a Narco Isotonic Myograph. In freely moving animals shell gape was recorded from electrodes attached to the shell using the impedance technique of Hoggarth & Trueman (1967).

<div align="center">RESULTS</div>

<div align="center">(*a*) *Spontaneous periods of activity and quiescence*</div>

In *Anodonta cygnea*, a rhythm of contraction and relaxation in the tonic portions of the adductor muscles results in the alternation of periods when the shell is open and the animal is active, with periods of prolonged shell closure and consequent quiescence (Barnes, 1955). During the active period, contractions of the phasic portions of the adductor muscles periodically eject faeces and pseudofaeces from the mantle cavity, and the alternate opening and closing of the siphons indicates an intermittent respiratory current which is independent of the shell rhythm (Koch & Hers, 1943). The contraction and relaxation of the tonic portions of the adductor muscles is apparently unrelated to any rhythm of the environment and has been previously considered to be a feeding rhythm (Salánki, 1966). More recently, Morton (1970) has shown that it can also be related to a rhythm of digestion associated with changes in the cytological structure of the digestive diverticula.

A similar rhythmic pattern of activity occurs in *Anodonta anatina*, and recordings of the ECG (Fig. 1) and ventricular pressure (Fig. 2) show marked changes in heart action during periods of tonic shell closure. At the start of a period of quiescence the closure of the shell takes place by a series of rapid adductions over a period of about 3 min, but the siphons close and ventilation stops at the first adduction (marked × in Figs. 1*a* and 2*a*). The onset of a period of shell closure is detectable, however, at least one hour earlier by the gradual decrease in shell gape at each phasic adduction. There is an initial small rise in heart rate which starts well before pumping stops and continues to increase for several minutes after the shell has completely closed. The rate then falls and remains at a low level until about 5 min before the start of the next active period. Whereas the decline in heart rate after shell closure is gradual, the increase in rate at the onset of activity is very rapid, and there is an overshoot of the normal heart rate for about 20 min after shell opening. The highest rates of beat therefore occur immediately after the start of the period of shell closure and immediately after the start of the active period; in both cases there is a well marked increase in rate before the movement of the valves.

Ventricular systolic pressure also shows a small initial increase as the valves start to close, but this falls several minutes before the reduction in rate and remains low throughout the period of closure (Fig. 2*a*, *b*). In recordings of ventricular pressure from six *Anodonta*, systolic pressure pulses were reduced from 3–4 cm to about 1 cm during closure. At the start of the active period there is no sudden large increase in systolic
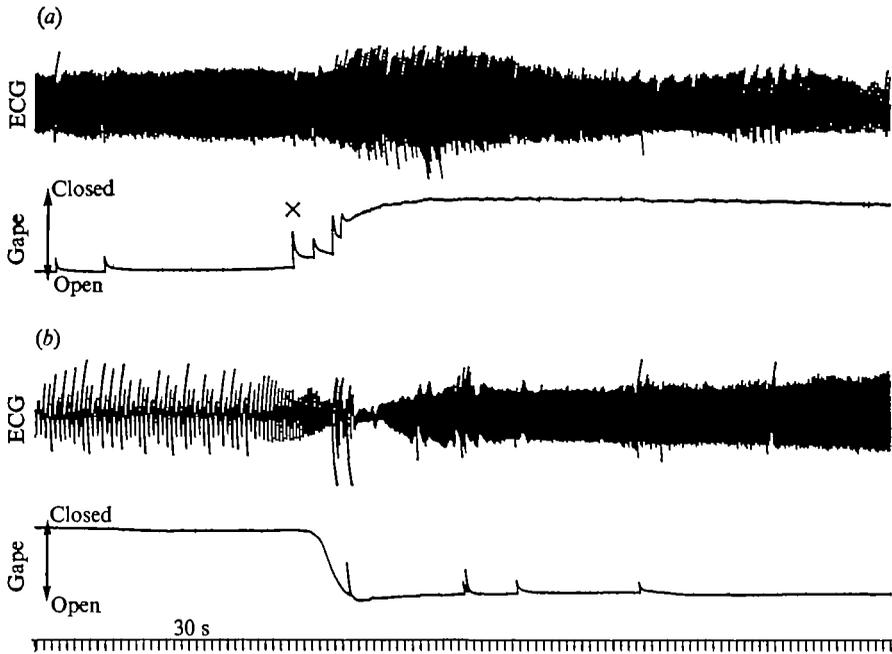
Fig. 1. Simultaneous recording of the ECG and shell gape of *Anodonta anatina* (*a*) at the start of a spontaneous period of tonic shell closure and (*b*) at shell opening after approximately 90 min closed. (A section of the recording during closure has been omitted.) After an initial small increase, heart rate and amplitude are reduced during the period of shell closure but rise rapidly when the shell opens. ×, siphons close and ventilation ceases.

pressure with an overshoot of the normal level, as there is with heart rate, but a steady increase over a period of about 30 min.

