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The Control of Hindgut Motility in the Lobster *Homarus gammarus* (L.)

3. Structure of the Sixth Abdominal Ganglion (6 A.G.) and Associated Ablation and Microelectrode Studies

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1. The structure of the sixth abdominal ganglion (6 A.G.) of *Homarus* has been determined using light microscopy. The ganglionic cortex is divided into anterior and posterior ventral lobes. A pair of dorsal lobes arises from the posterior ventral lobe. Four pairs of commissures cross the ganglion and six pairs of nerves arise from it.

2. The 6 A.G. is suggested to have been derived from three fused ganglia – the sixth and seventh abdominal ganglia and a terminal ganglion. Evidence is presented to support this hypothesis.

3. Lesion and ablation experiments were carried out on the 6 A.G. Motor activity from the posterior intestinal nerves (P.I.N.'s) is elicited by the activity of at least two pairs of interneurones (I1 and I2) which decussate in the 6 A.G. The somata of neurones controlling the defaecatory response are located in the anterior region of the posterior ventral lobe.

4. Cells producing unitary and bursting motor discharge down the P.I.N.'s were penetrated using glass microelectrodes. Three types of neurones are thought to be located in the hindgut control network at the level of the 6 A.G. These are unitary and bursting motor neurones and driver interneurones.

5. Our present knowledge of the hindgut control system of *Homarus* is summarised and compared with the system in the cockroach, *Periplaneta americana*.

INTRODUCTION

The sixth abdominal ganglion (6 A.G.) of *Homarus gammarus* exerts a considerable degree of control over the hindgut with respect to defaecation (Winlow and Laverack, 1972.1,2). Hindgut movements, however, are thought to be under the ultimate control of centres lying in the brain. These centres

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communicate with the 6 A.G. via a number (probably three) of paired interneurones which elicit motor output to the hindgut from groups of neurones within the 6 A.G. Two distinct neural networks have been postulated (Winlow and Laverack, 1972.2), the one producing a non-repetitive discharge and the other a bursting discharge.

It has recently been demonstrated in the lobster, *Homarus americanus*, that there is a high degree of constancy in the size, position and connections of any individual neurone (Otsuka, Kravitz and Potter, 1967). Cohen and Jacklet (1967) have shown that axons passing out through the same root of the metathoracic ganglion of the cockroach, *Periplaneta americana*, tend to be grouped in clusters, whilst Bentley (1970), working on the locust flight system, has demonstrated that the somata of functionally similar neurones innervating the same muscle lie adjacent to one another and their fibres remain in a compact bundle throughout the neuropile. Kandel and Wachtel (1968) have suggested that the somata of neurones controlling the various organs and muscles supplied by the abdominal ganglion of the gastropod mollusc, *Aplysia*, are grouped according to the organs which they supply. The neurones of these groups not only have different embryonic origins from one another, but in addition all those within a particular region show similar responses to a given transmitter.

Thus in invertebrates "the biochemical and functional properties of neurones correlate well with the topographical location of their somata" (Kandel and Kupfermann, 1970) within the ganglionic cortex. From this evidence it would seem that the somata of functionally similar cells innervating a given muscle, such as the circular muscle coat or the longitudinal muscle strands of the hindgut of *Homarus gammarus*, might lie in positions adjacent to one another.

As a preliminary to initiating intracellular microelectrode studies of the 6 A.G. in relation to hindgut function, we have attempted to define the general region in which the cell bodies of neurones controlling the hindgut lie. In order to do this it was first necessary to obtain a basic knowledge of the structure of the 6 A.G. Several authors have described the ganglion (Krieger, 1880; Retzius, 1890; Johansson and Schreiner, 1965), but none has given a particularly lucid or full account of its histological structure. All comment on the presence of a pair of dorsal groups of cell bodies in the posterior region of the ganglion and Horridge (1965) equates these with centres controlling hindgut function.

Following elucidation of the structure of the 6 A.G. it became possible to ablate various regions and to test the effect on the normal motor discharge to the hindgut. After this we proceeded with microelectrode studies of the region of ganglionic cortex which seemed to contain the somata of neurones associated with the defaecatory response.

MATERIALS AND METHODS

A. Anatomy of the Sixth Abdominal Ganglion

Specimens of the 6 A.G. were dissected out from *Homarus gammarus* and treated histologically by the methods outlined previously (Winlow and Laverack, 1972.1). Serial sections were cut in the three major planes and stained using either Azan or Mallory's triple stain. The sections cut in T.S. were then photographed and from the ensuing prints a model of the ganglion was constructed.

B. Ablation of the 6 A.G.

Two types of ablation experiment were performed on the 6 A.G. after its exposure and subsequent desheathing. First, the ganglion was split medially from anterior to posterior, using a fine scalpel. In the second series of experiments lesions of specific areas of the ganglionic cortex were induced using a heat probe constructed from fine tungsten wire (0.005 inch diameter) through which current was passed from a six volt power supply.

Prior to the induction of experimental lesions the abdominal ventral nerve cord (V.N.C.) was always crushed at the level of the 1–2 abdominal connectives. In normally functioning preparations this elicits co-ordinated hindgut movements. Preparations not giving a normal response were rejected. Following the lesions recordings of both spontaneous activity and activity evoked by stimulation of the V.N.C., were made from the posterior intestinal nerves (P.I.N.'s) and any changes in motor discharge as compared with the normal pattern (Winlow and Laverack, 1972.2) were noted. Finally the ganglion was prepared for light microscopy and the precise location of the induced lesion was determined. All experiments were carried out twice and in most cases three times.

C. Intracellular Stimulation of the Ganglionic Cortex

Stimulation of neurone somata in the region of the "hindgut control system" as localised by ablation and lesion experiments was carried out using 2 M. KCl filled glass microelectrodes of 15–20 megohm tip resistance. The desheathed ventral somata of the 6 A.G. were illuminated using a perspex light guide attached to a Prior high intensity dissection lamp. The microelectrodes were mounted on a Narashige micromanipulator and used to probe the cells of the ventral cortex. Shifts of tip potential on entry into neurone somata were displayed on the oscilloscope via a Bak high impedance preamplifier with a gain of one. Once entry into a soma was achieved positive going rectangular pulses were applied through the Bak bridge.

RESULTS

A. Structure of the 6 A.G.

The last abdominal ganglion is the most complex in *Homarus*. There are six pairs of nerves originating from the ganglion. These are, from anterior to posterior:

N1 – anterior nerves (to swimmerets)
N2 – uropod nerves
N3 – ventral telson nerves
N4 – dorsal telson nerves
N5 – anal nerves
N6 – posterior intestinal nerves.

