RESPIRATORY MOVEMENTS OF *ARENICOLA MARINA* L.: INTERMITTENT IRRIGATION OF THE TUBE, AND INTERMITTENT AERIAL RESPIRATION

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(Text-figs. 1–9)

Van Dam (1937, 1938) studied the respiratory movements of lugworms (*Arenicola marina* L.) in glass tubes. He found that they propelled water through the tubes by means of wave-movements running along the body, usually from tail to head, and that 'ventilation was intermittent; ventilation pauses alternated, sometimes very regularly, with ventilation periods; in some cases the pauses lasted as long as 40 minutes'. In the following paper, the mechanism and biological significance of this intermittence are investigated. The worms were studied in glass U-tubes. It will be shown, in another paper, that very similar behaviour occurs in the burrow, in sand.

Apparatus for Studying Intermittent Irrigation

Van Dam observed the worms visually, and measured the volumes of water pumped by collecting the output in a graduated cylinder. The period of time over which a worm can be studied in this way is necessarily rather limited. With the apparatus shown in Fig. 1, the behaviour of a worm can be continuously recorded on smoked paper for 2 or 3 days, and a rough idea of the volumes pumped can be got from the records.

The worm lies in a U-tube (of internal diameter 0·75 cm.). Each limb of the U is connected with a T-piece whose lower end is constricted, to discourage the worm from creeping farther upwards. The upper end of the T-piece communicates, through a 20 c.c. pipette bulb, with a wide cylinder (internal diameter 3 cm.). The side arm of the T-piece leads through a T-tap to the same cylinder. The side arms of the taps are connected by a capillary (bore about 0·15 cm.). The whole apparatus is filled with sea water. One of the wide cylinders contains an aeration jet. The other contains a paraffin float, connected with an isotonic lever writing on a slowly moving kymograph. The time trace is provided by a clock whose minute hand is bent forward and connected to a lever with a frontal writing point. This traces an approximation to a sine curve at 1 cycle per hr.

Most of the observations were made with the taps turned as shown in the figure. When this is so, the worm can circulate water along the U, through the 20 c.c. bulbs and wide cylinders and the capillary. Thus it can get a supply of freshly aerated water. Owing to the resistance of the capillary, any such pumping results in slight variations of level in the wide cylinders and will therefore be recorded on the drum. Rather different conditions arise if the taps are turned through 180°; these will be dealt with later.

The worm's output can be estimated as follows. The lever magnification was about 12. The capillary passed 6·7 c.c./min. at a pressure of 1 cm. sea water. Hence the flow rate through the capillary is $1·1\,d$ c.c./min., where d cm. is the displacement of the writing point from the zero position. The paper moved at 2·4 cm./hr. Hence the volume flowing through the capillary during any period is $27·5\,a$ c.c., where a cm.^{2} is the area between the tracing and the zero line. It must be borne in mind that the flow-rate through the U-tube is not necessarily the same as that through the capillary, owing to variation in the amount of water in the wide cylinders. A 1 cm. excursion of the writing point means a transfer of 0·6 c.c. of water from one cylinder to the other; if the writing point is moving away from the zero line, the flow-rate through the U-tube exceeds that through the capillary, and if the lever is moving towards zero the opposite condition holds.

The experiments lasted for many hours, and sometimes for 2 or 3 days. They were set up in an unheated room, where the temperature varied (over the whole period

Fig. 1. Apparatus for recording the irrigation cycles (see text).

of experimentation) from about 8° to 14° C.; in the course of a single experiment the variation was seldom more than 1 or 2 degrees. To avoid unnecessary stimulation of the worms, nobody but the writer, or visitors in
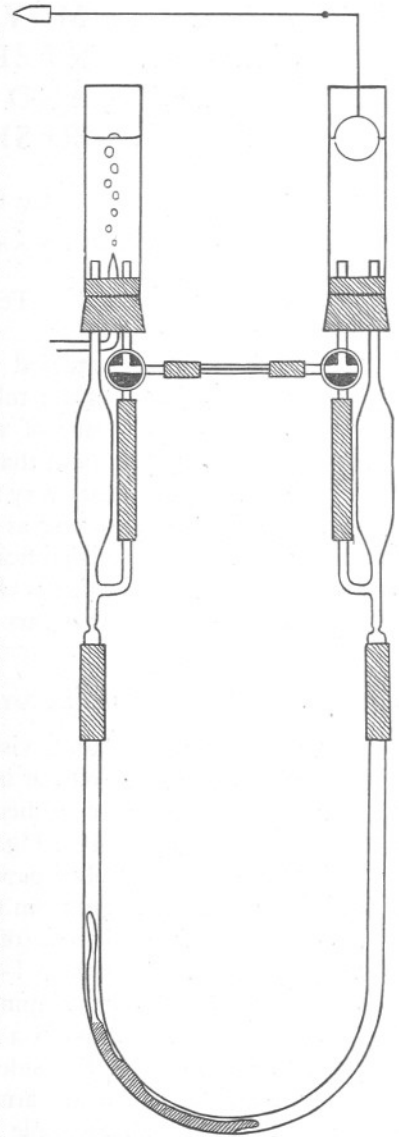
his company, ever entered the room; and, as it was necessary to interpret the records by watching the worms from time to time, the electric light was kept continuously on. Daylight was excluded.

IRRIGATION AND LOCOMOTION

The worms can displace the water in the U in several different ways, and before considering the records obtained, the characteristics of these various kinds of movement must be summarized. For further details, the works of Just (1924) and van Dam (1938) may be consulted. The movements depend on waves travelling along the whole length of the body, except the first three or four segments and the tail.

Irrigation. The worm lies in the tube, with its ventral and ventro-lateral surfaces pressed against the glass wall, but with a space (containing the gills) between the dorsal surface and the tube. Waves of swelling, which completely occlude this space, move steadily along the body and thus drive water through the tube. The waves generally run in a headward direction, but tailward waves are sometimes seen. It is of course obvious that in irrigation the direction of the water stream coincides with that of the waves.

