

Limulus Gill Cleaning Behavior

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Summary. 1. The gill cleaning movements of *Limulus* occur in definite periods (bouts). The sequence of movements in a bout, and the movements themselves, are highly stereotyped.

2. In a bout of gill cleaning the paired gill plates are adducted across the midline so that opposite gill plates can interact. The interaction consists of rhythmic flicking of the inner lobe of a gill plate between the book gill lamellae of the contralateral gill.

3. Each bout of cleaning lasts for approximately one minute and can be divided into four basic phases: pairing, crossing over, lateral cleaning, and medial cleaning (Fig. 2).

4. There are two distinct pairing arrangements of the gill plates during cleaning. During left leading (LL) cleaning all the gill plates are paired with an adjacent gill plate, except L_1 and R_5 . During right leading (RL) cleaning, which is the mirror image of LL cleaning, all the gills are paired except for R_1 and L_5 (Fig. 3).

5. Cleaning bouts are further organized into long-term patterns which last for hours (Fig. 4).

6. There are four major muscle groups involved in gill cleaning. Muscles 48/115 adduct the gill plate across the midline; muscles 113/114 flick the inner lobe, and muscles 20 (remotor) and 22 (promotor) control the anterior-posterior position of the gill plate during cleaning. The patterns of activity of these muscles are reliably different during RL and LL cleaning (Fig. 5).

7. Each abdominal ganglion controls the movements of a pair of gill plates. During a bout of cleaning one member of the pair is being cleaned (subpro-

gram A) and the other is not being cleaned (subprogram B). It is suggested that there are higher-order interganglionic neurons which control the expression of either the RL or LL patterns of cleaning. This is accomplished by dictating which gill plate of a pair uses subprogram A and which subprogram B, for all five ganglia.

8. It is concluded that a gill cleaning bout constitutes a moderately complex fixed action pattern, meeting the criteria of stereotypy within and between animals, intricacy of appendage movements, involvement of more than one effector system, and tendency to occur in its entirety in the absence of apparent stimuli (vacuum activity).

Introduction

Numerous studies have demonstrated that central nervous systems of both vertebrates and invertebrates are capable of generating rhythmic motor programs in the absence of sensory feedback (Grillner, 1975; Davis and Kennedy, 1977; Moffett, 1977). In some cases, it has been demonstrated that several more complex fixed action patterns are also of central origin (Dorsett et al., 1973; Koester et al., 1974). For example, contact with a starfish triggers a swimming motor program in the *Tritonia* central nervous system (CNS) that lasts for up to 30 s, and is comprised of four discrete stages (Dorsett et al., 1973; Willows et al., 1973). Even behaviors that last 3-4 h, such as insect molting or eclosion, have been demonstrated to be highly stereotyped, and largely centrally programmed (Truman and Sokolove, 1972; Carlson and Bentley, 1977).

It is then important to determine how long and complex a motor score can be preprogrammed in

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Abbreviations: CNS central nervous system; L_1 - L_5 left gill plates 1-5; LL left leading pattern of gill cleaning; R_1 - R_5 right gill plates 1-5; RL right leading pattern of gill cleaning

a CNS, and to what degree the day-to-day behavior of various animals is a manifestation of such innate mechanisms. In this and the following two papers we address these questions through an analysis of *Limulus* gill cleaning behavior in intact animals and as expressed by the isolated opisthosomal (abdominal) central nervous system.

Gill cleaning was first described by Hyde (1893) and later Patten (1912). However, in neither of these accounts was the behavior characterized in detail. This may have been due to the rather disorganized appearance of gill cleaning upon casual observation. However, on closer examination, I have found gill cleaning to be a highly stereotyped, complex fixed action pattern. In this paper I will present a description of gill cleaning in terms of the movements of the five pairs of abdominal appendages and the underlying muscle activity. The following paper (Watson, 1980) is concerned with the manner in which bouts of gill cleaning and related activities are organized into long-term patterns. Finally, the companion paper (Wyse et al., 1980) demonstrates that the neural correlates of both the gill-cleaning fixed action pattern and the long-term patterns of gill activity are expressed endogenously by the isolated abdominal CNS.

