Circulation in the Gippsland Giant Earthworm *Megascolides australis*

David R. Jones[1,*]
Peter G. Bushnell[1,†]
Barbara K. Evans[2]
John Baldwin[3]
[1]University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada; [2]Department of Zoology, University of Melbourne, Parksville, Victoria, Australia 3053; [3]Department of Ecology and Evolutionary Biology, Monash University, Clayton, Victoria, Australia 3168

Accepted 5/16/94

Abstract

Pressures have been measured in the dorsal vessel (DV), ventral vessel (VV), and lateral hearts (LHs) of the giant earthworm, Megascolides australis. *Mean pressure in the DV (22.1 ± 9.8 cm H_2O ± 1 SD) was similar to that in the VV (21.8 ± 10.1 cm H_2O) although pressures were much more pulsatile in the DV than VV. Peak and minimum pressures in the DV were significantly above and below, respectively, those in the VV. Contraction frequency of the DV was 6.8 ± 1.9 · min^{-1}. Neither imposing an orthostatic load by raising or lowering the tail, nor simulated autotomy, had any effect on pressure measured in the anterior segments of the worm. Injecting the tracer ^{99m}technetium into the anterior of the worm revealed that the circulation has two compartments; blood flow was rapid in the anterior 15 or 20 segments and exceptionally slow in the rest of the worm despite high blood pressure throughout the major distributing vessel, the VV. The anterior rapid circulation subserves the vital functions of the worm while the slow circulatory compartment is largely vegetative.*

Introduction

The closed circulatory systems of annelid worms have been the subject of considerable interest over the last 100 yr. Earthworms have a large dorsal

* Address for correspondence: David R. Jones, Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, B.C. V6T 1Z4, Canada.

† Present address: 1700 Mishawaka Avenue, Department of Biological Sciences, Indiana University South Bend, South Bend, Indiana 46634.

Physiological Zoology 67(6):1383–1401. 1994. 0031-935X/94/6706-9402$02.00

blood vessel (DV) and a large ventral blood vessel (VV), which are the major collecting and distributing vessels, respectively (Johnston and Johnson 1902; Johnston 1903; Johansen and Martin 1965). The VV distributes blood to the capillary circulations of the body wall and gut, which drain into the DV. The DV propels blood anteriorly by means of waves of peristaltic contraction. In the anterior region of the worm, the DV and VV are connected by paired commissural lateral hearts (LHs), one pair to a segment. The precise number of pairs of LHs varies between genera. The LHs are contractile and propel blood into the nonrhythmically contractile VV. Hence, the earthworm circulation can be fitted into the generalized scheme for closed circulations of collecting, propulsive, and distributing vessels (Johansen and Martin 1965).

This general description also appears to apply to the Gippsland giant earthworm (*Megascolides australis*) or at least as described by Spencer (1889) in his extensive monograph of the structure and lifestyle of this giant worm. Giant earthworms are found in a number of restricted Southern Hemispheric locations, leading to the plausible suggestion that they were isolated by the division of the continents. Giant worms, as their name implies, can attain lengths of 3 m and masses of 500–600 g, although much of this mass is soil in the gut. Physiologically, the circulation of these giant worms can be investigated by standard techniques of pressure recording and flow distribution (Johansen and Martin 1965).

In this series of experiments we explored the circulation in the Gippsland giant earthworm by making simultaneous pressure recordings in the DV, LHs, and VV, along with recordings of coelomic pressure, in more than one segment. Nearly all cannulations of the major blood vessels were non-occlusive, in contrast to the cannulations done by Johansen and Martin (1965). Furthermore, we investigated the pattern of the circulation by injecting ^{99m}technetium as a blood-flow tracer into the DV. The distribution of the tracer was followed for up to 30 min after injection. The major finding of this study is that the circulation has two compartments, one fast (anterior) and the other slow (posterior), despite high mean blood pressures throughout the major distributing vessel, the VV.

Material and Methods

Giant earthworms were collected from various locations in South Gippsland, Victoria, Australia. A pit or trench was dug by hand, and the earth brushed away between each spadeful until a wormhole was located. Wormholes were then carefully excavated with screwdrivers until a portion of worm

was located. Excavation of the burrow was continued until the worm was completely exposed. The worm was then removed from the burrow and placed in a 50-L plastic box that contained alternating layers of grass and burlap sacking. Worms were transported by car from the collection site to the laboratory and held in temperature-controlled rooms (15°–18°C) for several days before the start of any experiments.

All experiments were performed in temperature-controlled rooms in the Department of Zoology, Melbourne University. Several anesthetic regimes were tried (immersion in solutions of 7.5% $MgCl_2$ [wt/vol], 2% chloral hydrate [wt/vol], or 5% propylene phenoxetol [vol/vol]), but the most effective was to immerse the worms in a graded series of ethanol solutions (2%, 5%, 8%, 10% [vol/vol]) for up to 10 min at a time. Exposure to the ethanol was varied to suit the projected length of surgical intervention.

The relaxed worms were placed on a white enamel tray and observed with a binocular dissecting microscope. The DV and VV were exposed in the posterior regions of the body by longitudinal sections in the skin running over several segments. In the anterior segments the DV, VV, and LHs were exposed by making a hemicircumferential cut in the body wall of a single segment. Gut vessels were approached through incisions used to expose other vessels. Cannulae were made from P.E. 10 or P.E. 20 polyethylene tubing (Clay Adams, Parsippany, N.J.), which was pulled out over an alcohol flame to give a tip diameter of 50–200 μm. Cannulae with the smallest tip diameters were attached to an IPM oil-filled micropressure system (Model MP I or Model MP4; Instruments for Physiology and Medicine, San Diego, Calif.), whereas larger cannulae were attached to conventional pressure transducers filled with earthworm Ringer solution (Pantin 1962). The frequency response of the micropressure system was 10–30 Hz, whereas the standard pressure transducers were overdamped with a frequency response of 2.5 Hz when subjected to a "pop-test" (Jones 1970).