Antikinetic locomotion. In this case the direction in which the worm creeps is opposite to that in which the waves traverse the body. The body as a whole is elongated, and at most points clear of the tube. Waves of swelling run along the body and occlude and grip the tube. The waves act as fixed points, and the worm as a whole travels, driving water before it. Headward waves result in tailward locomotion and a tailward displacement of water, while tailward waves have the opposite effects. In either case, the notopodia are so oriented as to assist the movement by preventing any backsliding. Antikinetic locomotion can be very vigorous and swift, though it is not always so.

Synkinetic locomotion. In this case, the worm creeps in the direction of wave-travel. One often sees that a worm, which is vigorously irrigating in a headward direction, creeps gently headwards at the same time. The mechanism of this movement, which is never very swift, is obscure; perhaps the orientation of the noto- and neuropodia plays a decisive part. The water in the tube is propelled headwards, because the irrigation waves move much more rapidly than the worm as a whole. Theoretically, as all the movements appear to be reversible, a worm could creep gently tailward during tailward irrigation; but this has not been noticed, either by Just (1924) or by myself.

The most fundamental point, physiologically, seems to be the direction of wave-travel along the body. Headward waves can result in headward irrigation, more or less vigorous tailward locomotion, or gentle headward locomotion, and all of these variations merge into, and can smoothly change into, each other. On the other hand, a process involving headward waves only changes into one involving tailward waves after a definite pause, as if the two performances were quite distinct and incompatible.

DESCRIPTION OF THE IRRIGATION CYCLES

When newly put into the apparatus the worm is restless and its behaviour is unpredictable. Periods of similar restlessness may suddenly set in at other times; for instance, by narrowing itself and burrowing, so to speak, along its own ventral surface, a worm can easily reverse itself in a tube which, at other times, it seems comfortably to fill; sometimes this happens, after which, of course, the writing on the drum appears the other way up.[1] Or a worm may spoil a good record by 'running amok' and forcing itself through the
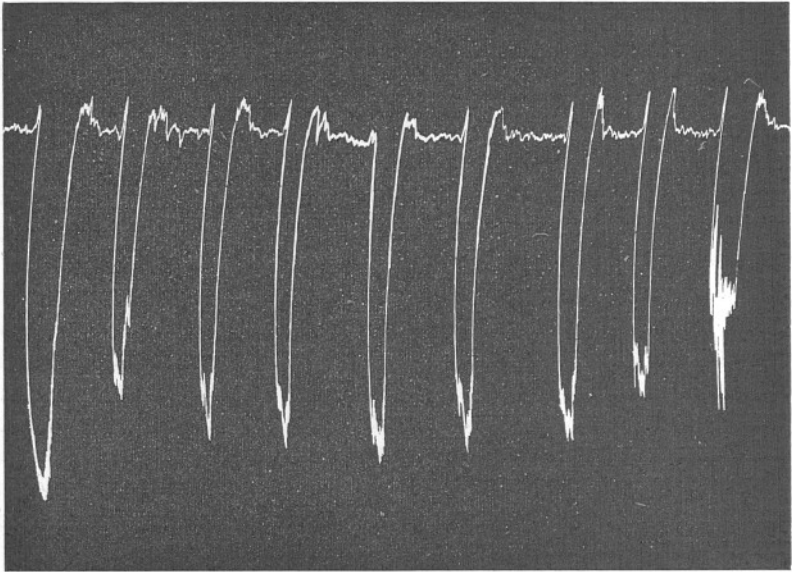

Fig. 2. Three-phase irrigation cycles, traced by a worm with its head towards the float. (Worm O 7.) Duration of printed extract 4 hr. 20 min. *In all records:* Read from left to right.

narrow constriction into one of the 20 c.c. bulbs. Generally, however, the animals settle down and show outbursts of irrigation alternating with rest periods, the cycle continuing—often for 12 hr. or so—with almost clock-like regularity.

The cycles, as traced on the record, vary somewhat in timing and in appearance from worm to worm, and, in the same worm, from day to day. Nevertheless, there is an underlying three-phase pattern, to which the outbursts always conform.

The essential features of this pattern can be seen in Fig. 2. In the relatively quiet intervals between outbursts, the worm was lying in the curved part of the

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[1] To avoid confusion, the extracts in the illustrations are chosen so that the worm's head is always towards the float. This means that a headward movement of water causes a downstroke of the writing point.

U, with its head towards the float and its body rather short and thick; it showed occasional slight movements, for example of the head and proboscis. At the beginning of each outburst it lengthened and waves began to travel headwards along its body. These resulted first in tailward locomotion, causing a short rise of the lever (phase 1). But soon the locomotion passed over into headward irrigation—a change brought about by an alteration of attitude, but not of the direction of wave-travel—and as this happened, the lever plunged down (phase 2). After a period of vigorous irrigation, during which the worm crept very gently back to about its original position, the waves slowed up and stopped. There followed a 'rebound' period, when the worm irrigated in the reverse direction, i.e. with tailward waves (phase 3). This gave a second, more prolonged rise of the lever. After this the worm became quiescent.
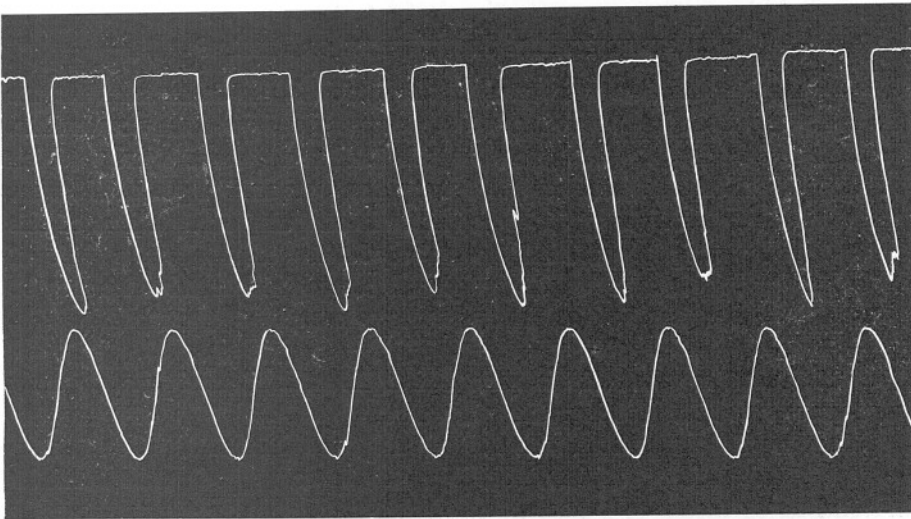