This nomenclature is derived from Keim (1915) except for N6 which was named by Alexandrowicz (1909). The structure of the ganglion is summarised in Figure 1. The zero mark for the scale given on Figure 1(A) is taken as the point at which the 5–6 connectives become fused into the sheath of the 6 A.G. The 200 mark is taken as the most posterior part of the ganglionic sheath.

1. *Non-nervous components of the ganglion*

Externally the 6 A.G. is bounded by a tough connective tissue sheath directly beneath which is a layer 100–200μ deep of highly vacuolated tissue of unknown function. This tissue completely packs the space between the connective tissue sheath and the nervous elements of the ganglion, except in the region of the non-vascular space which lies in the anterior dorsal region of the ganglion. This space is large, extending into the connectives and partially surrounding the anterior neuropile (Figure 1(B) to 1(D)). Injection of indian ink or methylene blue into the heart which is followed by disposal of the dye through the blood vessels of the animal reveals that this space in the ganglion is not of a vascular nature.

The blood supply to the 6 A.G. takes the form of several major sinuses from which are derived numerous capillaries that run through the neuropile and supply the neurone somata. The sinuses arise from a large median dorsal blood vessel which passes into the 6 A.G. from the anterior border and then gives rise to a ventral going vessel (Figure 1(B)). This vessel then bifurcates and the branches lie dorsal to the main mass of ventral cell bodies, forming the ventral sinus. This ventral sinus extends over the entire dorsal surface of the ganglionic cortex and wraps around the dorsal groups of cell bodies (Figure 1(G)). It is interrupted, at many points, by neurone tracts passing from the cortex (Figure 1(B), (E) and (F)). In the anterior region of the ganglion there is a major dorsal sinus, interposed between the non-vascular space and the neuropile, arising directly from the median dorsal blood vessel. This sinus

eventually peters out between scale marks 140 and 150, at the posterior limit of the neuropile. At several points the sinuses almost come to surround the neuropile (Figure1 (C), (D) and (F)). Many capillaries ramify throughout this region and appear to originate from the two major sinuses. The ventral sinus branches into the ganglionic cortex and these branches can often be seen to envelop individual cell bodies. Posteriorly the dorsal vessel is reconstituted and carries blood away from the ganglion.

2. *The ganglionic cortex*

For the most part the cortical region of the 6 A.G. lies ventral to the neuropile and nerve tracts of the ganglion. It is divided into anterior and posterior collections of neurone somata (Figures 1(A) and 2), joined by a narrow "waist" of cell bodies. Dorsal to the anterior ventral cortical lobe and lying between the dorsal sinus and the neuropile is a pair of superficial median dorsal cell bodies (Figure 1(A) and (C)) arranged in tandem. A further single isolated cell body, the deep dorsal cell body, lies ventral to the more superficial pair, directly below the most ventral division of the first commissure. It is about 10μ in diameter.

From the posterior ventral lobe there arises a symmetrically arranged pair of dorsal lobes (Figure 1(F) and (G)). These groups of cell bodies are found in the most posterior region of the ganglion. They lie lateral to the origins of the P.I.N.'s and wrap over their fibre tracts dorsally.

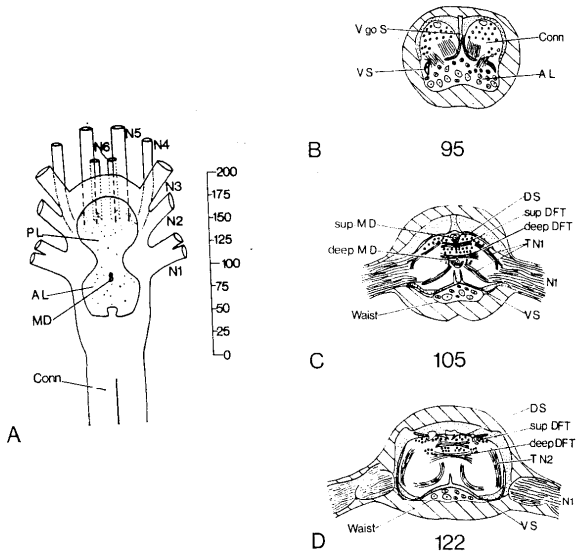
There are many large neurone somata in the cortex, some of which may reach 80–90μ in diameter (see Figure 1(G)), but the majority of cell bodies are between 10μ and 50μ in diameter in an average sized lobster.

3. *The neuropile*

Most of the neuropile proper lies between the first and fourth commissures (scale marks 100 to 155). Anterior to the first commissure (Figure 1(B)) the 5–6 connectives enter the ganglion and break up into tracts many of which pass ventrally to the anterior ventral lobe, whilst a smaller number travel dorsally into the posterior region of the ganglion. Posterior to the fourth commissure (Figure 1(G) and (H)), the neuropile gives way to the various nerve tracts which run out posteriorly. Many nerve tracts and several commissures can be discerned within the neuropile, as can the origins of the major nerve trunks.

a) *Commissures and tracts* Four groups of commissures lie within the neuropile and these are divisible into eight individual groups of fibres traversing the ganglion. The positions of these commissures are summarised in Table I.

In addition to the commissures there are numerous tracts running within the neuropile. The most obvious of these are shown in Figure 1(C) and (D).



Neurone somata.

Tracts and commissures:

a) In T.S.

b) In L.S.

Vacuolated tissue.

Non vascular space.

Blood vessels.

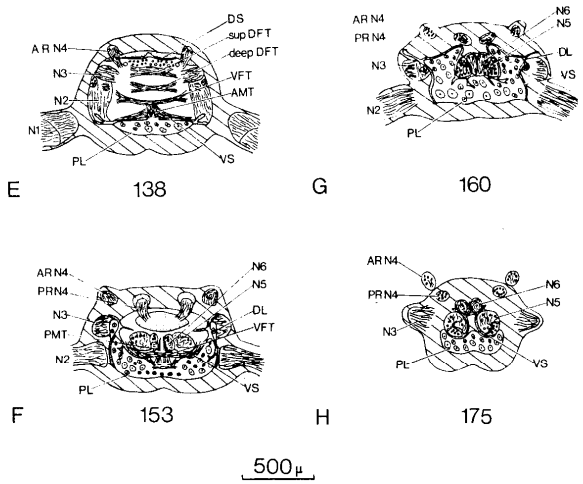


FIGURE 1

(A) Diagrammatic view of the ventral surface of the 6 A.G.
The region of light stippling denotes the ventral cell bodies, whilst the heavy stippling indicates the position of the dorsal cell bodies.
The scale marker is equivalent to 200 × 10μ transverse sections so that 200 = 2 mm. It is used as a reference scale in Figures (B) to (H).

