FACTORS AFFECTING THE HEART ACTIVITY AND BLOOD PRESSURE OF THE SWAN MUSSEL
ANODONTA CYGNEA

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(Received 5 August 1974)

SUMMARY

1. The rate of heart beat increased with temperature and was three times as high in the active as in the inactive animal.
2. The rate of shell valve movement rose and the rate of heart beat fell when the foot was extended.
3. The rates of heart beat and shell valve movement decreased when the water was saturated with carbon dioxide. This heart response remained when the visceral ganglion was destroyed.
4. Ventricular contraction occurred simultaneously over the whole chamber. The passage of blood into the posterior aorta could be restricted by the protuberances on its wall.
5. Pericardial cavity pressure rose by about 5 cm H2O at shell valve adduction and 0.25–0.6 cm H2O at ventricular diastole.
6. Pulse pressure changes of 0.25–0.6 cm H2O occurred in the auricle and 1–3 cm H2O in the ventricle and anterior aorta.

INTRODUCTION

The first object of this work has been to establish the normal patterns of activity for the freshwater swan mussel, Anodonta cygnea, over periods of several days. It has been known for some time that periods of activity during which the shell valves are mainly open alternate with periods of apparent inactivity during which they are closed (Koch, 1917; Hers, 1943; Barnes, 1955). This alternation will be referred to as the ‘slow’ adductor rhythm. During the active phase the unstriated fibres of the posterior and anterior adductor muscles are relaxed and at regular intervals the striated adductor fibres contract momentarily to close the valves and reduce the volume of the mantle cavity. This will be referred to as ‘phasic adduction’ resulting in a ‘fast’ adductor rhythm. During the inactive phase, the unstriated adductor fibres are in a state of tonic contraction. Barnes found that destruction of the visceral ganglion resulted in cessation of the phasic adduction and either permanent contraction or permanent relaxation of the tonic adductor fibres.

There are great variations in the values for the normal heart rate of A. cygnea claimed by various authors: for instance, Yung (1881), reported 12–15 beats/min; Baker (1897), 10–30/min; Willem & Minne (1898), 4–17/min; ten Cate (1923), 1–15/min; Hers (1943), 2–17/min and Hendrickx (1945) 3–4/min. W. Koch and Hers

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noted that the heart rate was higher during the active phase than during the inactive phase but only Koch stipulated the state of activity and the temperature during observation.

The second object of this work has been to find out to what extent the changes in heart rate associated with activity could be attributed to changes in hydrostatic pressure, influence of the nervous system, or the relative concentration of oxygen and carbon dioxide in the water surrounding the gills. Willem & Minne (1898) found that the frequency of beat varied with the degree of extension of the heart wall. They proposed that the coordination of the heart chambers and heart filling depended upon a volume-compensating arrangement between the auricle, ventricle and pericardial cavity whereby the combined volume of these three chambers was always constant. Hendrickx concluded that the coordination of the heart chambers depended upon a combination of local pressure changes and the conduction of electric potential from the contracting chamber(s) to the relaxed chamber(s) independent of the extrinsic nervous system. Brand (1972) working on *Anodonta anatina* found that the resting pressures in the heart chambers and pericardial cavity lay between 0.5 and 5 cm H₂O although the ventricular systolic pressure rose up to 10 cm H₂O as the foot was extended.

All the authors mentioned above except W. Koch, Hers and Brand were using surgical procedures in their investigations, which makes the significance of their findings in relation to the intact animal uncertain. In the following investigation an effort has been made to record the normal activity and heart pressures with the minimum of surgical interference.

**MATERIALS AND METHODS**

The mussels were 6- to 10-year-old specimens, 12-14 cm in length, collected from Whiteknights Park Lake in Reading. They were kept for up to six months in a large open-air tank and fed on oatmeal.

Two types of instruments were used to measure pressure changes; firstly, a closed water manometer (Davson & Purvis, 1959) which deflected a light beam to a recording camera [Chadwick (Sommerville), 1962] and secondly, a pressure transducer (Model P. 23, B. B. Statham Inst. Inc.) used in conjunction with a Grass 'Polygraph' pen recorder.