Fig. 3. Irrigation cycles in which the first and third phases are inconspicuous. Worm with head to float. (Worm O 49.) Time trace at 1 cycle per hr.

The second of the three phases—that of headward irrigation—is always the chief one, as long as the taps are turned as shown in Fig. 1. The others are more variable. The final 'rebound' phase may consist only of one or two very slow waves, taking place while the lever returns from the second phase and therefore leaving no trace on the record. Again, the backward locomotion in the first phase varies greatly in intensity. The worm of Fig. 3 gave only very slight, occasional tailward creeps, and only the faintest 'rebounds'. This is probably how the worms used by van Dam (1938) were behaving, as he makes no mention of the triphasic nature of the outbursts. The first part of Fig. 5 is particularly interesting because, as will be shown in another paper, it corresponds closely with the worm's normal behaviour on the beach. In this case, the

tailward locomotion phase is always well-marked. Starting from the bottom of the U, the worm crept up, at each outburst, until its tail had passed through the T-piece and extended for 1 cm. or so into the 20 c.c. bulb. Then, during the irrigation phase, it crept gently down again. The 'rebound' phase was vestigial, as the record shows.

In rough figures, the worm in Fig. 2 pumped about 20 c.c. of water at each burst, and the flow-rate through the capillary at the peaks was about 4·5 c.c./min. Corresponding figures for the other worms whose tracings are illustrated are: Fig. 3, 80 c.c., 6 c.c./min.; Fig. 5, 40 c.c., 7 c.c./min. The internal volume of the U-tube was 25 c.c., of which the worms occupied at least 5 c.c. It will be seen that the worms renewed all the water in the U-tube respectively once, four times and twice at each burst.

IS INTERMITTENCE SPONTANEOUS OR REFLEX?

The obvious explanation of intermittent irrigation is the reflex one. As the worm lies quietly in the tube, oxygen disappears and end-products accumulate. Presently, as we may suppose, the changes stimulate rhythmic activity, which ceases again when new water has been brought and the irritating conditions are removed. One should, however, be cautious in adopting explanations of this type. Isolated strip preparations from polychaetes often show periods of rhythmic activity alternating with periods of rest, so the intermittence may be spontaneous—i.e. produced solely by processes internal to the worm (Wells, 1939).

In the present case, there is little doubt that the intermittence is truly spontaneous, as the following evidence shows.

(i) If one pins out a worm with two pins near the front end and two at the base of the tail (being careful to avoid injury to the nerve cord) and records its movements by means of a glass hook passing under the middle of the body (Fig. 4), one often gets outbursts of activity, continuing very regularly, hour after hour, with about the same period as that of the irrigation outbursts. Now, the record in Fig. 4 is part of a very regular series of outbursts, which lasted for 13 hr. It was traced by a worm pinned to a weighted sheet of cork in a wide, shallow dish of sea water; the water was aerated and stirred by an air jet. One can hardly suppose in this case that the onset of each burst of activity is due to chemical conditions arising in the neighbourhood of the worm, and its cessation to the bringing of new water by the movements. This experiment shows that there is a 'clock' of some kind in the worm, of about the right frequency to account for the irrigation outbursts.

(ii) Van Dam (1938) found that the pauses did not disappear, or even shorten, when the oxygen content of the water was reduced by bubbling nitrogen through it. There was, however, a great increase in the amount of water pumped if the worms were given well-oxygenated water after a period

of oxygen lack. These experiments tend to exclude oxygen exhaustion as a possible stimulus for the outbursts, though they do not exclude the accumulation of CO_2 or other end-products.

(iii) The aerating effect of irrigation can be greatly reduced by turning the taps through 180° from the position shown in Fig. 1. The worm can still circulate the water and any such pumping will be recorded on the drum as before—but, as the water no longer circulates through the 20 c.c. bulbs and the wide cylinders, it can no longer be aerated. There is, in fact, a slight ebb and flow between the cylinders, corresponding with the excursions of the
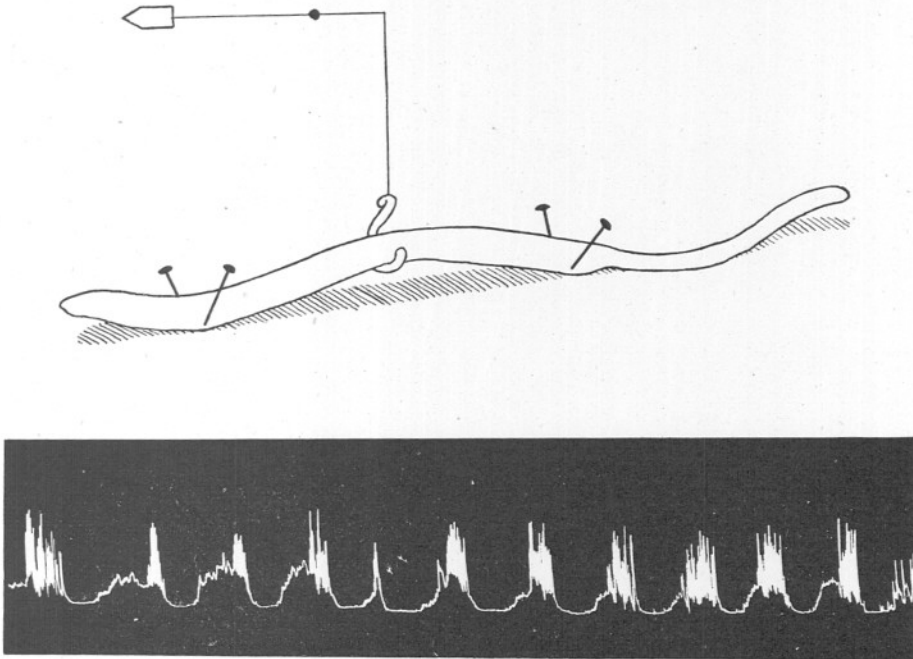