(B) to (H) Each drawing is a diagrammatic representation of a T.S. through the ganglion in the position indicated by the scale number (corresponding to the scale in Figure 1(A)).

Standard abbreviations used are as follows for both Figures 1 and 2.

Neurone Somata

A.L.	– anterior lobe of ventral cell bodies.
P.L.	– posterior lobe of ventral cell bodies.
D.L.	– dorsal lobes of cell bodies arising from the posterior ventral cortex.
deep M.D.	– deep median dorsal cell body.
sup. M.D.	– superficial median dorsal cell bodies.
Waist	– narrow waist of neurone somata connecting anterior and posterior ventral ganglion cortices.

Tracts

conn	– connectives.
N1	– anterior nerve.
N2	– uropod nerve.
N3	– ventral telson nerve.
N4	– dorsal telson nerve.
A.R. N4	– anterior root of N4.
P.R. N4	– posterior root of N4.
N5	– anal nerve.
N6	– posterior intestinal nerve.
T. N1	– tracts to N1.
T. N2	– tracts to N2.
A.M.T.	– anterior median tract.
P.M.T.	– posterior median tract.

Commissures

deep D.F.T.	– deep dorsal fibre tract.
sup. D.F.T.	– superficial dorsal fibre tract.
V.F.T.	– ventral fibre tracts.

Blood Vessels

D.S.	– dorsal sinus.
V.S.	– ventral sinus.
V. go. S.	– ventral going sinus derived from median dorsal blood vessel.

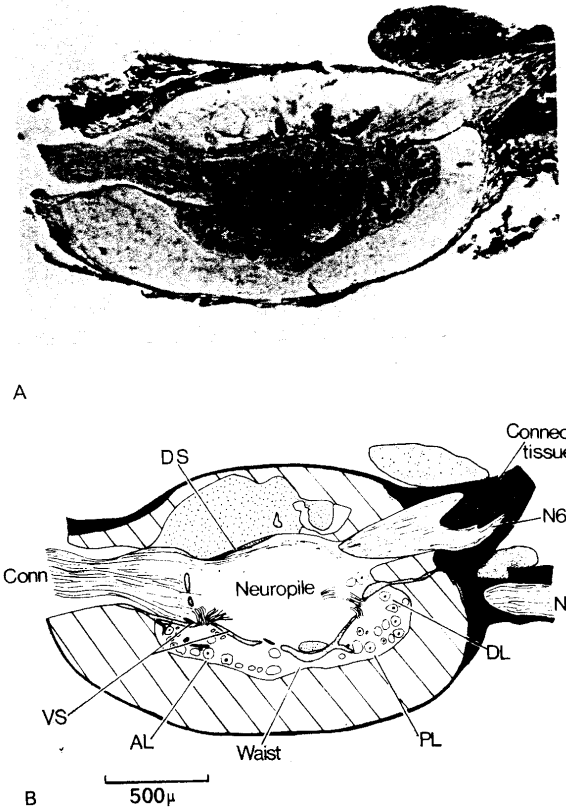


FIGURE 2 L.S. of 6 A.G. 25μ to the left of the midline.

(A) Mallory stained section.

(B) Diagrammatic representation of (A).

Abbreviations and shading as for Figures 1(B) to 1(H).

TABLE I

Commissure	Fibre tracts	Position relative to regions of neurone somata	Scale mark as on Figure 1(A)	See Figure
1st	a. Superficial dorsal b. Deep dorsal	Dorsal to waist	105	1(C)
2nd	a. Superficial dorsal b. Deep dorsal	ditto	120	1(D)
3rd	a. Superficial dorsal b. Deep dorsal c. Ventral	Dorsal to anterior region of posterior ventral lobe	140	1(E)
4th	Ventral	ditto	155	1(F)

They are on the whole symmetrically arranged and those in Figure 1(C) appear to run into the anterior nerve (N1) to the swimmeret musculature, whilst those in 1(D) are thought to be involved in the formation of the uropod nerves (N2). Two major medial tracts also occur; the anterior one ascending at the level of the third commissural group (Figure 1(E)). The posterior median tract lies posterior to the fourth commissure (Figure 1(F)) and many of the fibres ascend towards the origins of the P.I.N.'s which are already well formed.

b) *The origins of the nerve trunks within the 6 A.G.* The derivation of the main trunks is summarised in Table II. The anterior nerves divide into posterior and anterior branches soon after leaving the ganglion. The dorsal telson nerve is, however, more unusual in that it arises from two different roots which pass out separately from the posterior dorsal surface of the ganglion and then fuse. The P.I.N.'s arise medial to the anal nerves and from much the same region of the neuropile. They accompany the anal nerves for some way before passing from the posterior dorsal surface of the ganglion to supply the hindgut.

Many of the external features of the ganglion outlined here are quite variable, especially the positions of exit of the dorsal telson nerves and the P.I.N.'s. In all other respects the structure of the 6 A.G. is constant from animal to animal, especially with regard to the position of the neurone somata and the various commissures.

B. Effect of the Ablation of the 6 A.G.

1. *Splitting of the ganglion*

It was initially hoped that the ganglion could be split transversely at progressively more posterior positions in successive preparations. The damage caused to the ganglionic cortex by splitting further than about the level of

TABLE II

Nerve trunk	Region of origin and scale mark	Direction and point of exit (scale mark)	See Figure
Anterior N. (N1)	1st commissure 95–110	Laterally 95–120	1(C)
Uropod N. (N2)	2nd and 3rd commissure Mainly in lateral ventral neuropile 120–140	Obliquely posteriorwards 150–160	1(D) and (E)
Ventral Telson N. (N3)	3rd commissure Derived from lateral dorsal neuropile ventral to the anterior root of N4 135–140	Very oblique 170–180	1(E) to (H)
Dorsal Telson N. (N4): Anterior Root	3rd commissure Arises from lateral dorsal neuropile 135–140	Posteriorly 200	1(E) to (H)
Posterior Root	4th commissure Rudiments lie in dorsal neuropile medial to anterior root 145–155	Posteriorly 200	1(F) to (H)
Anal N. (N5)	4th commissure Arises in ventral neuropile lateral to to P.I.N.'s. 150–155	Posteriorly 200	1(F) to (H)
Posterior Intestinal N. (N6)	4th commissure Originates in ventral neuropile medial to anal nerves 150–155	Posteriorly 200	1(F) to (H)

of the first or second commissure (scale marks 105–122, with reference to Figure 1(A)), proved too great for us to detect any consistent effects on motor output. Splitting from the posterior end forward also caused much unwanted damage. The results which are summarised in Table III are limited to four experiments in which the ganglion was split longitudinally in the midline from anterior to posterior.

