

THE REFLEX CO-ORDINATION OF THE HEART BEAT WITH RESPIRATION IN THE DOGFISH

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INTRODUCTION

The linking of the heart beat with respiration was first noted in *Torpedo* by Schoenlein in 1895. He described a 1:1 co-ordination, a pattern reported by later workers in other elasmobranchs (Lyon, 1925; Lutz, 1930*a*). Lutz (1930*b*) demonstrated that in dogfish the cardiac vagus was concerned in this co-ordination but otherwise the phenomenon has received little attention. In this paper branchio-cardiac co-ordination and the mechanism effecting it will be described from the results of experiments on forty specimens of *Squalus lebruni* Vaillant. The major findings from this species have been confirmed on six specimens of *Mustelus antarcticus* Gunther. Finally, the suggestion will be advanced that this co-ordination of two systems jointly concerned in supplying oxygen to the tissues enhances the efficiency of this process.

MATERIAL AND METHODS

Mounting

Fish intended to provide information on branchiocardiac co-ordination were not anaesthetized, and were restrained by two clamps to the dorsal fins, in a rectangular tank filled with running sea water from the supply tanks of the University Marine Station. The fish weighed from 3½ to 6 lb. and no system of artificial perfusion was used. Sea-water temperatures varied from 4° C. in winter to 16° C. in summer.

When surgical procedures were intended, such as the cannulation of blood vessels, the fish were anaesthetized by 3 min. immersion in 1:1000 tricaine (MS. 222, Sandoz). They were then rigidly mounted underwater in a metal frame of the type described by Satchell & Restieaux (1958). In the few experiments in which curare was used the fish was artificially perfused through the spiracle.

Recording

Most of the records were made on an Ediswan 4-channel pen writer. The electrocardiogram (E.C.G.) was recorded with pre- and post-cordial leads consisting of insulated needles inserted through the body wall to lie ventral to the heart; signals from these were fed into a conventional E.C.G. amplifier. Respiration was recorded from two fine brass contacts clipped into the upper and lower jaws. When the jaws closed a 10 mV. pulse was fed into a second E.C.G. amplifier.

In some experiments brief inflations of the pharynx were made with a small

air-filled balloon connected by a spiracular cannula and polythene tube to a hand bulb and also by a side arm to a tambour pressing against a strain gauge, this last being connected through a d.c. amplifier to the pen writer.

Blood pressure was recorded from the first branchial artery (lateral ventral aortic pressure) and from the coeliac artery (lateral dorsal aortic pressure). Both arteries were cannulated with 1 in. long No. 17 hypodermic needles connected by 61 mm. lengths of 2 mm. P.V.C. tubing to two Statham P 23 AA pressure transducers. The transducers connected in this way have a response better than 0–22 cyc./sec. Their outputs after d.c. amplification were fed to the two beams of a Dumont 5 SP 11 A oscilloscope and photographed with a Grass model C 4 D kymograph camera.

Branchial blood flow was monitored by a photo-electric method. Light from a 6 V. bulb was passed through the gill on to a Philips OCP 71 red-sensitive photo-transistor tube, the output of which was displayed on the oscilloscope after d.c. amplification. Electrical stimuli were provided by a Grass square-wave stimulator.

The elasmobranch Ringer's fluid of Keynes & Martins-Ferreira (1953) was used to moisten nerves and to act as a diluent of such drugs as were used; injections were made into the anterior cardinal sinus.

RESULTS

The electrocardiogram

The E.C.G. of elasmobranch fish has been described by Kisch (1948); it is here used only to signal the heart beat and will not be described in detail. The shapes of the various deflexions vary considerably with minor changes in electrode placement; Fig. 1 A shows a typical trace. With pre- and post-cordial leads the *P* wave was either upright or inverted; it signals the onset of auricular contraction. The *QRS* deflexion was large; it signals the invasion of the ventricle by the cardiac impulse and the *P-R* interval thus corresponds to the time taken by the impulse to cross the auricle and the auricular-ventricular junction. At 12–16° C. the *P-R* interval was 0.3–0.4 sec. The *T* wave occurs as the ventricle starts to repolarize; it signals the end of the contraction; the *P-T* interval at 12–16° C. was 1.2–1.4 sec. The small excursion between *QRS* and *T* has been shown by Kisch (1948) to be due to the contraction of the conus.