Though there is some variation between recordings, the amplitude of ECG generally follows the pattern of change in ventricular systolic pressure. Heart impedance recordings are more variable and often show a marked overshoot of amplitude after shell opening.

The diastolic level of pressure in the ventricle increases slightly at shell closure (Fig. 2*a*). This increase is usually of 1–2 cm for most of the period of closure, but does not indicate a sustained increase in the venous return of blood to the heart: there is a similar increase in pressure in the pericardial cavity (Fig. 3) and probably elsewhere throughout the haemocoel, as a result of increased muscle tension during the period of tonic shell closure. Changes in the diastolic level of pressure in the ventricle and pericardial cavity during tonic shell closure occur without any movement of the valves for example, just before the shell reopens (Fig. 3*b*), indicating that changes in muscle tension during shell closure occur not only in the tonic portions of the adductor muscles, but probably also in other muscles such as the pedal muscles. It is of interest to note that small peaks of pressure in the pericardial cavity, which correspond to minute movements of the shell (Fig. 3*a* at A), continue for some time after tonic closure. These are probably the result of periodic increases in tension in the phasic portions of the adductor muscles, like those which Barnes (1955) (in *Anodonta cygnea*) observed to continue for some time after the contraction of the tonic portions.
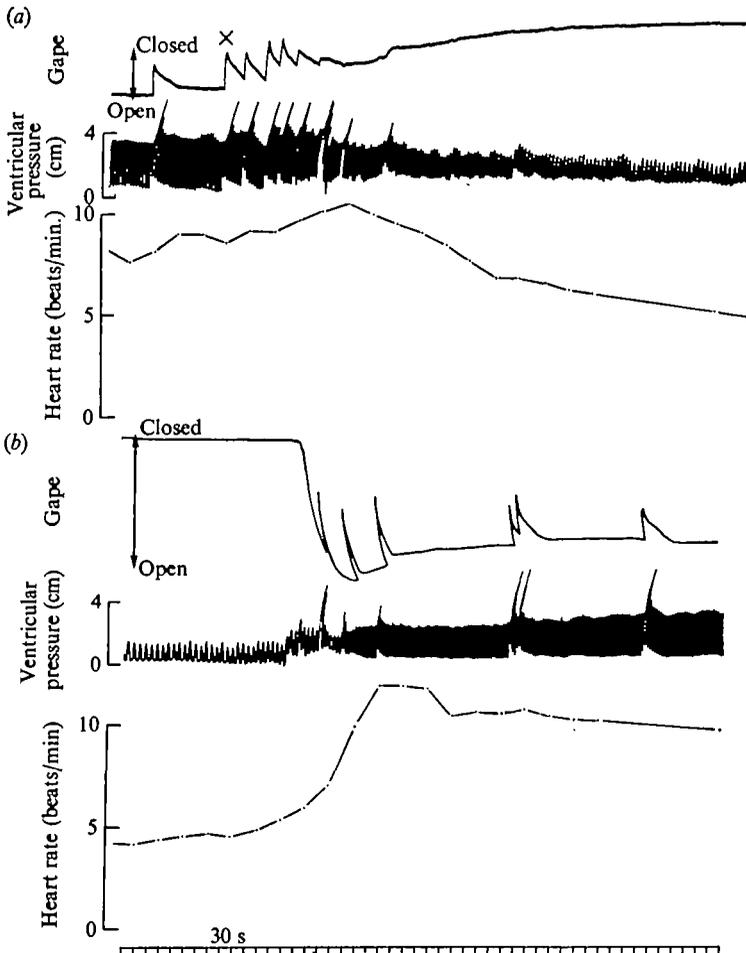
Fig. 2. Simultaneous recording of ventricular pressure and shell gape of *Anodonta anatina* (*a*) at the start of a spontaneous period of tonic shell closure and (*b*) at shell opening after approximately 90 min closed. Graphs of heart rate are drawn on the same time scale. ×, siphons close and ventilation ceases.