The manometers and transducers were connected to the animal through water-filled, ‘rigid’ Polythene tubing which terminated in an S 19 hypodermic needle (20 mm long; 0.3 mm bore). Unionid Ringer solution was introduced into the needle and adjacent tubing.

During experiments the instruments were frequently calibrated against static changes in pressure to check that the response was linear and the base-line steady. A cautious estimate of the response of the closed water manometer gave an amplitude accuracy of not more than 1% and not less than 5% up to a recording frequency of 0.69 c/s (McDonald, 1960). As this frequency is about five times that of the heart beat of *Anodonta*, the details of the pulse wave could be accurately recorded.

Heart rate and pressure recordings were carried out by inserting the hypodermic needle obliquely through a Polythene window which replaced the shell over one side
Heart activity and blood pressure of the swan mussel

of the pericardial cavity (Fig. 1). A window of 25 x 15 mm was sawn from the shell and a somewhat larger piece of heavy duty Polythene sheet was stretched to fit the shell curvature and fixed across the hole by sticking its border to the dried shell surrounding the window with 'UHU' adhesive. The heart could be observed sufficiently well to pass the needle into a particular part of the ventricle, the pericardial cavity, the anterior aorta and, less easily, the auricle of that side.

The heart activity was recorded for periods of 3–4 days using a closed water manometer in a darkened room. A relay switch, operated by a small electric motor running at one revolution/hour, turned on the camera motor, the lamp and the time marker for 12 min in every hour. Another method used to make permanent recordings of the heart activity over 3–12 days was to cannulate the pericardium. A round hole was sawn from the shell over one side of the pericardial cavity, (Fig. 1), a small hole was made in the pericardium-mantle and a ‘purse-string’ suture was tightened around the end of the cannula, as shown in Fig. 2. The rubber bung was fitted into the hole in the shell and the cannula withdrawn until its flange held the pericardium-mantle and nylon ribbon up against the bung. The purpose of the nylon ribbon was to prevent the cut edges of the shell damaging the delicate pericardium-mantle. The cannula was sealed by a small bung when not in use.

The apparatus shown in Fig. 3 was used to record fluctuations in pericardial pressure through the cannula. The tubing was filled with Unionid Ringer solution and required the displacement of 0.7 ml pericardial fluid to raise the float by 1 cm. The oscillation of the float with heart beat required the displacement of about 0.3 ml of fluid per beat. The movements of the float were recorded on a lightly smoked kymograph cylinder, 6 in. deep, 12 in. diameter, used in conjunction with a spiral attachment (C. F. Palmer Ltd.), which gave a recording time of 16 h/cylinder at a surface speed of 5 mm/min. Two kymograph drums were used alternately to prevent overheating. The movements of the posterior edges of the shell valves, to indicate the adductor rhythm, and the anterior edges of the valves, to indicate foot extension, were recorded by connecting kymograph levers to two lengths of monofilament nylon
Fig. 2. Pericardial cannula used to record heart beat.

Fig. 3. Apparatus used in conjunction with the pericardial cannula and kymograph, to record heart beat.
Heart activity and blood pressure of the swan mussel

which passed through pairs of small holes in the edges of the shell and shortened as the valves gapèd.

Some recordings of heart activity were made using this apparatus but replacing the pericardial cannula by a 70 mm long Polythene tube terminating in a fluid filled rubber balloon of 10 mm diameter. This was passed through the anus and along the intestine until the balloon lay within that part of the rectum which is surrounded by the ventricle.

The visceral ganglion was anaesthetized by injecting 3 mg sodium pentobarbitone in 0·1 ml Unionid Ringer solution over the ganglion. This was done by breaking away the posterior 5 mm of the shell valves and cutting the midline junction of the median gill lamellae. The lamellae were held aside by a plug of cotton wool, and a light was shone into the suprabranchial chamber where the ganglion could be seen lying on the ventral surface of the posterior adductor muscle. A long hypodermic needle (S15) was passed between the connective tissue and the muscle, and the anaesthetic injected onto the ganglion. Using the same approach, the visceral ganglion was destroyed by pulling it out with a pair of fine forceps.