Materials and Methods

Specimens of *Limulus polyphemus* (15–25 cm carapace width) were obtained from the Marine Biological Laboratory, Woods Hole, Mass., and were maintained in a 570 l recirculating seawater system (15°–19°C).

Experiments were carried out at room temperature in a 60 l glass-bottomed aquarium, allowing direct visualization and filming of the gill appendages. Films were utilized for analysis of the gill movements, and individual frames were printed for illustrative purposes.

Muscular activity was recorded chronically from intact animals using insulated 40 and 42 gauge stainless steel wires. Electrodes were inserted into muscles through holes in the overlying cuticle and cemented in place with Eastman 910 adhesive. Heart electrical activity was recorded with 40 gauge stainless steel wires inserted through small holes drilled along the dorsal midline of the opisthosoma, just over the cardiac ganglion. Amplified signals were simultaneously displayed on a dynagraph (Beckman Type RB) and tape recorded for subsequent photography.

Muscle Anatomy

Most of the relevant neuromuscular anatomy has been described previously (Lankester et al., 1885; Patten and Redenbaugh, 1900; Fournier et al., 1971; Wyse, 1972; Wyse and Page, 1976). Figure 1 is a simplified illustration of the major muscles and nerves involved in gill cleaning and ventilatory movements. Muscle 20 is the main ventilatory remotor muscle and muscle 22 is the major promotor. Both muscles are also involved in positioning the gill plates during cleaning. Muscles 48 and 115 are responsible for adduction of the

gill plates across the midline. In this study these two muscles were treated as a single functional unit. The other important muscles used during gill cleaning are 113 and 114. These two muscles, which were also grouped together for analysis, are responsible for the flicking movements of the inner lobes.

Results

Description of Gill Plate Movements During a Cleaning Bout

Limulus book gills are located on the ventral side of the opisthosoma (see inset of Fig. 1). There are 5 pairs of gill plates which have gill lamellae arranged like pages of a book on their posterodorsal surface (Fig. 1). During gill cleaning bouts the gill plates are adducted medially across the midline and the inner lobes are flicked between the lamellae of the gills on the opposite side. Each bout lasts for approximately 1 min and is almost always preceded by a period of ventilation or swimming. Each bout begins with the gill plates remotized (Fig. 2A), and then proceeds through four general phases: pairing, crossing over, lateral cleaning, and medial cleaning (Fig. 2).

During gill cleaning adjacent gill plates are paired in a distinct and stereotyped arrangement. In the 2–3 s of the pairing phase (Fig. 2B), the proper configuration of the gills is attained by remotizing some gill plates, promoting others, and holding a few stationary. Figure 2B is a photograph that was taken early in the pairing phase, when only a few gill plates had begun to pair. The left fourth gill plate (L_4) had started to pair with the left fifth gill plate (L_5). To do this, R_5 remained remotized, L_5 was actively promoted, and the medial portion of L_4 was slightly remotized so that it could slide under the right fourth gill plate which had itself moved slightly forward. The consequences of these pairing movements become more evident in Figs. 2C–E. These show that all the gill plates pair except for the first gill plate on one side (L_1 in this case) and the fifth gill plate on the opposite side (R_5). When all the gills are properly arranged they begin to cross over.

During the crossing-over phase (Fig. 2C), lasting about 3 s, gill plates are adducted across the midline so that gill plates on opposite sides can interact. This is a critical phase of cleaning because if the gill plates begin to cross over, and correct pairing is disrupted, the animal will often terminate the cleaning bout prematurely. This usually does not occur because during pairing the gills are also positioned in a V-shape, with their inner lobes held in close opposition (for example, gill plates L_4 and L_5 in Fig. 2B and 2C). During the latter part of the crossing-over phase the gill plates are positioned so that the lamellae are in