Recordings of pressure in the pericardial cavity during tonic closure (Fig. 3) differ most noticeably from ventricular pressure recordings (Fig. 2) in that pericardial pressure pulses are of greater amplitude during quiescence than during the active period. The pressure pulses in the pericardial cavity are generated by the amplitude or force of contraction of the ventricle (Brand, 1972) and it will be shown later that there is some evidence that the amplitude of these pressure pulses is related to the stroke volume output of the heart. During spontaneous periods of shell closure the stroke volume output may therefore be relatively high, but since there is generally a 50–60% fall in heart rate, a considerable reduction in total heart output is still likely.

As well as the pronounced bradycardia, there are generally changes in the rhythm of heart beat during periods of prolonged shell closure. This usually starts some time after shell closure and involves a regular variation of heart beat amplitude on ECG, heart impedance and ventricular pressure recordings (Fig. 4*a*, *b*). Most recordings
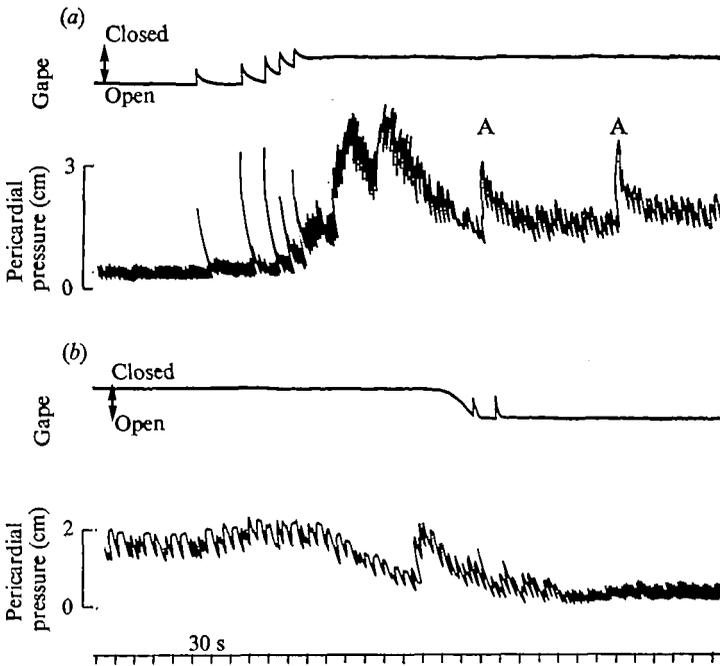
Fig. 3. Simultaneous recording of pericardial cavity pressure and shell gape of *Anodonta anatina* (*a*) at the start of a spontaneous period of tonic shell closure and (*b*) at shell opening after approximately 90 min closed. Pericardial pressure pulses are of greater amplitude during shell closure than during the active period. A, pressure peaks corresponding to minute movements of the shell which continue for some time after shell closure and are probably caused by contraction of the phasic portions of the adductor muscles.
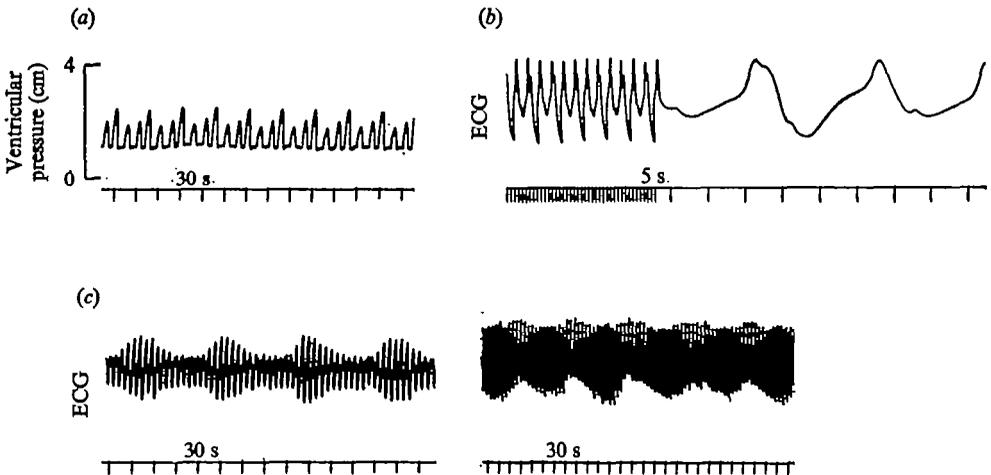

