SENSE ORGANS AND REFLEXES THROUGH THE ABDOMINAL NERVE CORD OF THE COCKROACH, *BLABERUS CRANIIFER*

A Thesis

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by

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INTRODUCTION

Sherrington's studies of mammalian spinal reflexes (Sherrington, 1906) provided a detailed basis for Eccles' studies of integration at the single cell level (Eccles, 1957; Granit, 1967). There is not yet a corresponding body of background information about insect reflexes, in spite of the recognition (Roeder, 1967) that insects carry out quite complex coordinations with, compared to vertebrates, surprisingly few nerve cells. This may mean that neural integrative processes are fundamentally different in insects or that the processes are simpler and should be easier to analyze. In either case insect central nervous systems are worthy objects of comparative study. Hughes (1965) has warned that an understanding of central integration in cellular terms may be delayed by the present shortage of information about reflex pathways.

The present study contributes to knowledge about insect reflex pathways, specifically those mediated by the six abdominal ganglia of the cockroach Blaberus craniifer. The research is based on the following questions which are directed towards a more complete understanding of the physiology of the abdominal nerve cord.

A. Where are the abdominal receptors located and what are their functions?

B. What are the intraganglionic reflex pathways and

effector organs served by these sensory receptors?

C. What are the interganglionic reflex pathways which could possibly serve to relay sensory information to distant abdominal effectors?

In cockroaches several abdominal receptors have been reported which have a bearing on the present study. Finlayson and Lowenstein (1958) found a single bipolar cell with stretch receptor function located longitudinally in the dorsal musculature of Periplaneta. A later study by Osborne and Lowenstein (1962) described a similar single celled stretch receptor vertically arranged in the dorsal musculature. Shankland (1966) recorded a stretch receptor response in a small nerve near the mid-ventral line in Periplaneta. A peripheral receptor in the vicinity of the pleural fold has been found by Florentine (1967) to respond to airborne sound. Farley, Case, and Roeder (1967) have reported unidentified abdominal receptors which fire during inspiration and expiration in Periplaneta; moreover, Farley and Case (1968) have shown that this sensory information is capable of altering the frequency of the respiratory rhythm.

Relatively little work has been done on either intraganglionic or interganglionic reflex pathways in cockroach abdomens, with the exception of the following two studies on Blaberus. Hughes and Wilson (1965) found sensory fibers which enter one abdominal ganglion and make

synaptic contacts in the next anterior ganglion. The resulting motor response returns to the nerve of the ganglion stimulated. Smalley (1963), in a study designed to map respiratory reflex pathways, established a number of the basic reflexes studied in more detail here.

MATERIALS AND METHODS

I. ANIMALS

Adult male cockroaches, Blaberus craniifer Burmeister, were used for most of this investigation. The larger size of the females made them useful in heart lateral nerve studies, but the fat bodies and egg cases interfered with ventral nerve cord experiments. Male adult Periplaneta americana were used in comparative histological studies of abdominal sense organs. Male and female Periplaneta americana nymphs were utilized in heart rate experiments, because the heart is visible through the dorsal cuticle.

The cockroaches were kept in 8" by 20" by 10" steel cages. Each cage contained several hundred male and female cockroaches of various ages. The animals were fed apples, Gaines dog food and oatmeal.

II. ANATOMICAL

To trace fine nerves to their sensory endings, 0.2 ml of reduced methylene blue was injected into the abdominal cavity. For temporary preparations a saturated ammonium molybdate solution was applied to stop the staining process after thirty minutes. If permanent whole mounts of sense organs were required, methylene blue was injected

for twenty to thirty minutes, followed by ammonium picrate for five minutes and ammonium molybdate for twelve hours. The preparation was then washed in distilled water, given two changes of tertiary butyl alcohol in two hours, cleared in xylene for thirty minutes, and mounted on a slide (see Stark, Smalley, and Rowe, 1968).

For histological studies of the peripheral sense organs serial sections were required. Newly molted Blaberus craniifer were fixed in alcoholic Bouin's. A sink aspirator was used to remove air in the tracheal system. Each successive stage of the standard alcoholic dehydration was also done under reduced pressure. Segments from the periphery of the abdomen were removed and embedded in paraffin. Sagittal, frontal, and cross sections were cut at five to ten microns. Several series of slides were stained with Luxol fast blue and phosphotungstic acid, while the best results were with Mallory's triple stain.

Photomicrographs of interesting whole mounts were taken with an American Optical Microscope with a Polaroid attachment. A Wratten 80A filter was used with outdoor color Polaroid film. A Wild camera and dissecting microscope were used with Polaroid black and white film to take pictures of the distribution of the dorsal nerve branches to the pleural fold.

III. PHYSIOLOGICAL

Prior to dissection all experimental animals were anesthetized with CO_2. Most animals were opened dorsally, pinned to a balsa block, and the gut and tergites were removed to expose the abdominal nerve cord. When it was necessary to eliminate extraneous activity, two adjacent ganglia, their peripheral nerves, and the connectives joining them were isolated from the rest of the nerve cord be severing the connectives anterior and posterior to the pair of ganglia.

In experiments on the lateral nerves of the heart, an animal was pinned to a waxed petri dish, one lateral incision was made, the gut was removed and the tergites were folded to the side and pinned down, exposing the abdominal portion of the heart. Once the ventral cord or the heart was exposed it was perfused periodically with saline (Yamasaki and Narahashi, 1959).

Fine silver wires (0.005 in.) served as recording and stimulating electrodes and were positioned by manipulators. The recording electrodes were connected through a Tektronix 122 low level preamplifier to a two-channel Tektronix 502 oscilloscope. Nerve activity was photographed with Grass C4 and Polaroid cameras. A Grass AM5 audio-amplifier was used to supplement the oscilloscope in monitoring nerve activity. Stimulus pulses were delivered from a Grass S4 stimulator through a Stimulus Isolation

Unit.

In several instances when stimulating or recording from very small nerves it was necessary to use even smaller wire electrodes. The wire was bent into the shape desired and sharpened electrolytically. Occasionally the nerve to be stimulated or recorded from was coated with Vaseline to prevent it from drying.

In the usual recording procedure, a nerve was lifted out of the saline with a small glass hook onto one recording electrode and the second recording electrode was placed in a drop of saline in contact with the animal. A nerve to be stimulated was placed on a pair of stimulating electrodes and lifted into the air. In most experiments the stimulus intensity varied between 1.5 and 6.0 volts, and the duration was held constant at 1.0 msec. In many experiments the thresholds increased as the preparations aged. This was compensated for by increasing the stimulus intensity. When working with "rebound" reflexes (in which sensory impulses enter and motor impulses leave the same nerve) the duration had to be reduced to 0.1 msec. to reduce the stimulus artifact. In reflexes involving more than one ganglion, connectives were cut systematically to further define interesting pathways.

Inherent in any electrical stimulating study is the possibility that non-physiological pathways may be activated. This was compensated for by using low stimulus

intensities.

Saline saturated with 100% CO_2 was usually used in experiments which called for initiation of the ventilatory rhythm. Less frequently 100% or 5% CO_2 was appled directly as a gas.

In experiments designed to determine whether or not a nerve terminates in a sensory structure two procedures were used. In many instances it was possible to cut the branch supplying the receptor and to record from a point distal to the cut. In nerve branches too small to be recorded from directly, records were taken from the deefferented main trunk.

In order to eliminate the effects of antifromic conduction resulting from electrical stimulation, various "natural" stimuli were applied to activate suspected but quiescent sensory elements. Groundborne vibrations, probing in the musculature, pressure on the sternites, tergites, and CO_2 were all capable of initiating a response in one receptor or another.

Heart rates were monitored with a transducer described by Miller (1968). The main components of this transducer are a battery-operated FM transmitter module and an FM tuner. A light wire lever is placed in contact with the heart. The movable end of the lever is placed near the antenna of the transmitter. As the lever moves, the effective capacitance of the transmitter antenna is varied

and this causes the output frequency of the transmitter to vary. Within the FM tuner the change in frequency is converted into a change in dc voltage proportional to the movement of the heart, and this voltage is displayed on an oscilloscope.

RESULTS

I. ANATOMICAL AND PHYSIOLOGICAL DESCRIPTION OF THE ABDOMINAL NERVES AND SENSE ORGANS

This section reports the structure, function and locations of the abdominal sensory elements and provides a physiological description of the peripheral nerves described anatomically by Smalley (1963).

Fig. 1 (A and B) shows the anatomical arrangement of nerves in the abdomen of Blaberus craniifer. The designation of nerves and ganglia follows that of Smalley (1963), modified only where necessary to include finer branches than were described in that study. The six abdominal ganglia are designated A-1 through A-6. The more anterior paired nerve in each ganglion is designated the dorsal nerve (DN) and the more posterior paired nerve is designated the ventral nerve (VN). Branches of each of these nerves are numbered in proximal to distal order. The smaller rami of these branches are designated by capital letters and further divisions (only occasionally necessary) are designated by lower case letters. Thus, VN-3Aa is a small division off the first ramus of the third branch of the ventral nerve.

The numbers of fibers given in the succeeding sections are based on the number of different spike heights recorded

Destinations of the abdominal nerve branches.

Dorsal Nerve

DN-1 inner sternal muscle

DN-2 spiracular, interpleural and inner tergal muscles

DN-2A branch connecting DN-2 with VN-3 of the anterior segment

DN-3

DN-3A and DN-3B several receptors associated with the lateral fold including the lateral chordotonal organ

DN-4

DN-4A primarily sensory, vertical and longitudinal single celled receptors

DN-4B inner tergal muscle, lateral nerve of the heart

Ventral Nerve

VN-1 terminates at the ventral body wall near the base of the tergo-sternal muscle

VN-2 tergo-sternal muscle

VN-2A joins with DN-2 of the same segment

VN-3 outer sternal muscle

VN-3A outer sternal muscle

VN-3Aa sensory, mid-sternal receptor

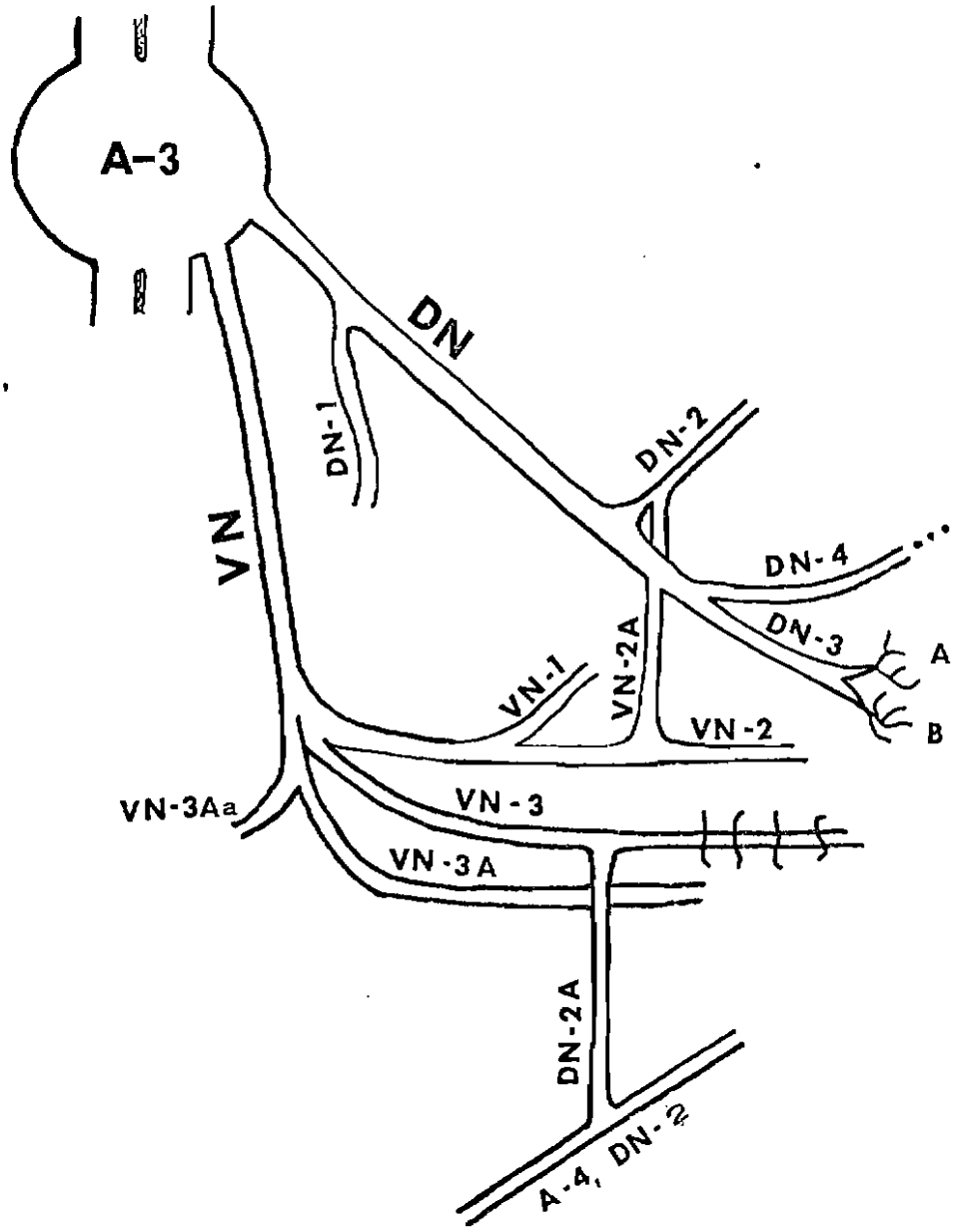


Figure 1-A. Diagram of major branches of dorsal nerve (DN) and ventral nerve (VN) of the third abdominal ganglion (A-3) of Blaberus. Minor variations in branching pattern and relative lengths of nerves exist on other ganglia. Destinations of these nerves given on opposite page.

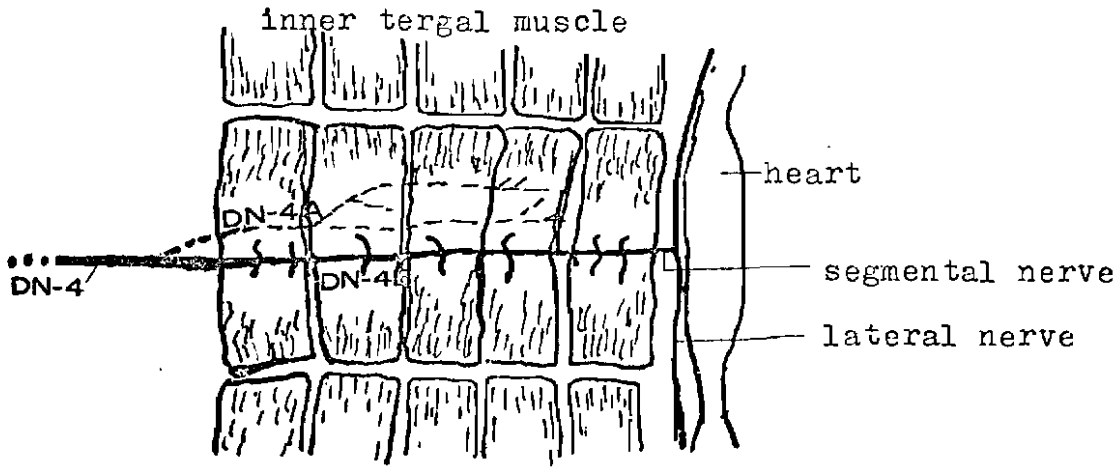


Figure 1-B. Diagram showing the relationship of DN-4 to the heart and to the inner tergal muscles.

from nerves firing spontaneously or under the influence of CO_2.

A. VENTRAL NERVES AND SENSORY ELEMENTS

VN-1

VN-1 branches from VN-2 and terminates in the vicinity of the lateral body wall. Two motor fibers are present. To test for sensory elements in VN-1, recordings were made from an isolated segment of VN-2 with only VN-1 functionally intact, and the area surrounding the nerve was subjected to sensory activating stimuli. No sensory elements could be demonstrated. Because of this and the difficulty of obtaining records from VN-1, due to its small size, its responses to stimulation were not tested in the ensuing reflex work.

VN-2

VN-2 innervates the tergo-sternal muscle and contains three large and one small motor fibers.

Possibly one receptor cell contributes to this nerve. On one occasion, a single afferent spike was found firing spontaneously. A careful histological study of the tergo-sternal muscle revealed no sensory elements among the muscle fibers. A small ramus branches from VN-2 to curve around the tergo-sternal muscle. Its terminations could not be followed and may possibly include a sensory

structure.

There is a small neural connection, VN-2A, between VN-2 and DN-2 of the same ganglion. Its anatomical designation as a branch of VN-2 is based on the following physiological observations: recordings from this nerve detached from DN-2 showed spontaneously firing motor fibers, and when recordings were made from the same connection detached from VN-2 the spontaneous activity stops. In the subsequent reflex study VN-2A was always cut to insure that dorsal nerve stimulation did not directly activate these ventral nerve fibers.

VN-3

VN-3 innervates the outer sternal muscle and the lateral intersegmental connective tissue. Three motor fibers are present and the nerve participates in the ventilatory rhythm. No sensory elements have been detected, histologically or electrophysiologically.

VN-3A and VN-3Aa

VN-3A innervates the outer sternal muscle. Distal to the small sensory branch, VN-3Aa, which passes mid-ventrally, the nerve is entirely motor. Three motor fibers are found which participate in a respiratory rhythm.

Methylene blue preparations show VN-3Aa passes under the ventral nerve cord and terminates in five bipolar

sensory neurons (Fig. 2, 3). The presence of this receptor was demonstrated electrophysiologically in ventral nerves of ganglia A-1 through A-6 in males and A-1 through A-5 in females. It is also present in Periplaneta (Fig. 4, 5), presumably contributing to the same ganglia as the receptors in Blaberus. This receptor will be referred to as the mid-sternal receptor.

Simultaneous recordings from VN-2, VN-3, and VN-3A indicated there are no bifurcating fibers.

ANATOMY AND PHYSIOLOGY OF THE MID-STERNAL RECEPTOR

Sections of this receptor stained with Mallory's triple stain show that the distal ends of the paired receptors of a single segment converge upon approximately the same spot on the cuticle (Fig. 6).

A thick layer of connective and fatty tissues overlies the cell bodies. These cell bodies are encapsulated by a blue-staining tissue which appears to be connective tissue or Schwann cell investment (Fig. 7). The large round nuclei of the receptor stained black with methylene blue and red with Mallory's stain. The distal ends of the bipolar cell bodies are enmeshed in a thick strand of connective tissue which in turn is attached to the cuticle at the mid-ventral line (Fig. 8). The nuclei of 20-30 non-neural supporting cells are found in close association with the receptor cell bodies. The connective tissue

Figure 2. Whole mount of the mid-sternal receptor (arrow) in Blaberus. VN-3Aa passes horizontally to join VN-3A, larger nerve along left side of photomicrograph (50X).

Figure 3. Whole mount of the mid-sternal receptor at a higher magnification. One nucleus visible along lower border (225X).

Figure 4. Mid-sternal receptor (long arrow) in Periplaneta. Note: the inner sternal muscle is found on either side of the receptor. The distal end of the receptor is visible (short arrow) (50X).

Figure 5. Mid-sternal receptor in Periplaneta showing four of the five nuclei of suspected receptor cells. One nucleus lies over another at the ventral (lower) end of the receptor (225X).

Figure 6. Cross section of the mid-sternal receptor. Both the cell bodies and point of attachment of the one receptor (short arrow) can be seen, but only the distal point of attachment (blue staining area, long arrow) of the other receptor is visible (50X).

Figure 7. Cross section of the mid-sternal receptor. Note the supporting cells (short arrow) and surrounding fatty tissue (long arrow) (225X).