For non-occlusive cannulation of the DV and VV, a hole was made in the vessel wall by using the tip of a 30-gauge hypodermic needle and the cannula tip was forced through the hole into the blood vessel. A purse-string suture, of 9-0 braided silk (Ethicon, Peterborough, Ontario), was used to secure the tip in the vessel. On other occasions, side branches of the DV, VV, LHs, and gut vessels were cannulated occlusively, and, after tying the cannula in place, the tip was advanced until it lay in the vessel of interest. This approach caused less stasis in the major vessels and was preferred. In the anterior end of the body the DV was occasionally cannulated occlusively in segments 5 and 6. This was quick and convenient and seemed to give recordings similar to those from non-occlusive

locations. Typical pressure tracings obtained with pressure pulses recorded with the micropressure system (fig. 1*a*, *b*) and standard blood pressure transducers (fig. 1*c*) are shown in figure 1. All these cannulations were non-occlusive. Dorsal vessel traces were more damped when recorded with standard blood pressure transducers but were still reasonable representations of the pulses compared with pressure pulses recorded with the micropressure system (fig. 1*b*, *c*). Ventral vessel pulses looked the same with both recording systems (fig. 1*a*, *c*).

The incision in the body wall was closed around the cannula(e) with interrupted sutures (8-0 braided silk was generally used). A separate cannula was placed in the coelomic cavity, attached to a standard blood pressure transducer, and held in place by one of the body wall sutures. Alternatively, coelomic pressure was recorded from unviolated segments by attaching a

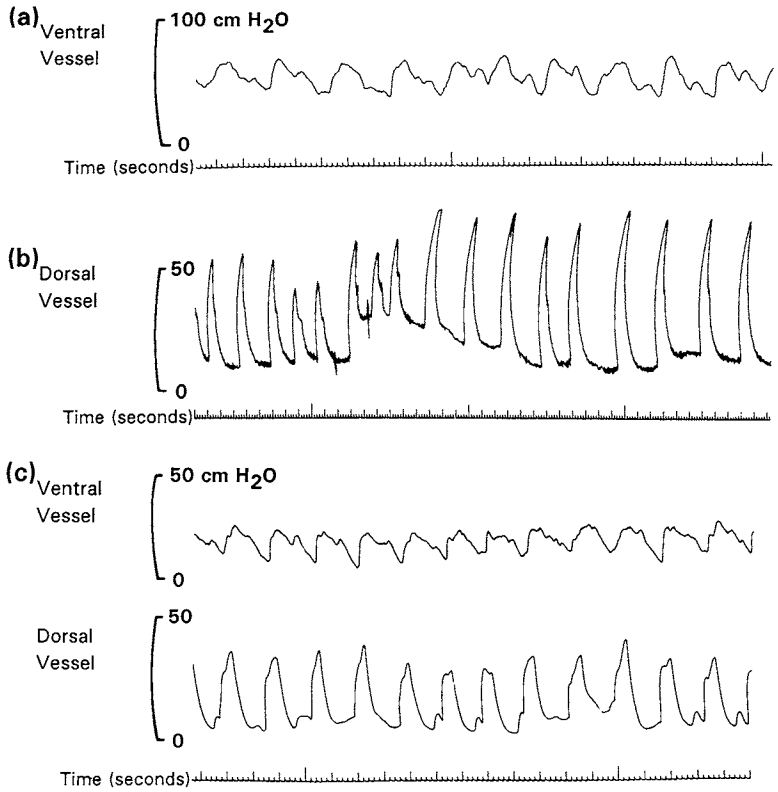

*Fig. 1. Pressures recorded non-occlusively in VV and DV by high-frequency micropressure systems (*a *and* b*) and low-frequency, overdamped, standard pressure manometers (*c*). The major difference between the pressures recorded by both systems was the loss of higher-frequency components with standard manometers.*

portion of hypodermic needle (30-gauge) to P.E. tubing and forcing the tip through the body wall. The tip was held in place by cyanoacrylate glue (Vetbond; 3M Products, St. Paul, Minn). All incisions, after closure, were also covered with a thin layer of Vetbond. Pressures were recorded on a Grass 6-channel polygraph (Model 7C; Grass Instruments, Quincy, Mass.) writing on curvilinear coordinates.

Animals were allowed several hours to recover from the effects of anaesthesia before any recordings began. Recordings were made over several days from cannulated animals. To encourage locomotion, one end of the dish was covered with black polyethylene and recordings were made while the worm crawled under it. The effects of various interventions such as raising or lowering the tail, or simulated autonomy, on circulatory dynamics were also investigated.

^{99m}Technetium (0.5–1 mCi in 100–200 μL of earthworm Ringer solution) was injected into the DV in the anterior end of the animals. Blood pressure in the DV was measured simultaneously. Distribution of the tracer was followed for up to 30 min with a G.E. STARCAM 300a gamma camera. A worm was coiled into an S-shape and placed on the patten of the inverted camera. Worms were covered with black polyethylene to discourage movement. Data were collected in both high- and low-resolution modes. Low resolution produced an image every 10 s (referred to as dynamic) whereas each high-resolution image required 1 min (referred to as static). Every image, or every other image, was processed with G.E. STARCAM software and stored on X-ray film. Some color pictures were also made of high-resolution images.

Chart records were analyzed to obtain mean, high, or low pressures from the DV, LHs, and VV. Contraction frequency (contractions · min^{-1}) was counted as the major frequency occurring over 10-min periods. However, more sophisticated analysis of rhythms was obtained from data digitized by SIGMASCAN (Jandel, San Rafael, Calif.). Digitized data were subjected to power spectral analysis with a coarse-graining spectral analysis program (CGSA) developed by Yamamoto and Hughson (1991). Digitized data of pairs of DV, VV, and/or LH pressure traces were cross-correlated with the cross-correlation function from the signal-processing toolbox of MATLAB (The Math Works, Natick, Mass.). The data were normalized so that the mean value of the data was zero, while the correlation function was normalized so that cross-correlation of two identical signals at zero lag was 1. When necessary, for figure preparation, digitized data were superimposed by using SIGMAPLOT (Jandel). Statistical analysis of data was done with SIGMASTAT (Jandel). Values in the table and text are means ± 1 SD.