Fig. 4. Rhythmic variations in the pattern of heart beat of *Anodonta anatina*. A regular alternation of two (*b*) or occasionally three (*a*) beats of different amplitude was commonly noted during spontaneous periods of tonic shell closure, in both ventricular pressure and ECG recordings. Conspicuous patterns of change in amplitude and waveform of heart beat of several minutes' periodicity were more common during the active period (*c*).

exhibit a regular alternation between two beats of different amplitude (Fig. 4*b*) but occasionally three beats of differing amplitude occur (Fig. 4*a*). This alternation of beat is occasionally noted during the active period, but a more extensive variation in heart amplitude is much more common during activity. This takes the form of a regularly repeated variation in the amplitude and waveform of the heart beat forming conspicuous patterns of beat of several minutes' periodicity (Fig. 4*c*).

To investigate further the mechanism controlling heart action, an attempt was made to eliminate the mechanical effects of shell movement. Glass cannulae were first inserted into notches cut in the edge of the shell in the position of the siphonal apertures so that water flow through the mantle cavity could be maintained. The shell valves were then sealed together rigidly around the entire mantle gape with black wax. The cannula over the inhalant siphon was connected to a reservoir of water, and flow through the mantle cavity controlled by a tap. When the flow of water through the mantle cavity is stopped (Fig. 5*a*), the heart rate immediately starts to fall and remains low until the water current is restored (Fig. 5*b*). Although the duration and extent of the changes in heart rate are smaller than those recorded during normal periods of shell closure, they do indicate the similarity between the two events. There are, however, certain differences. Firstly, closing off the water circulation through the mantle cavity causes an immediate decrease in heart rate, with no initial increase. Secondly, the increase in heart rate when the water current is continued is comparatively gradual with no overshoot of rate, though some impedance recordings show an obvious overshoot in amplitude. Finally, of course, there is no change in rate in anticipation of the change in water flow as there is during normal activity.

(*b*) *Burrowing*

Anodonta anatina burrows by the repetition of a cycle of movements, termed the digging cycle, which is essentially similar to that previously described for numerous other bivalves (Trueman, Brand & Davis, 1966; Trueman, 1968). The time from the start of burrowing until movement stops has been termed the digging period (Ansell, 1962).

Burrowing starts with the extension of the foot, accompanied by an immediate increase in ventricular systolic pressure pulses and a fall in heart rate (Fig. 6*a* at F). During the series of digging cycles which follow there are characteristic patterns of change in heart action recorded in both the ventricle (Fig. 6*a*, *b*) and the pericardial cavity (Figs. 6*c*, 7), which continue until burrowing stops (Fig. 6*b*). The changes in heart action during the different movements of the digging cycle (Stages i–vi as defined by Trueman *et al.* 1966), together with changes in pedal haemocoel pressure (taken from Brand, 1972), are summarized diagrammatically in Fig. 8. In the following account an attempt is made to reconcile the results obtained by the different recording techniques and to present an analysis of heart action consistent with previous knowledge of the haemodynamic condition prevailing in the circulatory system (Brand, 1972).

When the foot starts to extend and probe down into the substrate (Stages v and vi of the digging cycle) there is a good venous return of blood to the heart following the previous adduction and retraction movements (Stages iii and iv), and a low pressure in the foot providing little arterial resistance, so the heart beats at a high rate but with
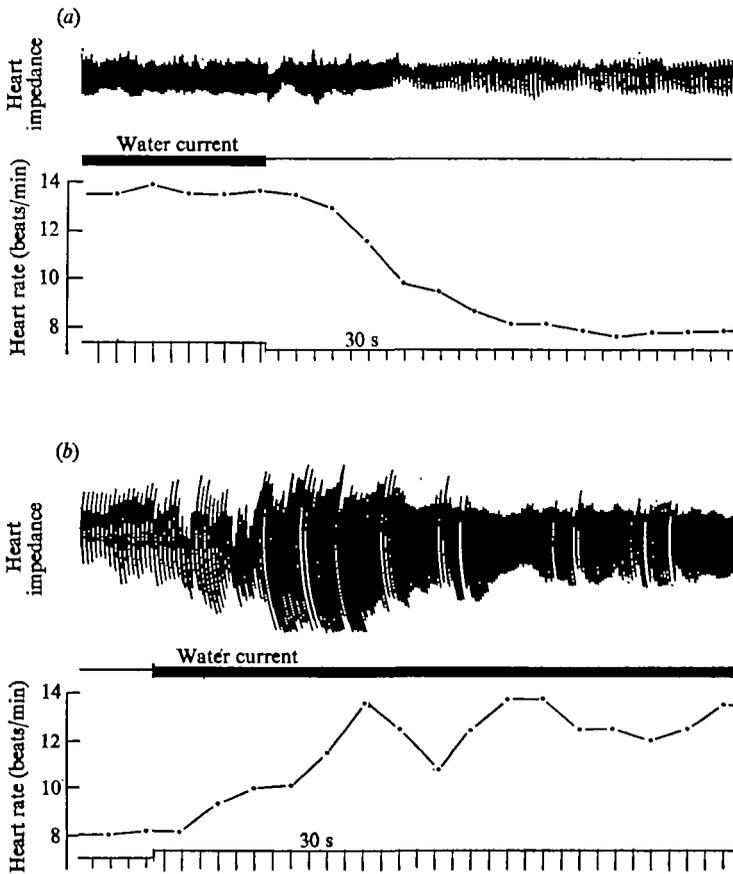
Fig. 5. A recording of heart action (heart impedance, upper trace) of *Anodonta anatina* with the shell valves sealed together. A water current was circulated through the mantle cavity (indicated by the thick line and also by the raised time-base line), by means of cannulae fixed to the edge of the shell in the position of the siphonal apertures. Water flow through the mantle cavity was stopped (*a*) and then continued 2 h later (*b*). Graphs of heart rate have been drawn on the same time scale. For further information see text.