The respiratory record

The pen writer records each respiration as an upstroke when the mouth opens and a downstroke when it closes. A respiratory cycle is considered as starting when the mouth opens and for the purpose of analysis has been divided into ten phases of equal duration (Fig. 1 B upper scale). From phases 1 to 7 the mouth is open, the gill slits are closed and the pharynx is dilating as it fills with water. Just after the start of the 8th phase the mouth closes and remains closed to the end of the cycle. During phases 8–10 the water in the pharynx is expelled from the gill slits. The time of most rapid water flow across the gills has been determined with the same pressure-recording device (Statham P 23 AA) as was used for recording blood pressure. The water-filled cannula was placed so that its opening was within

the 4th gill pouch. In this situation the outflowing water current was registered as a change in pressure at the cannula tip. In Fig. 1 B this trace was recorded on the oscillograph together with the mouth movement. It can be seen that the pressure recorded in this position reached a peak at the division between the 9th and 10th phases of the respiratory cycle.

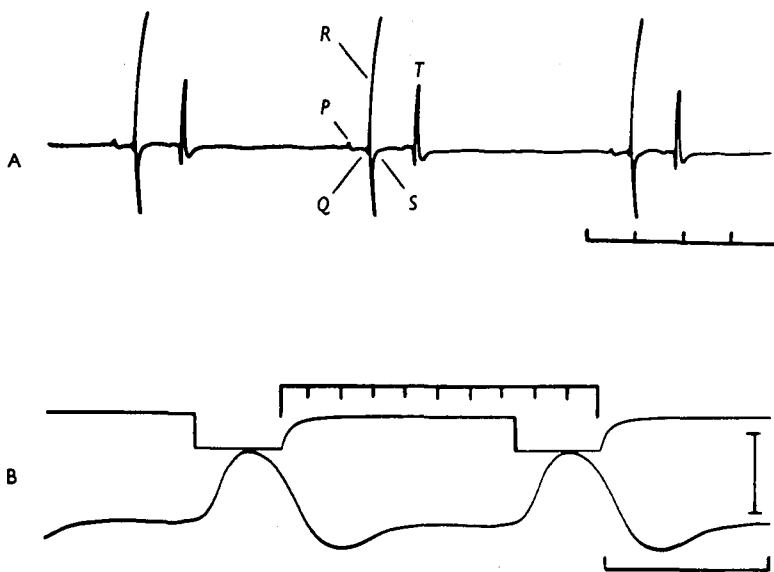


Fig. 1. A, E.C.G. of *S. lebruni*, 11° C. The deflexions have been given the conventional designations. B, Oscilloscope display of respiration. Top beam: mouth closure: opening = upstroke. Vertical strokes retouched. Lower beam: water pressure at gill opening indicating rate of expulsion of water across gills. Time marks in A and B = sec. Upper scale in B shows tenths of a respiratory cycle. Calibration = 1 cm H₂O.

The phenomenon of co-ordination

In all fish studied in this series the heart rate was lower than the respiratory rate; two patterns of co-ordination normally occurred. In some fish the interval between heart beats was consistently some simple multiple of the length of the respiratory cycle; rhythms of 1:2 (Fig. 2 A), 1:3 or 1:4 were observed for more than a hundred successive beats. *Mustelus antarcticus* provided some particularly striking runs of unchanging rhythm. More commonly the heart made a succession of beats at one multiple followed by a delayed beat at the next higher multiple of respiratory cycle length. The following sequence taken from *Squalus lebruni* is typical. (A space has been arbitrarily introduced after each longer beat.)

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The advent of the longer cardiac cycle cannot be predicted; its occurrence, no doubt, depends on the constantly fluctuating background of vagal tone, which is itself presumably related to the changing pattern of visceral and somatic stimuli impinging on the central nervous system. Lutz (1930b) has shown that a wide

variety of stimuli, both visceral and somatic, inhibit the heart beat. Fig. 2B is an example of alternating 1:2, 1:3 rhythm.