Results

Pressures within the Circulatory System

Pressures within the DV and VV were pulsatile with a mean frequency of 6.8 ± 1.9 min^{-1} ($N = 14$). In the absence of marked coelomic activity, mean pressures in DV and VV were similar (table 1), although peak DV pressure significantly exceeded VV pressure (table 1). Pressures were greatly affected by peristaltic waves moving along the body and rose along with coelomic pressure (fig. 2*a*, *b*).

In the DV pressure rose rapidly to a sustained peak during contraction and then declined. During relaxation pressures were constant, slowly declining or slowly increasing (figs. 1, 3). Very occasionally, pressure during the relaxation phase went below atmospheric pressure (negative) (fig. 3). Pressures during contraction or relaxation generally increased when coelomic pressure increased. However, in one instance, peak pressures were unaffected by increased coelomic pressure although pressures during the relaxation phase rose markedly. In another worm, DV contractions were inhibited by large increases in coelomic pressure, but not by small changes, that is, by 10–20 cm H_2O.

In an attempt to determine the rate at which a wave of contraction passed along the DV we recorded DV pressures in two segments. Unfortunately, even when the recording sites were close together a 1:1 relation was not obtained between the pressure pulses (fig. 3), so we could not access this variable by this technique. The DV is extremely sensitive and occasionally goes into spasm when cannulated. On several occasions we noticed that waves of contraction occurred ahead of or behind a segment in which the DV was in spasm. However, it was possible to obtain an estimate of wave velocity in the DV from experiments in which earthworm Ringer was injected in the DV (fig. 4). An injection of 100 μL of Ringer solution in segment 15 caused a positive inotropic effect on DV pressure recorded in segment 7 after a delay of 7 s (fig. 4). Hence DV wave velocity was 1 segment $\cdot$ s^{-1}.

The amplitude of the pressure wave in the VV was variable. On occasion, pressure waves in the VV were large and corresponded to waves in the DV, although phase relations between the two waves were variable (fig. 5). However, it was clear that the VV wave was not smooth but resulted from the summation of multiple smaller contractions (figs. 1, 2). Furthermore, even large-amplitude waves often had smaller waves superimposed on them (fig. 5). The pressure gradient along the VV was small. Pressure waveforms recorded at segment 50 were similar to those recorded in segment 10 (fig.

TABLE 1

Pressures in the DV and VV of Megascolides australis

Animal	Mass (g)	DV			VV			F_h (min^{-1})	Temperature (°C)
		Mean (cm H_2O)	Minimum (cm H_2O)	Maximum (cm H_2O)	Mean (cm H_2O)	Minimum (cm H_2O)	Maximum (cm H_2O)		
1		23	11	57	28	24	40	6.5	20
2	53	40	13	54	21	16	53	9	
3	87	45	18	73	41	36	60	6	
4	89	20	5	37	22.5	19	37	5	23.5
5	146	15	9	31	18	16	33	5.5	20
6	126	15	5	30	26	22	30	10	20
7		9.5	5	40	10.5	6	13		19
8		21	1	68	17	7	35	9	19
9	32	23	30	66	38.7	28	50	7	19
10	31	9	5	63				9	18
11	172	23.4	8	51	14	7	24	6	19
12	211	17	7	60				6.5	20
T1	135	21.4	0	57				6.5	20
T2	121	21.5	1	43	12.8	11	16	5.5	20
T3		27	3	66	12	10	18	3	20
Average	109.4	22.1	8.1[a]	53.1[a]	21.8	16.8[a]	34.1[a]	6.8	
SD	57.3	9.8	7.8	13.9	10.1	9.4	15.0	1.9	
N	11	15	15	15	12	12	12	14	

Note. Contraction frequency of the DV is designated by F_h (contractions · min^{-1}). Animals T1–T3 were used in the ^{99m} technetium studies.

[a] Corresponding DV and VV values are significantly different.