a low ventricular systolic pressure (Fig. 6*a*, *b* at the beginning of P). However, as the foot extends further into the substrate and terminal dilation begins (end of Stage vi and Stages i and ii), the arterial resistance rises due to the increased pressure in the foot. The reduction in diastolic pressure at this time in both ventricle and pericardial cavity (Fig. 6) indicates that there is probably also a reduction in the amount of blood returning to the heart, caused by the closure of Keber's valve (Brand, 1972). Diastolic filling of the ventricle is therefore slowed down and systolic emptying is resisted, so the heart beats more slowly but with a higher systolic pressure (Fig. 6*a*, *b* at the end of P). Thus, while the elevated systolic pressure is probably sufficient to supply some blood to the pedal haemocoel throughout most of the digging cycle (Brand, 1972), the stroke volume output of the heart towards the end of the pedal probing stage is probably very low. The major peaks of pressure during the adduction and retraction movements of the digging cycle (Fig. 6*a*, *b* at AR) and during normal phasic adduction
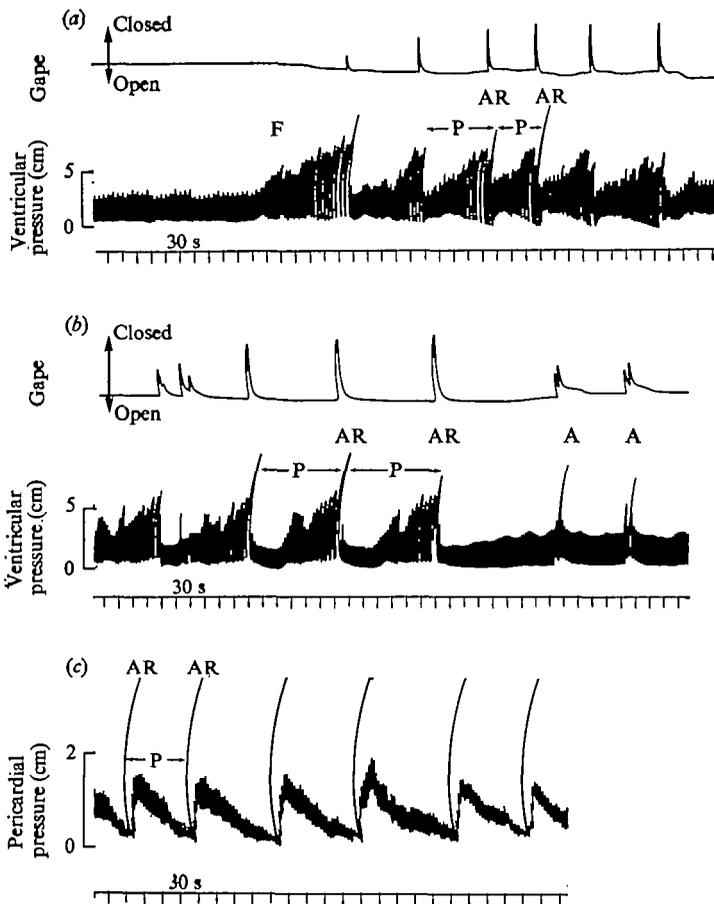
Fig. 6. Pressures recorded in the ventricle and pericardial cavity of *Anodonta anatina* during free burrowing. Simultaneous recordings of ventricular pressure and shell gape during a series of digging cycles (*a*) at the start of a digging period and (*b*) at the end of the same digging period after approximately 2 h burrowing. (*c*) Pericardial cavity pressures during a series of digging cycles. F, extension of the foot at the start of the digging period. AR, major peaks of pressure during the adduction and retraction movements of the digging cycle; P, period of pedal extension and probing.