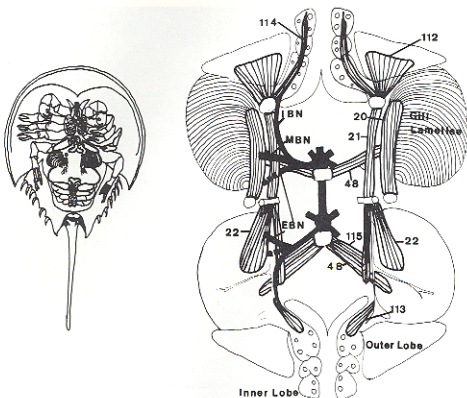


Fig. 1. Anatomy of gill cleaning musculature and associated nerves. Inset: ventral side of a *Limulus* with the first gill held forward to expose the underlying musculature and book gill lamellae. The first two gill pairs, positioned as in the inset, are shown enlarged on the right. Muscles: The inner lobe of the gill plate is the portion that flicks between the lamellae of the gill on the opposite side. Its movements are controlled by muscles 113 and 114. Muscles 48 and 115 adduct the gill plates across the midline. Muscles 20 and 22 are the main ventilatory remotor and promotor muscles, respectively. During cleaning they control the anterior-posterior position of the gill plate. Nerves: Each abdominal ganglion gives rise to 2 pairs of segmental nerves; branches of the posterior pair serve the gills. Muscles 113 and 114 are innervated by TBN (internal branchial nerve), muscle 20 by MBN (medial branchial nerve), muscle 22 by EBN (external branchial nerve), and muscles 48 and 115 by branches of MBN (not shown in the figure)

the proper orientation to be cleaned. This is accomplished by a pronounced promotion of all the gill plates, making them more accessible by spreading the gill lamellae somewhat so that the inner lobes can easily clean between them.

The complete sequence of pairing and crossing over is finished approximately 10–12 s after the start of a cleaning bout. The actual cleaning of the gill lamellae then commences. This consists of rhythmic flicking of the inner lobe of a gill plate between the lamellae of the contralateral gill. There are approximately 100 lamellae located under each gill plate; during this phase there is only time for the inner lobe to clean between several pairs of gill lamellae, using 2–3 flicks per pair. Gill plates are maximally adducted during this phase of cleaning (Fig. 2D, 2F) and so the most laterally positioned gill lamellae are cleaned first.

There is no firm delineation between lateral clean-

ing and medial cleaning because throughout a cleaning bout, gill plates gradually become more and more remoted and less adducted across the midline (Fig. 2F). However, there is a point, after about 10–15 s of lateral cleaning when marked relaxation of adductor muscles occurs, allowing the more medial portions of the gill plates to interact (Fig. 2E and 2F). The most characteristic features of medial cleaning are the rhythmic adductions of the gill plates that accompany the flicking movements of the inner lobes. Thus, medial cleaning can be further subdivided into distinct cleaning episodes. These are best understood in terms of the interactions of two contralateral gill plates (such as R_3 and L_3). In Fig. 2D, R_3 is cleaning the gill lamellae located underneath gill plate L_3 . The basic movements of R_3 are as follows (Fig. 2F): adduction and promotion (which bring the inner lobe in contact with the lamellae), two or three flicks of the inner lobe between the lamellae,