In all cases it proved impossible to elicit the normal defaecatory response after inducing the lesions which were, in all but the first instance, to the level of the first commissure only. After creating the lesion, normal paired spontaneous activity remained in the P.I.N.a.'s. This is shown in Figure 3, which is taken from experiment 4. However, it was impossible to either modulate the activity of these units or cause burst formation by stimulation of either connective in any of the experiments. That interneurones causing bursting

TABLE III

Experiment	Commissure(s) severed	Hindgut movements elicited by crushing V.N.C. 1. Prior to lesion	Hindgut movements elicited by crushing V.N.C. 2. After lesion	Occurrence of hindgut movements as lesion made	Activity in P.I.N.a.'s 1. Spontaneous (paired)	Activity in P.I.N.a.'s 2. Due to stimulation of V.N.C. a. Bursting	Activity in P.I.N.a.'s 2. Due to stimulation of V.N.C. b. Unitary
1	1st and 2nd	+	±	±	+	−	+
2	1st	+	−	+	+	−	−
3	1st	+	−	+	+	−	−
4	1st	+	±	+	+	−	+

The effect, on hindgut movements and motor activity down the P.I.N.a.'s, of splitting the 6 A.G. anteriorly in the midline.
+ indicates the presence of a particular kind of neural activity, or hindgut movements.
− indicates the absence of the above phenomena.
± indicates the presence of very weak hindgut movements.

FIGURE 3 Spontaneous activity in the P.I.N.a.'s recorded from a split ganglion preparation. Continuous trace. This recording was made from the preparation used in experiment 4 of Table 3. Normal "pairing" of at least 4 units takes place as is denoted by the arrows labelled 1 to 4. This discharge is comparable with the normal spontaneous output from the ganglion.

Upper beam – cut central end of right P.I.N.a.

Lower beam – cut central end of left P.I.N.a.

activity decussate in the first commissure is further borne out by the fact that the act of creating the lesion *always* causes hindgut motility.

In two cases (experiments 1 and 4) it was possible to elicit weak hindgut movements by crushing the V.N.C. In these experiments normal unitary output was also found to occur on stimulation of the abdominal connectives. Thus if the interneurones causing unitary output decussate it is probable that they do not do so in the first or second commissures since non-repetitive activity occurred in experiment 1 where both of these commissures were sectioned.

2. *Extirpation of neurone somata*

The effects of extirpation of various regions of the ganglionic cortex are summarised in Table IV and Figure 4. Only the dorsal cell bodies were not destroyed due to major difficulties in approaching them. The data obtained, however, show that they do not seem to play a part in control of hindgut movements.

Total ablation of the anterior lobe (Figure 4(A)) does not affect hindgut movements nor the normal activity patterns of the motor output to the hindgut. The same is also true of lateral or posterior regions of the posterior ventral cell bodies (Figures 4(C) and (E)). Nevertheless lesions induced in the

TABLE IV

Region Extirpated	Hindgut movements elicited by crushing V.N.C. 1. Prior to lesion	2. After lesion	Activity in P.I.N.a.'s 1. Spontaneous	2. Elicited a. Bursting	2. Elicited b. Unitary	Comments	See Figure
All anterior ventral cell bodies to level of 1st commissure	+	+	+	+	+	Hindgut control centre not in this region	4(A)
Posterior ventral cell bodies between 1st and 4th commissures	+	−	−	−	−	Control centre lies in this region	4(B)
Posterior ventral cell bodies posterior to 4th commissure	+	+	+	+	+	Control centre not in this region	4(C)
Medial posterior ventral cell bodies posterior to second commissure	+	±	−	−	+	Unitary units lie anterior to 2nd commissure	(4D)
Lateral regions of posterior ventral lobe	+	+	+	+	+	Control centre not in these regions	4(E)

The effect of extirpating various regions of the cortex of the 6 A.G. on hindgut movements and motor output in the P.I.N.a.'s.
+ indicates the presence of hindgut movements or neural activity.
− indicates the absence of these phenomena. This only occurs in the one case and presumably the hindgut movements were being driven by
± indicates the presence of a very weak response. non-repetitive units which produce a weak response (Winlow and Laverack, 1972.2).

FIGURE 4 Diagrammatic representation of the regions of the 6 A.G. extirpated as described in Table IV. Cross-hatching indicates the regions destroyed.

(A) Ablation of the anterior ventral cell bodies.

(B) Destruction of the anterior part of the posterior lobe to the level of the 4th commissure.

(C) Ablation of the posterior lobe posterior to the dorsal lobes.

(D) Ablation of the posterior lobe medially and posterior to the 2nd commissure.

(E) Lateral lesions of the posterior ventral cell bodies.

(F) Summary of the above results to indicate the most likely region of the ganglion in which the neurones controlling the hindgut movements should be found. Cross-hatching denotes regions of the ganglionic cortex whose somata are not connected with fibres to the hindgut. The dotted region indicates the area in which the somata of units responsible for hindgut motility are thought to occur. Non-repetitive units apparently lie in the anterior part of this region between the first (1st) and second (2nd) commissures whilst bursting units seem to lie posterior to the second commissure.

anterior regions of the posterior ventral lobe (Figure 4(B)) resulted in elimination of both hindgut movements and all motor output. This leads us to believe that any somata connected with motor neurones to the hindgut lie in the anterior central region of the posterior ventral lobe, as indicated in Figure 4(F).

We assume that no neurone somata of any significance to hindgut movements lie ventral to the dorsal lobes (i.e. between scale marks 145 and 170 with reference to Figure 1(A)). This area was left intact in the experiment represented by Figure 4(B), but no motor output was recordable in that experiment. The same is true of the cells in the dorsal lobes which, as mentioned above, were never destroyed. When neurone somata in the medial region of the posterior lobe, posterior to the second commissure, were destroyed, as in Figure 4(D), all activity except that of non-repetitive units was abolished. Thus it would seem that the non-repetitive units lie somewhere in the region of the first to second commissures (scale mark 105 to 125 with reference to Figure 1(A)). The units which respond repetitively are thought to lie between the second and fourth commissures (i.e. between scale numbers 125 and 155 with reference to Figure 1(A)). No evidence exists as to the position of units responding both repetitively and non-repetitively.

Whilst admitting that this is only a rough guide to the position of the somata controlling hindgut motility, it is useful in that a long search of the whole ganglion with microelectrodes is now unnecessary. This search can be restricted to the region shown in Figure 4(F).