Fig. 4. *Above:* worm pinned to a cork sheet, on the bottom of a flat dish. *Below:* record traced by the same. Duration of printed extract, 7 hr.

lever; but, as this consists of 2 or 3 c.c. of water at most, moving to and fro quite slowly, its aerating effect is negligible compared with that of the circulation before reversal of the taps. The bulbs were included to reduce this effect. The worms were occasionally seen to extend about 1–2 cm. of their tails into the 20 c.c. bulbs, but it is hardly likely that they could get much oxygen, or dispose of much CO_2, by this means.

If now the outbursts are reflexly produced, they should be prolonged and intensified when the taps are reversed. But nothing of the sort occurs. Fig. 5 shows a typical result; the taps were turned at X (the float was lifted out of the water and dropped again, to mark this moment on the record). The

outbursts continue; their frequency is slightly raised (but in other worms it was unaltered, or even lowered); and, though the tailward excursions continue, the phase of headward irrigation is diminished and sometimes fails to appear on the record at all.
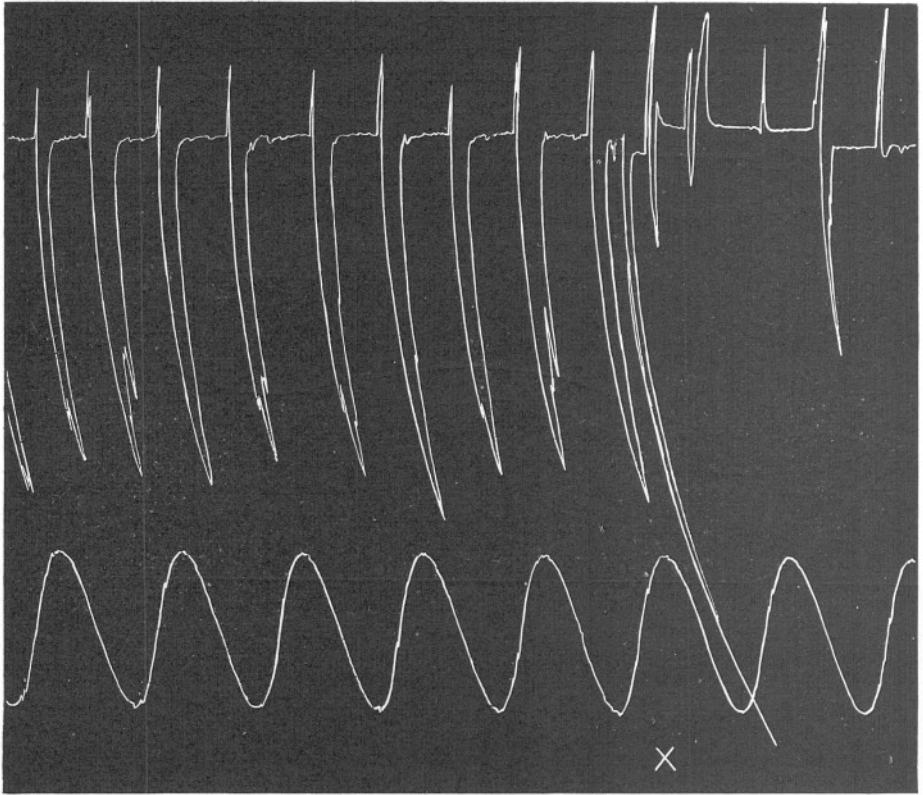

Fig. 5. Worm with its head to the float. At *X*, the taps are turned to 'no air'. (Worm O 48.) Time trace at 1 cycle per hr.

Fig. 6 shows the effect of turning the taps back to 'air' again, after a 7 hr. period of 'no air'. This worm had previously traced the record of Fig. 3. In the first part of Fig. 6, with the taps at 'no air', it was tracing outbursts at about the same frequency, but with much less voluminous irrigation. At the moment of turning the taps, there was a short spell of gentle headward, then tailward irrigation; this was probably a response to slight vibration of the apparatus caused by the handling of the taps. Then, when the next outburst fell due, the worm crept nearly to the T-piece, and began headward irrigation. It was not until this moment, that the aerated water first reached the worm. The response was very marked. Previously, the worm's movements had been