(A) have little effect on heart action since they are generated equally throughout the haemocoel. Such pressure peaks have been previously reported in many other species of bivalve and shown to be responsible for the dilation and anchorage of the foot in burrowing (Trueman, 1968).

The characteristic pattern of change in amplitude of pericardial pressure pulses during the digging cycle (Fig. 6c) therefore follows the suggested changes in heart output. The interpretation of pericardial cavity pressure pulses as indicating the stroke volume output of the heart is quite plausible since these pulses are generated by the amplitude or force of contraction of the ventricle (Brand, 1972). In this way it is possible to account for the marked differences between the patterns of pressure change in the ventricle and pericardial cavity during burrowing. If this interpretation is
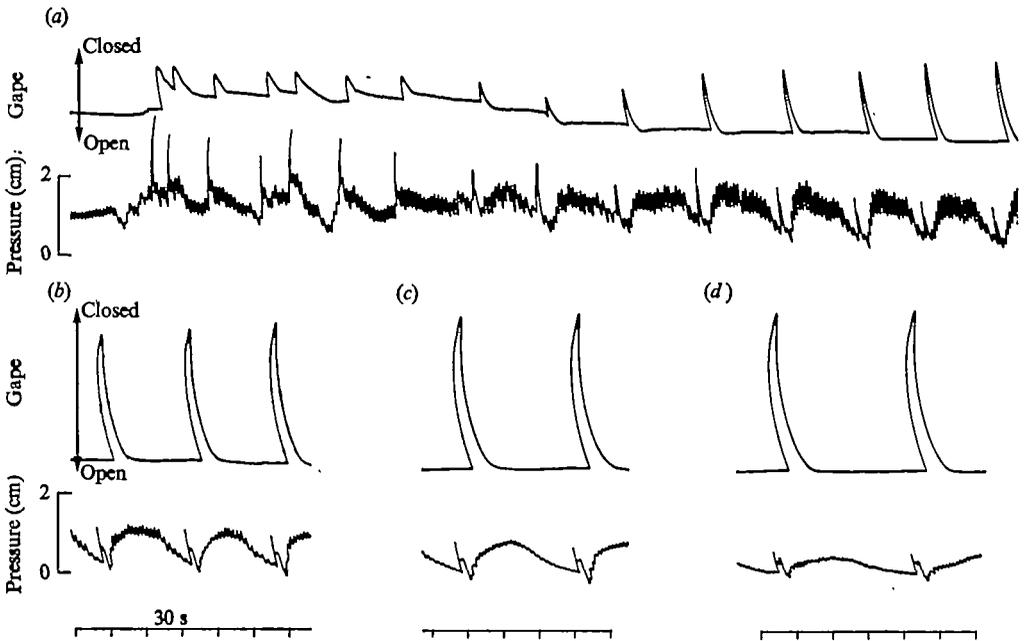
Fig. 7. (a)–(d) Sections of a continuous recording of pericardial cavity pressure and shell gape of *Anodonta anatina* during a digging period lasting several hours. The maximum amplitude of pericardial pressure pulses attained during successive digging cycles, and the diastolic level of pressure, fall progressively throughout the digging period.

correct, the reduction in amplitude of pericardial pressure pulses during successive digging cycles throughout the digging period (Fig. 7) indicates that the stroke volume output of the heart is reduced in later digging cycles. There are some observations which suggest that this may be so. As the digging cycle progresses, and the animal burrows deeper into the substrate, the foot becomes progressively more extended. If more blood is entering the foot during the digging cycle than is returning to the heart, which would seem on functional grounds to be most likely (Brand, 1972), then eventually, when the mantle and other sinuses have been emptied, the amount of blood returning to the heart, and therefore heart output, will be reduced. The progressive fall in the diastolic level of pressure in both ventricle and pericardial cavity throughout the digging period (Figs. 6 and 7) supports this explanation.