C. Microelectrode Penetration of the Posterior Ganglionic Cortex

The resting membrane potential of units in the posterior ganglionic cortex in our experiments lies between 40 and 50 mV (Zollman and Gainer, 1971, give values between 40 and 70 mV with a modal figure of 54 mV). The units impaled by us produced either non-repetitive or bursting activity in the P.I.N.'s, during stimulation, but never both types of activity. Figure 5 indicates the approximate locations of the units so far penetrated and these occur in the region designated above. However, no firm conclusions as to differences in the topography of the two types of unit can as yet be made.

Impaling and stimulating either unitary or burster units usually results in paired activity in the P.I.N.'s. Intracellular stimulation of a cell lying superficially and just to the left of the mid-line (position number 1 in Figure 5) was carried out (Figure 6). Stimulation at 12 Hz (Figure 6(A)) produced a paired output both ipsilaterally (upper beam) and contralaterally (lower beam). Stimulation of the neurone soma at 30 Hz (Figure 6(B)) produced rather a different effect. In this case higher frequency of stimulation caused the contra-

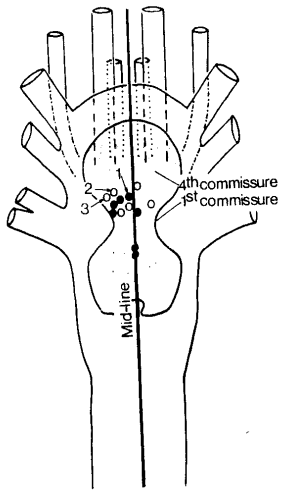


FIGURE 5 Ventral view of 6 A.G. to indicate the approximate positions of the neurone somata of units giving rise to unitary and bursting responses. Units causing a bursting response are represented by empty circles, whilst those causing unitary responses are indicated by filled circles.

1 – A single superficial unit causing non-repetitive responses in both left and right P.I.N.a.'s (and presumably the P.I.N.p.'s). Figure 6 shows the output produced by stimulation of this neurone soma.

2 – A single unit causing bursting activity in both P.I.N.a.'s as demonstrated in Figure 7. It lies one to two cells deep.

3 – A unit producing repetitive output in the left P.I.N.a. Its output is illustrated in Figure 8. It lies about one cell deep.

lateral unit to drop out. Such responses imply the presence of non-burster units which laterally excite one another.

The record displayed in Figure 7 is taken from the same preparation as that shown in Figure 6. The arrow on each figure denotes spontaneously active paired units in both left and right P.I.N.a.'s. Intracellular stimulation of a single neurone soma (number 2 on Figure 5), lying one to two cells deep on the left-hand side of the anterior part of the posterior lobe, causes three units to fire repetitively in the right P.I.N.a. Only one unit fires in the left P.I.N.a. and that is the very small spontaneously active unit which remains paired with the larger unit in the right P.I.N.a. even during burst formation. In several other experiments single units causing bursting activity of many neurones in both P.I.N.a.'s and P.I.N.p.'s have been detected. In the case shown in Figure 7

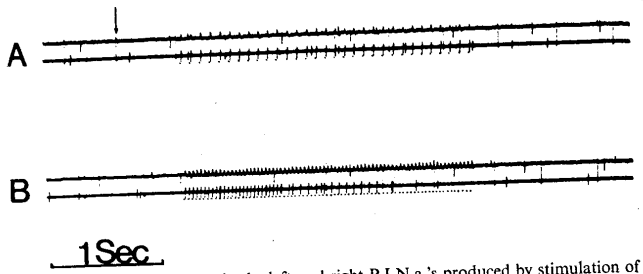


FIGURE 6 Unitary activity in the left and right P.I.N.a.'s produced by stimulation of a single unit lying just to the left of the mid-line in the anterior part of the posterior lobe (see Figure 5). The 6 A.G. was isolated from the rectum.

Upper beam – left P.I.N.a.

Lower beam – right P.I.N.a.

Dots (which have been retouched) indicate stimulus pulses delivered intracellularly.

(A) Stimulus pulses delivered at 12 Hz cause units to fire simultaneously in both left and right P.I.N.a.'s.

(B) Increasing the stimulus frequency to 30 Hz initially causes simultaneous unitary output in both P.I.N.a.'s, but the contralateral unit eventually slows down and then drops out. Two units, which laterally excite one another, have been postulated to explain this response. It is not thought likely that unitary output is caused by bifurcating axons (Winlow and Laverack, 1972.2).

The arrow denotes paired spontaneously active units firing simultaneously in both P.I.N.a.'s. Their rhythmical output is unaffected by direct stimulation of the non-repetitive unit on the left.

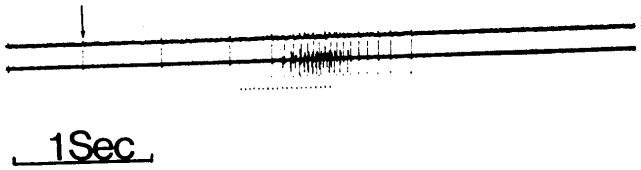


FIGURE 7 Bursting activity in the left and right P.I.N.a.'s of an isolated 6 A.G.

Upper beam – left P.I.N.a.

Lower beam – right P.I.N.a.

The arrow indicates the same pair of units as are arrowed in Figure 6. Stimulation of a single unit (number 2 on Figure 5) produces repetitive activity in both P.I.N.a.'s. The arrowed units always fire simultaneously. Immediately after the cessation of the burst there is a post-stimulatory depression of spontaneous activity, but this recommenced within two seconds.

it seems that no non-repetitive units fire in either P.I.N.a. Therefore, some major unit, driving several repetitively firing follower neurones, may have been penetrated. After cessation of bursting activity there was a period of post-stimulatory depression before the spontaneously active units commenced firing again. Figure 8 shows a single unit driven either directly or via an inter-neurone. The penetrated cell in this case lay on the left-hand side of the

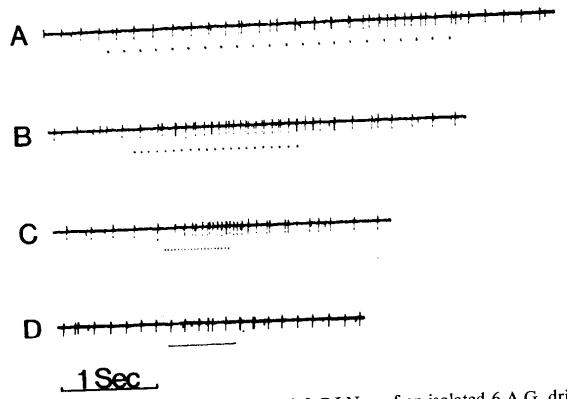


FIGURE 8 A single repetitive unit in the left P.I.N.a. of an isolated 6 A.G. driven at a variety of frequencies and at constant stimulus amplitude. The frequencies used were: (A), 6 Hz; (B) 12 Hz; (C), 30 Hz; (D), 60 Hz.