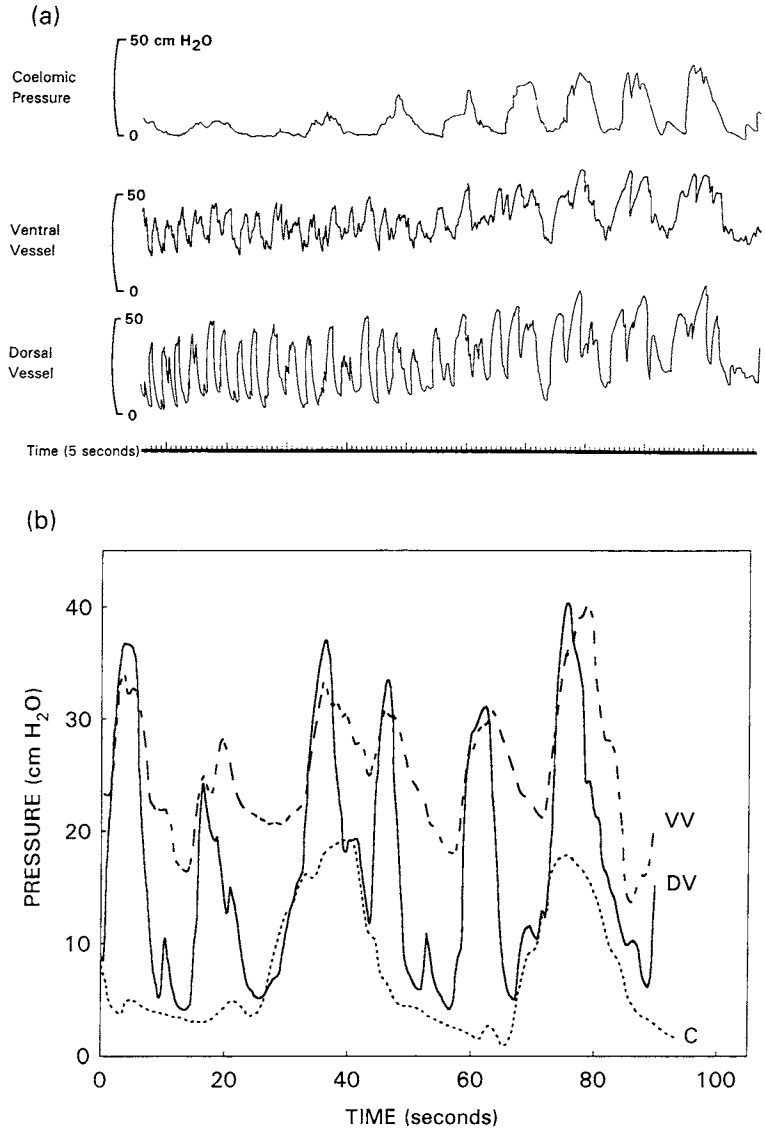

Fig. 2. a, *Pressures recorded in the coelom, DV, and VV at the anterior of a worm during peristaltic activity.* b, *A section of the above traces superimposed to show the pressure relationships.*

6). Mean pressure was reduced by 2 ± 1.67 cm H_2O ($N = 3$) between the anterior segment and segment 50.

The LHs, connecting the DV and VV, consist of multiple chambers, each one protected by valves. Pressures generated by individual chambers resembled those in the DV, but peak pressures were generally higher (fig. 7*a*, *b*). Also, vessels surrounding the gut connect the VV to the DV. Unfor-

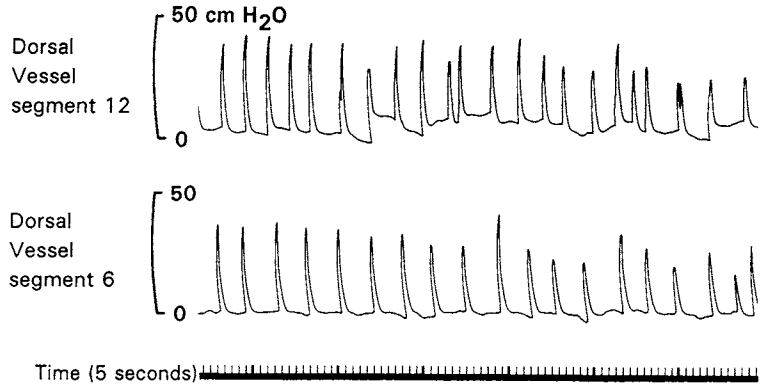

Fig. 3. Pressures recorded simultaneously from two segments of the DV. In segment 12 cannulation was non-occlusive, and it was occlusive and pointing upstream in segment 6.

tunately, pressures in gut vessels were only obtained from two animals. Gut vessel pressures were high and there were pressure oscillations, which presumably reflected oscillations in either the DV or VV (fig. 8).

Time series analysis of DV, LH, and VV pressures showed that the frequencies for maximum power of the spectral analysis were similar in seven of eight animals but varied between individuals from 3.37 · min^{-1} to 9.9 · min^{-1}. Cross-correlation of pairs of digitized DV, LH, and VV waves confirmed that the frequencies of their pressure oscillations were strongly related. In all cases R_n (the value of the normalized cross-correlation function) exceeded 0.3. Cross-correlations of DV and LH traces shown in figure 7*a* gave a value approaching 1 (fig. 7*c*). Values for R_n for LH and VV, and DV and VV were considerably weaker at 0.5. Nevertheless, values of 0.5 imply a common rhythmicity running through all traces, which in the case of figure 6 was at 7 · min^{-1}.

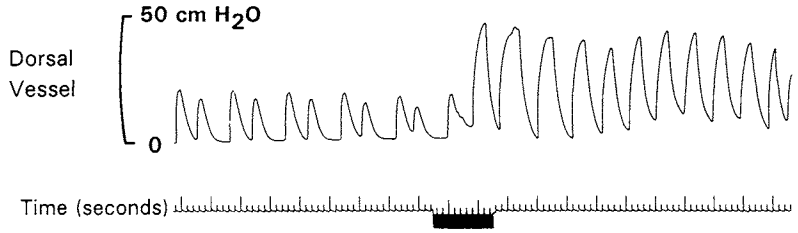

Fig. 4. Effect of injection of 100 μL of earthworm Ringer solution (at mark on time trace) into the DV (segment 15) on DV pressures recorded in segment 7. Wave velocity in the DV was approximately 1 segment · s^{-1}.

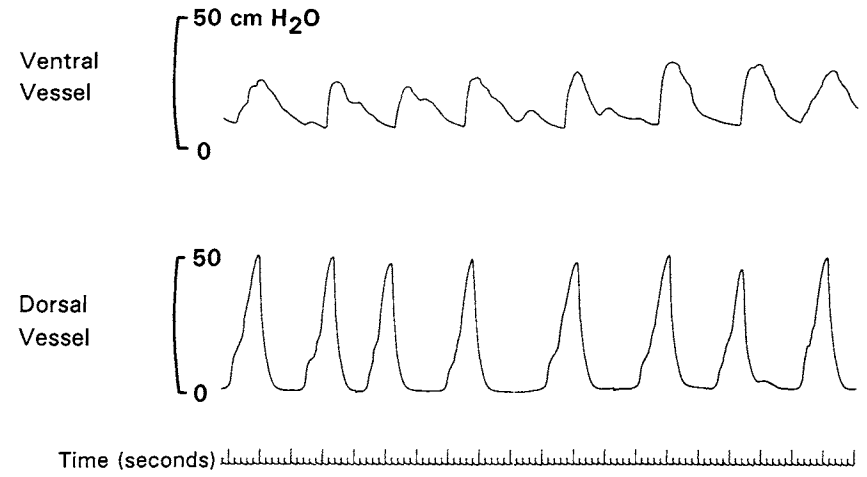

Fig. 5. Pressures recorded simultaneously in the VV and DV displaying common rhythmicity.