There is some indication (Figs. 2A and B) that the heart was beating at a particular phase of the respiratory cycle, the *P* wave tending to occur either just before (phase 10), or just after (phase 1), mouth opening. The point is better demonstrated in Table 1. Here one hundred consecutive heart beats from each of eleven fish (1 *Mustelus antarcticus*, 10 *Squalus lebruni*) have been placed in the phase of respiration in which they occurred. The totals for the ten *S. lebruni* analyses have been

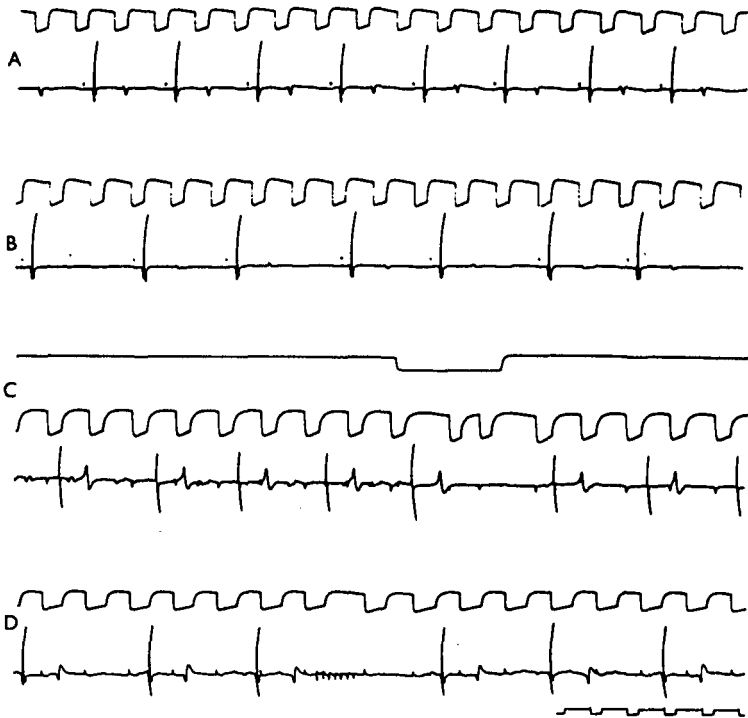


Fig. 2. Co-ordination in *S. lebruni*. All at 16° C. A and B. Upper trace: respiration; upstroke = mouth opening. Lower trace: E.C.G. The *P* wave is insignificant in this trace and its position is indicated by a dot. C. Upper trace: inflation of pharynx with a balloon; inflation downwards. Middle trace: respiration. Lower trace: E.C.G. The closing of the mouth switch makes a small down-going artifact in this experiment. D. Respiration and E.C.G. with upgoing respiratory switch artifact. After 3rd *T* wave, central end of cut branchial branch of the left vagus stimulated with 7 square wave 1 msec. 2 V. pulses. Shock artifact downwards. Time = sec.

added together and presented as a histogram (Fig. 3), which is thus a summary of the occurrence of 1000 heart beats from ten fish recorded at temperatures from 4–16° C. The co-ordination is manifested as a statistical trend—a tendency for the heart to beat immediately after the opening of the mouth. Phase 7, just prior to mouth closure, is the period in which the heart is least likely to beat, only 1.8% of the *P* waves originating at this time. Of thirty fish analysed in this way eighteen possessed this pattern of co-ordination. It has been accepted as 'normal' and others regarded as atypical for the following reasons.

Table 1. Number of heart beats in a series of 100 occurring in each tenth of a respiratory cycle from eleven fish (ten *Squalus lebruni*, one *Mustelus antarcticus*)

Species	T.	Phase of respiratory cycle									
		1	2	3	4	5	6	7	8	9	10
M.	10	26	7	1	—	—	—	—	—	4	62
S.	4	42	13	—	—	2	1	1	4	9	28
S.	8	29	22	16	8	1	1	2	1	4	16
S.	10	38	23	8	10	2	3	1	3	3	9
S.	10	24	22	20	11	10	6	—	1	—	6
S.	10	19	12	7	6	2	1	—	12	15	26
S.	10	33	29	15	6	5	2	—	—	1	9
S.	11	31	21	13	9	8	4	—	1	3	10
S.	15	22	8	9	11	6	11	7	6	4	16
S.	16	18	16	6	2	4	4	3	2	11	34
S.	16	20	9	7	2	1	—	4	7	20	30
Total		276	175	101	65	41	33	18	37	70	184