In order to irrigate the gills with oxygen-saturated or desaturated water, regardless of the animal's state of activity, oxygen or nitrogen was bubbled through boiled pond water which was led into the posterior end of the gill chamber through a tube sealed into notches in the edge of the shell valves. When the valves were closed, water escaped through a similarly arranged tube, mid-way along the chamber. The oxygen concentration was determined by 'Winkler' titration using standard tables to establish when maximal or minimal concentration had been achieved.

The experiments on the effects of varying the carbon dioxide content of the water were carried out by bubbling the gas through the water surrounding the animals. The posterior 5 mm of the shell valves was broken away to prevent the animal sealing off the gill chamber at valve adduction and a glass plate covered most of the tank to prevent gaseous exchange with the air. The pH of the water was measured at regular intervals to indicate the rate of saturation or desaturation with carbon dioxide.

EXPERIMENTS AND RESULTS

Direct observation of the heart

When a window was cut out of the shell over one side of the heart and the pericardium opened to reveal one auricle and the ventricle, it was noted that contraction of the auricle alternated with contraction of the ventricle. Occasionally, a second smaller contraction of the ventricle closely followed the first but this occurred most commonly in animals which had been subjected to some previous experimental interference. The ventricular contraction seemed to occur simultaneously over all parts of the chamber. Often the diastolic expansion of the ventricle began posteriorly and moved anteriorly.

There is a pair of valves at each auriculo-ventricular junction and a semilunar valve on the anterior aorta, about 1 cm from the ventricle, directed so as to prevent blood flowing back into the heart. There are two small protuberances at the beginning of the posterior aorta. Dye solution injected into the ventricle of a live animal passed readily into the anterior aorta but never into the posterior aorta unless the animal was
anaesthetized. In the unanaesthetized animal, dye could only be injected into the posterior aorta by passing the injecting needle from the ventricle through the restricting protuberances.

The effect of temperature and activity on rate of heart beat

The rate of heart beat was recorded over the temperature range 3–28.5 °C between the months of February and April, using both the closed water manometer and pericardial cannulation. The heart rate was higher in the active animal than in the inactive animal and was closely correlated with temperature in the active animal. This correlation was not so marked in the inactive state where the range of heart-rate variation was small. The results are summarized in the graphs shown in Fig. 4. The line for active heart rate based on the closed water manometer readings was not significantly different from that based on the cannulation readings.

The rate of adduction of the shell valves was taken as a quantitative index of activity. When the closed manometer was used to record heart activity, the phasic valve adduction was indicated by a rapid rise and fall in pericardial pressure of 3–7 cm H₂O. At the beginning of a period of inactivity, the pericardial pressure rose by 4–6 cm H₂O (Fig. 5) and remained at that level until activity was resumed.

The duration of each state of activity could vary greatly from animal to animal but each individual followed a regular pattern in which each period of activity was of similar length and somewhat longer than the periods of inactivity. There was no evidence of a diurnal variation in activity. The heart rate closely followed the general contour of the rate of valve movement except that:

1. There was usually a sharp rise in valve rate with no corresponding rise in heart rate at the end of a period of activity (Figs. 6, 7).
Heart activity and blood pressure of the swan mussel

Fig. 5. Pericardial cavity pressure changes measured by the Davson and Purvis manometer. Upper trace: transition from active to inactive state. Lower trace: (a) inactive state; (b) active state. (a) and (b) are successive recordings but the actual transition occurred while the recording apparatus was switched off.

Fig. 6. Variation in rate of heart beat with activity (cannulated pericardial cavity). O, Rate of heart beat; x, rate of shell valve movement.

2. The heart rate tended to fall progressively throughout a period of inactivity, reaching its lowest point just before activity recommenced (Fig. 7).

3. There was a sharp rise in valve rate accompanying foot movement while the heart rate remained unchanged or fell (Figs. 7, 8).