Pressure Response to Orthostasis and Body Transection

In virtually all worms the effect of an orthostatic load on the circulation was tested by raising or lowering the tail. Raising the tail by as much as 1 m had no effect on DV or VV pressures measured in anterior segments. However, in early experiments the anterior segments remained horizontal during tail elevation so there was a right-angle bend in the worm, which might have occluded the vessels. Hence, in later experiments the worms were suspended vertically from the head or tail. Even so, there was no effect on recorded pressures in the anterior segments.

Spontaneous autotomy of the hindmost segments is a characteristic feature of these worms so we tested the effects on the anterior circulation of transecting the body. Repeated whole body transection appeared to have no short-term effects on the circulation unless it was performed in the anteriormost segments (segments 5–20) when circulatory collapse ensued.

The Pattern of the Circulation

In three worms, 0.5–1 mCi of ^{99m}technetium was injected into the DV in segments 6 or 7. The volume injected was 100–200 μL. Injection artifacts were assessed by using the saline vehicle. Injection of 100–200 μL of saline caused an increase in both the peak pressure and frequency of contraction in the DV (fig. 4).

Within 2–3 min after injection, the label was distributed throughout the anterior segments (fig. 9*a*). After 4–5 min the label could be seen moving

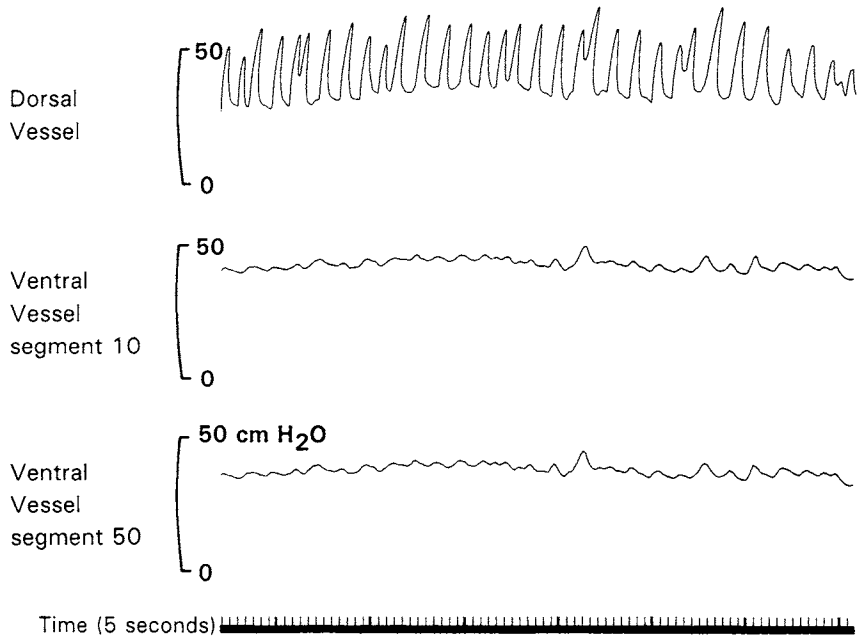

Fig. 6. Pressures recorded simultaneously in the DV and at two locations in the VV 40 segments apart. The VV waveforms are similar, and there is only a slight decline in pressure between segments 10 and 40.

along the VV (fig. 9). By 10–12 min after injection ^{99m}technetium label had reached about segment 40 (fig. 9*b*, *c*) and the label could be seen moving from the VV to the DV and penetrating further along the VV (fig. 9*c*). Scans were usually stopped after 25–30 min, when the label had traversed about one-third of the worm.

Discussion

The tracer experiments, using ^{99m}technetium, have shown that the circulation in the giant earthworm consists of two compartments: an anterior compartment, involving about the first 15 or so segments in which the circulation is rapid, and the posterior section of the body, in which the circulation is exceptionally slow. Obviously, this situation could not be deduced from pressure recordings alone and was not remarked upon by Johansen and Martin (1965), who supported their recordings of intravascular pressures with angiographic studies. However, with hindsight, their successive roentgen frames display a marked loss of resolution in the anterior end of *Glossoscolex giganteus,* which could have been brought about by more rapid and widespread circulation in the anterior compartment.