Figure 8. Cuticular attachment of the mid-sternal receptor. Note the large supporting cells in the cuticular epidermis (short arrow) and the connective tissue strands passing through the epidermis to the cuticle (long arrow). Fig. 7 and 8 are higher magnification photographs of the same section as shown in Fig. 6 (225X).

strands stain red with Mallory's stain and contrast with the blue-stained nerve cells.

The majority of the connective tissue strands terminate at the epidermal layer of the cuticle. Several central strands pass through the epidermal cell layer to fuse with what appears to be the laminated endocuticle. In the epidermis two large (trichogen? tormogen?) cells are located around the strands embedded in the cuticle.

The cuticle in the vicinity of the receptor is stained blue, in contrast with the rest of the cuticle, which is stained red with Mallory's. Florentine (1967) noticed similar staining differences in the vicinity of peripheral sensory structures and attributed them to local differences in cuticular permeabilities.

Cross sections of VN-3Aa show that at least seven axons are present (Fig. 9). Electrophysiologically, five of these axons can be shown to be sensory and two more can be shown to be efferent.

The five sensory cells were surprising in the range of stimuli to which the group responded and the degree of overlap in function between units. Two fibers responded with a discrete burst of activity to groundborne vibrations set up by tapping on the floor of the recording cage (Fig. 10). The smaller fiber responded to a single stimulus with a burst of 10-25 spikes while the larger fiber fired once or twice. Two to five fibers fired phasically in response to compression in the ventral

Figure 9. Cross section of VN-3Aa (arrow). At least seven axons are present (500X).

Figure 10. Response of mid-sternal receptor to groundborne vibrations.

musculature (Fig. 11). One fiber fired spontaneously in 90% of the preparations. CO_2 saturated solution evoked a response from three fibers. Tapping stimulation under these conditions also initiated a response from two fibers (Fig. 12). Exposure to CO_2 gas stimulated all of the fibers (Fig. 13). In a receptor stimulated by 100% CO_2 gas, it was impossible to initiate a further response to groundborne vibrations. Insect saline adjusted to pH 4 or 4.5 with HCl simulated the effects of CO_2 gas on the receptor.

Two efferent fibers were occasionally found firing spontaneously on VN-3Aa (Fig. 14). These efferents were shown to activate the receptor by the following experiment (see diagram in Fig. 15). The ventral nerve was cut near the ganglion and a pair of stimulating electrodes was placed distal to the cut. All peripheral connections except VN-3Aa were cut. A recording electrode was placed between the mid-sternal receptor and the stimulating electrodes. On stimulation, two fibers (A in Fig. 15) responded at a latency of 1 msec. This was followed by a highly repeatable burst of one or two fibers responding eight to thirty times per stimulus (B in Fig. 15). Two facts strongly suggest that response "A" is efferent and "B" afferent: response "A" remains but "B" drops out after cutting VN-3Aa at the receptor. The polarity of response "A" is opposite to that of response "B" (C in Fig. 15).

Obviously muscle tissue intermeshed with the

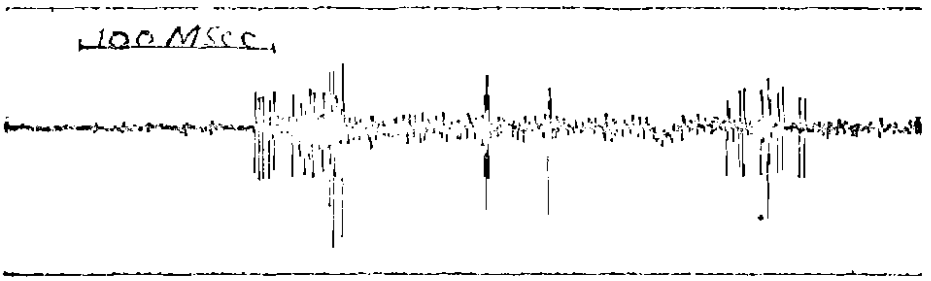


Figure 11. Response of mid-sternal receptor to compression of the ventral musculature.

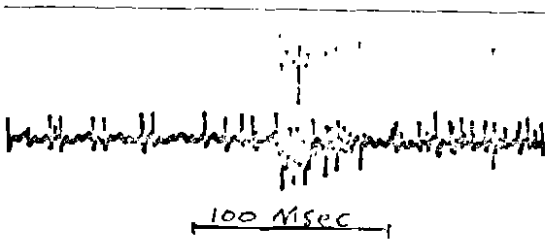


Figure 12. Smaller spikes responding to CO_2 in solution, larger responding to groundborne vibrations.

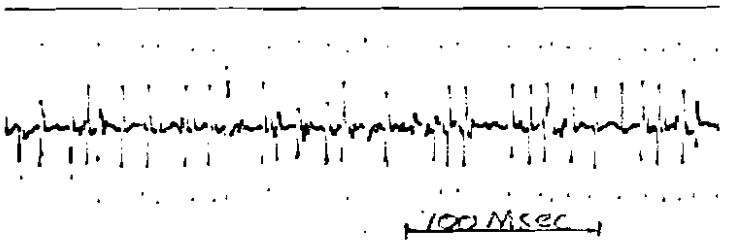


Figure 13. Response of mid-sternal receptor to 100% CO_2 applied as a gas.

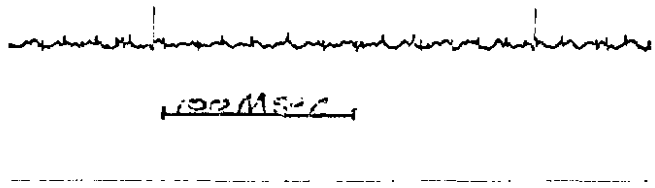
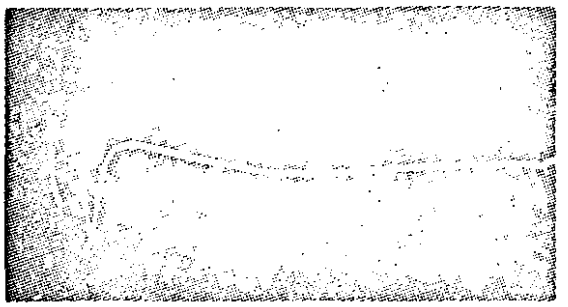
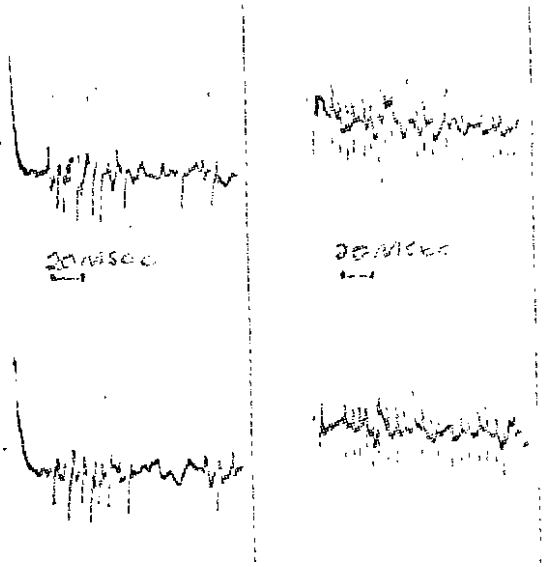


Figure 14. Spontaneous efferent activity on VN-3Aa. Nerve destroyed distal to recording electrode.



A.



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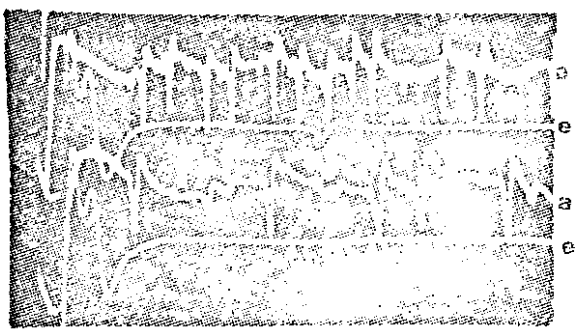

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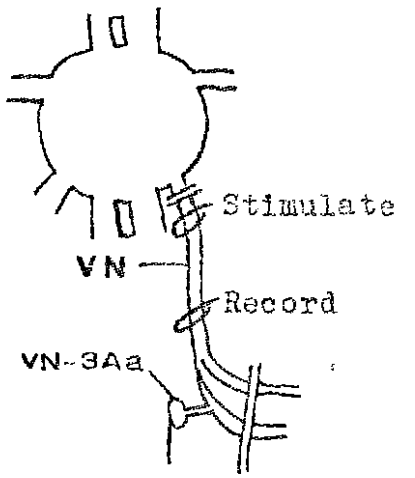


Figure 15. Experiments designed to show that ventral nerve efferents activate the sensory response. Recording conditions as shown in diagram.

A. Efferent response.
B. Two examples of the afferent response.
C. Records taken at two different speeds to emphasize the efferent response "e" and the afferent response "a" respectively. Note the reversal of polarity.

connective tissue strands would explain the observed response to efferent activity, but cross sections as thin as 5-7 microns fail to confirm the presence of muscle cells. A more definite statement on the question of whether or not there are muscle fibers in this receptor must await an electron microscope study.

Because the distal ends of both ventral receptors from a single ganglion lie in close proximity to one another, it was important to determine whether the activity in one receptor affected the other. Simultaneous recordings from both receptors during stimulation by tapping showed each receptor responded independently in terms of latencies, number of fibers participating and the intensity of the tapping required to initiate a response. Slight compression in the ventral musculature of one side of the animal caused only the homolateral receptor to respond. Electrical stimulation of the efferent input of one ventral receptor produced no response in the opposite receptor.

B. DORSAL NERVES AND SENSORY ELEMENTS

DN-1

DN-1 innervates the inner sternal muscle and consists of three large and one small motor fibers which participate in the respiratory rhythm. Stimulation of DN-1 results in a visible contraction of the muscle. There are no sensory elements associated with this nerve, as determined by

electrophysiological analysis and confirmed histologically.

DN-2

DN-2 innervates the inner pleural, inner tergal and spiracular muscles. It contains at least five small motor fibers which fire spontaneously and one large fiber which fires in bursts of 10-25 spikes per burst. The frequency of bursts is highly variable. The bursts may occur every few milliseconds or may be separated by intervals up to 60 seconds (Fig. 16). Occasionally, the bursting does not occur. When present, the spontaneous activity can be eliminated by cutting any connective anterior to the ganglion from which the recording is being made. This rhythmic activity appears to coincide with the normal respiratory rhythm which involves the rest of the motor fibers of DN-2 when the animal is perfused with CO_2 in solution.

No sensory elements could be detected on this nerve by electrophysiological or histological techniques.

DN-3

Smalley (1963) described DN-3 as "innervating the dorsal body wall in the region of the pleural membrane". Electrophysiological analysis indicates this nerve is primarily sensory and the histological analysis concurs.

In Periplaneta and Blaberus many hairs are found on

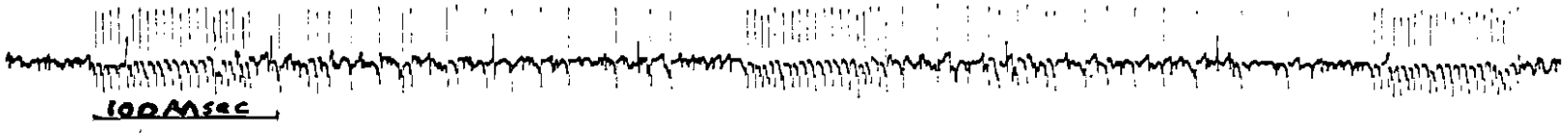


Figure 16. Rhythmic activity on DN-2.

the abdomen in regions innervated by DN-3. Wigglesworth (1950) states, "Nearly all the spines and hairs on the body surface (of an insect) are sensory end organs." This is certainly not true of all hairs on the abdomen in Blaberus and Periplaneta. In a series of methylene blue whole mounts (Fig. 17) and serial cross sections, no neural elements were found associated with the hairs on the dorsolateral cuticle.

Several millimeters from the pleural fold the nerve divides, and the "A" branch receives contributions from 20 to 30 small neurons originating in the pleural fold. The "B" branch originates from the wall of the cuticle adjacent to the spiracle (Fig. 18).

DN-3A

It is difficult to ascribe a function to the small nerves contributing to DN-3A, although electrophysiological analysis of DN-3 indicates most of them are sensory. Whole mounts of the pleural fold region show small darkened areas, possibly nuclei of receptor neurons, in several of the branches (Fig. 19). Unfortunately, serial sections have proven useless in attempts to define further these small nerve branches.

DN-3B

DN-3B has similar small nerve cells associated with

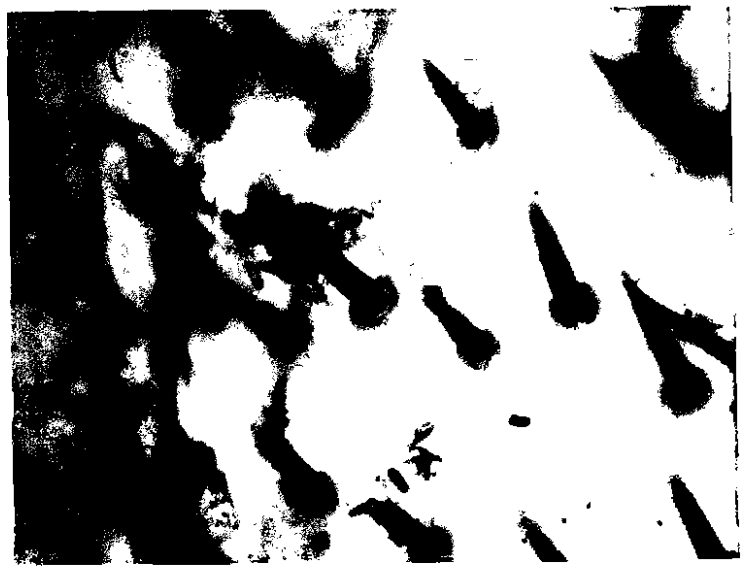


Figure 17. Methylene blue whole mount showing hairs on the abdomen of Blaberus in the vicinity innervated by DN-3 (50X).

Figure 18. Methylene blue whole mount of the pleural region in Blaberus showing the two major branches of DN-3 (225X).
A = DN-3A
B = DN-3B

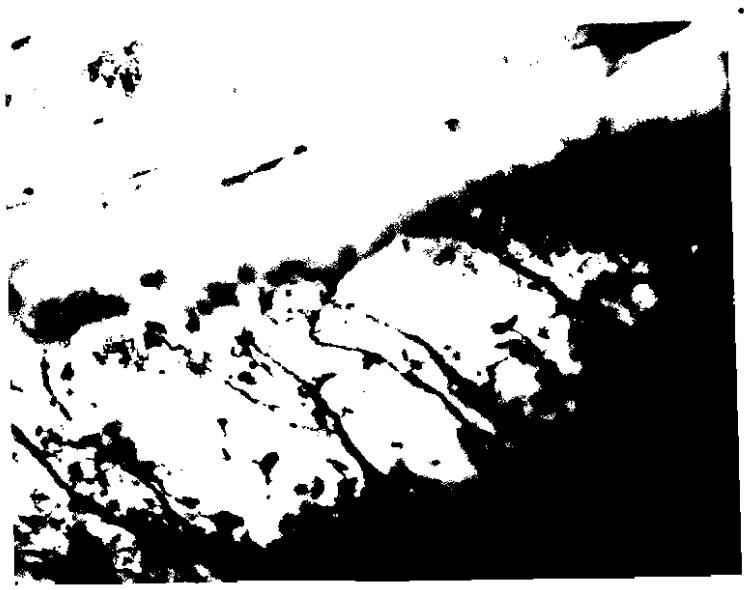


Figure 19. Methylene blue stained whole mount of the posterior pleural region of Blaberus showing the many fine branches of DN-3A and DN-3B (50X).

the cuticle and an important dorsal receptor, a heretofore undescribed chordotonal organ which was best seen in sagittal sections.

The receptor, which will be referred to as the lateral chordotonal organ, has two cuticular attachments. The first (to be called attachment 1) attaches to the posterior margin of the segment (Fig. 20, 21). It is located dorsal and medial to the line of fusion between the sternite and tergite. This attachment appears to be fan-shaped in three dimensions, and to consist of connective tissue fibers which stain blue with Luxol Fast Blue. The fibers pass anteriorly to the cell bodies which stain red with Mallory's stain (Fig. 22, 23). The sensory axons leave the cell bodies, pass anteriorly and dorsally, and eventually contribute to DN-3B. The cell bodies are encapsulated with blue-staining connective tissue. Several nuclei from supporting cells are associated with the sensory cell bodies. The second, more anterior, attachment is an extension of the line formed by attachment 1 and cell bodies, and is located at the lateral fusion line.

Fig. 24 shows the relationship of the receptor to the dorsal and ventral cuticle.

PHYSIOLOGY OF THE DN-3 RECEPTORS INCLUDING THE LATERAL CHORDOTONAL ORGAN

Since a minimum of 20 sensory cells contribute to

Figure 20. Sagittal section of the lateral chordotonal organ showing attachment 1 in the posterior intersegmental membrane (arrow) just medial to the lateral fold (50X).

Figure 21. Same as Fig. 20, but at a greater magnification to show fan-shaped attachment 1 (225X).

Figure 22. Encapsulated lateral chordotonal receptor showing nuclei of five sensory cells (225X).

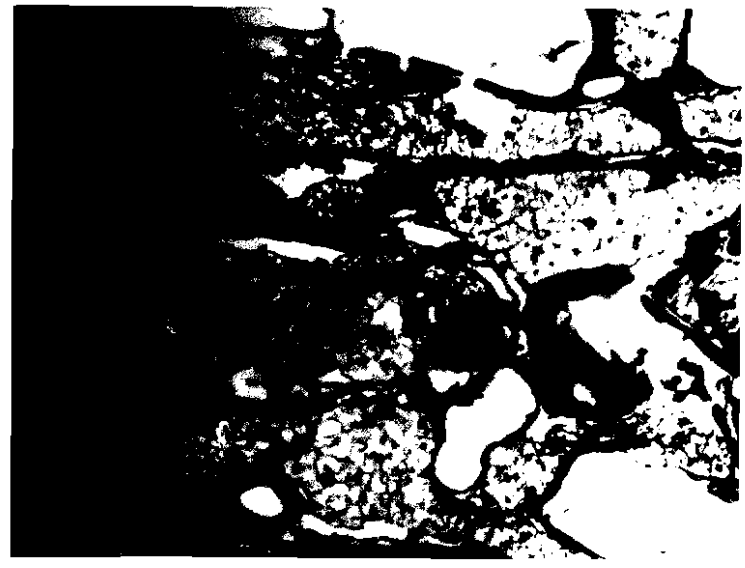


Figure 23. Lateral chordotonal receptor (arrow) in relationship to the dorsal musculature (50X).

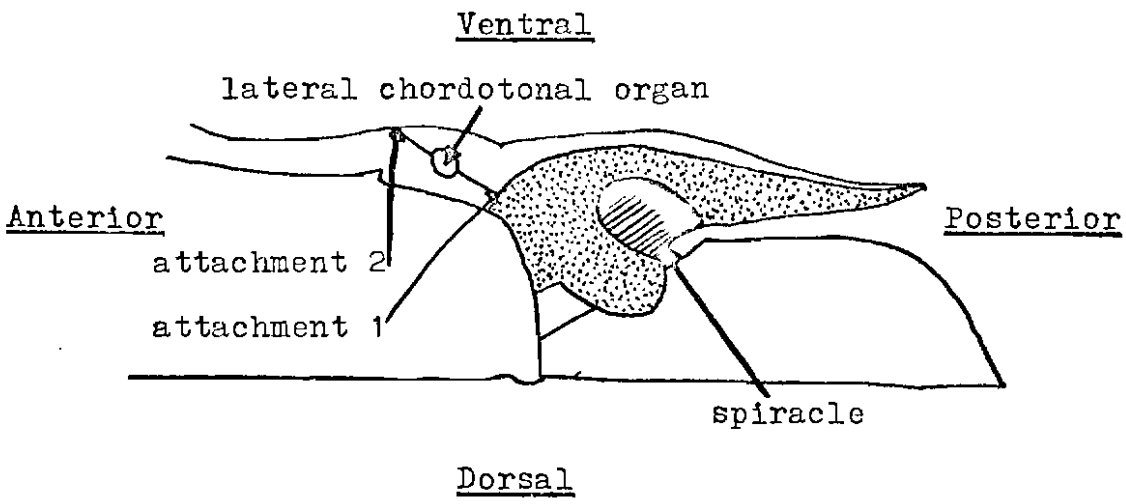


Figure 24. Diagram showing the relationship of the lateral chordotonal organ to the cuticle around the spiracle.