In (A) 17 stimuli were delivered before bursting activity was elicited, whilst in (B) and (C) only 7 or 8 stimuli were necessary. Presumably the excitatory potentials summating in the stimulated unit (which is number 3 of Figure 5) must have an initial slowly decaying phase, so that an increase in stimulus frequency from 12 to 30 Hz makes little difference to the number of stimulus pulses necessary to elicit the response.

In (D) a stimulus train delivered at 60 Hz produces no bursting response. The reason for this is unknown but it is possible that a driver cell was penetrated and the efficacy of its synapse breaks down at these higher stimulus frequencies. This correlates with the loss of repetitive output above 50 Hz demonstrated previously (Winlow and Laverack, 1972.2).

ganglion about one cell deep and in the position indicated by the number 3 on Figure 5. The output in the left P.I.N.a. was recorded and rhythmic, spontaneous activity was detectable. Stimulation of the penetrated soma, even at low frequencies, provoked repetitive discharge (Figure 8(A)). Increasing the stimulation frequency decreased the number of pulses necessary to cause burst formation, as is shown in Figure 8(B) and (C). This is presumably because the extent of decay of excitatory membrane potentials between stimulus pulses is greatly reduced. High frequencies of stimulation caused this unit to "switch

off" as is demonstrated in Figure 8(D). This suggests that the unit stimulated was a driver interneurone. In Figure 8(A) to (C) there is no indication of post-stimulatory depression.

DISCUSSION

Anatomy

As shown above the structure of the 6 A.G. is somewhat complex, though rather less so than that of the thoracic ganglia (Horridge, 1965).

The functions of the vacuolated cells, that lie external to the nervous elements of the ganglion, and of the non-vascular fluid space are unknown. The former may serve as a shock absorber to prevent damage to, or activation of, central neurones during violent activity such as the tail flick.

The delicate tracery of blood capillaries around the neurone somata of the 6 A.G. leaves one in little doubt as to the trophic function of the cell bodies. Many of the neurones are neurosecretory (Johansson and Schreiner, 1965; Schreiner, Staaland and Johansson, 1969) and it is conceivable that the axonal processes of these cells could discharge directly into the ventral sinus which underlies the dorsal surface of the ganglionic cortex.

Like other ganglia of the V.N.C., the 6 A.G. is bilaterally symmetrical, the two halves being linked by four groups of commissures. Kendig (1967) has demonstrated that three major commissural groups occur in the third abdominal ganglion of *Procambarus clarkii*, whilst Horridge (1965) indicates that there are only two in the first and second ganglia of *Astacus*. The four commissural groups in the 6 A.G. of *Homarus* demonstrate that the ganglion is a product of the fusion of somites during evolution. This proposition is strengthened by the presence of the two ventral and the two paired symmetrical dorsal lobes of the cortex (Johansson and Schreiner, 1965, described three dorsal lobes: we have seen only two). An inspection of the ganglionic roots of *Homarus* shows that the 6 A.G. is most probably derived from three separate ganglia. The first root of the 6 A.G. supplies the swimmerets of the fifth segment and is thus homologous with the first root of an anterior abdominal ganglion. The second root (uropod nerve) supplies the anterior oblique muscles as do the second roots of other abdominal ganglia, but it also innervates many muscles of doubtful homology which supply the uropods. These muscles may be equivalent to certain of the axial muscles of more anterior segments, thus making the second root of the 6 A.G. equivalent to a normal second root.

The third roots of abdominal ganglia one to five arise on the connectives posterior to the ganglia and supply the anterior and posterior oblique muscles as well as the superficial and deep flexors. The ventral telson nerve (third root) of the 6 A.G. supplies the anterior oblique muscles and also the anal compressors and dilators. It also supplies many of the muscles associated with the uropods. Larimer and Kennedy (1969) have suggested that the anal compressors and dilators respectively behave like the serial homologues of the phasic deep flexor muscles and the tonic superficial flexors. Thus the third root of the 6 A.G. is equivalent to a normal third root, but the additional nerve supply to the uropods suggests an affinity with the first root of other abdominal ganglia. Thus we have assumed the ventral telson nerve to be a fusion of the third root of a normal sixth ganglion with the first root of a seventh ganglion.

The dorsal telson nerve (fourth root of the 6 A.G.) supplies both anterior and posterior telson flexor muscles and the anal compressor muscles. The posterior and anterior telson flexors are both phasic and equivalent to the transverse and posterior oblique muscles of other segments respectively (Larimer and Kennedy, 1969). The transverse muscles are normally supplied by the second root of an anterior ganglion whilst the posterior oblique muscles are innervated by the third root. In addition the anal compressors are equivalent to the deep flexors (see above) normally supplied by the third root. Thus the fourth root of the ganglion is apparently compounded from normal second and third roots.

The anal nerve (fifth root of the 6 A.G.) is believed to be compounded from normal first and/or second and third roots. Larimer and Kennedy suggest that it is equivalent to the third root of more anterior ganglia since it supplies the anal compressor and anal dilator muscles. In addition this nerve contains afferent fibres from soft cuticle receptors (Winlow and Laverack, 1970, 1972.1). This suggests an homology with the first or second roots of the more anterior ganglia since these afferents are very similar to the mechanoreceptive afferents (Pabst and Kennedy, 1967) lying in those roots.

The sixth root of the 6 A.G. is the P.I.N., which is not homologous with any other root and would probably be associated with a terminal ganglion. The apposition of the origins of the anal nerves and P.I.N.'s (Figure 1(F)) implies that both may have arisen from the terminal ganglion.

From the above it seems that the fourth and fifth roots of the 6 A.G. are equivalent to the fused roots of two separate ganglia which have become telescoped into one another. The 6 A.G. would then be composed of a fusion of three segmental ganglia (see Table V). The first and second of these would be equivalent to other ganglia of the abdominal chain with the proviso that the appendages of the second would be the uropods rather than the swimmerets. The third ganglion would then be terminal and associated with the telson and proctodaeum. As such it would be lacking in appendages so that the anal nerve would be equivalent to fused second and third roots. The

affinities of the nerve roots of the 6 A.G. with those of other abdominal ganglia are summarised in Table V.