T. = temperature in ° C., M. = *M. antarcticus*, S. = *S. lebruni*

The atypical patterns vary widely, ranging from fish showing no co-ordination at all, in which approximately equal numbers of heart beats occur in each phase of the respiratory cycle, to fish in which the column of maximum occurrence lies closer to the start of the previous respiratory cycle in columns 7, 8 or 9. Experimental evidence to be presented in the next section suggests that a vagally mediated reflex is concerned in this co-ordination. A cyclically fluctuating pattern of cardiac inhibition, related to dilatation of the pharynx at each respiration, is superimposed on a tonic background of vagal activity related to blood pressure. Thus any lowering of this tonic activity caused by blood loss or injury might be expected to permit the heart to beat at a phase of the respiratory cycle closer in time to the cyclic peaks of inhibition resulting from respiration. Since this was just the type of deviation seen and as it tended to occur in fish with injuries sustained during their capture, it has been regarded as atypical.

A corollary of this co-ordination was that the time elapsing between one heart beat and the next, the E.C.G. interval, approximated to some whole multiple of respiratory cycle length. In fish showing the alternation of longer and shorter cardiac cycles (Fig. 2B) a histogram of cardiac cycle length showed a markedly bimodal distribution.

The mechanism of co-ordination

The co-ordination outlined in the previous section could be effected in various ways. The following three must be considered.

(1) If the heart were sensitive to stretch, the influx of venous blood resulting from the compression of the anterior cardinal sinuses during pharyngeal contraction might cause the heart to beat. The tendency for the heart to beat just after pharyngeal contraction has already been noted, and the failing dogfish heart can be made to beat by dilating it with Ringer's solution.

(2) The respiratory and cardio-inhibitory centres are anatomically closely related in the vertebrate medulla; it is possible that there might be some irradiation of

influences from one to the other. Rhythmical bursts of neuronal activity in respiratory centres might also activate the cardio-inhibitory centre through purely central pathways. Such explanations have been advanced to account for sinus arrhythmia in mammals (Heymans, 1929).

(3) The heart might be reflexly inhibited, the efferent pathway being the cardiac vagi. The afferent pathway could consist of receptors fired by pharyngeal dilatation and relaying their impulses to the medulla in the branchial nerves.

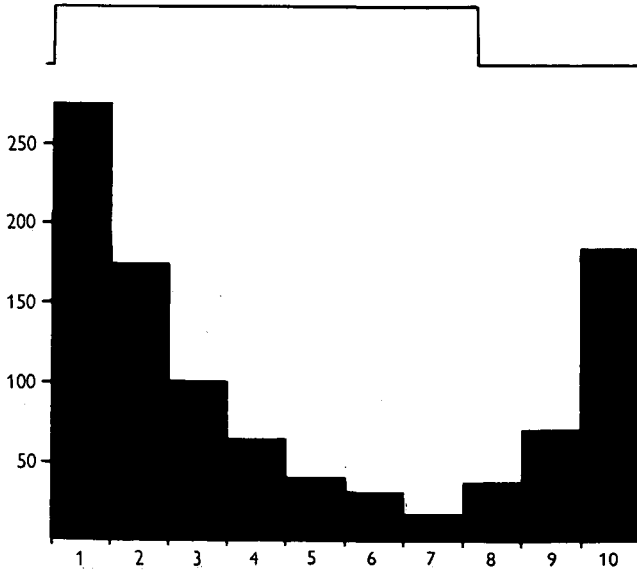


Fig. 3. The occurrence, in the ten phases of a respiratory cycle, of 1000 heart beats recorded as ten runs of 100 each, from ten specimens of *S. lebruni* between 4 and 16°C. Above, a respiratory cycle, with mouth opening indicated as an upstroke.