rather feeble and jerky, and its whole appearance suggested weakness and even injury by the 'no air' conditions; but now it suddenly revived and became alert and vigorous; and it began a burst of exceptionally powerful headward irrigation which lasted for 40 min. (total volume pumped 240 c.c., peak flow rate through capillary 8·25 c.c./min.). After this, the time intervals between outbursts were at first very short, and gradually lengthened out; but, even after the taps had been turned to 'air' for 10 hr., the rhythm was still quicker than at the beginning of the experiment (Fig. 3). As, however, the worm had been in the apparatus by this time for about 40 hr., an exact agreement is hardly to be expected.
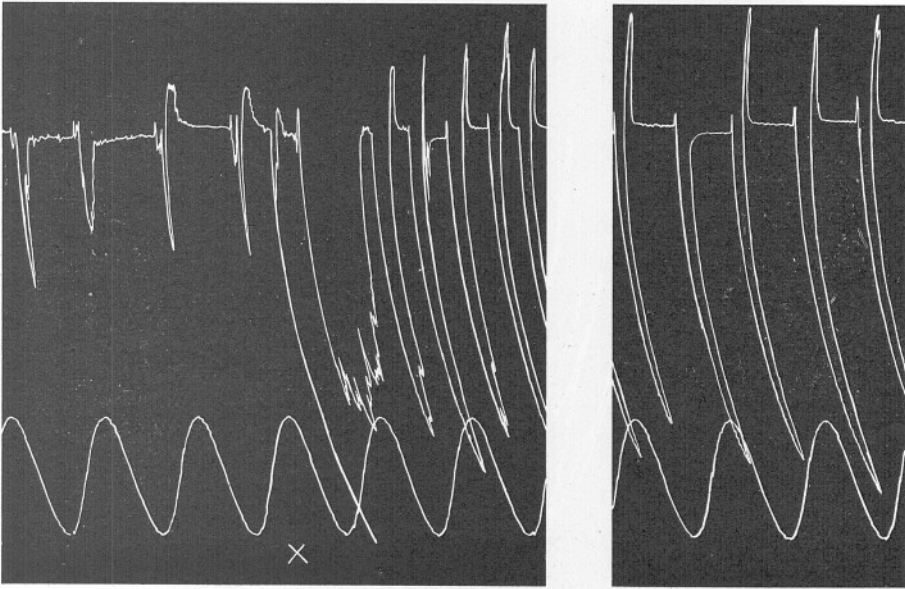

Fig. 6. Worm with its head to the float. The first extract begins with the taps in the 'no air' position. They are turned to 'air' at X. The second extract begins (still with the taps at 'air'), 3 hr. after the end of the first. (Worm O 49.) Time trace at 1 cycle per hr.

These results show that the cycles can be greatly modified, in amplitude, duration and frequency, by external conditions; but all the evidence tends to the conclusion that the intermittence itself is an inherent property of the worm. The case is analogous to that of the heart beat; rhythmicity is an inherent feature of the heart's organization, though the details of the rhythm can be modified by the vagus and sympathetic nerves.

LOCATION OF THE PACEMAKER

Wu (1939) studied the action of drugs on longitudinal body-wall strips from *Lumbricus* and *Arenicola*. He wrote: 'In contrast to the earthworm strips, those of *Arenicola* showed spontaneous activity only if the ventral cord was

present. The ventral strips were very active and often showed outbursts of rhythmic activity alternating with more quiet periods.'

To see whether the intermittent activity of isolated, innervated body-wall strips was at all comparable with the irrigation cycles, I made a series of experiments in the following way. The head, together with the first three chaetigerous segments, was removed by means of a transverse cut with a safety-razor blade. The tail, and the last two chaetigerous segments, were similarly removed. The middle part—of fourteen segments—was opened along
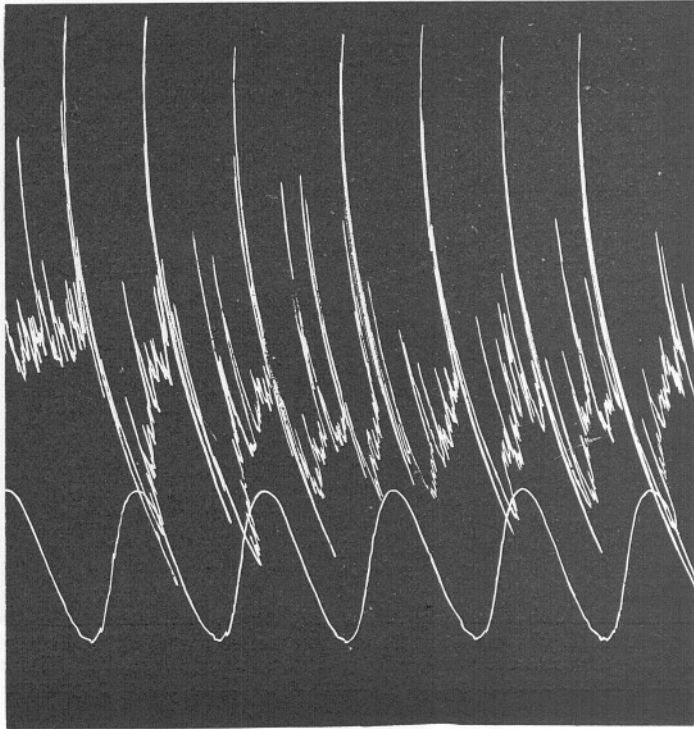

Fig. 7. Record traced by a body-wall strip, including the nerve cord, from the middle region of the body. Upstroke of lever means contraction of preparation. Time trace at 1 cycle per hr.

the mid-dorsal line, and the gut was removed. The body wall was then tied at both ends and suspended as a longitudinal preparation, in a large vessel of briskly aerated sea water, and connected to a light isotonic lever.

The resulting preparations showed continuous, rather irregular rhythmic activity, but one can generally see, on the tracings, bursts of outstanding vigour appearing at more or less regular intervals, with about the same timing as that of the irrigation cycles. Sometimes these were very evenly spaced, for several hours on end, as in Fig. 7.

In view of these results, and of Wu's observation that spontaneous activity occurs only in the presence of the ventral cord, one may reasonably place the pacemaker for the irrigation cycle, tentatively at least, in the nerve cord itself. The presence of the brain seems quite unnecessary.

INTERMITTENT AERIAL RESPIRATION

At high tide, the lugworm can get plenty of oxygen by circulating the water in its burrow. If, however, the tide recedes, leaving the surface dry and stagnant water in the lower part of the burrow, circulation is no longer possible and serious oxygen shortage could result. During an earlier study (Wells, 1945), I placed lugworms in glass U-tubes partly filled with sea water, which they were unable to circulate, and saw on several occasions what is evidently a method of aerial respiration. The worms crept backwards to the surface of the water, and drew air between their dorsal surfaces and the tube, so that it came in contact with the gills. This process might evidently be brought about by means of an adaptation of the irrigation cycle. The phase of tailward locomotion would bring the worm to the water surface and the following headward irrigation would then draw air down to the gills. If so, aerial respiration will be intermittent; and the experiments now to be described were made to find out whether this guess is true.

