PRESSURE DIFFERENCE IN ADJACENT SEGMENTS AND MOVEMENT OF SEPTA IN EARTHWORM LOCOMOTION

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SUMMARY

1. The nature and timing of septal movements during gentle crawling have been examined in relation to the coelomic pressure ($P_c$) in and between adjacent segments.

2. Between neighbouring anterior segments the phase lag was 0.05–0.1 s and the maximum $P_c$ difference 3.3 cm water. The mean $P_c$ in a leading segment exceeded that in a trailing segment by 0.9 ± 0.06 cm water.

3. In forward crawling, the septa bulged maximally backward and forward when segments were half elongated and half shortened respectively, and were flat when segments were longest and shortest: the area of a septum in an elongated segment was one quarter that in a shortened one and thus a septum is strongest (small and thick) when the $P_c$ to be longitudinally confined is highest.

4. Bulging of septa is closely related to the intersegmental $P_c$ difference. Bulging forces acting on a septum range from 0 to about 1 g wt.

5. The pressure drop along a worm is not linear and the ventral foramina may act as 'septal valves' to equalize coelomic volume and pressure when required. The influence of gut, septum and body wall movements on each other is discussed.

INTRODUCTION

When an earthworm crawls or burrows, successive segments leave the substratum, become thin and elongate, then shorten and thicken as they bear on the substrate again. In a vigorously crawling *Lumbricus terrestris*, high coelomic-pressure ($P_c$) pulses were recorded, electronically, from a segment during elongation and lower ones during full shortening. Pressure was lowest between these extremes (Seymour, 1969; 1971). In records from burrowing worms the pressure pulses associated with shortening of a segment predominated, as the worm dilated fissures in the soil. Often, especially during gentle crawling, elongation and shortening were less forceful; the high elongation peak was then lowered and the shortening peak disappeared.

When waves of segmental elongation and shortening pass along the body of the worm, considerable and fluctuating $P_c$ differences exist between different segments (Seymour, 1969) and are localized by the intersegmental septa (Newell, 1950). Newell described the cumulative effect of (about 30) septa in withstanding longitudinal

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transfer of liquid and of local high pressure induced in the coelom by injecting liquid. Commonly, activity obviously declines towards the trailing (usually rear) end of the worm, which is then dragged along by the actively crawling anterior body during forward locomotion (Yapp, 1956). This ‘activity gradient’ is reflected in a gradient of mean internal pressure along the worm (Newell, 1950; Seymour, 1969).

The septa, that maintain this pressure gradient, can be seen bulging backward and forward during locomotion in species (e.g. *Tubifex* sp. (Newell, 1950)) or individuals with little pigmentation in the body wall. In the work reported here, development and transfer of internal pressure in adjacent segments and the cause and role of septal bulging in crawling of earthworms has been examined by comparing timing and waveform of the pressure recorded from coelomic compartments separated by only a single septum.

**MATERIALS AND METHODS**

To record coelomic pressure (*P*<sub>c</sub>) in two adjacent segments of *L. terrestris* two cannulae made from slightly curved 0.7 mm bore hypodermic needles were clamped horizontally, so as to allow some relative movement, close to a flat, wax surface that was kept damp. Each cannula penetrated the lateral body wall of a segment and was connected by nylon tubing to a Sanborn 276 BC pressure transducer. Worms restrained by cannulae readily made crawling movements on the slippery surface and the two resulting series of simultaneous *P*<sub>c</sub> fluctuations were recorded on a Sanborn hot stylus chart recorder. Timings of segmental elongations and shortenings were added to the record from visual observations, using the event marker.

To observe movement of septa during locomotion, lightly pigmented individuals of various species of earthworm were examined under low magnifications. Timings of forward and backward bulging of a septum relative to its corresponding inter-segmental groove were noted with reference to the state of elongation or shortening of the segments immediately in front of and behind the septum as the worm crawled slowly forward over a level surface.

**EXPERIMENTAL OBSERVATIONS**

*Coelomic pressure relations between adjacent segments during gentle crawling*

Fig. 1, upper, shows typical simultaneous *P*<sub>c</sub> records from two adjacent anterior segments, 17 and 18, during forward crawling. As might be expected, the form of record from the two segments is closely similar. Mean length of locomotory cycles, between one peak (*e*) and the next, in all sequences was 7 ± s.e. 0.93 s. Phase lag (i.e. the delay between the appearance of a pressure pulse in one segment and a corresponding pulse in the adjacent segment) varied between 0.05 and 0.1 s. These figures agree well with estimates of delay time calculated by dividing the time for one cycle by the number of segments between corresponding parts of consecutive cycles.