DN-3, and different stimuli elicit characteristic and repeatable responses, it is obvious that the lateral chordotonal organ is not the only source of sensory information on this nerve.

Three, and occasionally four, fibers responded to groundborne vibrations (Fig. 25). Coating the lateral fold with Vaseline, a method which has been used to inhibit sensory hair responses (Haskell, 1956), failed to halt the sensory response to tapping.

Gentle rubbing of the ventral surface, in the vicinity of the lateral fold, initiated a sensory response of 4-6 fibers (Fig. 26). Several of these same fibers seemed to respond to compression of the tergites.

Uniform light pressure over the lateral junction between two tergites initiated a pronounced response of five to seven fibers (Fig. 27). This is the area which overlies the lateral chordotonal organ. Stronger compression on the tergites stimulated up to twelve fibers.

An air stream directed at the pleural fold initiated a response in up to 12-15 fibers (Fig. 28). Vaseline applied to the pleural fold and vicinity did not affect these responses. The air stream presumably exerts its influence through mechanical deformation and comes as close to activating all of the sensory elements as any stimulus.

Receptors in DN-3 responded to ventilatory movements. Three to five fibers respond 30 to 60 msec after the inspiratory motor bursts and one during expiration

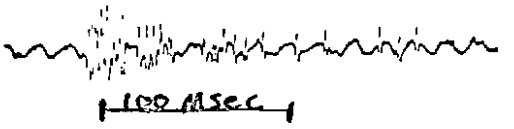


Figure 25. Afferent response on DN-3 to groundborne vibrations.

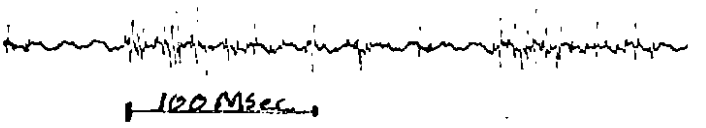


Figure 26. Response in the dorsal nerve to rubbing sternites.

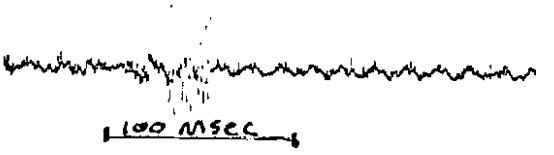


Figure 27. Response in the dorsal nerve to light pressure over the lateral junction between two tergites.

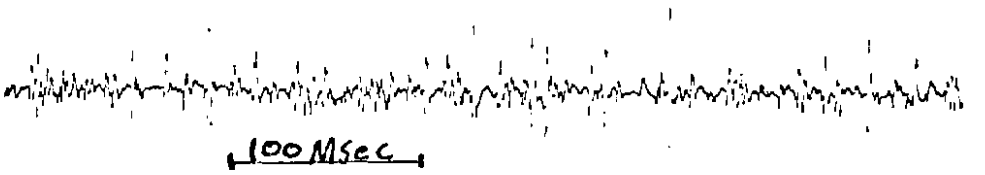


Figure 28. Response in the dorsal nerve to an air stream directed at the lateral fold.

(Fig. 29). A similar cell firing during expiration in Periplaneta was reported by Farley, Case, and Roeder (1967), although its anatomical location was not known.

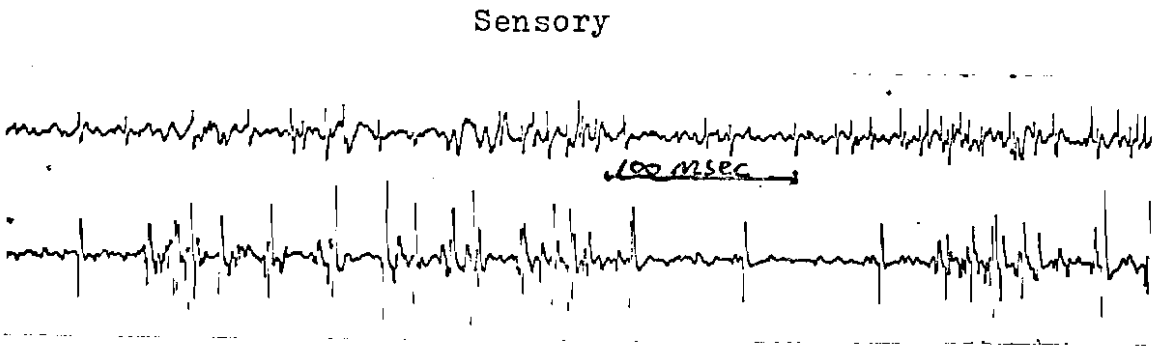
The sensory elements of DN-3 were tested for susceptibility to various chemicals in an attempt to activate a quiescent chemo-receptor, such as the possible CO_2 receptor which Case (1957) suggested as a logical means for an insect to monitor its internal environment. The nerve cord was removed, and the deefferented dorsal nerves were exposed to CO_2. No responses were noted.

The area of the pleural fold was then exposed to 1%, 5%, 10%, and 15% solutions of acetic acid, ethyl alcohol, sodium hydroxide, and sodium chloride in saline. Again no responses were noted. No afferent activity was initiated when distilled water was placed on the fold in an attempt to detect an osmoreceptor. The possibility of thermoreceptors was ruled out by applying saline heated between 30 and 50 degrees centigrade.

Stimulating dorsal nerve efferents while recording from DN-3 with sensory connections intact failed to initiate an afferent response. On the basis of this information the possibility of a muscle receptor organ contributing to this nerve was ruled out.

DN-4A

Finlayson and Lowenstein (1958) reported a single-



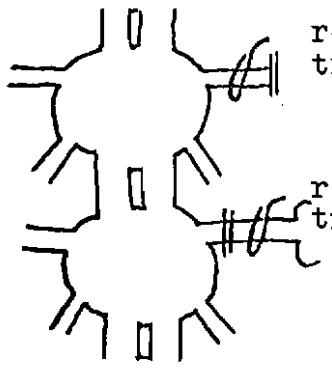


Figure 29. Simultaneous recordings from deafferented and deefferented dorsal nerve; ventilatory rhythm initiated by CO_2.

celled longitudinal stretch receptor under the fourth and fifth bands of the inner tergal muscle in Periplaneta. A later study by Finlayson and Osborne (1962) reported a similar vertical receptor near the longitudinal receptor. Both receptors are found in Blaberus (Fig. 30) and each contributes a fiber to DN-4A.

These receptors were destroyed during the usual dorsal dissections used in these experiments and were usually not included in the electrophysiological experiments. However, it was determined that electrical stimulation of DN-4 does not elicit a response in the homolateral ventral nerve, one of the major intraganglionic pathways under study.

Prelimary electrophysiological analysis of this nerve indicates several sensory cells in addition to the vertical and longitudinal stretch receptors (Fig. 31).

DN-4B, INCLUDING CARDIAC SEGMENTAL NERVE

DN-4B is of considerable importance to this study because the distal end terminates in the lateral nerve of the heart. In heart studies the dozen pairs of these distal branches have been referred to as the "segmental nerves" (Alexandrowicz, 1926; McIndoo, 1945). More proximally, DN-4B, which contained four motor fibers, divides into small branches to innervate the inner tergal muscle. It was possible on several occasions to record spontaneous activity which indicated at least two fibers were present in the

Figure 30. Methylene blue whole mount of the longitudinal receptor (long arrow) and vertical receptor (short arrow) in the dorsal body wall of Blaberus (225X).

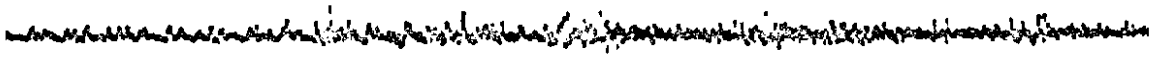


Figure 31. Afferent activity from DN-4A. Recording made from DN-4. Nerve cut proximal to recording electrode, DN-4B destroyed. Note: more than two spike heights are discernable.

cardiac segmental nerve.

There are no sensory elements in DN-4B, including the cardiac segmental nerve. Spontaneous activity on the cardiac lateral nerve does not contribute to or affect the activity on DN-4B. This has been determined by recording from a deefferented DN-4B connected to the lateral nerve.

Electrical stimulation of the lateral nerve resulted in a response of three fibers on DN-4B (Fig. 32). In view of the fact that lateral nerve activity is not conducted to the segmental nerve, these fibers are evidently antidromically stimulated dorsal nerve efferent fibers. The three responding fibers followed up to 50 stimuli per second.

Relationship of DN-4B Fibers to the Heart Rate

DN-4B participates in the respiratory rhythm. The following experiments (Table I) were designed to determine whether or not the respiratory rhythm affects the heart. The heart rate in the continous presence of high concentrations of CO_2 slows and eventually stops. To determine whether this slowing of the heart is a result of central neural inhibition or an intrinsic property of the heart itself, heart rates were counted in intact animals (Table I-A) and in isolated heart preparations (Table I-B) in the presence of CO_2. The heart rate slowed appreciably in both instances, indicating an effect of CO_2 independent

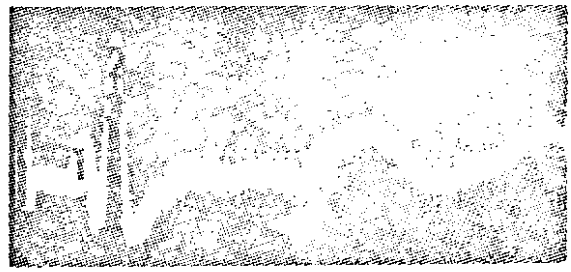


Figure 32. Response on DN-4B to stimulation of the lateral nerve. 1 = single spike; 2, 3 = two superimposed spikes.

TABLE I. Typical experiments showing the effect of CO_2 on the cockroach heart rate.

A. Decapitated, Otherwise Intact Cockroach. 100% CO_2 Administered In A Gas Chamber

Normal heart rate (beats per minute)	107	104	105		
Minutes	1	2	3	4	5
Heart rate (beats per minute) during application of CO_2	90	74	64	31	Narcosis

B. Isolated Heart. 100% CO_2 Administered In A Gas Chamber

Normal heart rate (beats per minute)	100	102	90	94
Minutes	1	2	3	4
Heart rate (beats per minute) during application of CO_2	51	24	28	Narcosis

All hearts were from adult male Blaberus.

TABLE I. Typical experiments showing the effect of CO_2 on the cockroach heart rate.

C. Isolated Heart - Lateral Nerve Intact. CO_2 Dissolved in Saline				
Normal heart rate (beats per minute)	60	62	66	
Minutes	1	2	3	4
Heart rate (beats per minute) during application of CO_2	54	52	46	27

D. Isolated Heart - Lateral Nerve Cut - In Six Places. CO_2 Dissolved In Saline				
Normal heart rate (beats per minute)	60	68	66	
Minutes	1	2	3	4
Heart rate (beats per minute) during application of CO_2	44	52	40	34

All hearts were from adult male Blaberus.

of central neural control. This experiment does not exclude the possibility that the cardiac lateral nerve could mediate the CO_2 effects. To test this, isolated hearts were exposed to CO_2 before and after the lateral nerve was cut in six places (Tables I-C and I-D). In both instances the heart slowed under the influence of CO_2. This result shows that the heart muscle is independently sensitive to CO_2, but it does not rule out the possibility that the lateral nerve may enhance the CO_2 sensitivity of the heart.

LATERAL CARDIAC NERVE

Six to ten fibers fire spontaneously on the lateral nerve. Several fibers exhibit opposite polarities to the majority of the fibers, indicating that the spikes travel both anteriorly and posteriorly (Fig. 33). At least two fibers which travel from posterior to anterior have a spike duration of about 4 msec (Fig. 34).

II. RESPONSES TRIGGERED BY VENTRAL RECEPTORS

Stimulation of the ventral nerve resulted in a large number of responses which are described in this section. Since, after an exhaustive search, the mid-sternal receptor was the only significant receptor found on the ventral nerve, it is probable that this receptor organ normally triggers all of the reflexes described here.

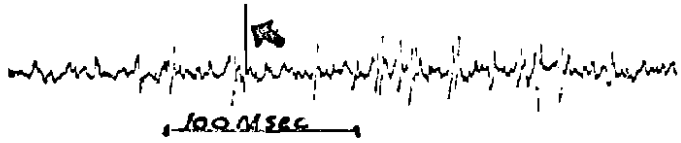


Figure 33. Activity recorded from lateral nerve. Arrow points to spike with polarity opposite to most spikes in record.

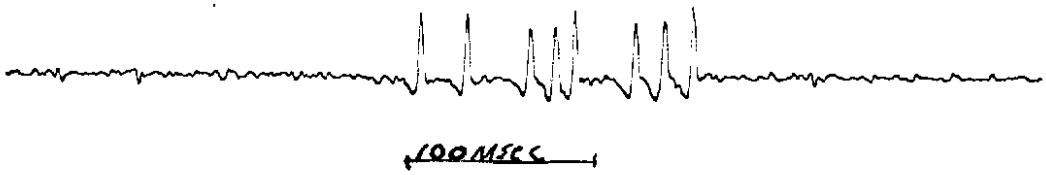


Figure 34. Long duration spikes on the lateral nerve.

A. VENTRAL NERVE TO HOMOLATERAL DORSAL NERVE PATHWAY

Stimulation of a ventral nerve initiated a response in the dorsal nerve of the same ganglion. Typically five to eight dorsal nerve fibers responded at a single threshold, which varied between 2.5 and 6 volts depending on the age of the preparation. Occasionally the response could be divided into a lower threshold group (Fig. 35) of two or three fibers and a higher threshold group of three or four fibers. The typical response followed up to 7 or 8 stimuli per second in freshly dissected animals. The stimulus strengths for the ensuing reflex studies were frequently adjusted to insure that the maximum number of fibers were activated.

This response to ventral nerve stimulation travels up the connective on the side stimulated to the next anterior ganglion where it synapses, then returns via the same connective to the dorsal nerve. This pathway was established by monitoring the response as it traveled through the reflex arc. Afferent spikes traveled at 2½ to 3 meters per second in the ventral nerve. Conduction time through the first ganglion normally required 1 to 2 msec, too fast for complicated synaptic events to occur. The response was conducted anteriorly through the connective at the slightly lower velocity of 2 meters per second, and followed trains of stimuli up to 40 per second. There was a 4 to 5 msec synaptic delay in the anterior ganglion (Fig. 36), where it

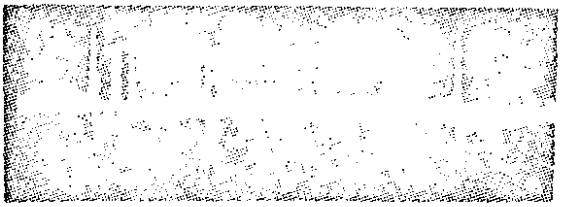


Figure 35. Primary response on the dorsal nerve to ventral nerve stimulation.

Figure 36. Data showing the delay in the ventral nerve to dorsal nerve reflex. Ascending afferent response in the connectives (short arrows) and descending motor response (long arrow).

appears some integration occurs. Unfortunately anticromically stimulated efferent fibers partially masked the afferent response and made an accurate evaluation of integration impossible. For the efferent half of the pathway the conduction rate was 2 meters per second in the connectives and 2 meters per second in the dorsal nerves. The conduction time in the posterior ganglion was 1 msec. When the anterior connective was stimulated the response on the dorsal nerve followed up to 100 stimuli per second, which indicates there are no synaptic events in this half of the reflex. The latency for the entire response was 12 to 15 msec, representing an average conduction velocity of 1.25 to 1.5 meters per second.

The dorsal nerve responses to ventral nerve stimulation could be traced to DN-1 and DN-4. On DN-1, two to three fibers were activated (Fig. 37) and it was possible to observe slight contractions of the inner sternal muscle, innervated by this nerve. Three to four fibers of DN-4 were also found to respond to ventral nerve stimulation (Fig. 38).

DN-2 and DN-3 did not respond to ventral nerve stimuli as strong as 8 volts.

When the mid-sternal receptor was subjected to natural or electrical stimulation, the afferent response was conducted centrally only. No responses were found on VN-2, VN-3 or distally on VN-3A i.e., no evidence for a peripheral synapse.

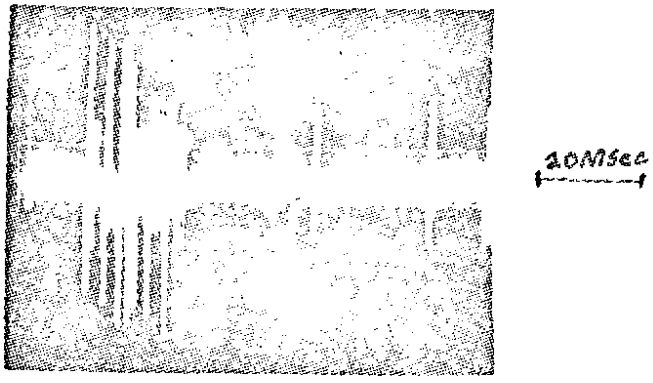


Figure 37. Response on DN-1 to ventral nerve stimulation.

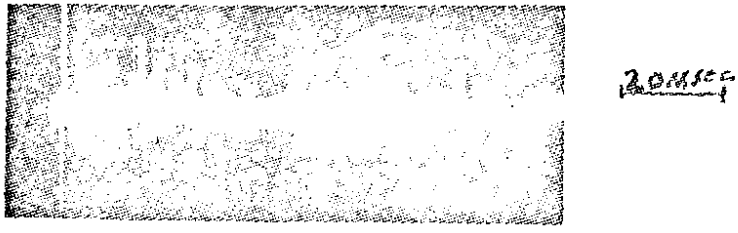


Figure 38. Response on DN-4 to ventral nerve stimulation.

B. VENTRAL NERVE TO HETEROLATERAL DORSAL NERVE PATHWAY

In addition to the homolateral pathway just described, stimulation of a ventral nerve also leads to excitation of fibers in the heterolateral dorsal nerve.

The heterolateral dorsal nerve responds with a latency of 10 to 14 msec. Most of the response travels up the homolateral connective to the next anterior ganglion, where it crosses over and returns to the heterolateral dorsal nerve via the heterolateral connective (Fig. 39). However, the response of one fiber requires only the ganglion stimulated; with the anterior and posterior connectives cut the fiber continues to respond to natural stimulation (Fig. 40).

The heterolateral ventral nerve does not respond to ventral nerve stimulation.

C. VENTRAL NERVE REBOUND PATHWAY

Stimulation of the main trunk of the ventral nerve results in a rebound reflex. The response consists of one VN-2 fiber firing several times in response to each stimulus. Unlike the dorsal nerve response to ventral nerve stimulation, the synaptic activity only occurs in the stimulated ganglion. The rebound portion of the response is lost when the nerve is cut close to the ganglion.