The apparatus was simple (Fig. 8). The worm was placed in the same U-tube as before, but now only partly filled with sea water. One end of the U was connected with pressure tubing to a float-recording device, so that the oscillations of the level in the U were written on the kymograph. For most of the time, the worms were left to write their own stories, but occasionally they were visited to see what they were doing, and once or twice they were watched continuously for an hour or so, and their behaviour was noted minute by minute.
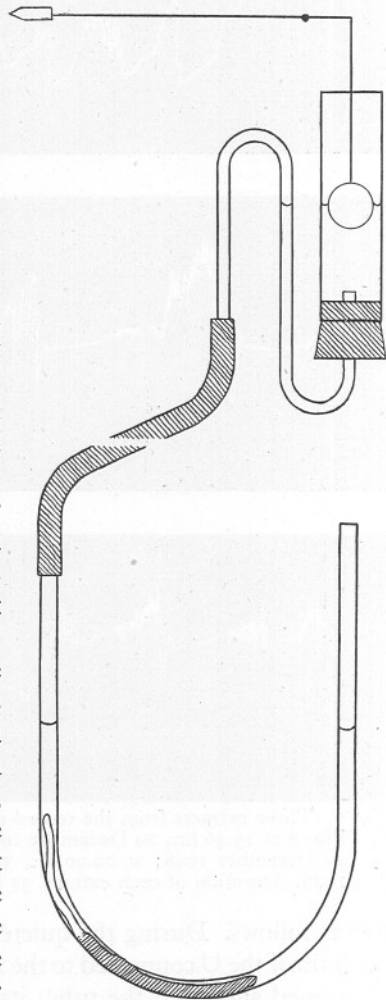

Fig. 8. Apparatus for recording aerial respiration (see text).

Parts of the tracings show confused, unanalysable activity, but usually the records are obviously periodic. The timing of the cycles varies considerably, as may be illustrated by the record of worm T 6 (Fig. 9). The worm was continuously watched during the last 2 hr. of the third extract, and its behaviour
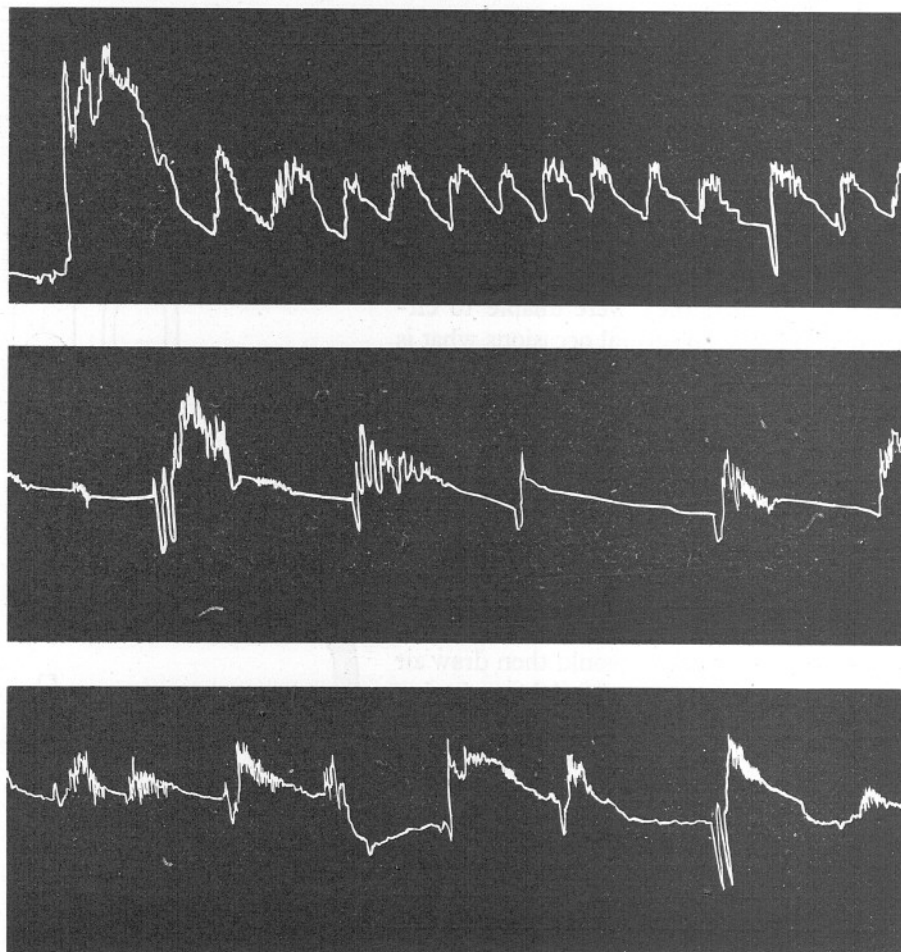

Fig. 9. Three extracts from the record of worm T 6. The worm was put in the apparatus of Fig. 8 at 15.46 hr., 29 December 1948. The three extracts start respectively at 19.00 hr., 29 December 1948; at 02.00 hr., 30 December 1948; and at 13.00 hr., 30 December 1948. Duration of each extract, 5½ hr.

was as follows. During the quieter parts of the record it was lying, tail up, in the limb of the U connected to the recording device; its body was shortened and broadened and filled the tube; its tail was short and thick, with its tip at, or near, the meniscus. As each of the bursts of rapid oscillation set in, the worm suddenly lengthened and narrowed its body. At this stage, there was usually

a drop of the writing point, presumably due to a slight upwards creeping of the worm, though this was not actually seen. Powerful headward wave-movements then began, the worm as a whole remaining in the same position. The waves began at the base of the tail, and resembled vigorous irrigation waves. Each wave drove air along the dorsal surface of the body, nearly to the most anterior gills; at this point, the bubble seemed to slip back past the wave and jerk up to the water surface again. During this phase, the water surface was mostly at the base of the tail. Each wave appears as a small oscillation of the writing point. Finally, the waves became gentler and died out, and the worm resumed its resting position.