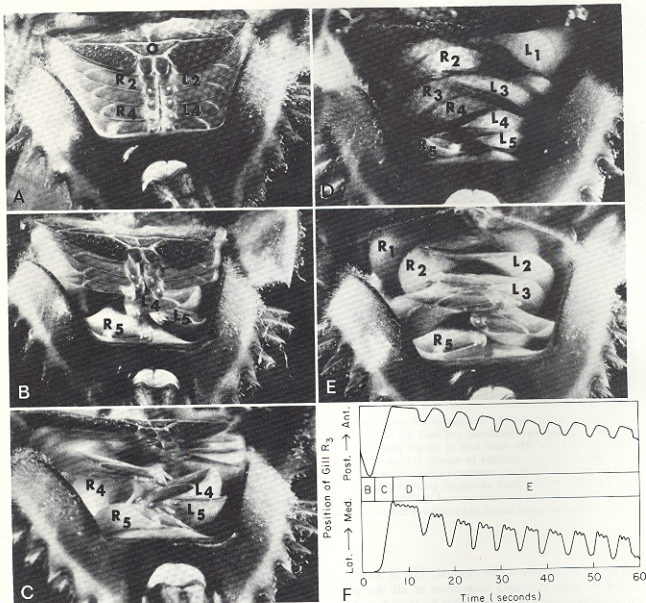


Fig. 2A-F. The four phases of gill cleaning. **A** Position of the gills (remoted) just prior to the initiation of a bout of cleaning. **B** Pairing. During this phase the gills pair in a fixed arrangement. The photograph, of early pairing phase, shows pairing between gill plates L₄ (left fourth) and L₅. **C** Crossing Over. After all the gills have paired they are adducted across the midline, allowing interaction with gills on the opposite side. Note the V-shape of each pair, which helps prevent their separation during adduction. **D** Lateral Cleaning. At this point the gills are fully interlocked in a fixed arrangement such that all the gills are paired except for R₂ and L₁. The gills are also fully promoted, which helps to expose and spread the book gill lamellae for cleaning. During this phase the inner lobes clean between the most lateral lamellae (for example in this photograph the inner lobes of gill plates L₂ and L₃ are visible between the lamellae of gill R₁). **E** Medial Cleaning. As in lateral cleaning, the inner lobes clean between the lamellae of the gills on the opposite side. But now the gills are less adducted and promoted, so that only the more medial gill plates are being cleaned. **F** Schematic diagram of the movement of a single gill (R₃) during an entire bout of cleaning. Top: movement in the anterior-posterior plane. Bottom: movement in the lateral-medial direction. Letters correspond to the phases described in B-F. above. Note the durations of the 4 phases and the rhythmic adductions and promotions during lateral cleaning. See text for details

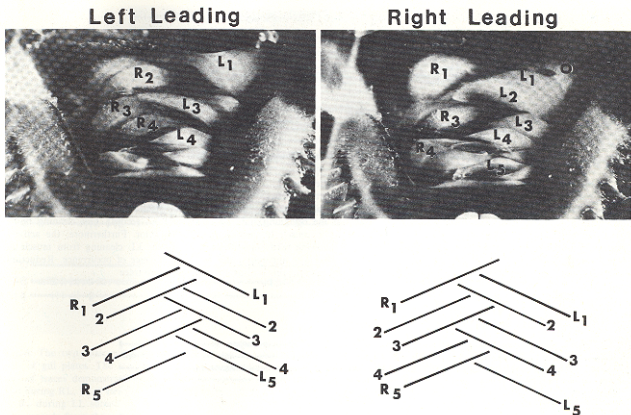


Fig. 3. Left-leading (LL) and right-leading (RL) cleaning. There are two ways which the gill plates are arranged during cleaning. This figure shows photographs and schematic diagrams of each type. In LL cleaning all the gills are paired except R_5 and L_1 . In RL cleaning, which is a mirror image of LL, all the gills are paired except L_5 and R_1 . During RL, gills R_1 , R_3 , R_2 , L_2 , and L_4 are cleaned, while during LL, R_2 , R_4 , L_1 , L_3 , and L_5 are cleaned. Long-term recordings (>24 h) indicate that the ratio of LL to RL is approximately 1:1. Thus, with time, all gill plates are cleaned equally. O = genital operculum

abduction (probably passive), and remotion. After a brief pause the cycle is repeated, 10–12 episodes occurring in a bout.

The cleaning bout ends with a nearly synchronous remotion of all the gills, which by this time are nearly fully uncrossed. Following this remotion, ventilation or swimming usually resumes immediately.

Left Leading (LL) and Right Leading (RL) Cleaning

There are two types of gill cleaning, which I have defined according to the pairing arrangement of the gills (Fig. 3). During left leading (LL) cleaning (which is the type illustrated in Fig. 2), all the gills are paired except for L_1 and R_5 . Right leading (RL) cleaning is a mirror image of LL, with all the gills paired except for R_1 and L_5 . The type of cleaning occurring at any given time is most easily identified by compar-

ing the relative positions of the fifth pair of gill plates; R_5 is not paired in LL, and L_5 is unpaired in RL.

The use of both types of cleaning arrangements insures that all gills eventually are cleaned; most of the gills (except the fifth pair) being cleaned by two gill plates at the same time. Therefore, during LL cleaning: L_5 is cleaned by R_5 , R_4 by L_4 and L_5 , L_3 by R_3 and R_4 , R_2 by L_2 and L_3 , and L_1 by R_1 and R_2 . During RL cleaning: R_5 is cleaned by L_5 , L_4 by R_4 and R_5 , R_3 by L_3 and L_4 , L_2 by R_2 and R_3 , R_1 by L_1 and L_2 .