Simultaneous records from the dorsal and ventral

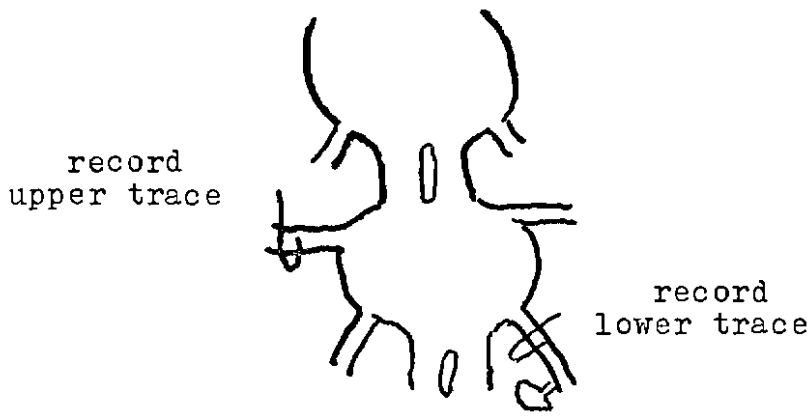
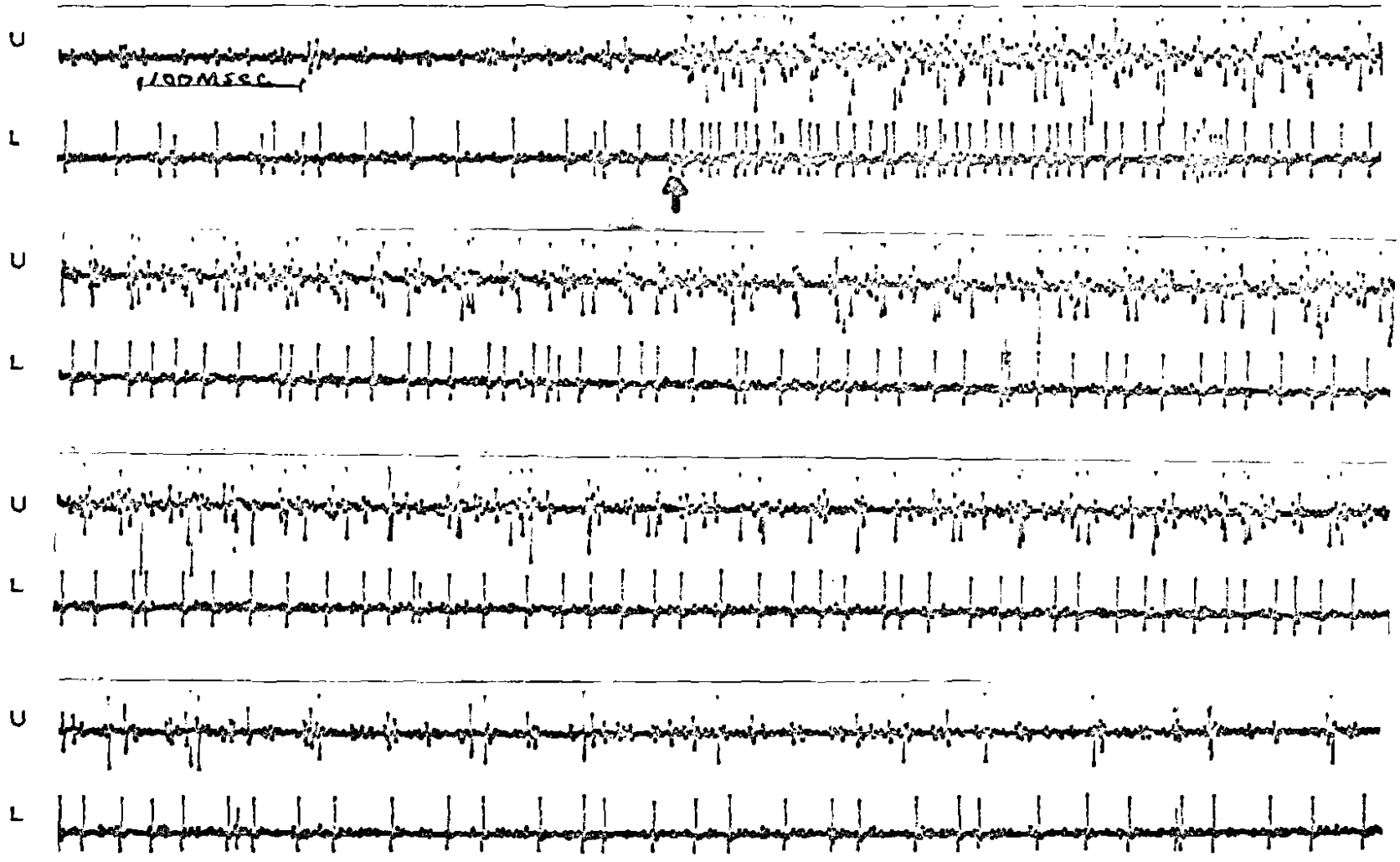
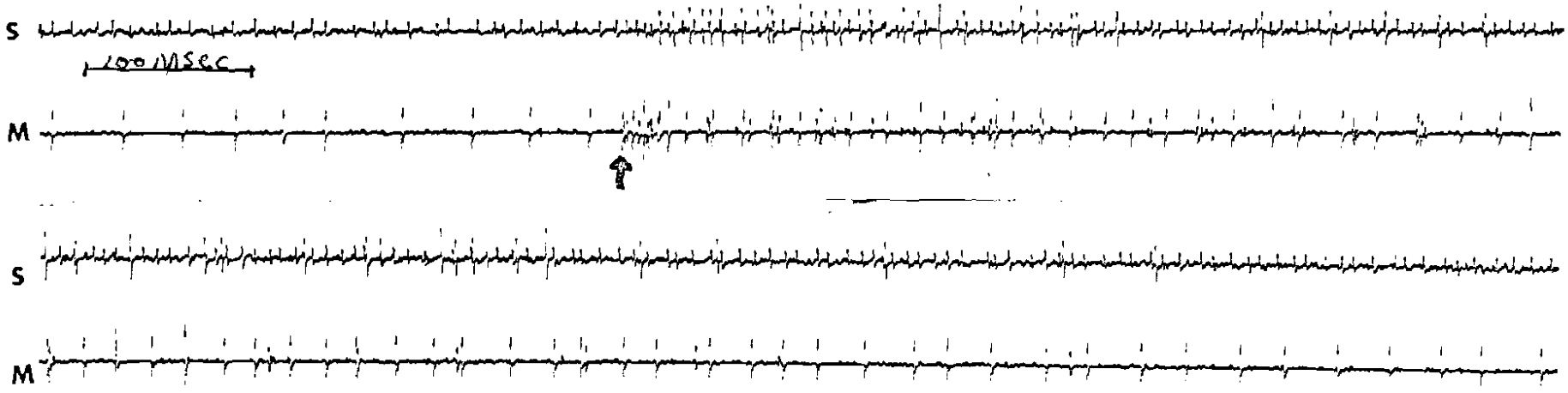


Figure 39. Response on the heterolateral dorsal nerve to pressure in the ventral musculature which activated the mid-sternal receptor. The response utilizes the interganglionic and intraganglionic pathways described in text. Diagram indicates electrode placement. Arrow indicates approximate time of stimulation.



U = upper trace - dorsal nerve

L = lower trace - ventral nerve



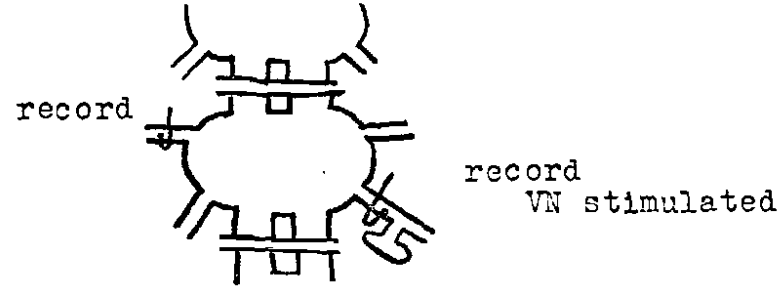


Figure 40. Same as Fig. 39, except connectives cut anterior to ganglion recorded from (see diagram). Upward-directed arrow indicates beginning of receptor response and downward directed arrow indicates beginning of single fiber response in dorsal nerve.

S = sensory input M = motor response

nerves during stimulation of the ventral nerve indicate that the ventral rebound response is synchronized with the dorsal response (Fig. 41). The long latency of the rebound reflex, 10 to 12 msec, could be the result of either slow-conducting fibers or a long synaptic delay. By arranging the stimulating and recording electrodes to observe the input as well as the output, a ganglionic delay of 5 to 6 msec is observed (Fig. 42). If it is assumed that the efferents conduct at the same rate as the afferents, $2\frac{1}{2}$ meters per second, the synaptic delay could account for the synchronization of responses.

D. REPETITIVE RESPONSE IN HOMOLATERAL CONNECTIVE

An additional response to ventral nerve stimulation was found in the anterior homolateral connective. With stimuli of 1 to 2 volts above the threshold for the normal ventral nerve to dorsal nerve response, an additional fiber in the connective began to fire at 8 to 10 spikes per stimulus (Fig. 43). This may be the activity of a higher threshold sensory fiber with an axon which passes through the ganglion, or it may be indicative of the occurrence of ganglionic synaptic events. In either case, this fiber does not participate in the ventral nerve - dorsal nerve reflex.

E. RESPONSES OF THE CARDIAC LATERAL NERVE

Electrical stimulation of the ventral nerve stimulates one to three fibers on the lateral nerve (Fig. 44).

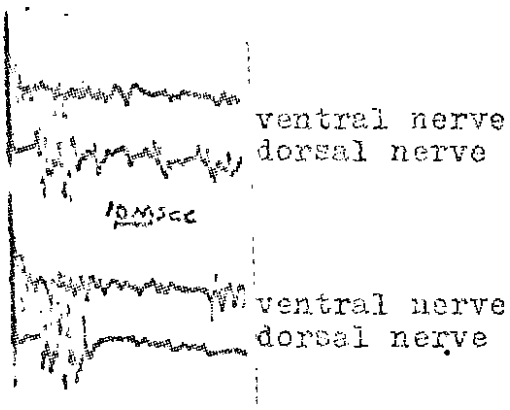


Figure 41. Ventral rebound and simultaneous dorsal nerve response to ventral nerve stimulation.

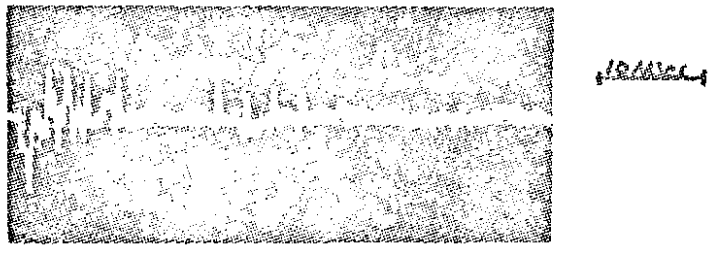


Figure 42. Activity on the ventral nerve following its stimulation at a point distal to the recording electrodes. The first burst of spikes represents the afferent activity. The second burst is efferent.

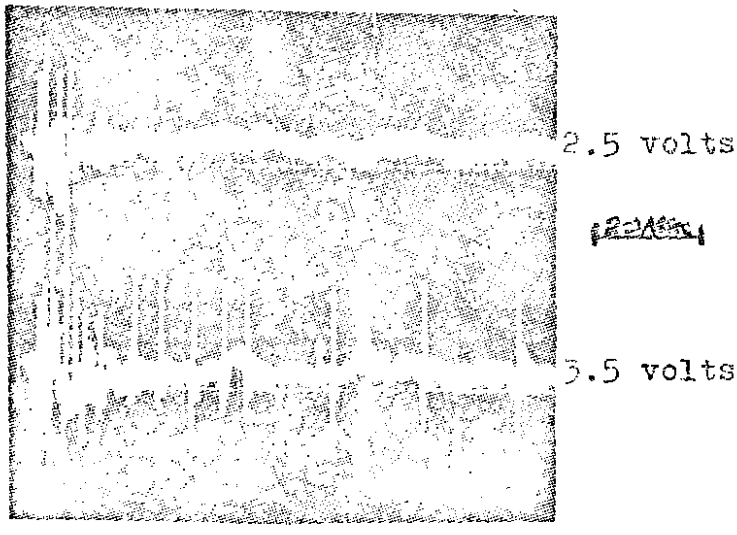


Figure 43. Recetitive response (lower trace) in the homolateral connective to ventral nerve stimulation. Upper trace shows connective response at stimulus strength required to activate ventral nerve to dorsal nerve response.

The latencies depend on the distance the recording electrode is from the segmental nerve-lateral nerve junction. In the experiment described by Fig. 44 they vary between 14 and 16 msec. In the record described, the geometry of the stimulating and recording electrodes was such that the spikes had to travel from posterior to anterior.

Natural stimulation of the mid-sternal receptor was also observed to evoke a response in the homolateral lateral nerve. The duration of the response appeared to be proportional to the strength of the input.

Utilizing the FM wireless transducer to monitor heart contractions, attempts were made to show that segmental nerve input can modify not only lateral nerve activity but also heart rate. There were no observable changes in the heart rate when a single dorsal nerve was stimulated at intensities up to six volts and at frequencies of one to fifty per second. However, heart rate increases were obtained when two dorsal nerves were stimulated, as shown in Fig. 45. In this example the rate before and after stimulation was 80 per minute and during stimulation it was 90 per minute, or 12% increase during stimulation.

F. EXPERIMENTS TO ESTABLISH FUNCTION OF VENTRAL NERVE-DORSAL NERVE REFLEX

Of the responses to ventral nerve stimulation described above, the responses of the dorsal nerve involve

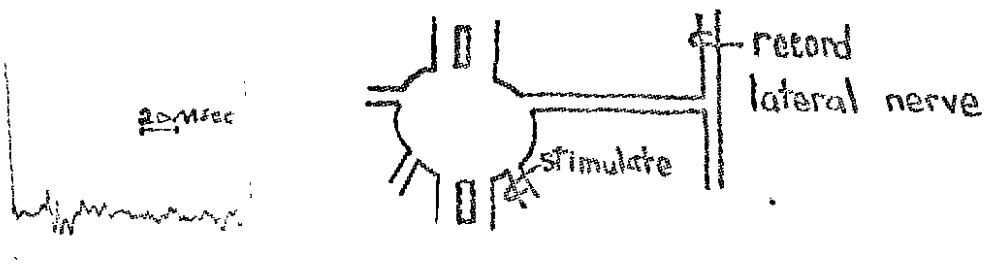


Figure 44. Lateral nerve response to ventral nerve stimulation.

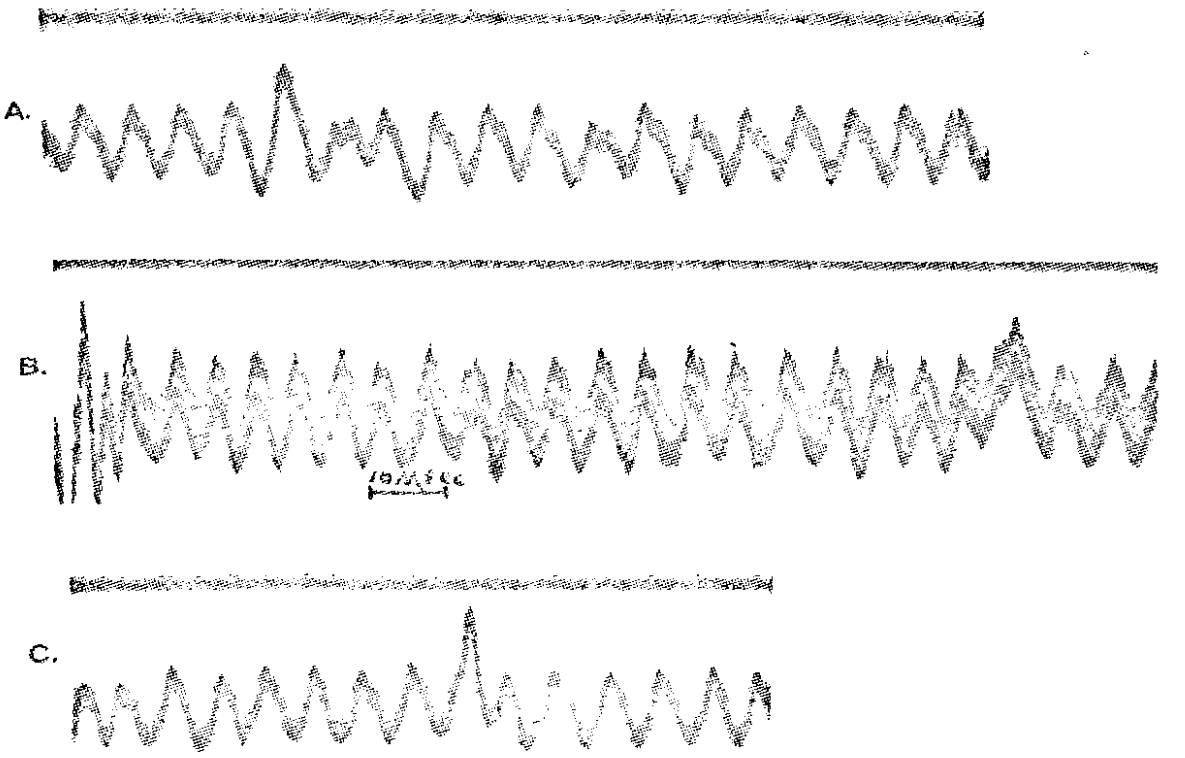


Figure 45. Changes in the heart rate during stimulation (3 volts - 20 per second) of two dorsal nerves.
A. Heart rate before stimulation.
B. Heart rate during stimulation.
C. Heart rate after stimulation.

the largest number of efferent fibers and have received the most attention. For the detailed mapping which was the purpose of that part of the study, precisely controllable electrical stimuli were necessary, but to determine the function of this reflex, "natural" stimuli were more appropriate.

Of the three forms of natural stimulation found to stimulate the mid-sternal receptor, only exposure to carbon dioxide and compression of the ventral sternites elicit a full dorsal nerve response. Groundborne vibrations fail to elicit a response. The effects of each are described in this section.

1. VENTRAL NERVE-DORSAL NERVE REFLEX INITIATED BY THE CO_2 SENSITIVE ELEMENTS OF THE MID-STERNAL RECEPTOR

The following experiments on carbon dioxide effects were designed to determine whether the mid-sternal receptor initiates or modifies ventilatory activity. Two ganglia were isolated by cutting all their connections except for one ventral nerve. Large sections of the ventral cuticle adjacent to the receptor were removed, and the animal was pinned over a longitudinal hole in a wax-filled petri dish. A mound of clay was inserted under the two ganglia to ensure isolation from the CO_2-saturated saline. The sensory connections of the ventral nerve were checked to be sure

that they were intact. A small drop of CO_2-saturated saline was placed on the receptor with a small pipette. Excess saline drained through the holes in the cuticle. Under these conditions it was possible to observe a gradual increase in the CO_2-induced afferent activity and a concomitant increase in dorsal nerve motor activity (Fig. 46). Once an induced increase in spike frequency was obtained, additional CO_2 placed on the receptor had no further effect on the dorsal nerve activity. Since great care was taken to insure the drop of saline touched only the receptor it appears that the afferent activity initiated the dorsal nerve spike frequency change. However, two other explanations are possible. The CO_2 may antidromically stimulate ventral nerve motor fibers which activate the dorsal response, or enough CO_2 may come out of solution to affect the ganglion or dorsal nerve directly. No evidence on these points is presently available.