The whole performance is clearly identical with the irrigation outbursts seen in the apparatus of Fig. 1. The variability of timing is paralleled by the irrigation records. In particular, there is an attractive resemblance between Fig. 6 and the upper extract in Fig. 9; in both cases, a prolonged outburst of great amplitude is followed by a series of bursts at short intervals. Now the worm of Fig. 9 spent the first $3\frac{1}{2}$ hr. of its time in the apparatus lying very still with its head up the open limb of the U, at about the level of the meniscus. In these circumstances it cannot have got any significant oxygen supply; its first respiratory movements are shown in Fig. 9; so the common features of the two figures may be attributed to previous oxygen shortage.

The first and second phases of the irrigation cycle are usually evident on the air-breathing tracings. The third ('rebound') is not detectable on the records; but as one watches the worm, one sometimes sees a slight, slow wave-creep in the tailward direction as the outburst passes off.

Cyclic aerial respiration of this type was seen or recorded in 13 of the 15 worms used. That it is adequate to support the worm for a considerable length of time was proved by worm no. T 5, which spent 120 hr. in the apparatus, always with the same 15 c.c. of sea water, and was in excellent condition at the end.

We may infer from these results that the worms in the field breathe air intermittently under low-tide conditions, and that they do so by adapting the irrigation cycle. Whether they continue to feed and defaecate when the tide is out will presumably depend on the mechanical properties of the drying sand.

DISCUSSION—THE FUNCTIONAL SIGNIFICANCE OF INTERMITTENCE

Van Dam (1937, 1938) made experiments on the respiration of animals from various phyla, several of which showed intermittent respiratory movements, and he assembled a number of other examples from the literature. The mechanism of intermittence may clearly be very different in different cases. The behaviour of *Arenicola* may profitably be contrasted with that of the larvae of the caddis fly, *Phryganea grandis*. These were studied by van Dam, after he had induced them to assume celluloid cases. They irrigate their cases by means of undulatory movements of the abdomen, and the following citations

from van Dam give the physiological picture: 'Periods of ventilating often very regularly alternated with intervals during which no movements occurred.... Crawling and struggling increased the oxygen need of the animal and so caused the intervals to be shortened.... That it was really oxygen want which brought about the respiratory movements, was proved in the following way. A tube was attached to one end of the case and a current of water was forced through it. In a current of air-saturated water no ventilation movements occurred (e.g. not for 27 min.), even if the animal moved in its case. However, if water poor in oxygen was used, the intervals were shortened and finally ventilation became uninterrupted.... Water containing from about 2 to 29 % CO_2 had no marked influence on the respiratory movements.' This is a clear case of reflex response to change in oxygen tension. With *Arenicola*, on the other hand, the position is completely different. Neither in the experiments of van Dam nor in those here described were the pauses abolished or shortened by oxygen lack, and intermittence is seen in worms surrounded on all sides by air-saturated water.

Can one read any functional significance into intermittence? Wolvekamp & Vreede (1941) suggest economy of effort. If the worms are watched, one sees that their whole attitude changes as the irrigation outbursts appear. 'During the pauses the body was contracted and, except the posterior end, pressed everywhere against the tube; the gills were also contracted. The animal usually lay motionless in its tube. Before resuming ventilation the animal elongated its body' (van Dam, 1938). Perhaps this change in posture means an increase in muscle tone and in the pressure of the body fluids, for clearly the latter factor must be high if effective irrigating movements are to be performed. If this be true, it might be economical to pump the necessary amount of sea water in bursts, rather than to do it gently and continuously, for the cost of maintaining an alert posture would be saved during the intervals in the former case. Against this viewpoint, however, it may be pointed out that the worms appear to be more active between the bursts when in sand than they are in glass tubes. This will be shown in another paper. In the absence of measurements of the metabolic cost of the worm's various kinds of activity, the 'economy' argument is not wholly convincing.

The problem can perhaps be more profitably approached from another angle. If the experiment illustrated in Figs. 5 and 6 were carried out on a reflexly irrigating animal, such as a *Phryganea* larva, the result would be as follows. The animal would irrigate more and more violently and continuously —but to no purpose—when the taps were turned to 'no air'; presently it would be exhausted and would cease to show respiratory movements; after this stage has been reached, the turning back of the taps would be of no avail, since the animal must co-operate if it is to get the oxygenated water. *Arenicola*, on the other hand, behaves in a way making for long survival under the conditions of the experiment. When the taps are turned to 'no air', its irrigation

outbursts decrease in intensity; they may perhaps be interpreted as a periodic testing of the conditions; and only when the taps are turned back, and the movements bring aerated water again, is their vigour increased.

It is of course unreasonable to suppose that the worm is adapted to the special conditions of a laboratory apparatus, and one might question whether a similar situation would ever occur in the field. At high tide, the worm has a plentiful supply of oxygenated water at its disposal, and at low tide, if the sand surface dries, it can breathe air. If, however, the burrow were covered with surface water at low tide, then circumstances might arise in which behaviour of the *Phryganea* type would be injurious or even fatal, while behaviour of the *Arenicola* type would save its exhibitor.

The surface water in summer weather is often several degrees hotter than the underlying sand. Linke (1939) studied an *Arenicola* beach near Wilhelmshaven, and found the following temperatures towards the end of a long tidal exposure in July, 1935: water in surface puddles, 26·2° C.; sand at a depth of 10 cm., 21·3°; at 30 cm., 19·4° C. I have noticed similar differences, though of less extent, when collecting worms at Thorpe Bay, on the Thames estuary. This is a beach which is exposed for a couple of hours only; nevertheless, it is very noticeable in summer that worms taken away in water collected from the sea travel better than those taken in surface water from the sand flats. When experimenting on dissected worms, or keeping stocks in the laboratory, I regard 20° as about the upper limit for good results. Thamdrup (1935, p. 66) found that the O_2 consumption of *Arenicola* rose from 2° to 10° C., and from 10° to 20° C., but fell from 20° to 28° C.