Artificial inflation of the pharynx with a small balloon provided evidence on this question. If such inflations were small enough, it was possible to avoid provoking the cough reflex and to show that they evoked respiratory inhibition and cardiac slowing (Fig. 2C). The respiratory inhibition has been described in a previous paper (Satchell, 1958); it is believed to be evoked by the activity of receptors fired by pharyngeal movement. When the anterior cardinal sinuses of both sides were opened and blood flow through them prevented by plugging them anteriorly and posteriorly, neither co-ordination nor the response to inflation was disrupted. But cutting the cardiac branches of the vagus caused the heart to accelerate from 12 to 18 beats per min., whilst co-ordination disappeared and the cardiac, but not the respiratory, response to inflation was lost. These findings are opposed to a haemodynamic explanation since a mechanism dependent on blood flow ought to be affected by plugging the anterior cardinal sinuses but ought not to be disrupted by cutting the cardiac vagi.

The action of atropine is also opposed to a haemodynamic explanation. Intravenous atropine 0.2 mg./kg. produced the same effects as cutting the cardiac vagi;

co-ordination and the cardiac response to inflation disappeared and the heart accelerated. Atropine did not cause further cardiac acceleration in the vagotomized fish, indicating that its cardiac effects were exerted on the vagal terminals rather than on the heart itself. The respiratory response to inflation persisted, suggesting that it does not involve an atropine-sensitive cholinergic link. Likewise, destruction of the medulla caused the heart to accelerate and the response to inflation to disappear. These findings implicate the cardiac vagus and its cholinergic link with the heart in this co-ordination; they do not distinguish between the second and third explanations.

That the co-ordination was not effected through purely central pathways, but involved a peripheral link, was suggested by the action of curare. When the respiratory muscles were paralysed the characteristic variation from beat to beat in cardiac cycle length was lost. Records of nerve action-potentials in the branchial branches of the vagus demonstrated that the respiratory centre continued to send out its volleys for many hours after curarization, if a stream of water was directed through the spiracle. That curare was not blocking the central and efferent pathway was shown by the ease with which respiratory and cardiac inhibition could still be produced when the pharynx was artificially inflated. But the absence of any spontaneous movement would deprive a cardiac inhibitory reflex of its afferent component and thus prevent co-ordination.

The following facts may be adduced in favour of the reflex explanation. An efferent limb, the cardiac vagi, has already been established in the process of excluding the other hypotheses. In a previous paper (Satchell, 1958, Fig. 3) it has been shown that bursts of action potentials could be recorded in the distal end of a cut branchial nerve of *S. lebruni* synchronous with each pharyngeal contraction. Inflation of a balloon in the pharynx produced a discharge containing a phasic element at inflation and deflation, and a sustained response throughout the period of inflation. Some of these fibres and the receptors connected to them could well constitute the afferent limb of the reflex. The presence of a system of reflexly linked cardio-inhibitory fibres in the branchial nerves has been established by tetanically stimulating the central end of a cut branchial nerve (Fig. 2D). Cardiac inhibition was always produced, as has been shown in the eel by Mott (1951) and in the dogfish by Lutz (1930b).

Significance of the branchio-cardiac reflex

It is possible that a reflex that links the activity of two muscle pumps, one propelling blood through a system of sinuses, and the other water over them, might enhance diffusion by synchronization of the periods of rapid flow. With this hypothesis in mind, attempts have been made to determine the time course of the pressure differential across the gill vessels. The input pressure to the gill capillaries has been sampled by cannulating the first afferent branchial artery, the pressure beyond the gills by cannulating the coeliac artery so that the cannula tip lay in the dorsal aorta within 3 cm. of the point of entrance of the epibranchial arteries. The type of manometers and their connexions have already been described. As this is the first time that fish blood-pressure traces have been recorded with modern

electrical manometers having a high frequency response some general comments may be made.

The pressures recorded were as follows, in mm. Hg.