2. EFFECTS OF RESPIRATORY MOVEMENT ON DORSAL AND VENTRAL NERVE AFFERENT ACTIVITY

Compression of the ventral musculature occurs during a normal respiratory movement. During the rhythmic respiratory pumping movements, motor bursts correspond to bursts of ventral afferent activity. Simultaneous records of afferent activity from dorsal and ventral nerves indicate they both fire in synchrony to the abdominal displacement (Fig. 47

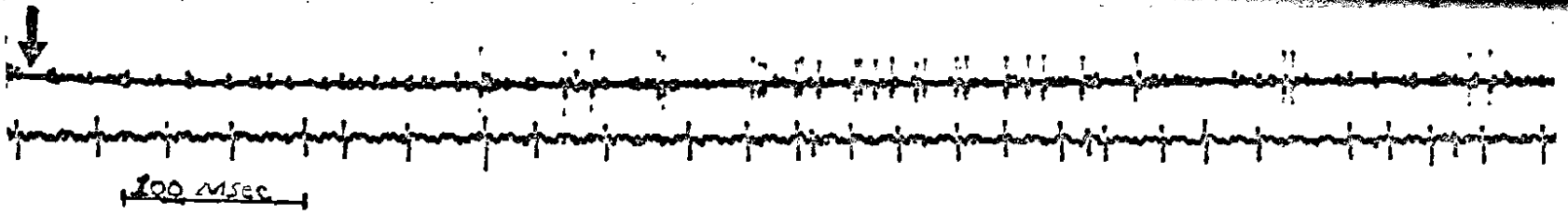


Figure 46. CO_2-induced response from the mid-sternal receptor activating the dorsal nerve. Arrow indicates the time of CO_2 application. Upper trace: ventral nerve with intact mid-sternal receptor. Lower trace: motor activity on the dorsal nerve.

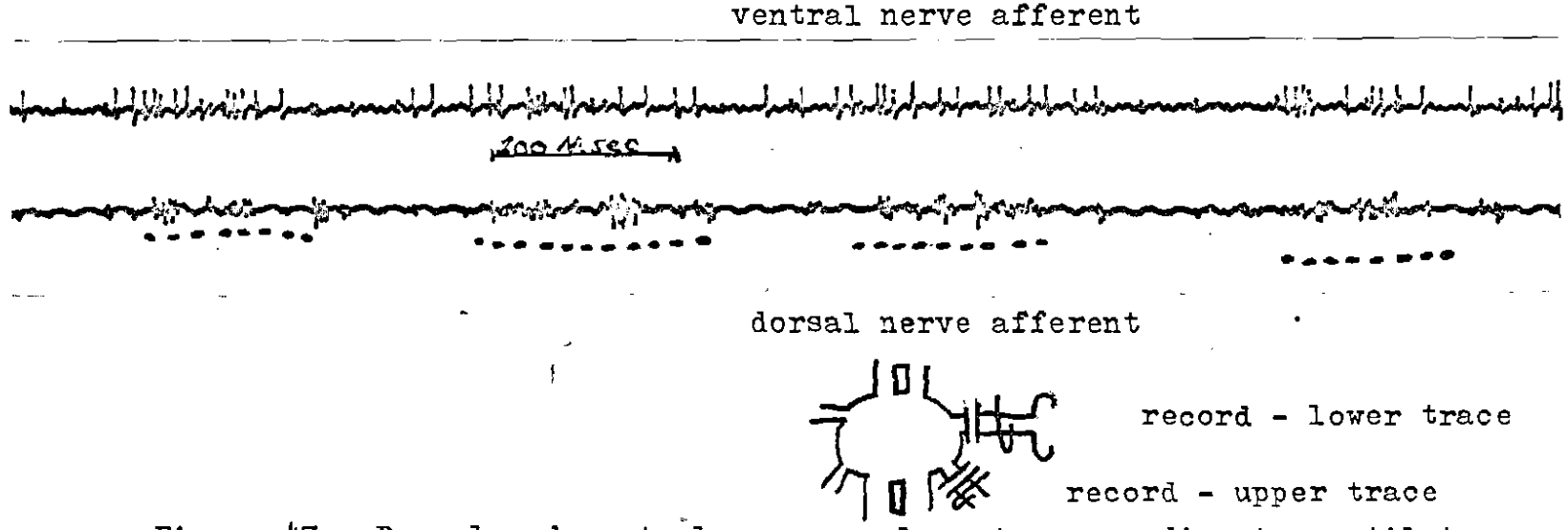


Figure 47. Dorsal and ventral sensory elements responding to ventilatory pumping movements. Dots indicate compression.

3. REFLEX RESPONSES TO PRESSURE, WHICH ACTIVATES THE MID-STERNAL RECEPTOR

In order to determine whether abdominal compression is capable of initiating a response on the dorsal nerve the following experiment was carried out. Two ganglion were isolated and deafferented, with the exception of a ventral nerve. Recording electrodes were placed under the ventral nerve and its homolateral dorsal nerve. By gently compressing the ventral musculature with a small glass rod it was possible to activate the receptor. The dorsal nerve was found to respond under these conditions (Fig. 48 A and B). The efferent response varied with the intensity of the input.

In addition to the dorsal nerve response, compression stimulated a response in the thoracic connectives. When the mid-sternal receptor of A-1 was stimulated naturally a response was found between the connectives of the second and third thoracic ganglia (Fig. 49); but, the heterolateral thoracic connectives did not respond. Afferent activity from A-3 did not reach the thoracic connectives.

4. REFLEX RESPONSES TO GROUNDBORNE VIBRATIONS

The third possibility, that the mid-sternal receptor serves to relay information about groundborne vibrations to

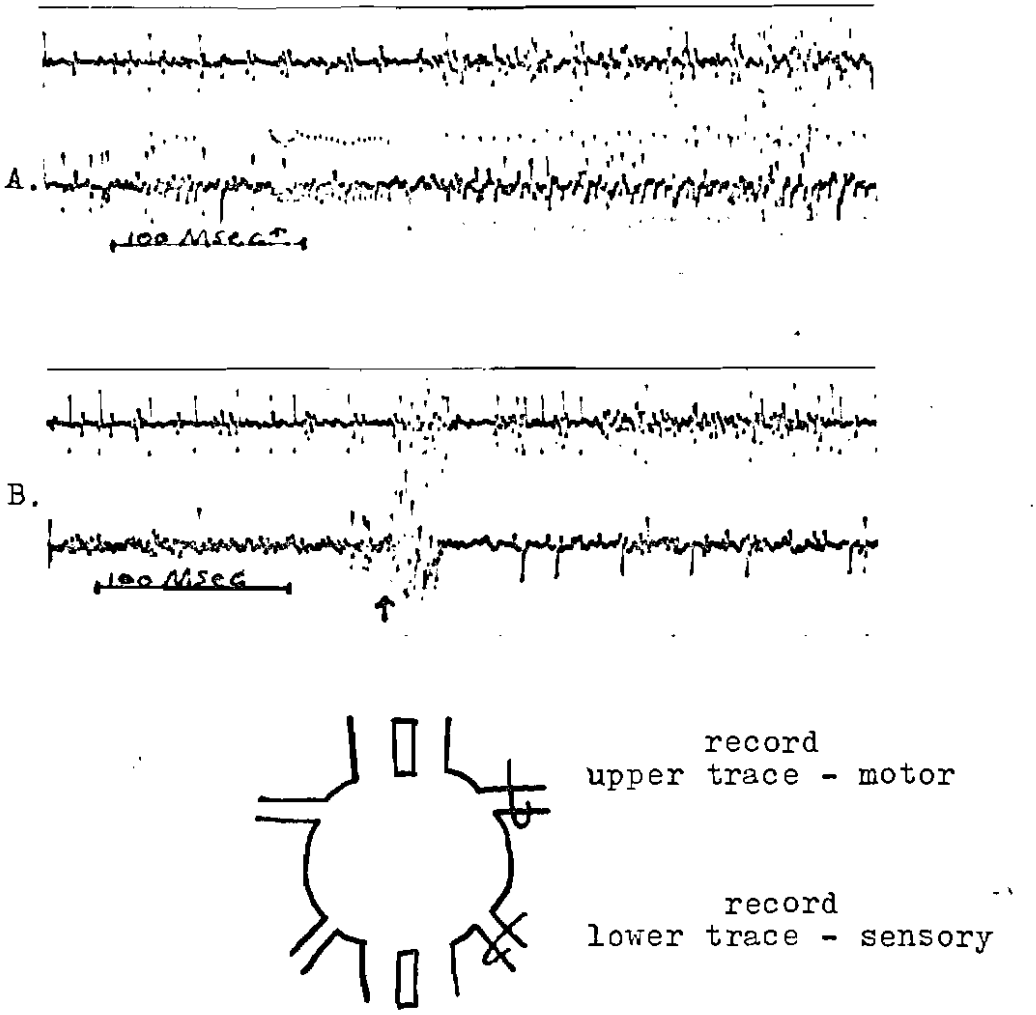


Figure 48 (A and B). Ventral nerve to homolateral dorsal nerve reflex induced by compression in the ventral musculature, which activates the mid-sternal receptor.

Figure 49. Response on the thoracic connectives, upper trace, between T-3 and T-2 to natural stimulation of the mid-sternal receptor of A-1, lower trace. Arrow indicates approximate time the stimulation was begun.

the dorsal and ventral musculature, was tested in the following way: two abdominal ganglia were isolated and all peripheral nerves were cut, except one ventral nerve which was to provide sensory input. Recording electrodes were placed on the ventral nerve and on the homolateral dorsal nerve, to monitor both sensory input and motor output. Analysis of 12 records of such experiments failed to turn up dorsal nerve responses to tapping stimulation (Fig. 50). It is possible that the sensory response to tapping is too weak to activate the synapses necessary for the dorsal response.

It did not seem entirely reasonable that the clear-cut sensory response to tapping would completely fail to produce a motor response, so responses were sought on other nerves. No responses were found on the other motor nerves of the same ganglion, but a response to tapping was recorded from the posterior homolateral connective (Fig. 51).

III. RESPONSES TIGGERED BY DORSAL NERVE RECEPTORS

A. DORSAL NERVE TO HOMOLATERAL VENTRAL NERVE PATHWAY

Stimulation of DN-3 results in a response on the homolateral ventral nerve. Two thresholds are present in fresh preparations. At a threshold of 2.5 volts, one and sometimes two fibers responded to single well-spaced stimuli (Fig. 52). At 3 to 3.5 volts three or four additional fibers responded. These responses followed trains of stimuli up to 12 per second. The central pathway of this

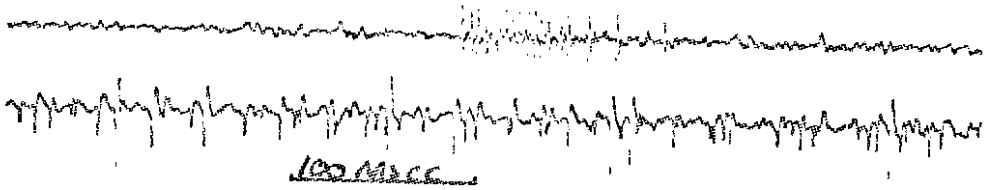


Figure 50. Simultaneous recording of dorsal nerve efferent activity (lower trace) and ventral nerve afferent activity (upper trace) during stimulation by groundborne vibrations.

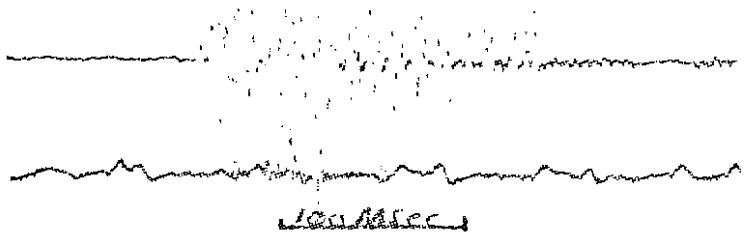


Figure 51. Simultaneous records of sensory input on an intact ventral nerve (upper trace) and response on posterior homolateral connective.

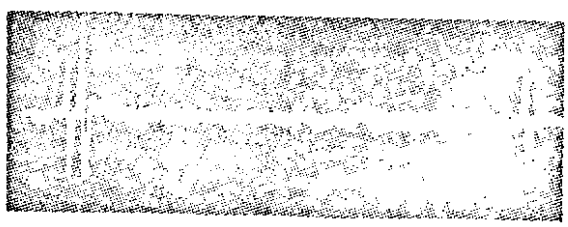


Figure 52. Primary response on the main trunk of the ventral nerve to dorsal nerve stimulation.

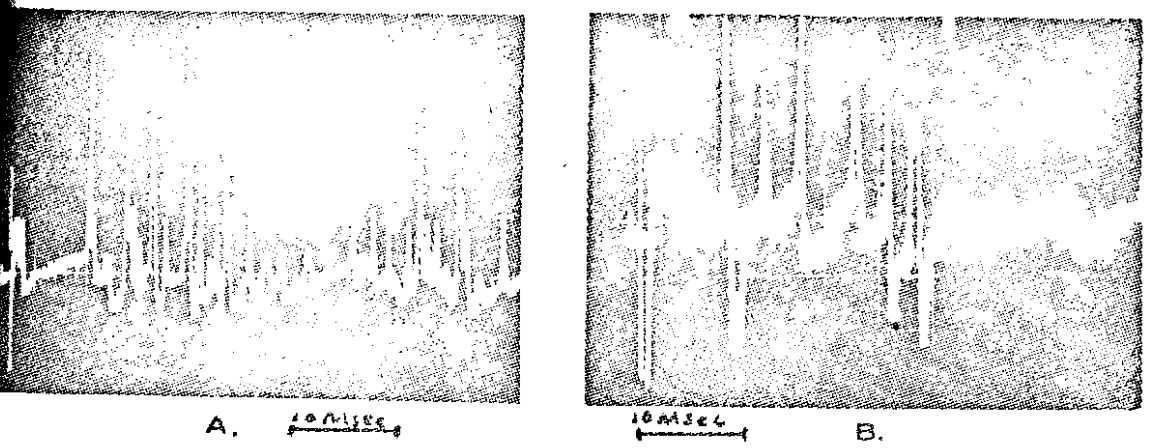
response is confined to the ganglion stimulated, since the response remains after anterior and posterior connectives are cut. The latency varied from eight to nine msec, representing an average conduction velocity of 2.25 to 2.50 meters per second.

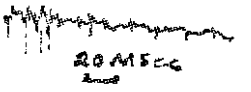
The response to dorsal nerve stimulation can be traced to DN-2 (three to four fibers activated), VN-3 (two fibers), and VN-3A (one to three fibers) (Fig. 53 A, B, C).

B. DORSAL NERVE REBOUND PATHWAY

The stimulation of DN-3 or the main dorsal nerve trunk initiates a rebound reflex. This reflex must travel to the next ganglion to make synaptic contact. It then returns on the same side to activate the dorsal musculature. The response, which lags 1-2 msec behind the ventral response (Fig. 54), has a latency of 10-12 msec, representing an average conduction velocity of 2 to 2.5 meters per second. The synaptic delay is on the order of 4.5 to 5 msec (Fig. 55). These reflexes are not as closely synchronized in time as the dorsal and ventral nerve responses evoked by ventral nerve stimulation. Six to eight fibers constitute the total response.

In terms of number of fibers activated the dorsal nerve rebound reflex is of more importance to the animal than the dorsal nerve to ventral nerve reflex. In the rebound reflex two fibers respond on DN-1 (Fig. 56-A),





C.

Figure 53. Responses on branches of the ventral nerve to dorsal nerve stimulation.
A. Response on VN-2.
B. Response on VN-3.
C. Response on VN-3A.

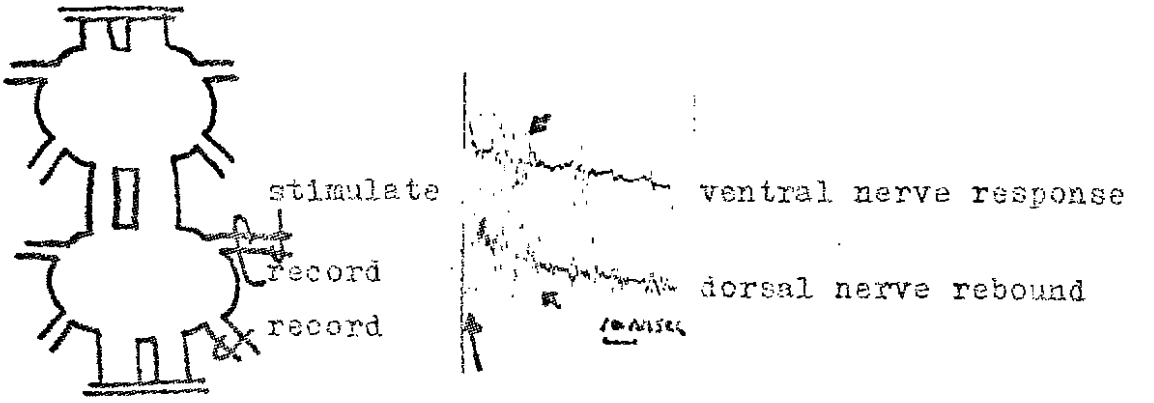


Figure 54. Dorsal rebound and ventral response to stimulation of the dorsal nerve. Afferent response marked by long arrow and efferent responses marked by short arrows.

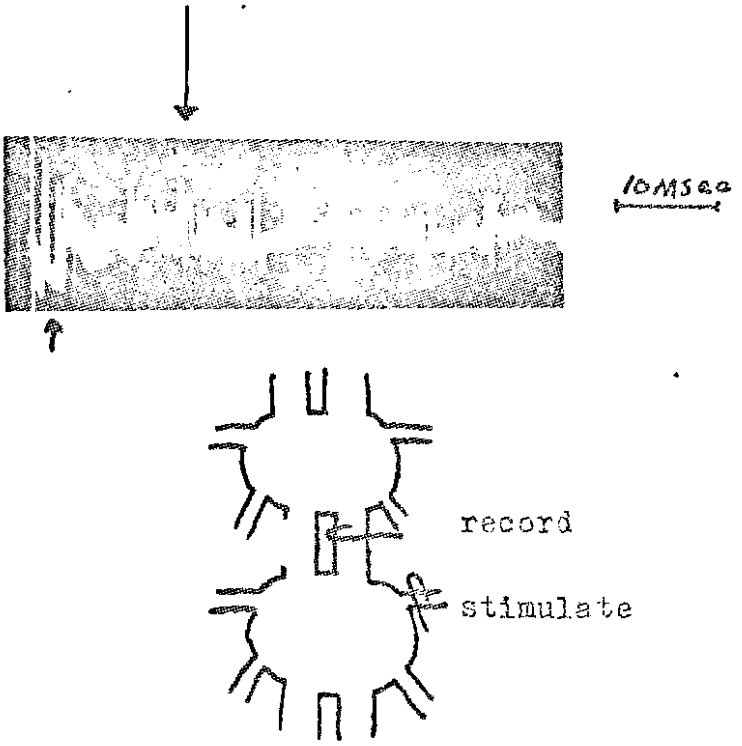


Figure 55. Dorsal nerve rebound reflex recorded in the anterior connective. Afferent ascending response (short arrow) and descending efferent response (long arrow).

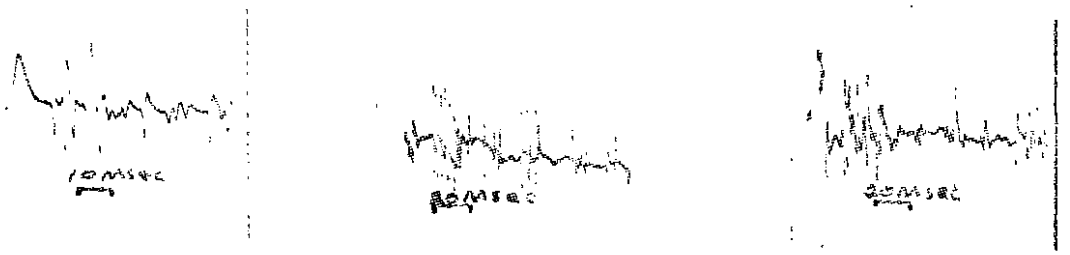


Figure 56. Dorsal nerve rebound reflex on the peripheral branches receiving efferent information.
A. Response on DN-1.
B. Response on DN-2.
C. Response on DN-4.

four fibers on DN-2 (Fig. 56-B), and three to four fibers on DN-4 (Fig. 56-C). When DN-1 or DN-4 was stimulated no rebound reflex was initiated and this served as a control on the above data.