In Fig. 1, lower, differences in *P*<sub>c</sub>, measured at 0.4 s intervals, are plotted as excess of leading-segment pressure (*P*<sub>cL</sub>) over trailing-segment pressure (*P*<sub>cT</sub>)(the following extreme and mean values are based on all the data). Maximum excess, +3.3 cm water, occurred as elongation pulse *P*<sub>cL</sub> approached maximum. Minimum pressure excess (i.e. maximum *deficit* in *P*<sub>cT</sub>, −0.75 cm water, was seen as both segments
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Fig. 1. *Lumbricus terrestris*. Simultaneous records of coelomic pressure ($P_c$) from two adjacent segments (17 and 18) during gentle crawling over a smooth surface. $e$, pressure peaks as segments elongate. Below is plotted excess of $P_{c17}$ over $P_{c18}$. Vertical axis, $P_c$ in cm water; time in s.

Fig. 2. Diagram showing how changes in segmental shape, coelomic pressure differences between two adjacent segments and bulging of septa are related in a gently crawling earthworm. Segmental shape changes are greatly exaggerated for clarity. Further explanation is in the text.
shortened. A comparison of mean excess pressures confirms the existence of a $P_o$ gradient, falling in the direction of movement of the locomotory wave (here anterior–posterior); mean excess of $P_mL$ over $P_mT$ was 0.9 ± 0.06 cm water. Mean excess of $P_mT$ over $P_mL$ was only 0.3 ± 0.02 cm water. Despite the overall excess of $P_mL$ over $P_mT$, total times during which one segment showed excess or deficit with respect to the other were about equal.

In the example shown in Fig. 1, from two anterior segments of L. terrestris, the instantaneous pressure difference can be resolved into two components; first the delay as the locomotory pressure wave develops in successive segments and secondly an ‘excess factor’ that is detected as an extra hump in the $P_mL$ waveform (top), directly above the positive peak in the difference curve (bottom). The excess factor may result from independent movement of the neighbouring muscular gizzard and the action of the especially muscular septa suspending it (see Newell, 1950).

**Shape of segments and movement of septa in gentle crawling**

When a worm paused during crawling its segments tended to remain short, with the septa flat; if locomotion did not resume after about a minute, segments slowly elongated to a ‘rest’ configuration over the next few minutes and the septa bulged anteriorly. As shown earlier (Seymour, 1969) this relaxation was accompanied by a gradual pressure drop.

In the earthworm locomotory waves are retrograde (see Vles, 1907), i.e. they travel along the body in a direction opposite to that in which the whole animal moves with respect to the substratum. So in forward crawling a wave of sequential segmental elongation and shortening runs backward. Each segment, and the septum anterior to it, behaves consistently as follows during forward locomotion (and see Fig. 2).

<table>
<thead>
<tr>
<th>Segment</th>
<th>Septum</th>
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<tbody>
<tr>
<td>a Short</td>
<td>Flat, expanded</td>
</tr>
<tr>
<td>b Half elongated</td>
<td>Bulges posteriorly to maximum</td>
</tr>
<tr>
<td>c Long</td>
<td>Flat, contracted</td>
</tr>
<tr>
<td>d Half shortened</td>
<td>Bulges anteriorly to maximum</td>
</tr>
<tr>
<td>(a₁) Short</td>
<td>Flat, expanded</td>
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</tbody>
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Bulging $a$–$b$ is less pronounced in segments behind the clitellum than in those in front. Septa take up slack as the diameter of their attachment to the body wall decreases ($c$–$d$) by contraction of their intrinsic muscles (Newell, 1950) and by elastic recoil of the septum. Resilience of septa is well shown by probing them in an opened worm.

**Correlation of locomotory $P_m$ fluctuations and changes in segmental shape with movement of septa**

Newell (1950) said that in Tubifex sp. ‘... septa ... bulge into segments where the pressure is low but remain taut during all phases of contraction and relaxation of the body wall muscles’. This work has shown that the latter observation does not apply to larger, terrestrial oligochaetes; indeed the greatest septal distortion is seen when
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segments are actively changing shape. However my observations on the bulging of septa agree with Newell’s. From the data presented here on $P_e$ fluctuations and differences, and on movement of septa, both in relation to segmental shape, it can now be shown how these factors are related during crawling in the earthworm.

In Fig. 2, ‘ideal’ $P_e$ curves (middle) yield a peaked difference curve like those derived directly from segmental pressure records as in Fig. 1. The inter-segmental septum is shown bulging on the segment diagrams (above) and the direction of bulging is plotted below.