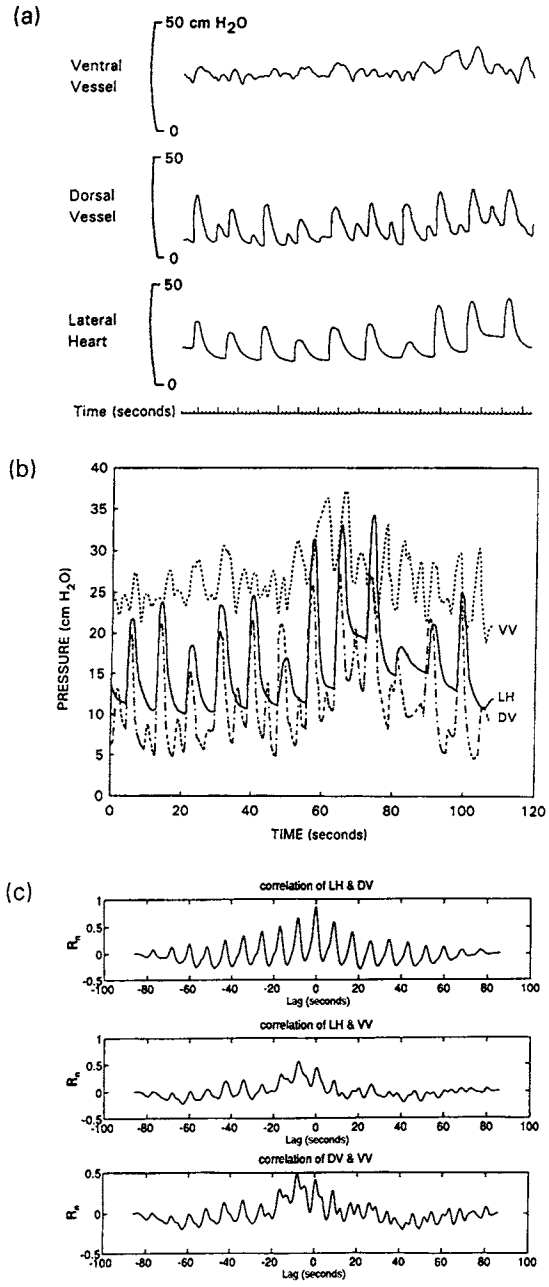

Fig. 7. a, *Pressures recorded simultaneously in the DV, VV, and in an LH.* b, *Superimposition of the three pressures shown in part* a. c, *Cross-correlation of pairs of pressure waveforms shown in part* a. *Upper panel, DV and LH, showing a strong correlation at a predominant frequency of 7 · min^{-1}. For the cross-correlations of LH and VV (middle panel) and DV and VV (lower panel) the correlation is weaker, although the predominant frequency is the same for DV, LH, and VV.*

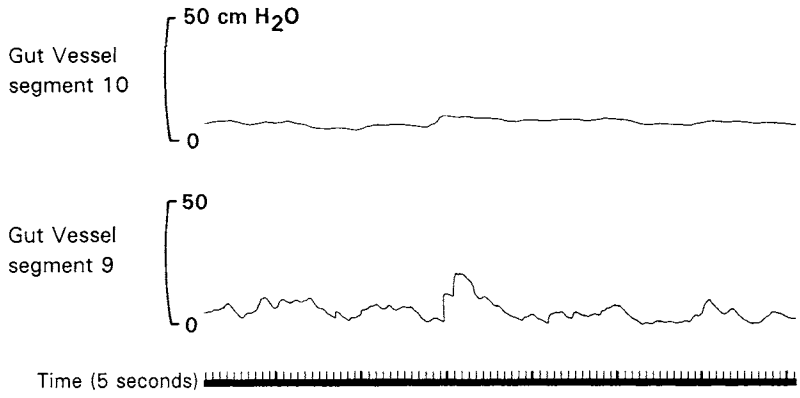

Fig. 8. Pressures recorded simultaneously from gut vessels in two segments.

The classic work on the circulation in the earthworm, *Lumbricus,* was done by visual observation by Johnston and Johnson (1902) and Johnston (1903). The direction of the circulation was adequately revealed by their observations and is supported by the present experiments. However, it is not known whether the pattern of fast and slow circulatory compartments is common to all earthworms or only occurs in giant representatives such as *Megascolides.*

The VV is the major distributing vessel for both the fast and slow circulations. The VV is narrow and unvalved although the pressure gradient along its length is small, due to the low flow. Obviously, it is the gut and cutaneous vessels that provide the major flow resistance in the posterior end of the body. Johansen and Martin (1965) suggested that one set of segmental vessels arising from the DV also supplied the capillary circulation. This contrasts with the view of Johnston and Johnson (1902), who argued that the position of the valves in the dorsal segmental vessels of *Lumbricus* means that these vessels are afferent to the main DV. Hence, in their view the VV supplied all subsidiary segmental circuits. Our own observations agree with this interpretation, for in segments in which the DV was in stasis all segmental vessels connecting to the DV were greatly swollen with blood.

In the anterior region of the body (segments 6–13), the DV and VV are connected by paired LHs. Each lateral heart itself consists of up to 10 chambers, with valves between each chamber. In contrast, the LHs of *Lumbricus* are muscular tubes with a narrow dorsal and ventral bulbous portion (Johnston 1903). In fact, the classic study on the anatomy of *Megascolides* by Spencer (1889) also diagrammed the LHs as large commisures, which contrasts with our observation that the LHs resemble a "string of sausages" that

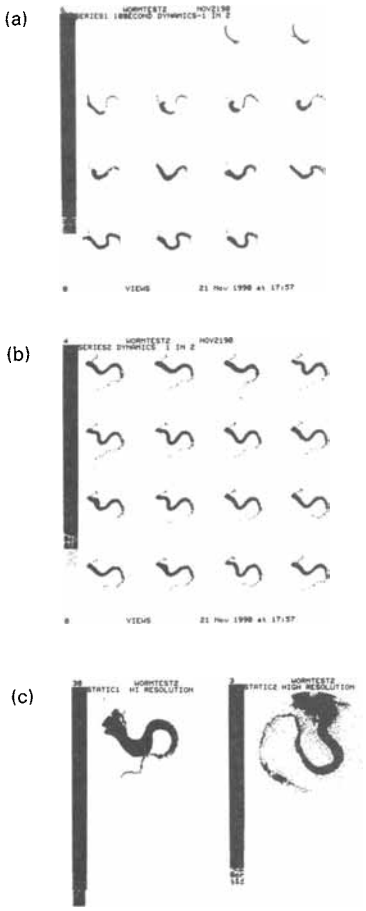

Fig. 9. Gamma camera images tracing the distribution of ^{99m}technetium injected into the DV at the anterior end of the worm. The injection period was 40 s. a, *Dynamic traces (10-s resolution), every other one being displayed. The first image (upper panel, first row, third column) shows the outline of the injection cannula. Time progresses left to right and top to bottom.* b, *Dynamic traces starting about 1.5 min after the last image in part* a. *(c) high-resolution traces (1-min resolution) taken between parts* a *and* b *(left) and after the last image in part* b *(right). The blurring of these images, particularly on the right, was caused by movements of the worm and excretion of ^{99m}technetium.*

meander around the segment, being three to four times longer than a direct connection between the DV and VV requires.