The rebound reflex also reaches the lateral nerve. When a dorsal nerve was cut, then stimulated distal to the cut, a response of three to four fibers was found on the lateral nerve (Fig. 57). When the dorsal nerve was left connected to the ganglion, both short and long latency responses were obtained (A and B, respectively, in Fig. 58). Response B was probably the rebound response.

C. DORSAL NERVE TO HETEROLATERAL DORSAL NERVE PATHWAY

Natural or electrical stimulation of a dorsal nerve leads to a response of the heterolateral nerve of the same ganglion (Fig. 59). Cutting experiments show that the main response travels up the homolateral connective to the next anterior ganglion, crosses over, presumably makes synaptic contact, and returns via the heterolateral connective to the heterolateral dorsal nerve. When either right or left anterior connective is cut the typical response is lost. Fig. 60 shows the response within the heterolateral connective. The cut below the recording point eliminated the possibility of recording from fibers which crossed over in the posterior ganglion.

A single efferent fiber receives synaptic input in the stimulated ganglion since it continues to respond to

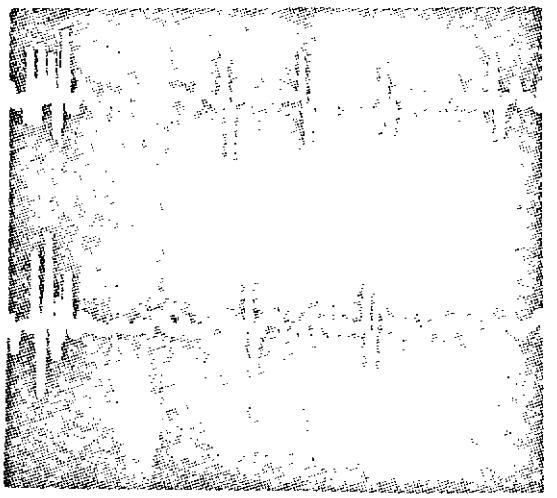


Figure 57. Two records showing response of lateral nerve to stimulation of dorsal nerve. Dorsal nerve cut at ganglion.

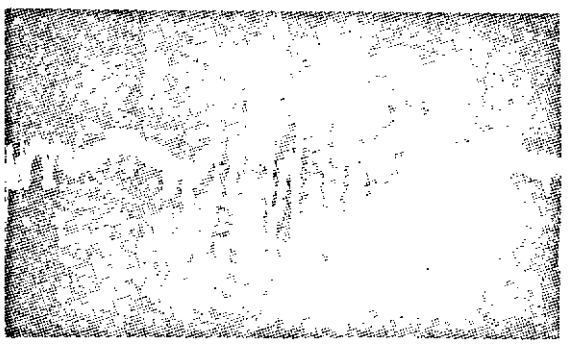
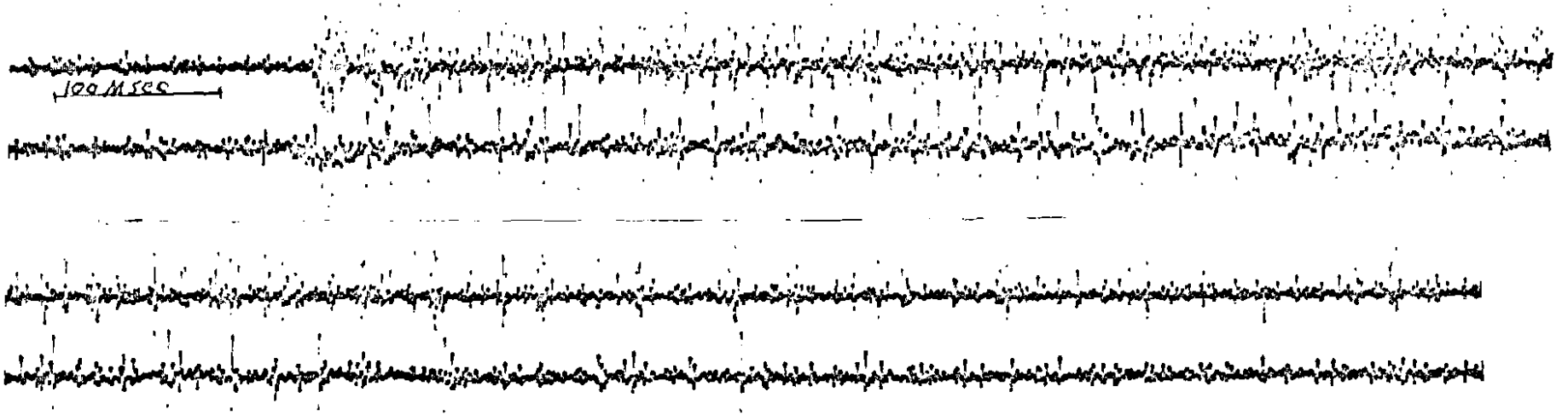


Figure 58. Same as Fig. 57, but connection to ganglion intact.



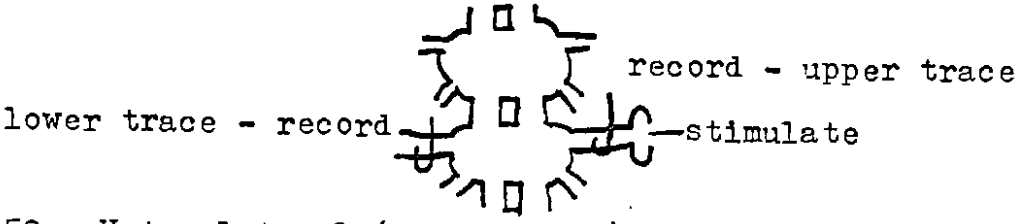


Figure 59. Heterolateral (upper trace) and homolateral dorsal nerve response (lower trace) to natural stimulation of the DN-3 receptors.

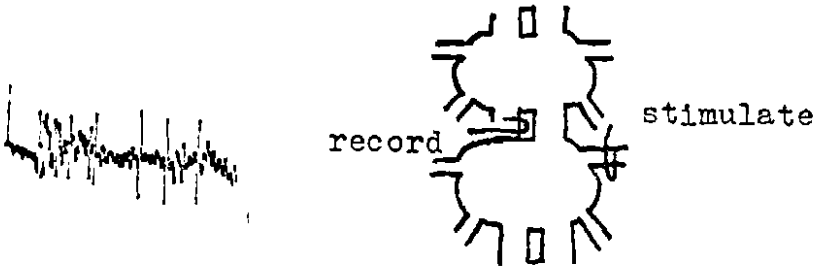


Figure 60. Response to DN stimulation on the cut heterolateral connective.

natural stimulation after the anterior connectives are cut (Fig. 61). This is the same fiber which receives input from the heterolateral ventral nerve of the same ganglion under the same recording conditions. This fiber has also been shown to respond to cercal nerve stimulation (see diagram, Fig. 62 which emphasizes the importance of this fiber).

In addition to these responses in the dorsal nerve, a response to dorsal receptors could be traced to the cardiac lateral nerve. Natural stimulation of one set of dorsal receptors evoked a response on the heterolateral lateral cardiac nerve (Fig. 63).

There is no response to dorsal nerve stimulation on the heterolateral ventral nerve.

D. EXPERIMENTS TO ESTABLISH FUNCTION OF DORSAL NERVE TO VENTRAL NERVE REFLEX

Mechanical pressure in the region of the dorsal receptors initiated a motor change on the ventral nerve (Fig. 64). The response varied with the intensity of the afferent input. Stimuli of this nature appear to simulate the normal pressure changes observed during the respiratory rhythm.

Tapping stimuli sets up groundborne vibrations which initiate responses in three to four fibers of the homolateral ventral nerve (Fig. 65). This indicates that a receptor contributing to DN-3 serves the physiological

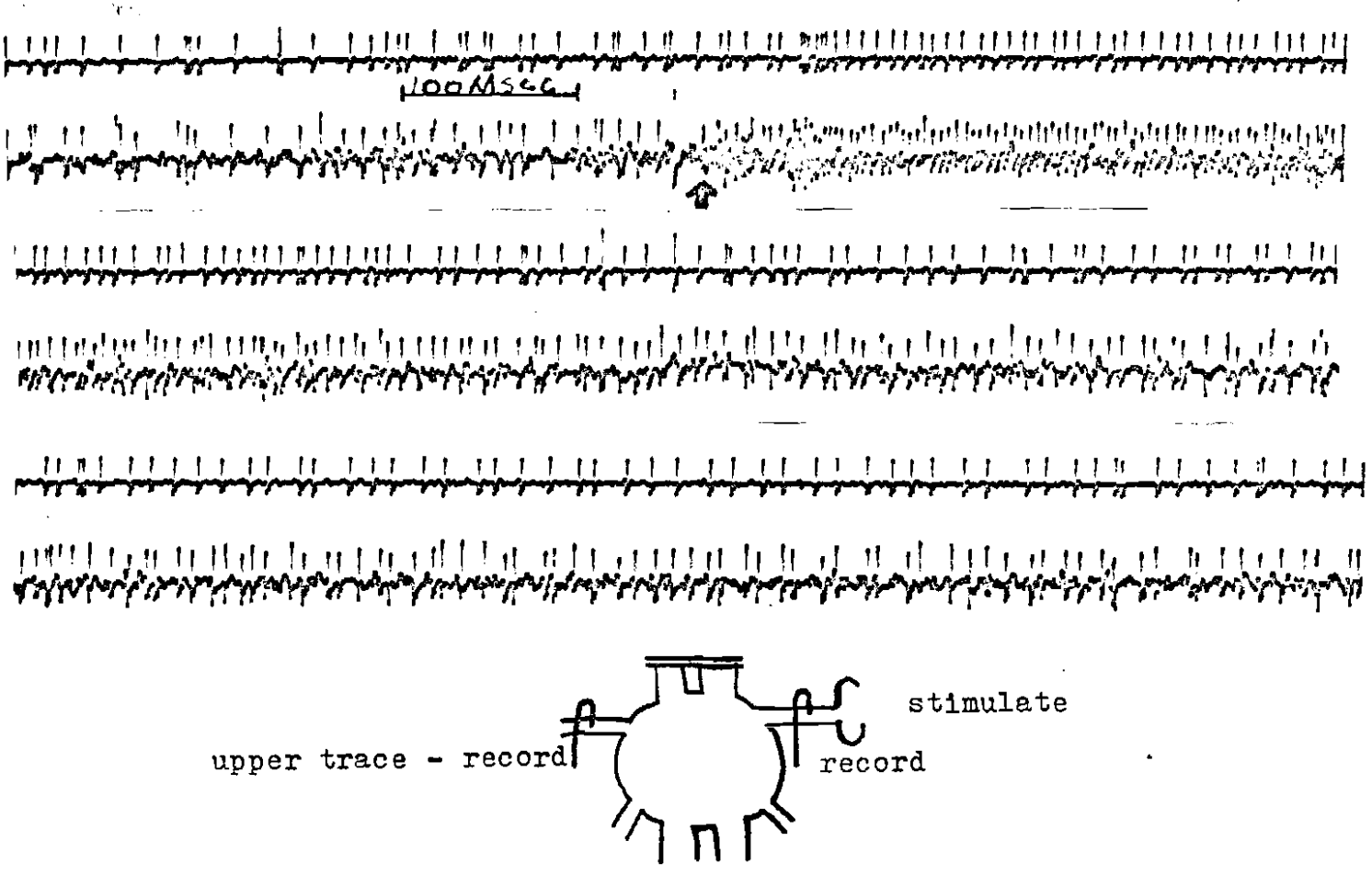


Figure 61. Response to dorsal nerve stimulation in the heterolateral dorsal nerve. Anterior connectives cut, so that the major response is lost.

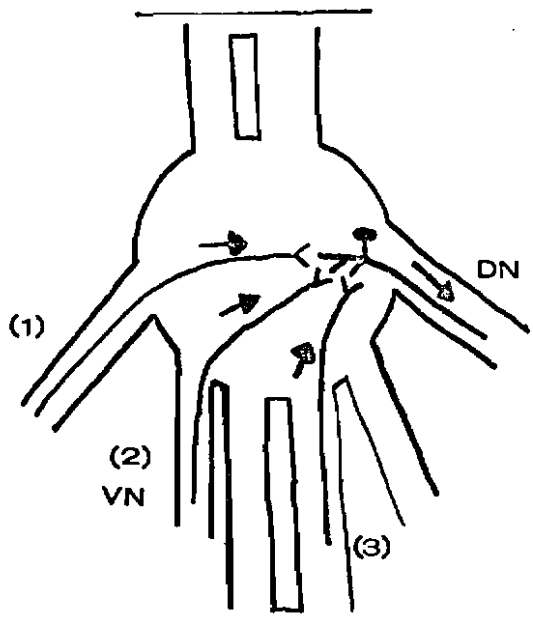
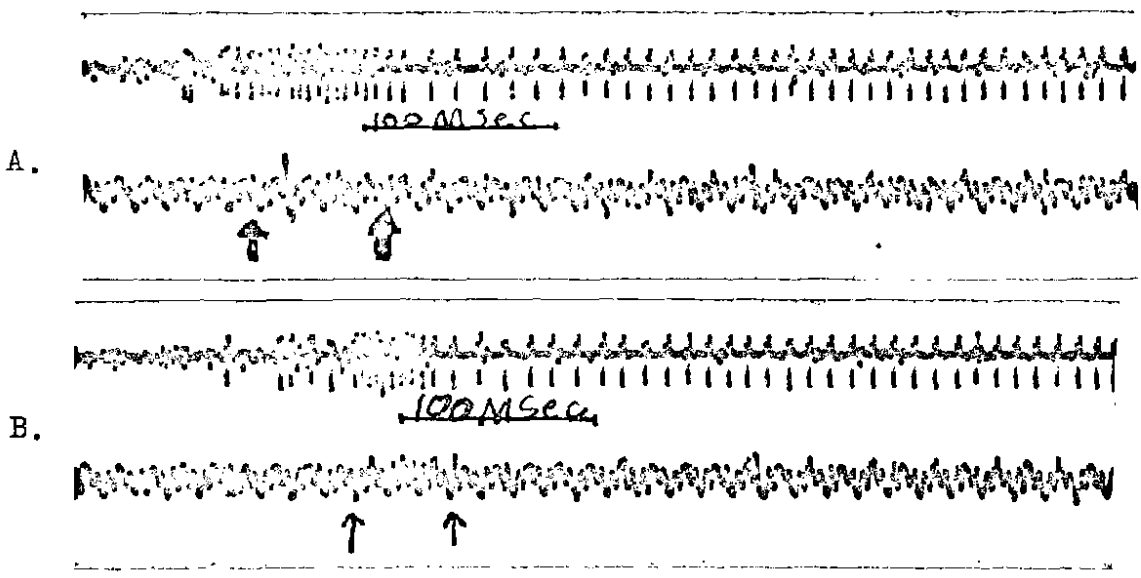


Figure 62. Diagram emphasizing the dorsal nerve fiber which responded to multiple sensory inputs. This cell, which was spontaneously active, also responded to stimulation of the heterolateral dorsal nerve (1), heterolateral ventral nerve (2), and homolateral cercus (3).



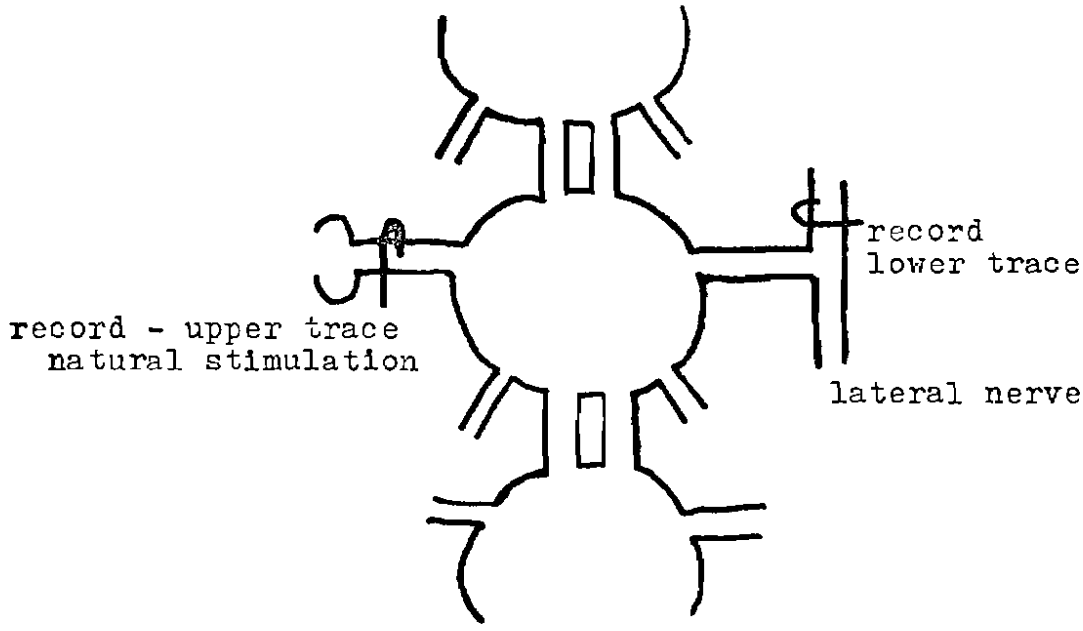


Figure 63. Two examples (A and B) of the response on the heterolateral lateral nerve to natural stimulation of the dorsal nerve. Upper trace is the dorsal sensory input. Lower trace is the response (between arrows) on the lateral nerve.

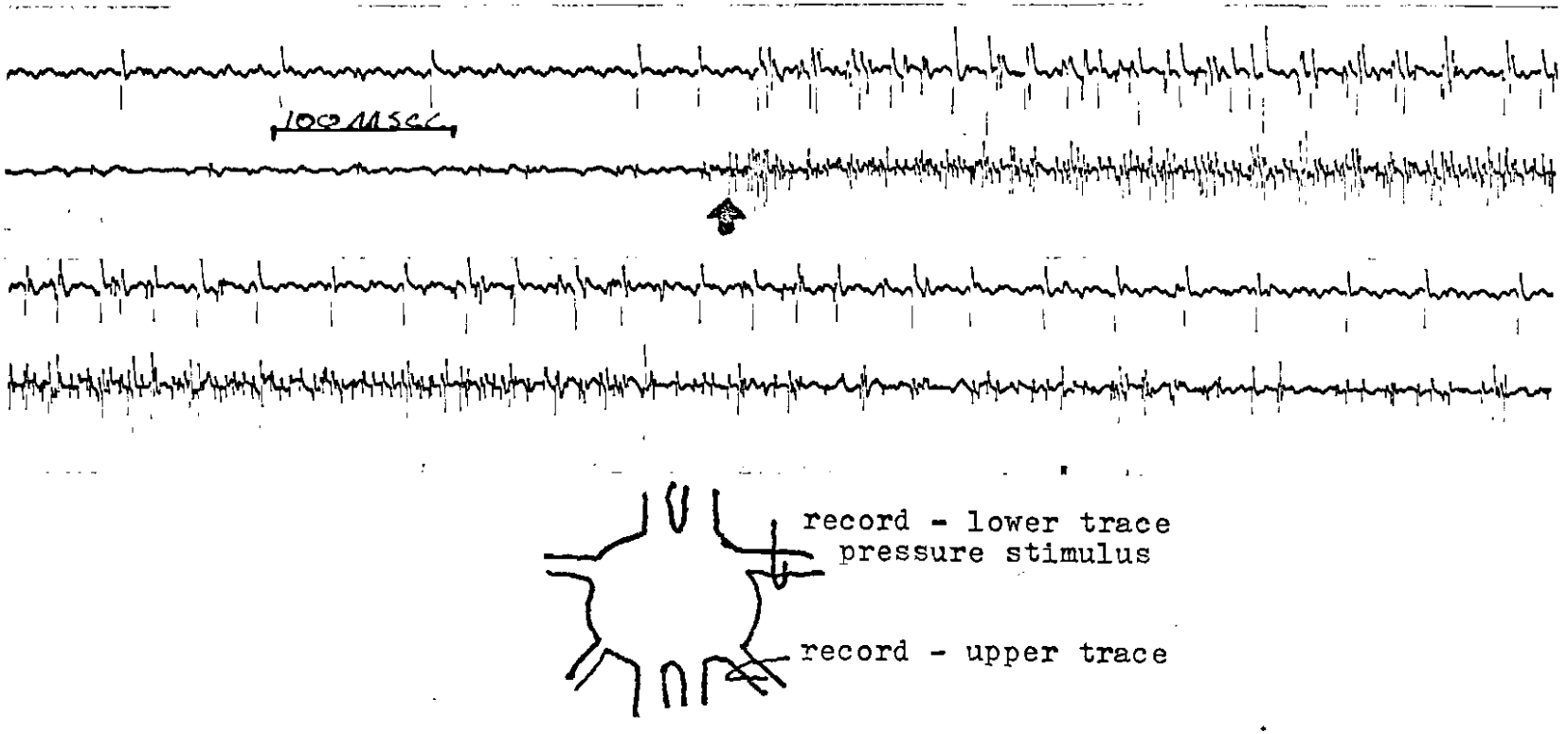


Figure 64. Responses on the homolateral ventral and dorsal nerves to pressure stimulation of the dorsal receptors. Arrow indicates approximate time stimulation was begun.