Gill cleaning bouts usually alternate with periods of ventilation or swimming. During long-term sequences of periodic gill cleaning and ventilation, both types of cleaning are employed (Fig. 4). The two types do not alternate or occur in any readily predictable sequence. However, over long periods of time the two occur in roughly equal proportions. For example, over a 24-h period one animal executed 137 bouts of LL cleaning and 125 bouts of RL cleaning.

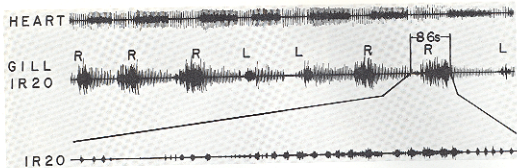


Fig. 4. Long-term pattern of gill cleaning. Gill cleaning usually alternates with ventilation in regular long-term patterns. A portion of such a pattern is presented in the top two dynamograph recordings, and the activity of muscle 20 during one of the individual cleaning bouts had been expanded in the bottom trace. During ventilation muscle 20 fires in discrete bursts which appear as single deflections in the dynamograph record (they can also be seen more clearly at the beginning and end of the bottom record). Gill cleaning bouts are easily identified by the large amplitude activity of the units in muscle 20 used during this behavior. Furthermore, the activity in muscle 20 differs consistently for the two types of cleaning, allowing ready identification of RL or LL cleaning from muscle 20 activity. Note that the two types of cleaning do not appear to have any apparent order to their sequence of occurrence. Reduction in heart rate is also an integral part of the gill cleaning fixed action pattern; this is clearly visible in the top trace

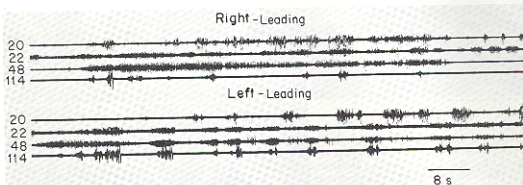


Fig. 5. EMG records of LL and RL gill cleaning. Each record shows activity of the 4 major cleaning muscles of the right first gill plate during an entire cleaning bout. Three cycles of ventilation are also included at the end of the top record. During LL cleaning (bottom) the basic episodes of cleaning are clearly visible: adduction (4–6 s bursts in muscle 48) and promotion (muscle 22) of the gill plate, accompanied by flicking of the inner lobes (short, multiple bursts in muscle 114). These episodes are separated by abduction and retraction (muscle 20) of the gill plates. The retractions increase in strength as the bout progresses, thereby gradually closing the gills. Likewise the degree of cross-over (and thus the amplitude of the bursts in muscle 48) slowly decays throughout the bout. During RL cleaning the muscle activity is quite different. This difference is due to the fact that during LL, R_1 is cleaning L_1 , but not being cleaned itself; whereas in RL, R_1 is being cleaned, but not cleaning. Therefore, the basic cleaning episodes are not as prevalent. There is reduced activity in muscle 114, and nearly continuous activity in muscles 20, 22, and 48. Further discussion in the text

Muscle Activity During Gill Cleaning

Muscle activity recorded during gill cleaning is distinguishable from activity recorded during any of the other respiratory movements (Fig. 5). Muscles 48 and 115 are usually quiet, but during gill cleaning they are active in long duration, high amplitude bursts. Muscles 113 and 114 also fire in bursts during cleaning; these are of short duration (0.3–1 s), and usually occur in doublets or triplets. The regular rhythmic activity in muscles 20 and 22 during normal ventilation switches to sporadic discharges during gill cleaning. Units active in muscle 20 during cleaning are

usually larger than those recorded during ventilation. Thus, differences in both frequency and amplitude of activity in muscle 20 allow for a clear distinction between gill cleaning and ventilation during long-term recordings (Fig. 4).