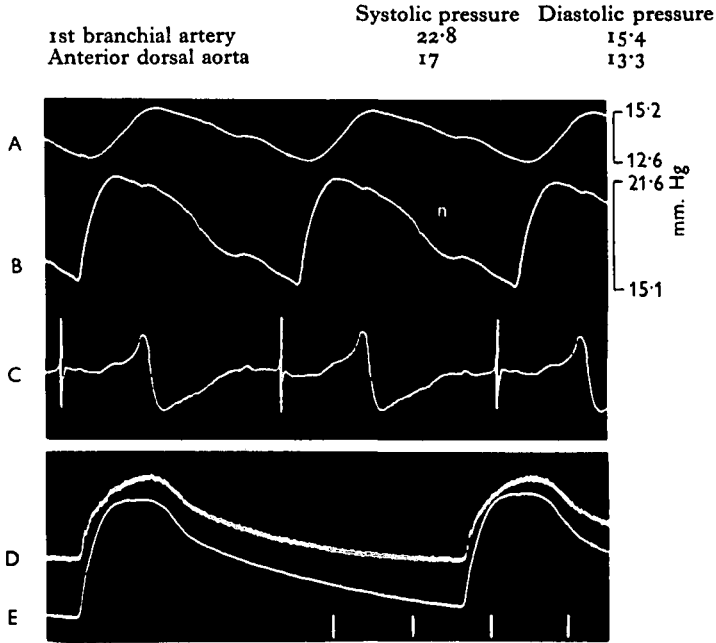


Fig. 4. Oscilloscope tracings all from one specimen of *S. lebruni*, 14°C. A and B recorded simultaneously. C. Placed in appropriate time relation. D and E recorded simultaneously. A and B: blood pressure from coeliac artery and 1st afferent branchial artery, respectively. *n* = dicrotic notch; calibration on right. C. E.C.G. The QRS stroke has been retouched. D. Gill opacity recorded with phototransistor. E. Afferent branchial artery blood pressure. D and E after curarization. Time = sec.

These pressures are within the range of those recorded by other workers from fish of comparable size (4½ lb.) (see Brown, 1957, for references). They are probably lower than normal, due to the trauma resulting from the double cannulation; in fish in which only the branchial artery was cannulated systolic pressures as high as 33 mm. Hg were recorded.

The afferent branchial artery trace shows a steeply rising front, following the ventricular contraction, and a more gentle decline. The dicrotic notch, as the semi-lunar valves closed, is just visible (Fig. 4 B, *n*), and the valves thus stayed open for 1.55 sec. at a heart rate of 22/min. The closure of the valves occurs after the *T* wave of the E.C.G., suggesting that, as in mammals, it is the relaxation of the heart muscle, leading to a decline in intraventricular pressure and a backward flow of blood, that initiates closure. The small peaks of blood pressure before and after the dicrotic notch were observed to be caused by expiration.

The trace from the dorsal aorta shows the expected lower pulse pressure, and the delay in the onset of the rise following systole and expiration.

As the circulatory system of fish has the smaller vascular bed of the gills in series

with the larger vascular bed of the body, enough blood must flow through the gill vessels, early in each cardiac cycle, to distend the large elastic reservoir of the peripheral circulation. As this occurs, pressures should rise in the dorsal aorta, the pressure differential across the gills should fall and the rate of flow through them should slacken. Thus immediately following ventricular systole there should be a brief period of rapid flow through the gills. To test this hypothesis ten successive branchial artery and aortic pressure traces have been projected on to graph paper, and the pressure values, at twenty-three successive points, determined and averaged. From these the two curves A and B in Fig. 5 have been constructed. By subtraction, curve C has been derived, representing the pressure difference across the gills. It

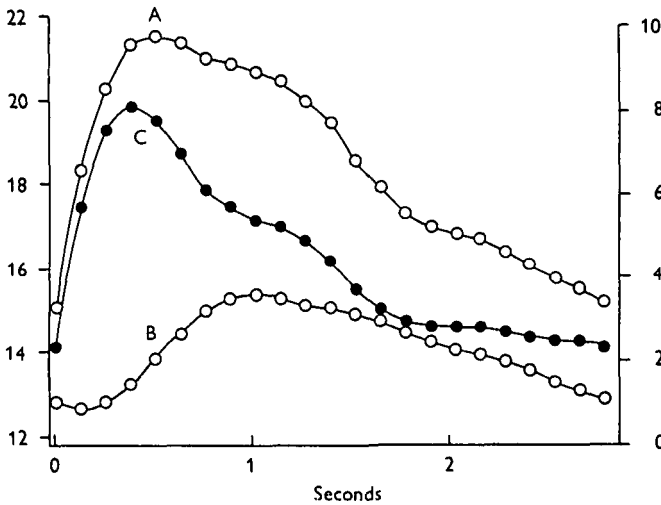


Fig. 5. *S. lebruni*, 14° C. Blood-pressure records from A, the 1st afferent branchial artery, and B, the coeliac artery, derived by averaging ten simultaneously recorded consecutive pairs of traces. C. Differential pressure across the gill circulation, derived by subtracting B from A. Ordinate for A and B on left, for C on right, in mm. Hg.