Once again, both ECG and heart impedance recordings during burrowing show greater variability than the pressure recordings. The ECG generally follows the same pattern of change as the ventricular systolic pressure, with increased amplitude prior to adduction and retraction. Heart impedance recordings, by contrast, usually respond like the pericardial cavity pressure pulses with a reduction in amplitude at this time. Since the amplitude of pericardial pressure pulses probably indicates the stroke volume output of the ventricle, these observations support the recent use of the heart impedance technique to obtain an index of gill perfusion in studies of respiratory regulation (Bayne, 1971; Taylor & Brand, 1975); though the relationship between heart output and gill perfuson has yet to be confirmed.
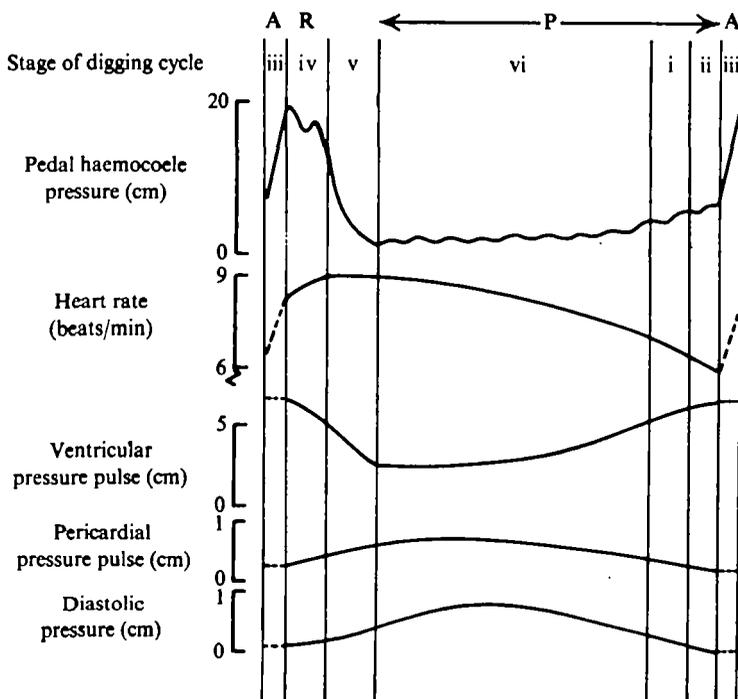
Fig. 8. Diagram summarizing the changes in heart action and pedal haemocoel pressure in *Anodonta anatina* during the different stages of the digging cycle. The pattern of change in pedal haemocoel pressure is taken from Brand (1972). Stages i–vi of the digging cycle are defined fully by Trueman *et al.* (1966). A, adduction stage of the digging cycle; R, retraction stage of the digging cycle; P, duration of pedal extension and probing. For further information see text.

DISCUSSION

It has long been known that the heart rate of bivalve molluscs is reduced when the shell is closed and increases rapidly upon shell opening (Baker, 1898; Koch, 1917; Schlieper, 1955), and an essentially similar basic response occurs in a range of bivalves in response to various forms of respiratory stress (Trueman & Lowe, 1971; Coleman & Trueman, 1971; Bayne, 1971; Lowe & Trueman, 1972; Brand & Roberts, 1973; Taylor, 1976).

An initial increase in heart rate at shell closure, as found in *Anodonta*, has also been recorded in *Cardium edule* (Trueman, 1967; Boyden, 1972) but was not detected in many studies on other species (Schlieper, 1955; Coleman & Trueman, 1971; Trueman & Lowe, 1971). A similar tachycardia has, however, been recorded in *Pecten maximus* (Brand & Roberts, 1973), *Mytilus edulis* (Bayne, 1971) and *Arctica islandica* (Taylor & Brand, 1975) as an initial response to hypoxia, and these authors have shown that the increased heart activity is part of a respiratory mechanism, mediated by the nervous system, which regulates oxygen consumption in response to declining oxygen tension. However, the increase in heart rate in *Anodonta* generally starts several minutes before ventilation stops, and though mantle cavity oxygen tension has not been recorded, it would seem unlikely to fall significantly before shell closure. Since no initial increase occurs after stopping the flow of water through the mantle cavity in animals with the

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valves fixed together, the possibility remains that the increased heart rate results from haemodynamic changes in the circulatory system brought about by the increase in muscle tension prior to shell closure. A more critical study of ventilation, oxygen availability and heart action is required before this question can be resolved.