TABLE V

Root of 6 A.G.	Muscles supplied	Homologue of root in abdominal ganglia 1 to 5	Ganglion with which roots are associated
N1 – anterior nerves	Swimmeret muscles and pleura	1st	
N2 – uropod nerves	Anterior oblique muscles and muscles to uropods	2nd	6th
N3 – ventral telson nerves	Anterior oblique muscles Muscles to uropods Anal compressor } muscles Anal dilator } muscles	3rd + 1st	7th
N4 – dorsal telson nerves	Anterior and posterior telson flexor muscles Anal compressor muscle	2nd + 3rd	
N5 – anal nerves	Anal compressor and dilator	2nd + 3rd	Terminal
N6 – P.I.N.'s.	Muscles of hindgut	No homologue	

Fusion of ganglia is presumably the result of either reduction in number or shortening of body segments. In such cases fusion of neuropile regions would occur with a probable eventual loss of duplicated units and a considerable shortening or even loss of interneurones involved in interganglionic communication. A reorganisation of ganglionic cortices would also be expected with migrations of clusters of cell bodies into regions other than those with which they were originally associated. In the case of the 6 A.G. the anterior and posterior ventral lobes probably arose from the sixth and seventh ganglia respectively. The paired dorsal lobes might then have originated as part of the cortex of the terminal ganglion although the somata of the neurones controlling the hindgut now lie in the region of the cortex of the seventh ganglion. Perhaps they originally lay between the two dorsal lobes to form a single terminal cortex, but after fusion moved anteriorwards so displacing the medial region of the seventh ganglion (or filling the space left by it) into the region we have termed the waist of the ganglion.

On the basis of the above hypothesis it must be supposed that the dorsal cortical lobes contain the motor neurone somata of fibres supplying the anal compressor and dilator muscles since the anal nerves innervate these muscles. However, the anal nerves also pass to the telson to supply the multitudinous

sensory structures lying thereon. The cell bodies of these receptors have never been detected and it is possible that they lie in the dorsal lobes of the 6 A.G. Alexandrowicz, and Whitear (1957) provide evidence that sensory cell bodies may lie within the central nervous system and the somata of the soft cuticle receptors described by Pabst and Kennedy (1967) and ourselves (1970 and 1972.1) are centripetal in that they lie within major nerve roots.

Physiology

The two types of motor discharge recordable from the P.I.N.'s (Winlow and Laverack, 1972.2) indicate that at least two sets of interneurones impinge on the hindgut control centre in the 6 A.G. Our split ganglion preparations show that the command interneurones (I2) eliciting bursting motor discharge decussate in the first commissure of the ganglion. On the basis of Table III it seems most unlikely that the interneurones (I1) which produce a unitary discharge decussate in either the first or the second commissure. However we (1972.2) have already presented evidence of decussation of I1 since high frequencies of stimulation of the V.N.C. result in loss of responsiveness of units in the ipsilateral P.I.N.'s. Further, direct driving of non-repetitive units results in loss of the contralateral response at high stimulus frequencies (Figure 6) and we have also shown (1972.2) that an increase in conduction time occurs when ipsilateral rather than contralateral units are stimulated. The profiles of the interneurones producing motor discharge may be envisaged as in Figure 9. We have no evidence relating to the profiles of the second category of I1's we previously described (1972.2).

As shown in Figures 4(F) and 5 the somata of units controlling hindgut function lie in the anterior part of the posterior cortical lobe and not in the dorsal lobes as stated by Horridge (1965). Although the results obtained using microelectrodes are still somewhat sparse a consideration of these and the extracellularly recorded output from the ganglion (Winlow and Laverack, 1972.2) does tell us something of the interactions of the cells involved in hindgut control. Our results indicate that unitary and bursting neurones exist as two physiologically differentiated types. Stimulation of the soma of a non-repetitive cell will produce a typical paired response which drops out contralaterally at high stimulus frequencies (Figure 6). This strengthens the argument (1972.2) for a network of non-repetitive units, individuals of which drive their partner cells by lateral excitation. With regard to repetitive discharge, stimulation of a single soma may often induce a discharge from several cells and this activity is usually paired (Figure 7). The multiplicity of units driven by a single neurone suggests that driver interneurones synapsing onto numerous repetitively discharging cells have some part to play in this system. Whether the repetitively discharging units cross-excite one another is unknown.

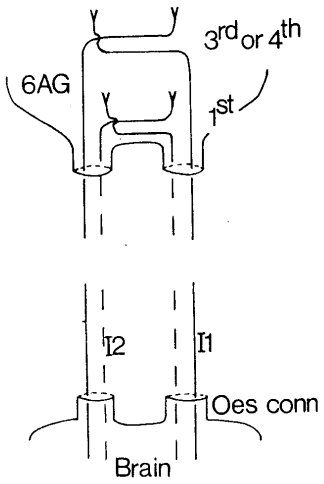


FIGURE 9 Decussation of command interneurones activating the defaecatory mechanisms within the 6 A.G.

I1	– interneurone(s) activating non-repetitive motor units.
I2	– interneurone activating burster motor units.
Brain	– tritocerebral region of the brain.
Oes conn	– oesophageal connectives.
1st	– first commissure.
3rd or 4th	– third or fourth commissure.

It is possible that both types of output are dependent on the bursting or unitary properties of the command or driver units which impinge onto them, but it is our opinion that three types of units occur within the 6 A.G.; unitary and bursting motor neurones and driver interneurones. However, if driver interneurones do exist they may be different in form from those interneurones described by Kennedy, Selverston and Remler (1969). These authors suggest that the interneuronal soma is separated from its major ramifications by a long thin strand, which makes it difficult to elicit active electrical responses in the unit by stimulation of its soma.

CONCLUSIONS AND COMPARISONS

The hindgut of the lobster is under direct central control from the 6 A.G. with respect to the defaecatory response. Central patterning initiates the response

which may then be carried on by the highly excitable hindgut muscles. The rectum is divisible into anterior and posterior sections controlled by the P.I.N.a.'s and the P.I.N.p.'s respectively. The innervation of the hindgut resembles that of the somatic muscles. No myenteric plexus capable of independent co-ordinating activities is thought to exist and the hindgut is capable of unco-ordinated low amplitude excursions which are myogenically initiated by pacemakers within the muscles. The muscles probably exhibit a graded or passive response on stimulation.