Patterns of muscle activity recorded from a given gill plate are different during the two types of cleaning. During LL cleaning (Fig. 5, bottom), the right first gill (R_1) is not being cleaned itself, but is actively involved in cleaning L_1 (see Fig. 3 for clarification of the position of each gill plate during the two types of cleaning). Muscles 48/115 are active in 4–6 s bursts, corresponding to adductions of the gill plate. Each

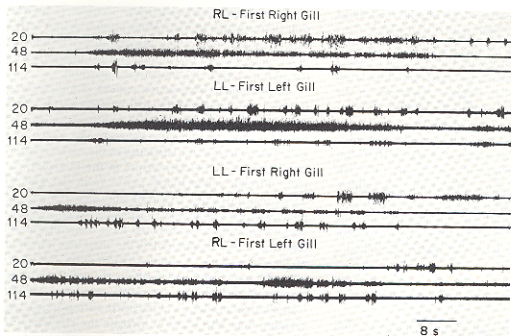


Fig. 6. The two basic gill cleaning subprograms as demonstrated by a comparison of muscle activity between opposite sides of a pair of gill plates. The top two sets of traces represent the motor program for gills that are being cleaned, while the bottom two sets of traces demonstrate the typical activity of gill plates that are not being cleaned. During the LL cleaning R_1 is cleaning L_1 and during RL, L_1 is cleaning R_1 (see Fig. 3 for schematic of gill positions during LL and RL cleaning). Therefore, the muscle activity in R_1 during LL should be the same as that seen in L_1 during RL, and vice versa. Such a comparison is shown in this figure. The records from the muscles of the right gill plate were made from one animal, while those from the left were made from another animal. This further demonstrates the similarity of the underlying motor programs from animal to animal, as well as within a single ganglion

of these bursts is accompanied by bursting in muscle 22, and short multiple bursts in muscles 113/114. Each individual burst in 113/114 results in a flick of the inner lobe. Muscle 20 is fairly quiet in the beginning of the cleaning bout, but gradually the bursts become stronger and occur more frequently, as the remotion between episodes becomes more pronounced.

The basic differences between LL and RL cleaning are represented in the EMG records. During RL cleaning (top of Fig. 5) R_1 is not engaged in cleaning, but it is being cleaned by L_1 and L_2 . There are fewer bursts in 113/114 (thus fewer flicks), nearly continuous bursting in 48/115, and the bursting in muscles 20 and 22 is less discrete than during LL cleaning. These differences are probably less pronounced in the other gill pairs because, unlike the first pair of gill plates, they are always involved in the cleaning, whether they are being cleaned or not.

Motor Subprograms

The available evidence indicates that there are two gill cleaning subprograms. There is one for gills that

are being cleaned (A), and one for gills that are not being cleaned (B). Viewed in terms of a single pair of gills, the muscle activity in one gill plate during LL cleaning is similar to the pattern seen in the contralateral gill plate during RL cleaning, and vice versa. This similarity is apparent even in comparisons between different animals, indicating stereotypy between animals as well as within the same animal. For example, Fig. 6 compares activities of muscles of the first right gill plate (R_1) of one animal with those of the first left gill plate (L_1) of another animal. As shown in the upper two sets of traces of the figure, gill plates engaged in cleaning but not being cleaned (R_1 during LL, L_1 during RL) had comparable patterns of motor output, as did gill plates that were being cleaned, but were not actively cleaning (R_1 during RL, L_1 during LL cleaning; bottom two sets of records of Fig. 6).

The first pair of gill plates, which are the most accessible for recording purposes, unfortunately are atypical because they are the only gills that get cleaned while not engaged in cleaning a more anterior gill at the same time. To test whether the muscle activity patterns recorded are unique to the first pair of gill

plates, it would be necessary to obtain recordings from all the muscles in each pair of gill plates. This is very difficult because of the geometry of the gills, which leads to interference with the electrodes during cleaning. This problem does not exist with muscle 20, however, because one can implant electrodes in the dorsal insertions. By comparing the activity of muscle 20 in all five pairs of gill plates the relationship between the activity in those gills and that recorded from the first pair was determined. Judging from this analysis the two subprograms seen in the first pair are typical for all gill pairs. Therefore, the subprogram seen in the top two traces of Fig. 6 is probably the same for all gills that are not cleaned and the bottom two traces are characteristic of the subprogram utilized by all the gills that are being cleaned.

Discussion

My analysis of *Limulus* gill cleaning indicates that it is a complex fixed action pattern. Cleaning bouts are stereotyped within and between animals, last approximately 1 min, are accompanied by reduction in heart rate, and are organized into long-term patterns which last for hours. Each bout is itself divided into four identifiable phases, and these can be further subdivided into separate fixed acts, or episodes. Finally, bouts of cleaning always tend to occur in their entirety, usually in the absence of any apparent stimuli (vacuum activity). While we have yet to complete a thorough analysis of gill cleaning at the level of individual neurons, the aforementioned characteristics make this behavior potentially valuable for investigating the neural basis of a complex fixed action pattern. In fact our experiments thus far, as reported in the accompanying paper, demonstrate that all the characteristics of gill cleaning observed in the intact animal persist in the isolated abdominal CNS (Wyse et al., 1980).