Bulging of the septum is obviously correlated with $P_e$ difference. When the two segments are near their minimum length $P_L$ equals $P_T$ and so the expanded septum is flat ($a, a_1$). As $P_L$ rises in advance of $P_T$, excess of $P_L$ increases to a maximum bulging the septum posteriorly ($b$). With both segments near their maximum length, $P_L$ then levels off and begins to fall as $P_T$ continues to rise; their difference becomes zero and the septum is again flat ($c$). But this time it is maximally contracted and thickened by its intrinsic muscles. As the segments shorten and $P_L$ continues to fall ahead of $P_T$, pressure excess in the trailing segment reaches its peak, bulging the septum forward maximally ($d$). With continued shortening, pressures equalize when the leading segment is just past its shortest and the trailing segment just before its shortest; this is stage $a_1 (= a)$ and the cycle continues in the same way for as long as locomotion occurs.

The cycle described affects all active segments sequentially, so that at a given moment there are one or two ‘feet’, or points d'appui, each consisting of a group of short, low-pressure segments with septa more or less bowed towards the centre of the group; separating the feet are groups of long segments with high coelomic pressure and their septa more or less bowed away from the middle of the group. In each case the centre of the group contains a few segments whose septa are flat or nearly so. In a living worm the locomotory stages shown in diagrammatic form in Fig. 2 (top) would appear in a given segment about 0.05 s apart.

Size of a septum and bulging forces acting on it

To compare the maximum and minimum sizes a septum assumes during locomotion, the septum between segments 42 and 43 was examined in two worms of the same size, one fixed fully extended and the other fully shortened. The difference in size is striking. Fig. 3 shows that relative to the short, wide segment (right), the total cross-sectional area of the elongated segment is about one-third (34.5%), and of the septum only about one-quarter (27%) of the septum on the right; correspondingly the septum in the elongated segment is nearly four times as thick (37%) as that in the shortened segment. The great difference in size and thickness at different stages of locomotion affects the total bulging forces acting on a septum and the results they have.

The force acting on a septum obviously varies throughout the locomotory cycle and can be estimated, knowing the $P_e$ difference across the septum and the area of the septum. Where the difference is zero (Fig. 2a, c) the net force is also zero. The force is greatest at $b$ and $d$, when $P_e$ excess in one segment, and bulging of the septum, are greatest. As previously shown (Seymour, 1969), segmental diameter changes roughly linearly with time during locomotion, and so, the diameter of the septum at
Fig. 3. Scale diagrams drawn from transverse sections of two fixed specimens of \textit{L. terrernis} both weighing 67 g, showing relative cross-sectional areas of body- and gut-wall, septum between segments 42 and 43 (stippled), and total body (hatching), when the segments were fully elongated (left) and fully shortened (right). The square represents 1 mm$^2$.

$b$ and $d$ (Fig. 2) lies about half way between the two extremes shown in Fig. 3. For the purposes of calculating the force acting on a septum, the degree of bulging can be ignored since the thrust, parallel to the worm’s long axis, on the curved surface of the septum is the product of the $P_c$ and the area of the septum projected on a plane normal to the long axis (Alexander, 1968). Subtracting the cross-sectional area of the gut, the cross-sectional area of a typical septum at $b$ and $d$ was 5 mm$^2$. Since maximum pressure differences recorded here were 3.3 cm water (acting backward) and 0.75 cm water (acting forward), the maximum bulging forces on the septum during locomotion were:

$$3.3 \text{ g/cm}^2 \times 0.05 \text{ cm}^2 = 0.16 \text{ g wt (at } b, \text{ backward), and}$$

$$0.75 \text{ g/cm}^2 \times 0.05 \text{ cm}^2 = 0.04 \text{ g wt (at } d, \text{ forward).}$$

These can be expressed as $b = 160$ dynes ($= 1.6 \times 10^{-3}$ N) and $d = 36$ dynes ($= 0.36 \times 10^{-3}$ N).

During a previous study (Seymour, 1969), the highest $P_c$ recorded in one segment, during (very active) crawling, was 25 cm water (i.e. five times the maximum recorded during these observations on gentle crawling). On this basis, maximum pressure difference could be about 17 cm water and maximum bulging force sustained by one septum about 750 dynes ($7.5 \times 10^{-3}$ N). Thus the force on the anterior face of a septum can fluctuate during forward crawling between 0 and nearly 1 g wt. Given that in a sphere, $T = P \times \frac{r}{2}$ (where $T =$ tension in the wall, $P =$ internal pressure and $r =$ radius) (see Alexander, 1968), tension in a bulging septum can be estimated. Radius of curvature of a septum at maximum bulging (Fig. 2b, d) is about 3 mm. Substituting the pressure values noted above, i.e. 3.3 and 17 g/cm$^2$, and ignoring the presence of the gut, tension is estimated as about 0.6 and 2.5 g/cm.
DISCUSSION