Whether or not there is an initial increase in heart rate, an extensive bradycardia appears to be the eventual response of all bivalves to shell closure or severe hypoxia. Details of the mechanism controlling the onset of bradycardia are not known in any bivalve, although it has been suggested that the build-up of CO_2 (Schlieper, 1955) or the depletion of O_2 (Bayne, 1971) in the mantle cavity water is responsible, through the stimulation of some receptor system. Direct mechanical effects of shell closure are obviously not important in *Anodonta* as bradycardia occurred in the experiments on animals with the valves sealed together. However, in these experiments the artifacts on ECG and heart impedance recordings caused by tissue movements or changes in muscle tension are generally suppressed within about 10 min of stopping mantle cavity water flow, as they are during normal tonic shell closure. In other words, preventing water passing through the mantle cavity affected not only heart rate but also other events associated with a normal period of tonic shell closure. If this is so, it would indicate that the circulatory, muscular and ventilatory systems of *Anodonta* are much more closely integrated than was formerly thought. Salánki & Pecsi (1965), working on *Anodonta cygnea*, demonstrated the existence of sensory pathways running from the heart to the visceral ganglion. This was confirmed in *Anodonta anatina* by stimulating the heart electrically through the electrodes normally used for recording the ECG. The coordination of the events which occur during a spontaneous period of shell closure is therefore rather complicated and further research is necessary to determine its neurophysiological mechanism.

In addition to the rapid and pronounced bradycardia, prolonged aerial exposure of *Mytilus edulis* leads to a rhythmic suppression of heart beat (Helm & Trueman, 1967). This response is considered to be an adaptation to intertidal life (Coleman & Trueman, 1971; Coleman, 1973), and would appear to be under the control of the nervous regulatory system. By contrast, the simple alternating pattern of heart beat amplitude that occurs in *Anodonta* during periods of tonic shell closure is probably mechanically determined. A similar alternation of heart beat amplitude has been reported in *Tridacna crocea* following removal of part of the shell and pericardial wall (Purchon, 1955). It is probable, as Purchon suggests, that the heart rhythm is limited by the rate at which blood is returned to the heart: after surgical opening of the pericardial cavity of *Tridacna*, and during periods of quiescence in *Anodonta*, the venous return of blood is insufficient to maintain the regular rhythm of heart beat. Experiments on isolated *Anodonta* ventricles support this interpretation (Brand, 1968), in showing a similar alternation of beat amplitude when perfusion pressure stretching the ventricle wall fell to very low levels. Thus, purely mechanical factors probably account for the simple alternation of heart beat amplitude in *Anodonta*.

The rapid increase in heart rate and initial overshoot of the normal level on shell opening has received much attention in recent investigations. The overshoot is probably generally associated with the repayment of an oxygen debt in most bivalves (Helm & Trueman, 1976; Coleman & Trueman, 1971), though other factors are undoubtedly involved in some species (Boyden, 1972; Brand & Roberts, 1973). In *Anodonta*, like

Isognomon alatus (Trueman & Lowe, 1971), the heart rate starts to increase before any movement of the valves. These observations suggest that this is a nervously controlled mechanism to ensure blood flow through the respiratory surfaces immediately mantle cavity ventilation recommences. The major acceleration of heart rate in all species coincides with the start of mantle cavity ventilation, though the rate of increase and extent of overshoot vary between species and also with the severity of previous respiratory stress (Brand & Roberts, 1973; Taylor, 1976). Thus the absence of an overshoot, when water flow through the mantle cavity is resumed in *Anodonta* with the valves sealed together, is probably due to the comparatively short duration of respiratory stress (1–2 h).

Although the major changes in heart activity during spontaneous periods of activity therefore appear to be controlled largely by the extrinsic nervous regulatory system, the variations in heart action recorded during burrowing seem more likely to result from haemodynamic changes in the peripheral circulation, with little influence by the nervous regulatory system. In any case, the nervous regulatory system, functioning as it does by the production of neurohumours, does not seem well suited for controlling these regularly repeated short-term variations in heart action. Longer term variations such as those occurring during spontaneous periods of activity and quiescence, and the changes in heart rate associated with variations in the rate of ventilation (Walne, 1972) and level of feeding (Widdows, 1973), are undoubtedly integrated parts of physiological mechanisms controlled by the nervous regulatory system. Control of the heart by the extrinsic nervous regulatory system is therefore apparently of much greater importance in relation to respiratory control, than in relation to the haemodynamic functioning of the fluid-muscle system in locomotion.

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