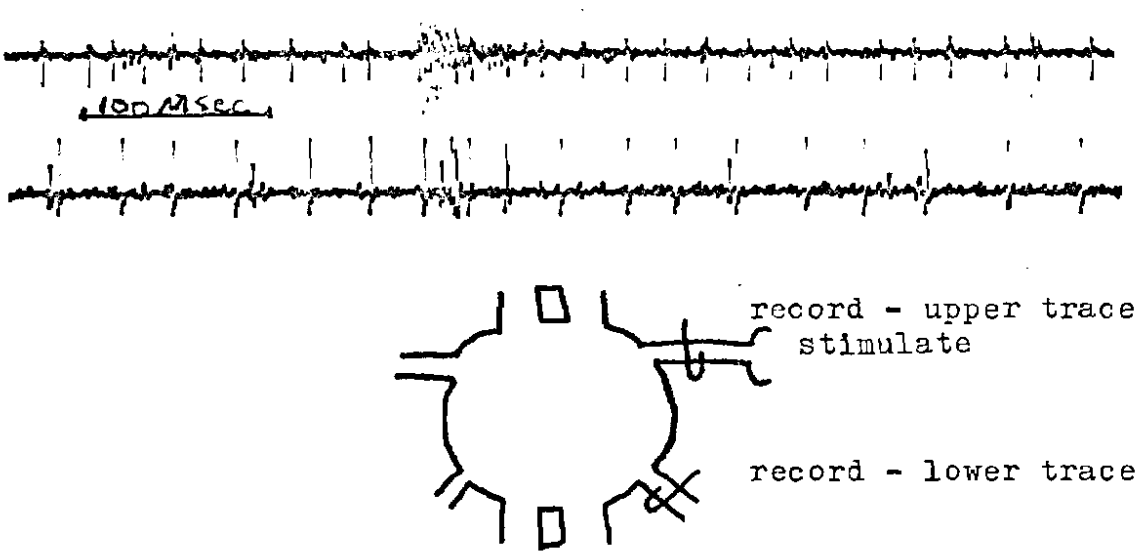


Figure 65. Afferent response to groundborne vibrations (upper trace) on the dorsal nerve activating an efferent response on the ventral nerve (lower trace).

function of responding to vibrations.

IV. STABILITY OF REFLEXES

The dorsal nerve to ventral nerve and ventral nerve to dorsal nerve reflexes differ not only in the number of fibers participating but also in their stability. A limited study on their longevity was undertaken to aid in planning experiments.

Thresholds were measured every 15 minutes using well spaced stimuli. The ventral nerve to dorsal nerve reflex remained viable for up to an hour and half. The less sensitive dorsal nerve to ventral nerve reflex remained for up to three hours, sometimes longer. The thresholds progressively increased in both reflexes as the preparation aged (Fig. 66). When the ventral to dorsal nerve response was lost in the dorsal nerve, a response could still be obtained in the connectives. This indicates that it was the synaptic activity in the next anterior ganglion which was lost. When the tracheae and ventral diaphragm supplying the nerve cord were completely removed the longevity of both reflexes was diminished. This indicates that oxygen deficiency is at least partly responsible for the loss of synaptic activity.

The difference in longevity of the two responses implies there are no common interneurons between reflexes.

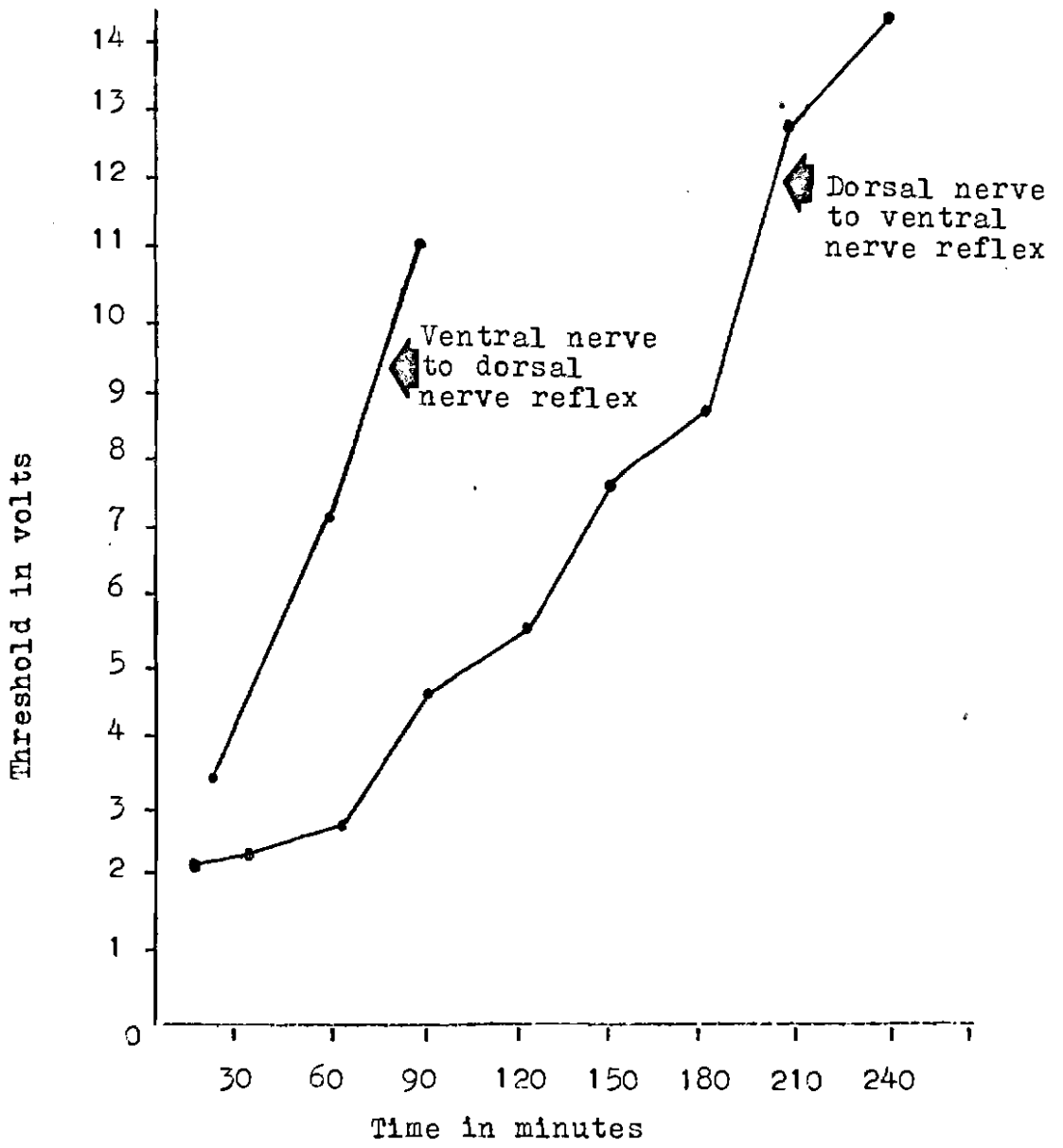


Figure 66. A typical experiment comparing the thresholds of the dorsal to ventral nerve reflex to the ventral to dorsal nerve reflex.

V. FURTHER INTERGANGLIONIC PATHWAYS

The reflexes described to this point involve activity on the homolateral dorsal and ventral nerves belonging to a single ganglion. The following survey was undertaken to determine possible broader distribution of sensory information in the abdominal nerve cord. The results are summarized by Tables II and III. Primarily abdominal ganglia 2-5 have been used because of their accessibility. By studying pathways stimulated both electrically and by natural stimulation it was possible to ascribe a physiological function to pathways whose significance would be otherwise undetermined. This technique, combined with the cutting of connectives, has made it possible to ascertain gross regions of synaptic activity in several instances.

Because high stimulus intensities may activate non-physiological pathways, only those reflexes have been presented which have thresholds below 7 volts. Since repetitive stimulation has been noticed to have similar undesirable effects, only responses triggered with well spaced stimuli were normally used. Smalley (1963) reported that stimulation of a dorsal or ventral nerve can produce a response in any of the connectives leading from the ganglion of the nerve stimulated, depending on the stimulus intensity. Under the more conservative levels of stimulation used here the dissemination of sensory information appears to follow more restricted pathways.

An approximate threshold is reported for each reflex. Since the thresholds vary with the age of the preparation, those reported are from freshly dissected animals.

Latencies for a single reflex are variable from animal to animal but never by more than several milliseconds. The calculated conduction velocities were obtained by dividing the length of the presumed pathway by the latency of the earliest response. Since the latency value includes synaptic delays of unknown duration, the average conduction velocity will always underestimate the conduction velocities of the axons carrying the response.

The calculated conduction velocities are averages for the fastest fiber(s) participating in the response.

The maximum rate at which a reflex can follow stimulation is also presented. In conjunction with latencies and average conduction velocities, this value may indicate the complexity of the synaptic activity.

The connectives traveled are only reported for reflexes of some interest. The natural stimulation methods described in this section are the same as described previously. A plus sign in the appropriate box of Tables II and III indicates the reflex may be induced by natural stimulation of one receptor or another. A minus sign in the box indicates the appropriate receptor was stimulated but did not induce an efferent response. A blank space indicates the reflex was not tested.

Tables II and III summarize the wider distribution

of responses to dorsal and ventral nerve stimulation within the abdominal cord.

A. SPREAD OF VENTRAL NERVE INPUT

Responses to ventral nerve input were traced anteriorly two ganglia (Table II, pathways 1-6). On the homolateral side, both ventral and dorsal nerve responses were found on the first and second anterior ganglia (Table II, pathways 1-4). On the heterolateral side, single stimuli produced responses on the ventral and dorsal nerve of the first anterior ganglion (Table II, pathways 5 and 6). The heterolateral ventral and dorsal nerves of the second anterior ganglion could also be stimulated, but only by repetitive stimulation (Table II, pathways 7 and 8).

The posterior spread of ventral nerve input was limited to a response on the homolateral dorsal nerve of the first posterior ganglion (Table II, pathway 9). No response was seen on the first posterior ventral nerve (Table II, pathway 10) and no responses were seen on posterior ganglia on the heterolateral side (Table II, pathways 11-14).

B. SPREAD OF DORSAL NERVE INPUT

Responses to dorsal nerve input spread anteriorly to ventral nerves and dorsal nerves on both sides of the next two anterior ganglia (Table III, pathways 1-8). Latencies for all of these responses were of the order of

10-15 msec. The homolateral ventral and dorsal nerves of the first anterior ganglion were able to follow stimulation at a higher frequency (8-10 per second) than was true of the other anterior pathways (which responded up to 3 per second).

The posterior spread of responses to dorsal nerve input was more restricted than the anterior spread (Table III, pathways 9-14). On the homolateral side, dorsal nerve responses were found on the first and second posterior ganglia (Table III, pathways 10 and 12) but ventral nerve responses were found only on the first posterior ganglion (Table III, pathways 9 and 11). On the heterolateral side, single stimuli elicited no responses on posterior ganglia but repetitive stimulation produced a response on the ventral nerve of the first posterior ganglion (Table III, pathways 13 and 14).

C. SEVERAL GENERALIZATIONS ABOUT THE DISSEMINATION OF SENSORY INFORMATION

Several generalizations about the dissemination of sensory information may be drawn from the results summarized by Tables II and III.

(1) The spread of responses tends to be stronger to the homolateral side than to the heterolateral side (II-3, 4 vs. II-7, 8; III-9, 10 vs. III-13, 14). The most complex response patterns (in terms

TABLE II. Interganglionic pathways. Responses to ventral nerve stimulation.

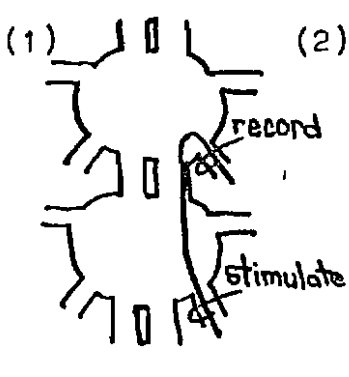
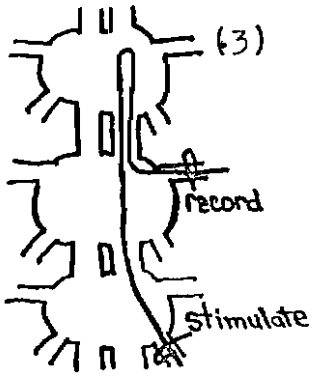
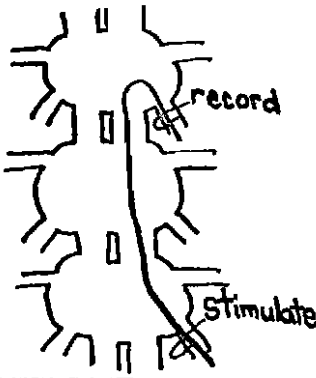
	Ascending Pathways		
			
Number of fibers participating in the reflex	3-4	3-4	1-2
Threshold in volts	2.5	3	3.5
Conduction rate (meters per second)	2.0	1.5-1.7	1.5
Latency (msec.)	8-10	10-12	12-15
Maximum frequency followed (stimuli per second)	8-10	7-8	5-6
Responds to natural stimulation	+	+	+

TABLE II. Interganglionic pathways. Responses to ventral nerve stimulation.

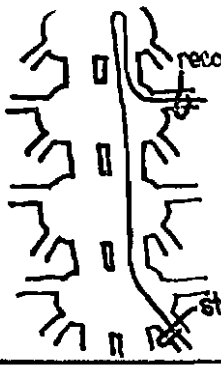
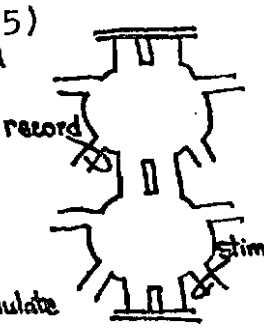
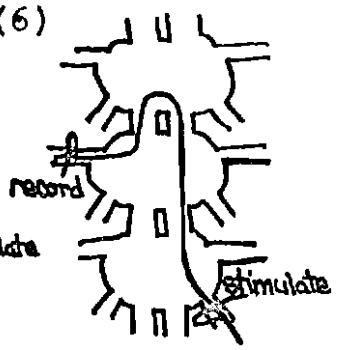
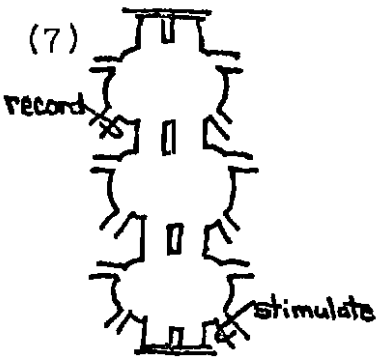
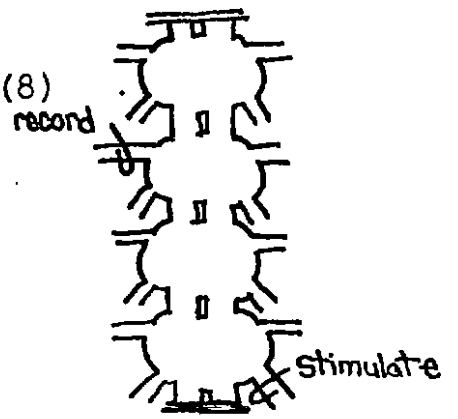
	Ascending Pathways		
	(4) 	(5) 	(6) 
Number of fibers participating in the reflex	3-4	1-2	4-5
Threshold in volts	3.5	4	6-8
Conduction rate (meters per second)	1.5	1	1
Latency (msec.)	10-15	8-10	13-18
Maximum frequency followed (stimuli per second)	4-5	6	1-2
Responds to natural stimulation	+		Easily activated by repetitive stimulation.

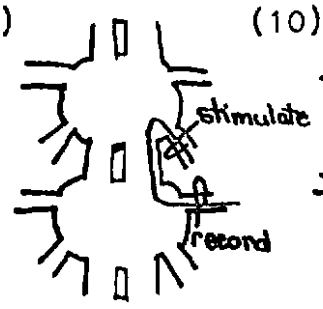
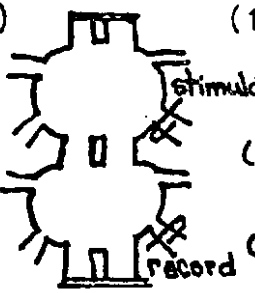
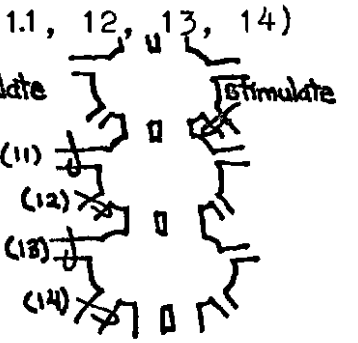
TABLE II. Interganglionic pathways. Responses to ventral nerve stimulation.

	Ascending Pathways	
	(7) 	(8) 
Number of fibers participating in the reflex	3-4 *	3-4 **
Threshold in volts		
Conduction rate (meters per second)		
Latency (msec.)		
Maximum frequency followed (stimuli per second)		
Responds to natural stimulation	+	

* Responds only to repetitive stimulation, 4 volts, 20 per second.

** Responds only to high frequency repetitive stimulation, 3-5 volts, 20-30 per second.

TABLE II. Interganglionic pathways. Responses to ventral nerve stimulation.

	Descending Pathways		
	(9) 	(10) 	(11, 12, 13, 14) 
Number of fibers participating in the reflex	2-3	*	*
Threshold in volts	4		
Conduction rate (meters per second)	1.25		
Latency (msec.)	12-15		
Maximum frequency followed (stimuli per second)	3		
Responds to natural stimulation	+		

* No response to well-spaced stimuli.

TABLE III. Interganglionic pathways. Responses to dorsal nerve stimulation.