It seems clear that the surface water may become hot enough to be dangerous to the animals, and we may guess that a worm, whose burrow was left at low tide under a pool of hot water, would behave rather like the animal of Fig. 6. It would refrain, for obvious reasons from irrigating its burrow; under the influence of its internal 'clock', it would make occasional testing excursions towards the surface; and, after the returning tide had brought a supply of cooler water, it would begin vigorous irrigation at the next testing excursion. A hard frost, or a heavy rain, might perhaps make the surface water dangerous at low tide, and here again behaviour of the *Arenicola* type would be useful.

The fact that the cycles typically begin with tailwards creeping adapts them to the purpose of testing the surface water, since the worm is thereby brought nearer to the surface. The intensity of the second phase, of headward irrigation, can vary, as we have seen, with the conditions. The third, or 'rebound' phase, may also have its uses; it could expel any harmful water drawn down during testing irrigation, and (since irrigation and antikinetic locomotion are closely related), it might conceivably serve to bring the worm away from the surface if the second phase has been cut out.

These suggestions imply, of course, that the worm can survive long periods of oxygen lack. The animal of Fig. 6 responded promptly to the renewal of the

oxygen supply after 7 hr., during which it can have had little external oxygen except that dissolved in the water in the U-tube, the capillary and the short connecting tubes.[1] No analyses of oxygen tension were made, but the conditions were at any rate stringent enough to induce a marked change in behaviour soon after turning the taps to 'no air' (Fig. 5).

On the question of the possible value of haemoglobin as an oxygen store, the available data are meagre. Estimates of the oxygen consumption of the worms (when shaken in a little sea water in a manometric apparatus) and of the oxygen capacity of the worms' blood were made by Barcroft & Barcroft (1924), who deduced that the oxygen in the blood, at saturation, would be 'enough to suffice the worm for an hour or thereabouts'. Similar measurements and calculations were made by Borden (1931), who concluded that the oxygen in the blood would last 71 min.—a result in good agreement with that of Barcroft & Barcroft, although the figures on which it is based are considerably higher.[2] Thamdrup (1935) made measurements of the oxygen consumption at various temperatures with the Winkler technique; his figures fall between those of Barcroft & Barcroft and those of Borden.[3] Two further points should be borne in mind. The first is that the calculations just cited assume that the worms will continue, in the absence of an external oxygen supply, to consume oxygen at the same rate as when it is abundantly available. This has not been shown to be true, and the behaviour of the worms in Figs. 5 and 6 suggests that, on the contrary, the energy usage is reduced when the oxygen supply falls. The second is that *Arenicola* has recently been found to have haemoglobin in its muscles, besides that in its blood (Fox, 1949). Both of these factors will tend to prolong the period over which the stored oxygen will last. Van Dam (1938) accepts the earlier values (about 1 hr.'s supply) and suggests that the function of the haemoglobin is to supply the worm in the intervals between consecutive irrigation outbursts. According to the hypothesis here put forward, unfavourable surface conditions may force the worm to do with little or no external oxygen during the whole of the low-tide exposure period.

SUMMARY

The worms were housed in glass U-tubes, and were able to get a supply of aerated water from above by making pumping movements. The water movements were recorded kymographically. The experiments generally lasted for 24 hr. or longer.

The worms generally settled down to give outbursts of irrigation separated

[1] Total volume of water about 35 c.c.; the total O_2 content of this would be, at the start, about 0·2 c.c.; the worm weighed 4·8 g.

[2] The oxygen consumptions, in c.c. O_2/g./hr., are 0·01 (Barcroft & Barcroft) and 0·02–0·04 (Borden). The oxygen capacities of the blood, in c.c. O_2/g. of worm, are 0·008–0·013 (Barcroft & Barcroft) and 0·030–0·049 (Borden).

[3] Oxygen consumption, in c.c. O_2/g./hr., 0·0064 at 2°, 0·015 at 10°, 0·034 at 20°, 0·018 at 28°C.

by periods of rest, the alternation continuing with great regularity for many hours at a stretch.

An irrigation outburst consists of three phases: (*a*) tailward locomotion, (*b*) headward irrigation and slow headward creeping, (*c*) tailward irrigation. These three phases always follow each other in that order, but their relative prominence is variable. The second phase is the most conspicuous, whenever a plentiful supply of oxygenated water is available.

The following facts show that the intermittence is spontaneous, i.e. produced solely by conditions internal to the worm:

(i) If worms are pinned down in large vessels of well-aerated and stirred sea water, they often show outbursts of rhythmic activity corresponding in timing to the irrigation cycles.

(ii) Van Dam (1938) found that the pauses between outbursts are neither shortened nor abolished by lowering the oxygen tension in the water.

(iii) If the experimental conditions are so arranged that the worm can circulate the water in its U-tube without thereby getting an oxygen supply, the irrigation cycles continue with their previous timing, but with the vigour of the outbursts greatly reduced. If, after some hours under these conditions, aerated water is again admitted, irrigation is very greatly increased.

Observations on the rhythmic activity of body-wall strips indicate that the pacemaker for the irrigation cycles is in the ventral nerve cord.

If worms are placed in U-tubes partly filled with water, so that circulation is impossible, they creep tailwards to the water surface and draw air down into contact with their gills. Aerial respiration is intermittent, and is brought about by an adaptation of the irrigation cycle.

Intermittence, determined by an internal pacemaker, might have survival value if, at low tide, the burrow was covered by surface water which got too hot, or otherwise dangerous, for the worm.

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