can be seen that this curve reached a maximum of 8 mm. Hg before the peak of the afferent artery pressure curve, and that after the semilunar valves had closed (12th–14th points on the graph) the curve of pressure difference changed slope and declined more slowly. At this stage the pressure difference across the gills was only some 2½ mm. Hg and gradually decreased as the elastic reservoir of the ventral aorta poured its contents into the emptying reservoir of the peripheral circulation.

Changes in pressure across the gills would lead to comparable changes in flow only if the resistance of the branchial vessels remained constant. Cyclic activity in a system of branchial vasoconstrictor fibres could minimize the fluctuations in flow. The evidence of previous workers is against the existence of such a system (Wyman & Lutz, 1932), but to gain further evidence on this the opacity of the gill was monitored with a red-sensitive phototransistor and light source. The device proved to be remarkably sensitive to changes in the amount of blood in the gill and Fig. 4D and E show the simultaneous recording of gill opacity and afferent branchial

arterial blood pressure in a curarized dogfish. The opacity curve followed the pressure curve so closely as to suggest strongly that the vessels must be compliant, increasing in diameter as the pressure rose and narrowing as it fell. In some experiments, but not in the one depicted in Fig. 4, even the small excursion of the dicrotic notch produced a corresponding change in the opacity. Whilst there is thus no evidence of active vasoconstriction of branchial vessels, their passive dilatation might be expected to affect the pressure-flow relationships. The equations concerning the flow of blood through a compliant tube have not yet been completely solved (Rashevsky, 1945; Branson, 1945), but as flow is proportional to the 4th power of the radius (Poiseuille's Law) the early peak of pressure difference across the gill must result in a greater increase of flow than a linear pressure/flow relationship would predict.

It remains to demonstrate that this early period of rapid blood flow through the gills coincides with the phase of rapid water flow past them. In the experiment depicted in Fig. 4, the simultaneous recording of the two blood pressures was followed by the recording (also simultaneous) of the afferent branchial pressure and the electrocardiogram. It has thus been possible to calculate that the time elapsing between the occurrence of the *P* wave of the E.C.G. and the start of the pressure rise was 0.690 sec. (S.D. = 0.0146 sec.) and from the data used in the construction of Fig. 5 the time from the start of the pressure rise to the peak of the differential pressure was determined as 0.251 sec. Adding these, it can be said that under the conditions of this experiment ($T = 14^{\circ} \text{C.}$) 0.94 sec. elapsed between the start of a heart beat and the peak of pressure difference across the gills. The respiratory rate in ten unanaesthetized fish recorded at temperatures of $14\text{--}16^{\circ} \text{C.}$ was 54.2 (S.D. = 3.79), so each tenth of a respiratory cycle endured for 0.11 sec. If, for convenience, all heart beats originating in phase 1 (the phase of maximum occurrence) were regarded as starting at the same instant half-way through the phase (0.05 sec. from the start), the lapse of 0.94 sec. would bring the time of peak blood-pressure difference across the gills to 0.99 sec. after mouth opening. With each phase of respiration enduring for 0.11 sec., the peak of blood pressure difference would occur at the division between the 9th and 10th phases ($9 \times 0.11 = 0.99$) of the respiratory cycle. Reference to Fig. 1 B shows that this is indeed the time when water pressure in the pharynx was maximal. The evidence thus indicates that heart beats with the *P* waves starting immediately after mouth opening will result in a peak of blood flow through the gills coincident with the maximum flow of water over them.