Anal movements are monitored by sensory cells responding to deformation of the soft cuticle of the anal lips. Their input does not modulate motor discharge at the level of the 6 A.G. and their central connections are unknown. They may synapse onto interneurones which are responsive to opening of the anal valve (Wiersma and Hughes, 1961). Other receptors are also thought to exist on the rectum (Alexandrowicz, 1909; Orlov, 1926), but these have not been physiologically demonstrated.

Unitary and burster units control hindgut motility. The non-repetitive units are thought to lie in lateral networks, whilst the burster units may lie medianly. Non-repetitive units interact with one another by lateral excitation. Some burster units may be multibranched and send axonal branches to all the P.I.N.'s. Burster units alone are capable of driving the powerful defaecatory response, whilst unitary discharge is thought to "prime" the muscles of the hindgut, but it can also drive the longitudinal and radial muscles rhythmically. The different types of units may utilise different transmitters. These networks only represent a final motor pathway and are ultimately controlled by several interneurones originating in the brain, presumably in the tritocerebral region (see Figure 10). It is our view that a specific relationship exists between hindgut and foregut function in *Homarus gammarus* (L.). This relationship may eventually be revealed by an electrophysiological study of the tritocerebral region of the brain.

The somata of the units controlling the defaecatory response have been localised. They lie in the anterior region of the posterior cortical lobe of the 6 A.G.

The 6 A.G. may have been derived from three fused ganglia – the sixth, seventh and terminal abdominal ganglia. The longitudinal muscles of the hindgut and the extrinsic radial muscles of the anus are thought to have the same embryological origins.

Finally we have made a comparison between the lobster hindgut control system and that of the cockroach as elucidated in a number of recent publications (Belton and Brown, 1969; Brown and Nagai, 1969; Nagai and Brown, 1969; Nagai, 1970) which report the results of work carried out on the procodaeal muscles of *Periplaneta americana* L. The hindgut of the cockroach is very similar to that of *Homarus* except that the six symmetrically placed

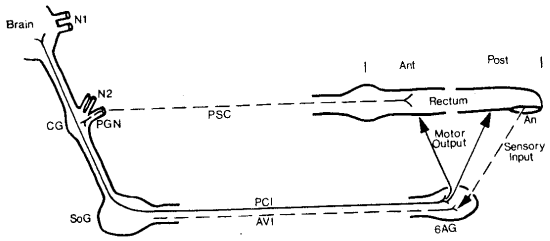


FIGURE 10 The innervation of the hindgut in relation to the central nervous system of *Homarus gammarus*.

The bipolar sensory cells lying on the hindgut are not shown. The cell bodies of Orlov's (1926) pyloric sensory cells lie on the pylorus and their axons pass to the commissural ganglion.

Brain	– tritocerebral region of the brain.
6 A.G.	– sixth abdominal ganglion.
C.G.	– commissural ganglion.
So.G.	– suboesophageal ganglion.
P.G.N.	– posterior gastric nerve.
N1	– nerves to oesophageal and stomatogastric ganglia.
N2	– nerves to oesophageal ganglion.
Ant.	– anterior region of the hindgut.
Post.	– posterior region of the hindgut including the extrinsic anal musculature. The hindgut is broken to indicate the independence of anterior and posterior regions.
An.	– anus.
Motor output	– motor output down the P.I.N.s.
Sensory input	– sensory input from the receptors of the anal lip.
A.V.I.	– interneurones responding to opening of the anal valve (Wiersma and Hughes, 1961). Their proximal terminations are unknown.
P.C.I.	– presumed command interneurones probably originating in the brain.
P.S.C.	– pyloric sensory cells of Orlov.
Dashed lines	– primary sensory fibres and the interneurones onto which they discharge.
Solid lines	– motor fibres and command fibres.

longitudinal muscle strips lie external to the circular muscles and only stretch over the anterior two-thirds of the rectum. In the posterior part they are replaced by six symmetrical dilator muscles which are distally attached to the body wall in a manner reminiscent of the five radial muscle groups of the lobster.

The nerves supplying the cockroach hindgut arise in the sixth abdominal ganglion. The hindgut is supplied bilaterally by the protodaeal nerves (a branch of nerve XI, the cercal nerve). These nerves are divisible into anterior and posterior branches as in *Homarus*. The anterior branches supply the longitudinal muscle straps, the ventral dilators, the circular muscles of the anterior rectum and all the muscles of the midgut, whilst the posterior branches run to the dorsal and lateral dilators and the circular muscles of the posterior rectum. Thus the hindgut of *Periplaneta* may be almost as completely divided into two regions as that of *Homarus*.

Stimulation of the 5–6 connectives of the cockroach elicits motor activity in the proctodaeal nerves and this activity can be knocked out by ganglionic blocking agents. Thus the motor fibres are thought, by Brown and Nagai (1969), to be centrally controlled. The somata of motor neurones to the hindgut have been shown to lie in groups of four to six cell bodies, on either side of the midline, in the posterior region of the sixth abdominal ganglion. This is very similar to the position of the motor neurone somata in *Homarus*.

Afferent activity has been recorded from sensory cells lying below the circular muscle layer. Such cells may be similar to those described by Alexandrowicz (1909) in decapod crustacea. Ganglion cells have never been observed on the cockroach hindgut although its surface is interlaced with a periproctodaeal net which is thought to be made up of modified muscle fibres rather than nerve fibres.

Two types of motor output exist, one of which is rapidly conducted (0.5 metres/sec.), whilst the other is much slower (0.2 metres/sec.). Both conduction velocities are much less than those occurring in *Homarus*. Only the fast fibres evoke p.s.p.'s in muscles of the hindgut. The function of the slow fibres is unknown.

The longitudinal muscle fibres of the cockroach proctodaeum are innervated multiterminally and polyneuronally. Muscle action potentials are of the graded type (as is suspected in *Homarus*) and could be triggered either by summation of centrally generated p.s.p.'s or by a smoothly fluctuating muscle membrane potential of critical amplitude. The longitudinal muscles of the cockroach proctodaeum appear to be myogenic, but under the control of the central nervous system. We have reached precisely this conclusion for the hindgut musculature of *Homarus*. In the cockroach, rhythmic muscle action potentials can also be evoked by stretch of the proctodaeal muscles. According to Nagai (1970) these properties are similar to those of vertebrate smooth visceral muscles, as well as the papillary muscles of the mammalian heart. Their pacemaker sites are of variable location.

As can be seen from the review of recent literature set out above, the control mechanisms for defaecation are apparently very similar in cockroaches and lobsters, although hormonal mechanisms are also thought to be involved in the cockroach system (Davey, 1962, 1964). However in both cases the hindgut is centrally controlled and the rhythmicity of the visceral muscles is thought to be myogenic in origin.

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