In the nine cannulated specimens used, the valve movements were recorded mechanically as already described, and in three of these, recordings were made for three days before cannulation to ascertain the effect of this interference upon activity. Fig. 8 shows a marked rise in activity for 12 hours following cannulation with the
Fig. 7. Variation in rate of heart beat with activity (cannulated pericardial cavity). O, Rate of heart beat; x, rate of shell valve movement; †, foot extended.

Fig. 8. Variation in rate of heart beat with activity (cannulated pericardial cavity). O, Rate of heart beat; x, rate of shell valve movement; †, foot extended.
Heart activity and blood pressure of the swan mussel

Fig. 9. Variation in pericardial cavity pressure at transitional states of activity (cannulated pericardial cavity). (a) Upper pair of traces: transition from active to inactive state. (b) Lower pair of traces: transition from inactive to active state. (Open water manometer and kymograph).

valve activity falling to reach the original level between 24 and 36 h after. Figs. 6 and 7 are based on recordings made 24–36 h after cannulation, and Fig. 7 still shows a falling level of activity. The values for heart rate used in Fig. 4 were taken at least 24 h after cannulation.

Figs. 5 and 9 show how the fast adductor rhythm usually continued for 5–10 min after the tonic adductor fibres had contracted at the beginning of a period of inactivity and commenced just before relaxation of the tonic fibres at the end of the inactive period. During a period of activity, the heart rate was unaffected by the momentary rise and fall in pressure at phasic valve adduction, although the heart rate fell rapidly as the valves closed at the beginning of a period of inactivity.

Fig. 9 also shows a rhythmic undulation in the base-line pressure of 0.3 cm H₂O at a frequency of about 0.6/min which was sometimes seen when the animal was active and was unrelated to the fast adductor rhythm. A manometer, connected to a fluid-filled balloon lying within the rectum and ventricle, registered the contractions of the ventricle and adductor muscles but showed no evidence of any other rhythmic activity at the time of recording.

The effect of the visceral ganglion on shell valve and heart activity

When the visceral ganglion was anaesthetized or destroyed, the fast adductor rhythm stopped with the adductor muscles either relaxed or contracted. The heart usually stopped beating for about 10 min and then recommenced at approximately twice the previous rate (Fig. 10). The effect of the anaesthetic lasted at least 7 h and not more than 24 h, after which normal activity was resumed.

The effect of the oxygen and carbon dioxide content of the water on shell valve and heart activity

In order to find out whether the concentration of oxygen in the water surrounding the gills could account for the variation in rate of heart beat with activity, the gills
were irrigated with water through which a succession of air, oxygen and nitrogen was bubbled. Each gaseous treatment was maintained for 2–4 h. Experiments were carried out on five animals with cannulated pericardia and on three animals using the closed water manometer to record heart activity. The state of oxygenation of the water did not affect the rate of heart beat or of shell valve adduction.

To investigate the effect of varying the concentration of carbon dioxide in the water, a closed water manometer was used to record heart activity in three uncannulated mussels. Ten minutes after carbon dioxide had started bubbling through the water the pH had fallen from 6·9 to 4·6 and the heart rate began to fall. After 45 min the pH reached 4·4 and the heart rate about 2/3 of its initial level. The heart rate usually continued to fall slowly until the carbon dioxide was replaced by air or oxygen. The pH then took 1½–2 h to return to 6·9 whereas the heart rate did not begin to rise for 1–3 h and took 1–2 h more to reach the initial level. Statistical analysis of the results from one animal (part of which are seen in Fig. 10) showed that although the rate of heart beat and valve movement varied in a similar manner as the gaseous treatment was changed, there was no significant correlation between the two within any particular treatment. This meant that the interdependence of heart rate and activity could be discounted as a complicating feature in the interpretation of the
Heart activity and blood pressure of the swan mussel

Table 1

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<th>Air/oxygen</th>
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<td>Rate of heart beat</td>
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<td>Rate of valve movement</td>
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Levels of significance of the variation in rates of heart beat and shell valve movement under different gaseous treatments.

Fig. 11. Pressure changes measured simultaneously in the pericardial cavity and ventricle, and in the auricle and ventricle (Davson and Purvis manometers). Upper trace: pericardial cavity and auricle. Lower trace: ventricle.

results. The rate of heart beat and rate of valve movement were significantly lower under the carbon dioxide treatment than under the oxygen treatment (Table 1).