It is the contractile activities of the DV and LHs which contribute to the rapidity of flow in the anterior circulation. Consequently, the connections

between the VV and DV must be of low resistance in the anterior region. In fact, pressures in the gut vessels of the anterior segments are high (5–10 cm H_2O), which, this being a high-flow area, indicates low-resistance connections to the VV. In essence, the earthworm circulation is analogous to the situation in a vertebrate in which a major shunt between artery and vein is opened at the top of a limb. Limb blood flow continues but flow in the central circulation is greatly enhanced because cardiac output is increased enormously (Burton 1972).

The DV in each segment is contractile. The DV is valved at the intersegmental septa and connects to eight pairs of LHs, anteriorly. In segments 9–13 the LHs are also supplied by a major gut vessel, whereas the LHs in segments 6–9 arise solely from the DV. In earthworms, a peristaltic wave passes anteriorly along the DV, and we confirmed this by visual observation. However, apparently the wave was not arrested at segments that were in spasm, although it is possible that a new wave arose on the rostral side of the spastic region. In this respect, Stübel (1909) believed that all parts of DV could initiate contraction. The contraction frequency of $6.8 \pm 1.9 \cdot \text{min}^{-1}$ in *Megascolides* is similar to that of the giant earthworm *Glossoscolex* (Johansen and Martin 1965) but lower than rates generally recorded in the smaller *Lumbricus terrestris* at similar body temperatures (Stübel 1909; Fourtner and Pax 1972; Drewes et al. 1981). However, in our experiments, DV contraction frequency was somewhat labile as was shown by pressure recordings made in two segments, so it may be that comparisons of DV contraction frequencies in earthworms is of little heuristic value. Similarly, our estimate for the velocity of the wave of contraction of 1 segment $\cdot s^{-1}$, although similar to that recorded by Haffner (1927) in *Lumbriculus,* is only one-twelfth that obtained by Johansen and Martin (1965) in *Glossoscolex.* Obviously, more data are required for this variable from other annelid species.

The neurogenic versus myogenic origin and conduction of DV rhythmicity has been the subject of discussion for nearly a century (Stübel 1909; Gaskell 1919; Aoki 1930; Prosser and Zimmerman 1943; Fourtner and Pax 1972; Drewes et al. 1981). The strongest evidence for myogenicity comes from intracellular activity patterns in intact and isolated vessels (Drewes et al. 1981). Ramplike depolarizations occur during filling, and Drewes et al. (1981) suggest that stretching may be an important feature in inducing the ramp. Allied to the observations of Fourtner and Pax (1972) that DV beating frequency was slowed by occlusion and increased by increasing intraluminal pressure, Johansen and Martin's (1965) suggestion that DV filling might control both rate as well as force of contraction seems supported. However, our own observations suggest that

the influence of stretch on force predominates over that on frequency (fig. 4). Furthermore, intraluminal DV pressures often fell throughout the noncontraction phase and even went negative on occasion, which suggests considerable variation in stretch of the wall of the DV which had no overt effect on frequency of contraction.

Rhythmic pressure waves occur in all parts of the circulation. It is tempting to suggest that these waves originate in the DV and are transmitted to the VV by the LHs. Certainly, the high degree of correlation for the cross-correlation between DV and LH pressure waves supports this view for the collecting and propulsive vessels. In fact, this result is not unexpected, for many authors reported that DV and LHs beat in perfect synchrony (Biedermann 1904; Stübel 1909; Haffner 1927; Aoki 1930; Stephenson 1930) although later work was often contradictory (Prosser and Zimmerman 1943; Johansen and Martin 1965; Fourtner and Pax 1972). In addition, spectral analysis of the waveforms showed that similar frequencies occurred in DV, LHs, and VV while cross-correlation analysis revealed that the pressure waveforms in DV and LHs, DV and VV, and LHs and VV were well correlated. This suggests that there is a fundamental rhythmicity to the waves of contraction traversing the annelid circulation, although the precise relationships existing throughout the circulation are labile.

Mean pressures in the DV and VV were similar and peak pressures in the DV often exceeded those in the VV, providing an apparent pressure gradient for flow. Pressures in the DV were higher and pressures in the VV much lower than those recorded by Johansen and Martin (1965) in *Glossoscolex.* In theory, only the pressure in the last segment of the lateral hearts needs to exceed VV pressure, but in practice the pressure relations we recorded were reassuring. In contrast, Johansen and Martin (1965) never recorded a pressure in the DV or LHs that exceeded that in the VV.

Johansen and Martin (1965) attributed large VV pressure waves in *Glossoscolex* to synchronous contractions of the LHs. It is possible that this occurs in *Megascolides* because the LHs have fewer chambers in the most anterior segments. So if a wave of contraction is set in train by DV peristalsis, moving posterior to anterior, then it is possible that the last segments of all pairs of LHs will empty synchronously. However, the chambers of the LHs are bigger in the posterior segments and receive blood from both the DV and gut. It seems more likely that these LHs will dominate in terms of both pressure and flow generation in the VV. Certainly, the VV pressure waves are not smooth; a number of smaller waves contribute to the formation of the dom-

inant pressure profile in the VV, indicating asynchronous emptying of LHs into the VV.