DISCUSSION

It is now reasonably established that in fish as in mammals blood pressure is reciprocally related to heart rate. In the eel (Mott, 1951) and the dogfish (Lutz & Wyman, 1932) raising the blood pressure slows the heart. The structure and location of the pressor receptors in the branchial vessels of dogfish have been studied by Boyd (1936); bursts of action potentials in branchial afferent fibres, synchronous with cardiac systole and evoked by increasing blood pressure, have been demonstrated by Irving, Solandt & Solandt (1935) in dogfish. Cardiac inhibition evoked

by electrical stimulation of the central end of a cut branchial nerve has been described by Mott (1951) in the eel, and by Lutz (1930b) in the dogfish. We may thus safely conclude that there is a reflex control of heart rate, the number of respirations intervening between one heart beat and the next depending on the level of tonic vagal activity. The cyclic inhibition reflexly induced by respiratory movement is superimposed on this, controlling the position within a given respiratory cycle at which an incipient beat will occur. Whether receptors distinct from those subserving the blood-pressure reflex are concerned in the branchiocardiac reflex is unknown.

Hughes & Shelton (1958) have shown that in teleosts the opercular suction pump alternates with the buccal pressure pump to maintain a flow of water across the gill throughout almost all of the respiratory cycle. There is no operculum in recent elasmobranchs, but Woskoboïnikoff (1932) has suggested that the outer portion of each gill pouch acts as a suction pump, and that the two pumps act synchronously. Water flow across the gills is thus rapid during approximately one-third of the respiratory cycle and less rapid during the remainder. Were the period of rapid blood flow to occur when the water flow was minimal, it might be that partly deoxygenated blood would be poured into the peripheral circulation. The branchiocardiac reflex, by causing the periods of peak flow to coincide, ensures a maximum gradient of oxygen tension across the gill epithelium, and hence the most effective oxygenation of the blood. Van Dam (1938, quoted in Krogh, 1941) has shown that, in fish, water and blood flow on a counter-current pattern. This results in the most highly oxygenated blood being partnered with the most highly oxygenated water, so that the greatest gradient of oxygen tension is maintained along the length of the vessel. The branchiocardiac reflex may be regarded as achieving a temporal coincidence of flow rates analogous to the spatial coincidence of oxygen tensions secured by the counter-current arrangement of the gill circulation.

SUMMARY

1. The hearts of *Squalus lebruni* and *Mustelus antarcticus* beat at intervals that approximate to some simple multiple (1-4) of respiratory cycle length.
2. The beat tends to be initiated during a particular phase of the respiratory cycle, most commonly just before or just after the opening of the mouth.
3. Possible mechanisms of this co-ordination are considered and evidence is presented to show that it is reflexly mediated. Fibres from receptors fired by pharyngeal dilatation are believed to constitute the afferent limb, and the cardiac vagi the efferent limb of the reflex arc.
4. Simultaneous records of blood pressure have been made from the 1st afferent branchial artery and the coeliac artery. By subtraction, the differential pressure across the gill vessels has been calculated and found to have a peak early in the cardiac cycle.
5. Simultaneous photo-electric records of gill opacity and branchial blood pressure show the gill vessels to be compliant. It is concluded that there is a brief period of rapid blood flow early in each cardiac cycle.

6. Calculations from simultaneous records of the electrocardiogram and branchial blood pressure showed that heart beats originating near the time of mouth opening caused a rapid flow of blood through the gills at the time that water was expelled across them.

7. It is suggested that this synchronization of the periods of rapid flow of blood and water serves to maintain the diffusion gradient of oxygen across the gill epithelium.

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Note added in proof

The paper 'The mechanism of gill ventilation in the dogfish and the skate', by G. M. Hughes (*J. Exp. Biol.* 37, 11-27, 1960) did not arrive in New Zealand in time to be considered in this study. Hughes divides the respiratory cycle into four phases. Mouth opening (the start of the respiratory cycle in this paper) occurs half way through phase 4; mouth closing occurs at the end of phase 2. Hughes Fig. 4 (p. 18) suggests that heart beats originating in column 1 (the time of maximum occurrence) would result in peak blood flow through the gill vessels during the operation of the buccal pressure pump. Beats originating in column 7 (the column of minimum occurrence) would result in peak flow coinciding with Hughes' phase 2 when water pressure across the gills is minimal.