The mean $P_e$ drop between the leading and trailing segment of a pair at the leading end of a worm was about 1 cm water. If this drop were to continue between successive pairs of segments, $P_e$ would fall to zero long before the locomotory wave reached the last segments. Although, as noted above, the last half or third of a worm may be inactive and will then have a very low $P_e$ (Seymour, 1969), records made earlier (Seymour, 1969; 1971) from distant segments simultaneously show that the $P_e$ differences along the worm in the direction of the locomotory wave is usually less than that predicted by linear extrapolation of the pressure drop existing between anterior segments. The form of the $P_e$ drop curve along the worm has not been completely determined, but it must fall abruptly anteriorly and gradually flatten out to approach or reach zero between the median and terminal segments. The point at which the curve reaches zero will depend upon the pressure in the segments at the leading end of the worm, and the vigour of the activity in the remaining body segments. These in turn depend on the speed of locomotion, whether the worm is crawling or burrowing, and the possibility or penetrability of the substratum in each case.

Other factors may affect the pressure curve: anterior and posterior segments are markedly different in proportions, those in the anterior third of the body being much longer. Also there are indications, discussed in Seymour (1969) that the locomotory effort can at times be reinforced, increasing the $P_e$, some way along the body of the worm.

At full segmental elongation and shortening there is no $P_e$ difference for a septum to withstand, and so the great differences in area, thickness and stiffness of the septum are irrelevant. However, the forces on the septum near full elongation and shortening are very different, because, although the $P_e$ difference between adjacent segments may be similar, the absolute $P_e$ is higher in long segments (see Fig. 1). Also the septa, when small and thickened, are best able to isolate from shortened, low-pressure regions the $P_e$ necessary for extension of the worm, against external resistance, especially at the front end.

The muscular and resilient septa connect a body wall and gut that are themselves resilient and muscular, and activity in any one component must directly affect the other two. Locomotory movements of the body wall, acting via the septa, tend to pull the gut in the direction of movement of the body as a whole during segmental shortening; and in the opposite direction during segmental elongation (see Fig. 2). The other main effect on the gut is that it tends to be pulled open as the septa bulge and a radial stress is set up in them, when a segment increases in diameter ($c$ to $a$, in Fig. 2) and especially when both these effects coincide (i.e. around $d$ in Fig. 2). Thus an ‘induced peristalsis’ acts on the gut during locomotion. It is not known to what extent the gut and septal muscles reduce or modify these effects on the gut, but Arthur (1965) showed by X-rays how the gut was squashed together longitudinally within a shortened group of segments and stretched out in an elongated group.

Possible effects of this body wall movement on the gut are to mix the contents, so as to aid digestion, and, by its rapid and vigorous action, to promote thixotropic liquefaction of the soil mixture, and so help transport by the slower, less energetic
intrinsic gut rhythm. The cyclically-recurring high and low pressure in the coelomic fluid surrounding the gut must have the effect of a peristaltic pump, which mixes and transports the gut contents. Arthur (1965) however, disregarded this effect and supposed that the long body and high pressure of the worm are disadvantageous for food transport. He concluded that a ‘force pump’ (pharynx + gizzard) is needed to urge ingested soil down the gut.

Since the gut has its own intrinsic peristaltic rhythm (as seen in dissected preparations) gut movements might modify the body wall locomotor cycle.

As Newell (1950) showed, each septum has a hole with a sphincter muscle, the ventral foramen, through which the ventral nerve cord passes. From injection and X-ray experiments Newell concluded that coelomic fluid does not pass from one segment to the next across the intervening septum during locomotion. Such isolation is to be expected where large pressure differences have to be maintained between regions separated by only a few segments (see Seymour, 1969). The ventral foramina are equipped to open and close but it is not clear from Newell’s model when and why they do so.

I propose that the ventral foramina are pressure-equalizing valves that, by leaking a small volume of coelomic fluid through each septum at certain phases of the locomotor cycle, ensure that the volume of each segment is kept within an optimum range, in which the longitudinal and circular muscles surrounding that segment work most efficiently. The most likely phase of locomotion at which the foramen opens is (a) (Fig. 2) where the septum is stretched to its largest diameter, tending to open the foramen, and no very great $P_c$ difference needs to be sustained.

The ventral foramen, or ‘septal valve’ will need to open and equalize volume and pressure when segmental volume is changed by any of the following: (1) Temporary accumulations of gut contents, which will increase the volume of one segment or several adjacent segments. (2) Loss of gut volume which occurs temporarily in a large group of posterior segments following defaecation. (3) Shrinkage in regions surrounding the genital tracts as gametes are shed. (4) Excretory flow from the nephridia which lowers the volume of segments, perhaps unequally. (5) Slow leakage, or, often, more considerable loss of coelomic fluid from some segments through the dorsal pores.

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REFERENCES