When the visceral ganglion was anaesthetized or destroyed, the heart rate response to variations in the carbon dioxide content of the water was the same as in the intact animal. The conditions of the experiment illustrated in Fig. 10 seem to have interfered with the slow adductor rhythm as there was no period of sustained tonic adduction over the three days before the visceral ganglion was anaesthetized.

Pressure measurements

Two 'Davson and Purvis' closed water manometers and two Statham pressure transducers were used to measure pressure changes in various parts of the circulatory system. Sample traces are shown in Figs. 11 and 12. The pericardial cavity pressure showed a pulse change of 0.25–0.6 cm H₂O with the contraction of the ventricle, the peak point corresponding with ventricular diastole. Rapid adduction of the shell valves caused a rise and fall in pressure of 5 cm H₂O, and the heart cycle in progress
Time: 30 sec int.
Pressure: 1 cm H₂O

Fig. 12. Pressure changes measured simultaneously in the ventricle (upper trace) and the anterior aorta (lower trace) (Davson and Purvis manometers).

usually took slightly longer than the one immediately before or after (Figs. 5 and 11). The auricular pulse pattern seemed identical to that of the pericardial cavity. The ventricular pressure showed a pulse change of 1–3 cm H₂O sometimes with a secondary peak on the ascending limb, as in Fig. 11, which corresponded with the end of auricular systole. This second peak probably marked the point at which the atrio-ventricular valves closed. The pressure pattern in the anterior aorta was similar to that of the ventricle but lacked the slightly flattened peak contour. In Fig. 12 the aortic pulse is somewhat greater and more regular than that of the ventricle, presumably because of haemodynamic effects due to the recording needles pointing in opposite directions and the blood passing from the ventricle into the narrower aorta.

DISCUSSION

The ventricle of Anodonta is long and narrow with an aorta leading out of each end so that a unidirectional peristaltic contraction of the chamber could effectively supply blood to only one aorta. Willem & Minne (1898) and W. Koch (1917) observed that the contraction of the ventricle began at the anterior end. ten Cate (1929) reported the contraction beginning in the lateral lobes of the posterior end and moving medially and forwards to fill first the posterior and then the anterior aorta. Hendrickx (1945) stated that the contraction could begin at either the posterior or anterior end of the chamber. It seems probable that these observations may have been based upon abnormal ventricular activity occasioned by opening the shell or pericardium since the visual observations made during the present work revealed no significant delay in contraction of any part of the ventricle. It also appeared that the blood flow into the posterior aorta could be limited by the protuberances on the inner wall near its junction with the ventricle.

W. Koch's measurements of normal heart rate were carried out in the summer on one-year-old animals, over the temperature range 14–17 °C. His figures of 0.5–1/min (inactive phase) and 4–7/min (active phase) are appreciably lower than those reported here which were made during the winter on 6–10-year-old animals. Hers (1943) carried out his experiments at 15–18 °C so it seems likely that this is the temperature
Heart activity and blood pressure of the swan mussel

range for which he records a heart rate of 2-4/min (inactive phase) and 12-17/min (active phase), making his values exceptionally high compared with Koch’s and my own. The discrepancy between the three sets of figures is difficult to account for, since it is unlikely that the oblique insertion of a fine hypodermic needle just through the pericardium would influence the heart rate to any great extent, particularly since the recordings were made for several hours with no intervening interference. However, many of the long term recordings of activity reported in this work were made by monitoring pericardial cavity pressure changes through a cannula of 2 mm bore, so it is important to assess how this technique affected the normal activity of the animal. Since there was no significant difference between the heart rate values recorded by the closed water manometer and those recorded by the open water manometer, it seems reasonable to assume that, apart from the initial 24 h, cannulation did not noticeably affect the normal pattern and level of activity.