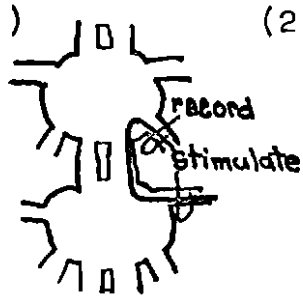
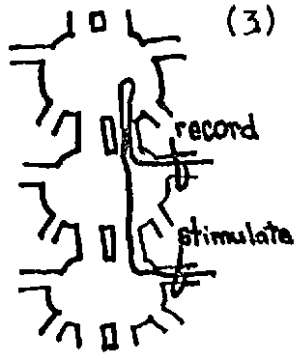
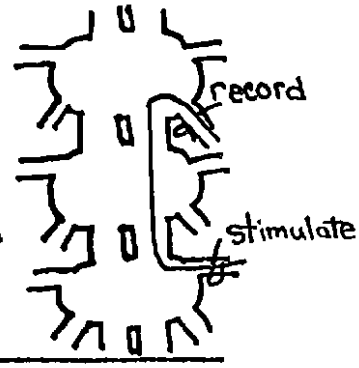
	Ascending Pathways		
	(1) 	(2) 	(3) 
Number of fibers participating in the reflex	4-5	4-5	3-4
Threshold in volts	3	3½	3
Conduction rate (meters per second)	2	1.5	2
Latency (msec.)	10	12-15	10-13
Maximum frequency followed (stimuli per second)	10	8-10	5-7
Responds to natural stimulation	+	+	

TABLE III. Interganglionic pathways. Responses to dorsal nerve stimulation.

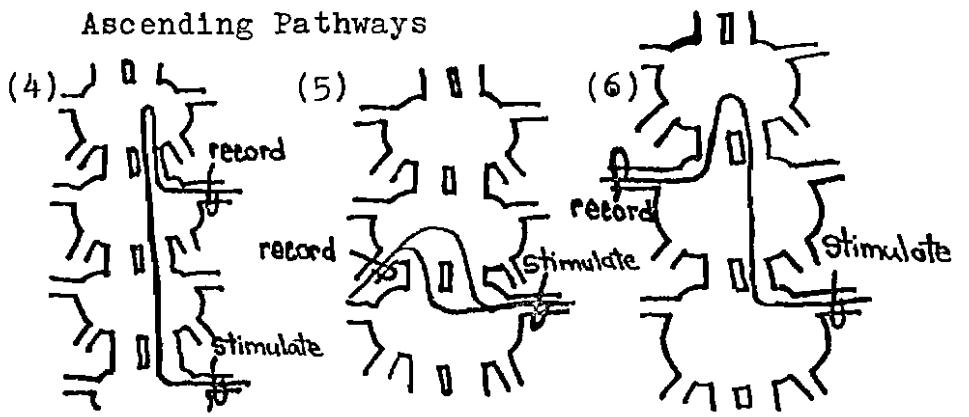
	Ascending Pathways		
			
Number of fibers participating in the reflex	3-4	2	3-5
Threshold in volts	4-5	5-6	5-6
Conduction rate (meters per second)	1 to 1.5	1	1 to 1.5
Latency (msec.)	13-15	10-12	12-15
Maximum frequency followed (stimuli per second)	3-4	2-3	2-3
Responds to natural stimulation		+	+

TABLE III. Interganglionic pathways. Responses to dorsal nerve stimulation.

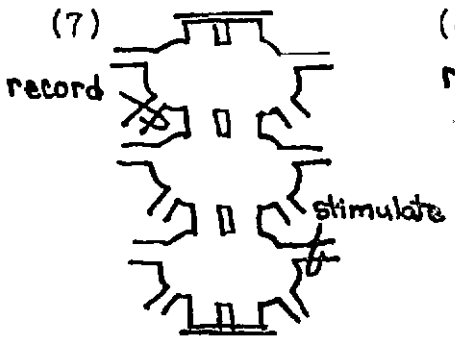
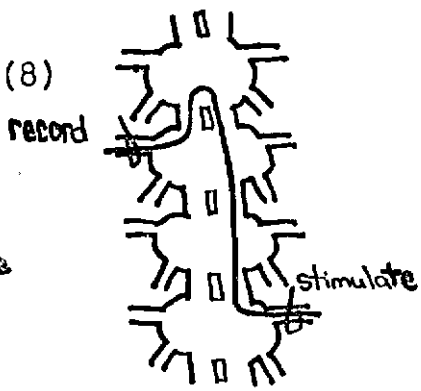
	Ascending Pathways	
	(7) 	(8) 
Number of fibers participating in the reflex	1-2	4-5
Threshold in volts	6	6
Conduction rate (meters per second)	1	1
Latency (msec.)	12-13	12-15
Maximum frequency followed (stimuli per second)	2-3	2-3
Responds to natural stimulation		

TABLE III. Interganglionic pathways. Responses to dorsal nerve stimulation.

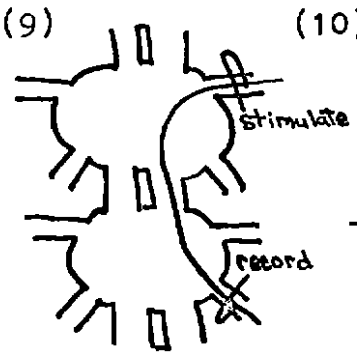
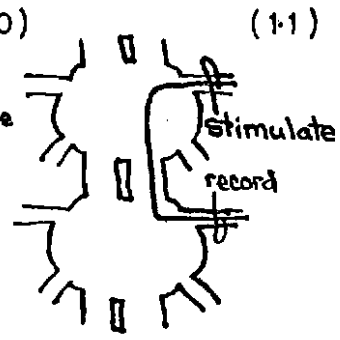
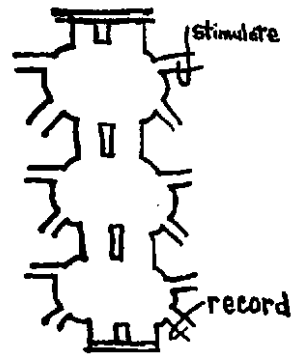
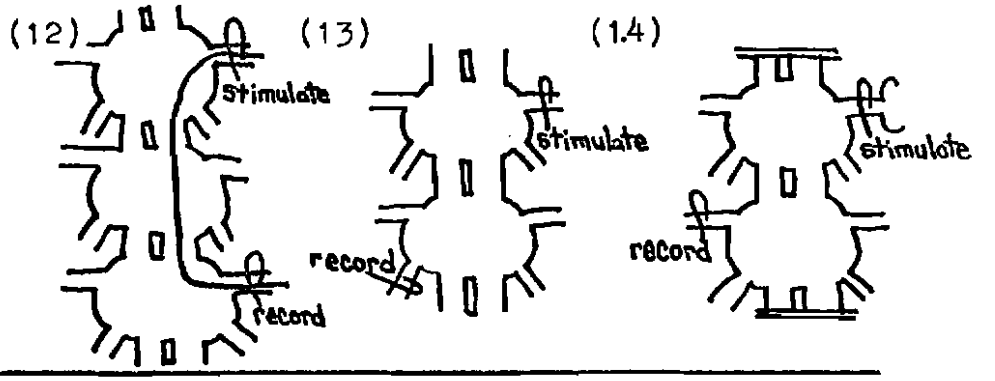
	Descending Pathways		
	(9) 	(10) 	(11) 
Number of fibers participating in the reflex	1	2-3	No response
Threshold in volts	6-8	4	
Conduction rate (meters per second)	1.5	1.25-1.5	
Latency (msec.)	12-15	12-15	
Maximum frequency followed (stimuli per second)		5-6	
Responds to natural stimulation		+	

TABLE III. Interganglionic pathways. Responses to dorsal nerve stimulation.

	Descending Pathways		
			
Number of fibers participating in the reflex	3-4	* 2-3	No response
Threshold in volts	4		
Conduction rate (meters per second)	1-1.5		
Latency (msec.)	15-18		
Maximum frequency followed (stimuli per second)	5-6		
Responds to natural stimulation		+	-

* Responds only to repetitive stimulation.

of ease of fatique, variability of latency, etc.) recorded during this part of the experiment were recorded on heterolateral nerves (II-7, 8).

(2) The spread of responses tends to be greater to anterior than posterior nerves (III-4, 5 vs. III-11, 14; II-1, 6 vs. II-10, 12).

(3) The spread of responses tends to be stronger to nearby ganglia than to more distant ganglia (III-9 vs. III-11; III-14; II-7, 8).

(4) In any dorsal nerve response to ascending input it can be seen that both the next anterior ganglion and the connective homolateral to the responding dorsal nerve are required (III-2, 4, 6, 8; II-2, 4, 6). The probable anatomical basis for this result is that the cell bodies and synapses of the dorsal nerve cells lie in the next anterior ganglion and their axons must pass through the homolateral connective en route to the dorsal nerve. This is consistent with a conclusion reached earlier in this paper (see section II) and by Smalley (1963).

(5) In dorsal nerve responses to ascending input it was shown that the connectives homolateral to the sensory input must be intact (III-2, 4, 6, 8; II-2, 4, 6). Evidently the afferent part of the pathway in these responses passes up the homolateral connectives and no crossing-over of

sensory information occurs in ganglia posterior to the ganglion in which synapses take place. However, in pathways which lead to excitation of ventral nerve fibers there appears to be some crossing over posterior to the ganglion in which the synapses are located (III-5).

(6) Ventral nerve responses do not require a ganglion anterior to the responding nerve in ascending reflexes (III-1, 3, 5, 7; II-1, 3, 5, 7) nor in descending response do they require a ganglion more posterior than the one on which the ventral nerve responded (III-9). The probable anatomical basis for this generalization is that the synapses for the ventral nerve fibers all lie within the ganglion of origin of a ventral nerve.

(7) The dorsal nerve responses also tend to have longer latencies and higher thresholds than do the ventral nerve responses. In general the dorsal nerve responses have more labile properties, suggesting more complex synaptic properties and more complex integrative phenomena. This is consistent with another indicator of more complex synapses; in an earlier section of this paper (section IV, Fig. 66) it was shown that the thresholds of dorsal nerve responses rise more rapidly and are more sensitive to detracheation than are dorsal nerve responses.

VI. EVIDENCE FOR PROPRIOCEPTIVE REFLEX SYSTEM: BEHAVIORAL OBSERVATIONS

One very likely function for reflexes studied here is that of proprioception. Although antigravity reflex systems have been described in the abdomens of other insects (Weevers, 1966) and in cockroach thoracic legs (Pringle, 1940), there appears to be no published evidence for a proprioceptive reflex system in the cockroach abdomen, and the following experiments were accordingly carried out. The effects of adding weights to the abdomens of male Periplaneta were observed. Small drops of warm wax were progressively layered on the posterior dorsal abdomen of anesthetized roaches until the desired weights were reached.

The normal roach walks with abdomen elevated and parallel to the ground. Four out of six roaches tested were capable of carrying loads up to 110 per cent of their body weight. When the loads were placed well to one side of the midline, the animal continued to maintain a normal posture with loads up to 20 or 30 per cent of total body weight.

Animals with their connectives cut between A-3 and A-4 continue to walk naturally and maintain a normal posture; however, a load of 10 per cent of their total body weight is enough to cause the abdomen to drop when walking. Similar results were found when the connectives were cut at two points, between A-2 and A-3, and between A-3 and A-4. When the connectives were cut between

A-1 and the third thoracic ganglion, the abdomen could not be held up and was dragged as the animal walked.

DISCUSSION

I. MID-STERNAL RECEPTOR

Shankland (1966) recorded afferent impulses from nerve B-1 of Periplaneta (which corresponds to a branch of the ventral nerve of Blaberus) and inferred the presence of a midventral stretch receptor. On the basis of methylene blue preparations he concluded that the afferent impulses originate from a connective tissue strand suspended between two points on adjacent sternal plates, although he could not find the cell bodies or ascertain the number of fibers constituting the stretch response. A careful histological study of the midventral region of Blaberus in this laboratory indicates the mid-sternal receptor described here is the only sensory element present. Furthermore, methylene blue preparations in Periplaneta confirm the presence of bipolar cell bodies in the same location as in Blaberus. It must be concluded in the light of this new evidence that Shankland has attributed the physiological activity of the mid-sternal receptor to the wrong anatomical structure.

In addition to cells responsive to stretch, this study demonstrated some cells capable of responding to both CO_2 and stretch. These results raise two questions: are the responses to CO_2 part of the normal physiology of these cells? If so, are there "bimodal" receptor cells which respond to both CO_2 and mechanical stimuli in the

normal functioning of the organism? There are no previously reported CO_2 receptors in insects, although Case (1957) pointed out the reasonableness of such an organ. On the basis of the evidence presented here it would be premature to assign a definite CO_2 receptor function to the mid-sternal receptor. The argument that this is a CO_2 receptor could be strengthened by data linking this receptor with the respiratory center or data showing that the CO_2 concentrations which stimulate this receptor are within physiological limits. Until such data become available, the following conservative conclusion must stand: the mid-sternal receptor serves a mechanoreceptor function and three of its cells are unusually sensitive to CO_2.

II. LATERAL CHORDOTONAL ORGANS

Florentine (1966) recorded from an abdominal receptor sensitive to substrate and airborne vibrations in Periplaneta. Based on his histological study, which utilized cross sections of the lateral fold region, it was concluded that the anatomical structure responsible for the physiological response was a fan-shaped multicellular hair receptor. The present histological study on Blaberus and a confirming study on Periplaneta (Smalley, 1968; unpublished) indicate that what Florentine considered to be sensory cell bodies were actually part of attachment 1 (Fig. 20) of the lateral chordotonal organ described in this study. Light pressure on the tergite juncture, the

approximate location of the lateral chordotonal organ, evokes afferent spikes of a different spike height than those induced by groundborne vibrations. In the light of this evidence it must be concluded that Florentine attributed a physiological response to the wrong anatomical structure.

Although this study has ruled out the structure postulated to be responsive to groundborne vibrations an alternative has not been found. Because Vaseline does not inhibit the receptor activity and the histological study does not show innervation of the hairs, hair receptors seem to be ruled out. It is probable that several of the small nerves contributing to DN-3A and DN-3B are the true vibration receptors.

III. FUNCTIONS OF THE MID-STERNAL RECEPTOR AND LATERAL CHORDOTONAL ORGAN

A. RHYTHMOMETER FUNCTION

The dorsal and ventral receptors probably serve both as proprioceptors and as rhythmometers. The idea of a rhythmometer was suggested in 1928 by Eggers, who postulated sense organs coordinating respiration and circulation. Hughes (1956) has found afferent fibers from unidentified receptors in the locust which respond to inspiration, others which respond to inspiration and expiration, and a third group which is inhibited during

inspiration. He suggested this information is used to modulate ventilatory movements. Farley and Case (1968) have verified Hughes' hypothesis in the American cockroach. They have shown that the afferent input from unidentified abdominal receptors is capable of altering the frequency of the respiratory movements. The nature of their stimulation techniques was such that they probably activated the mid-sternal receptor.

For a receptor to modulate the activity of the thoracic respiratory center, it must be capable of activating a pathway which reaches the respiratory center. The mid-sternal receptor meets this requirement, since this study shows that its response to natural stimulation can be found as far anterior as the thoracic connectives. The CO_2-sensitive property of this receptor could possibly be a factor in initiating the entire ventilatory cycle.

Both the lateral chordotonal organ and mid-sternal receptor fire during abdominal pumping movements, so in actuality either or both receptors could serve as rhythmometers. The answer to the question, which receptor is more important in modulating the respiratory rhythm, must await additional experiments designed to eliminate one set of receptors while leaving the other functionally intact during induced respiratory movements.

B. PROPRIOCEPTOR FUNCTION

The reflexes under consideration in this study

appear also to serve a proprioceptive function.

The behavioral observations suggest that roaches carrying a load in some manner compensate for the additional weight. The similar work of Planck (described by Wilson, 1968), with stick insects carrying weights on their backs, concludes that proprioceptive loops compensate for the additional load.

A function for the dorsal nerve to ventral nerve reflex is suggested here. In response to load, the dorsal nerve mechanoreceptors are activated. The response on the ventral nerve of the same segment activates the outer sternal and tergo-sternal muscles. The rebound response on the dorsal nerve activates the inner sternal, tergal and spiracular muscles. Since inner and outer sternal muscles serve as retractors of the sternum, while the tergal muscles serve as retractors of the tergum (Shankland, 1966), the predicted result of stimulating the dorsal receptors is a shorting and general stiffening of the abdomen.

When it is considered that similar reflex events are occurring on both sides of the animal as well as up and down the nerve cord, it is reasonable to conclude that the dorsal receptors are involved in postural control.

IV. SPONTANEOUSLY ACTIVE FIBER RESPONDING TO MULTIPLE SENSORY INPUT

Several cells have been shown to fire spontaneously on the dorsal nerve of an isolated abdominal ganglion.

Roeder (1955) reports similar cells present on isolated thoracic ganglia. Wiersma (1962) feels that an understanding of the functional significance of such spontaneously active cells would enhance our knowledge of the transmission of impulses in the central nervous system. It can be conclusively stated that one cell firing spontaneously receives multiple sensory input from the heterolateral mid-sternal and DN-3 receptors and the homolateral cercus (see Fig. 62). The synapses for this fiber, unlike those of other dorsal nerve cells, are in the ganglion from which the dorsal nerve originates.

V. NEURAL CONTROL OF THE HEART

In 1926 Alexandrowicz described the lateral and segmental nerves of the heart. Since that time there has been a great debate among physiologists as to the function of these nerves. The evidence presented in this study was directed toward proof of functional neural pathways which could convey cardiac regulatory information to the heart.

Evidence for a regulatory function was sought by stimulating cardiac segmental fibers. Stimulation of a single dorsal nerve did not alter the heart rate, but stimulation of two dorsal nerves did increase the heart rate up to 12 per cent over the normal values. This evidence implies neural control over the heart. All of the heart data presented in this paper are consistent with the conclusions of Miller and Metcalf (1968) who feel the

heart is myogenic with a superimposed neural control. It is worth pointing out that Wigglesworth (1950) anticipated this conclusion.

SUMMARY

The purpose of this study was to investigate major reflex pathways through the abdomen of the cockroach Blaberus craniifer. Attention was also given to the structure and function of sense organs which provide the normal input to these reflexes.

Two previously undescribed abdominal receptors were found in this study and named the mid-sternal receptor and the lateral chordotonal organs.

The five bipolar sensory cells making up the mid-sternal receptor are located at the midventral line and contribute their axons to the ventral nerve. The distal ends of the receptors of a segment converge at approximately the same spot on the cuticle, giving the receptors a V-shaped appearance in cross section. Electrophysiologically two motor fibers have been shown to activate the receptor and their presence has been confirmed histologically. Three of the five cells are unusally sensitive to CO_2, two cells respond to groundborne vibrations and all five cells respond to compression of the ventral musculature.

The lateral chordotonal organ, located in the lateral fold, is a seven-celled mechanoreceptor which contributes its axons to dorsal nerve branch three (DN-3). At least 14 additional sensory cells contribute axons to

DN-3. Three to four of these cells respond to groundborne vibrations, four to six to rubbing on the ventral surface and the remainder to cuticular deformation.

Twenty-nine reflexes, initiated by stimulating either the dorsal or ventral nerves, have been studied. Special emphasis has been given to reflexes through a single ganglion.

One reflex studied in detail was the response of a dorsal nerve to stimulation of the homolateral ventral nerve of the same ganglion. The latency of the response is 12-15 msec, representing a conduction velocity between 1.25 and 1.5 meters per second. The response is found on branches innervating the inner sternal and tergal muscles, and the lateral nerve of the heart. Ventral nerve stimulation also results in a rebound intraganglionic reflex synchronized with the dorsal nerve response. This response returns to the tergo-sternal muscle.

The heterolateral dorsal nerve responds to ventral nerve stimulation with a latency varying between 10-14 msec. The major response travels up the connectives on the side stimulated to the next ganglion, where it crosses over and returns to the dorsal nerve via the heterolateral connective. One fiber utilizes an intraganglionic pathway. This cell, which responds to heterolateral ventral nerve input, also receives input from the heterolateral dorsal receptors and the homolateral cercus.

All of the major branches of the homolateral ventral nerve respond to dorsal nerve stimulation. This reflex utilizes an intraganglionic pathway. Dorsal nerve stimulation also initiates a rebound response on the same nerve. In this response, synaptic contact is made in the anterior ganglion before the response returns to activate the dorsal musculature.

There is also a major dorsal nerve to heterolateral dorsal nerve pathway which makes synaptic contact in the next anterior ganglion before returning to the dorsal nerve via the heterolateral connective.

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