Raising or lowering the tail caused no marked or consistent changes in DV or VV pressure. The DV is valved segmentally, which could ameliorate some of the orthostatic effects. However, the VV has no valves. The VV is narrow but is definitely not a resistance vessel, the pressure drop along its length being small. Consequently, it must be capable of being shut off in response to a positive or negative orthostatic load. Johansen and Martin (1965) found the muscular elements in the VV were well developed and suggested that they played a role in vasoactive adjustments. Whether these muscular elements play a role in orthostasis is unknown. We felt that an indirect indication of VV closure would be an increase in the VV oscillations as the overall volume of the VV would be reduced. In fact, this was observed on a couple of occasions but the effect was not consistent. A method to minimize orthostatic effects might be expected in an animal whose burrows are frequently oriented vertically, and the method by which it is achieved is worthy of further investigation. Also, autotomy is a characteristic shared by many earthworms and the value of autotomy occurring in the region of the slow circulatory compartment is obvious. In this respect, Martin and Johansen (1992) report that the blood volume of autotomized *Glossoscolex* was actually higher than the average blood volume of intact worms, which indicates no appreciable blood loss.

Motor activity by the worms had a considerable affect usually on both minimum and peak pressures. Since the DV has valves at each intersegmental partition, changes in coelomic pressure due to motor activity will be transmitted across the DV wall. However, the VV lacks valves and changes in coelomic pressure in one region would be expected to be dissipated throughout the whole volume of the VV, reducing pressure changes due to motor activity. This was the case on some occasions but not on others, perhaps another indication that the VV is capable of extreme vasomotor action.

This research adds to the considerable body of work on the circulation in the earthworm and extends it in several areas. An important contribution is our finding of fast and slow circulatory compartments. What is not known is how unique the circulatory situation in this giant representative is compared with its more common and garden relatives. In the giant worm the anterior segments contain many vital organs, cerebral ganglia, salivary glands, gizzard, reproductive organs, and small nephridia, whereas the posterior segments are very similar morphologically and subserve nutritive, excretory, and respiratory functions. Hence the circulation may be viewed as compartmentalized to serve vital (fast) and vegetative (slow) functions.

Acknowledgments

This research was supported by operating and equipment grants from the Natural Sciences and Environmental Research Council of Canada (NSERC; to D.R.J.), the Agricultural Research Council (ARC; to B.K.E.), and the University of Melbourne. Travel and maintenance support was provided by NSERC (to D.R.J. and P.G.B.) and the University of Melbourne (to D.R.J.). We are grateful to the staff of the Gippsland Giant Earthworm Museum for help on the "digs" and for advice on maintaining the worms in captivity. Frazer Hercus, Douglas Gimesy, Richard and Michael Hardwick, and Dailan Evans assisted on the digs. D.R.J. and P.G.B. are thankful to Colin and Marian Hardwick for providing social "support" on our visits to Melbourne. Finally, we are grateful to Yeh Yuan for the time series analysis, Geoff Gabbott for preparing the figures, and Linda Kachur for typing the manuscript.

Literature Cited

Aoki, K. 1930. Preliminary studies on the physiology of the pulsating blood vessels of the earthworms. Sci. Rep. Tohoku Univ. 5:717–738.

Biedermann, W. 1904. Studien zur vergleichenden Physiologie der peristaltischen Bemegungen. I. Die peristaltischen Bemegungen der und Würmer der Tonus glatter Muskeln. Pflügers Arch. 102:475–542.

Burton, A. C. 1972. Physiology and biophysics of the circulation. 2d ed. Year Book Medical Publishers, Chicago.

Drewes, C. D., M. R. Denney, B. O'Gara, and E. P. Vining. 1981. Intracellular recording of electrical activity in muscle cells of intact and isolated dorsal blood vessel of the earthworm *Lumbricus terrestris*. J. Exp. Biol. 93:149–165.

Fourtner, C. R., and R. A. Pax. 1972. The contractile blood vessels of the earthworm, *Lumbricus terrestris*. Comp. Biochem. Physiol. 42A:627–638.

Gaskell, J. F. 1919. Adrenalin in annelids. J. Gen. Physiol. 2:73–85.

Haffner, K. von. 1927. Untersuchungen über die Morphologie und Physiologie des Blutgefasssystems von *Lumbriculus variegatus* Mull. Z. Wissenschaftliche Zool. 130:1–82.

Johansen, K., and A. W. Martin. 1965. Circulation in a giant earthworm, *Glossoscolex giganteus*. J. Exp. Biol. 43:333–347.

Johnston, J. B. 1903. On the blood vessels, their valves and the course of the blood in *Lumbricus*. Biol. Bull. 5:74–84.

Johnston, J. B., and S. W. Johnson. 1902. The course of the blood flow in *Lumbricus*. Am. Nat. 36:317–328.

Jones, D. R. 1970. Experiments on amphibian respiratory and circulatory systems. Exp. Physiol. Biochem. 3:233–293.

Martin, A. W., and K. Johansen. 1992. Circulation in the giant earthworm, *Glossoscolex giganteus*. Pages 315–325 in Stephen C. Wood et al., eds. Physiological adaptations in vertebrates: respiration, circulation, and metabolism. Dekker, New York.

PANTIN, C. F. A. 1962. Notes on microscopical techniques for zoologists. Cambridge University Press, London. 77 pp.

PROSSER, C. L., and G. L. ZIMMERMAN. 1943. Effects of drugs on the hearts of *Arenicola* and *Lumbricus*. Physiol. Zool. 16:77–83.

SPENCER, B. W. 1889. On the anatomy of *Megascolides australis,* the giant Earthworm of Gippsland. Trans. R. Soc. Victoria 1:2–60.

STEPHENSON, J. 1930. The Oligochaeta. Oxford University Press, Oxford. 978 pp.

STÜBEL, H. 1909. Studien zur vergleichenden Physiologie der peristaltischen Bemegungen. IV. Die Peristaltik der Blutgefässe des Regenwurmes. Pflügers Arch. Gesamte Physiol. Menschen Tiere 129:1–34.

YAMAMOTO, Y., and R. C. HUGHSON. 1991. Coarse-graining spectral analysis: a new method for studying heart rate variability. J. Appl. Physiol. 71:1143–1150.