Koch (1917) found that decreasing the oxygen content of the water had no effect on the rate of heart beat of *Anodonta*, although saturating the water with oxygen resulted in an increased frequency of beat. In the present experiments there was no significant change in rate of heart beat with the degree of oxygen saturation. Hers (1943) found that the heart rate fell when animals were kept for 24–36 h out of water under anaerobic conditions. This was probably not due to a depletion of oxygen but rather to a build-up of carbon dioxide, which could not occur during the present work since the ventilation of the gills was maintained.

The change in heart rate in response to variation in the carbon dioxide content of the water may have been in response to a change in pH, as Motley (1934) stated that the normal pH of the blood of freshwater lamellibranchs is 7·8 and heart rate is depressed when the pH falls below 5. However, this cannot be the sole basis for the normal depression of heart rate seen during a period of inactivity, since the rate falls by 60% within 5 min of the onset of tonic adductor contraction, during which time the carbon dioxide accumulation would be insignificant. The continuing steady decline in heart rate throughout the inactive period might be attributed to accumulating carbon dioxide. The fact that under natural conditions the heart rate begins to rise just before relaxation of the tonic adductor fibres is further evidence in favour of a direct nervous control, although the carbon dioxide level may influence the pattern of nervous activity. Koshtoyants & Salanki (1958) are of the opinion that the periodic variations in activity are primarily the result of metabolic changes due to an interaction between changes in the ‘medium’ and the central nervous system. Barnes (1955) found that the phasic adductor contractions continued for some time after the tonic contraction had begun and that destruction of the visceral ganglion resulted in cessation of the phasic contractions with either prolonged contraction or relaxation of the tonic fibres. He concluded that the adductor rhythms were determined by an intrinsic pattern of nervous activity independent of peripheral conditions. The present work confirms his observations and, to the extent that there was no evidence of diurnal variation in activity, suggests that the adductor rhythms are determined by an inherent activity pattern which is independent of light and small temperature fluctuations.

Koch & Hers (1943) and Barnes (1955) noted an opening and closing of the siphons which produced an intermittent respiratory current unrelated to the fast adductor
rhythm. This may account for the regular small variations in the pericardial cavity pressure sometimes noted in the active animal.

Brand (1972), measuring heart and pedal haemocoel pressures during the digging cycle of *A. anatina*, also found that the heart rate was unaffected by rapid adduction of the shell valves. His recordings showed a slowing in heart beat rate towards the end of the digging cycle as pressure built up in the pedal haemocoel, presumably due to the closure of Keber’s valve. This explains the drop in heart rate, accompanying extension of the foot, noted in my long-term recordings. The values for pulse pressure in *A. cygnea* obtained during the present work agree with those of Brand for resting *A. anatina* (ventricle 2–4 cm H$_2$O, auricle 0.5–1 cm H$_2$O and pericardium 0.5 cm H$_2$O), except that the ventricular pressure of 2–3 cm H$_2$O is at the lower limit of his figures, but these were based upon more measurements than mine.

Until differential pressure measurements between the lateral venous plexus, auricle and pericardial cavity have been made, it is not possible to assess the importance of the volume-compensation mechanism in heart filling (Willem & Minne, 1898; Krijgsman & Divaris, 1955). This hypothesis has been criticized in relation to the *Helix* heart (Sommerville, 1973a, b), but does seem tenable in *Anodonta* where the pericardial walls are functionally rigid, there is strict alternation of contraction between auricles and ventricle, and the pericardial pressure is always relatively low. However, it must be borne in mind that the reno-pericardial opening is large and that the cannulated specimens used during the present work maintained apparently normal function including foot-extension for recording periods of 3–12 days, with a hole of 2 mm diameter in one side of the pericardium. Despite these breaches in the pericardium, the compensation mechanism might still function providing there was sufficient resistance to rapid translocation of fluid through the openings.

I wish to thank Professor A. Graham for his advice, encouragement and for the facilities of the University of Reading where most of this work was carried out; Dr H. Davson and Mr C. Purvis for their advice and gift of manometers; Dr R. H. Nisbet and Professor R. J. Linden for their help; my husband, Dr A. Chadwick, for his great help with the work and the preparation of this paper; and Professor J. M. Dodd and the Department of Pure and Applied Zoology, University of Leeds, where this work was finished.

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Heart activity and blood pressure of the swan mussel


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