The functional significance of gill cleaning has not been investigated. One possibility is that it serves to rid the gill lamellae of *Bdellura candida*. This triclad turbellarian is found only on *Limulus*, and it can be seen on nearly every animal examined in its natural habitat. It is presently considered to be ectocommensal (Hyman, 1951; Jennings, 1974); however, its egg cases appear to damage the lamellae and this may interfere with efficient gas exchange (unpublished observation).

Another hypothesis is that gill cleaning helps to clear lamellae of debris that is abundant in the natural habitat of *Limulus*. Although little is known about the natural history of *Limulus*, they are bottom dwellers and are often found buried in the sediments.

However, preliminary tests show no obvious correlation between the amount of suspended debris in the experimental chamber and the duration or frequency of cleaning. In fact, one animal cleaned intermittently for 14 h in a virtually debris-free aquarium.

The complete fixed action pattern of gill cleaning includes simultaneous bradycardia (see Fig. 4). This may serve two functions: (1) to maintain the proper hemodynamic relationship between the heart and gills; (2) to increase the efficiency of the entire respiratory system. The blood pressure in the branchial canals, through which blood passes from the gills to the pericardial cavity, is considerably increased during gill cleaning (Watson and Freedman, unpublished results). Pressure increases could have a significant effect on cardiac function unless the heart was inhibited at the same time. A similar explanation has been put forth to explain the inhibition of the heart during respiratory pumping in *Aplysia* (Koester et al., 1974). Concomitant inhibition of the heart during apnea and cleaning may also serve to increase the efficiency of the respiratory system by matching cardiac output with oxygen uptake. In fact, the frequencies of the heart and gill rhythms have been shown to covary at all times (Watson and Wyse, 1978). The neural mechanisms responsible for this covariation are presently under investigation and the results should help shed light on the interganglionic coordination of different activities during complex fixed action patterns.

Although the interactions between all five pairs of gill plates are complex, those between plates of a pair are fairly straightforward; one plate is using subprogram A and the other subprogram B during RL cleaning, and vice versa. Thus, as in *Limulus* ventilation (Hyde, 1893), and lobster swimmeret beating (Davis, 1969; Stein, 1971), the basic motor subprograms are probably located in each ganglion, and coordinated by interganglionic interneurons. Evidence for this hypothesis comes from lesion studies and personal observations. If lesions are made between ganglia of the ventral cord, the more posterior gills will sometimes clean, while the gills anterior to the cut ventilate (Patten, 1912). If the ganglia are split lengthwise then each hemiganglion is capable of performing cleaning movements (Hyde, 1893). Even in the intact animal single gill plates have been observed undergoing crude, but distinguishable, gill cleaning movements. Intersegmental control and coordination of these ganglionic pattern generators is complicated by the existence of two subprograms. To get reciprocity between a pair and coordination between all five pairs, there must be interganglionic interneurons that select which gill plate of a pair uses subprogram A and which subprogram B, for all five ganglia. This type of coordination and control is par-

ticularly intriguing because of the unique pairing arrangement and the unpredictable order of occurrence of LL and RL cleaning.

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References

- Carlson, J.R., Bentley, D.R.: Ecdysis: neural orchestration of a complex behavioral performance. *Science* **195**, 1006-1008 (1977)
- Davis, W.J.: The neural control of swimmeret beating in the lobster. *J. Exp. Biol.* **50**, 99-118 (1969)
- Davis, W.J., Kennedy, D.: Organization of invertebrate motor systems. In: Handbook of physiology, Sect. 1, Vol. I, Part 2. Geiger, S.R., Kandel, E.R., Brookhart, J.M., Mountcastle, V.B. (eds.), pp. 1023-1087. Bethesda: American Physiological Society 1977
- Dorsett, D.A., Willows, A.O.D., Hoyle, G.: Neuronal basis of behavior in *Tritonia*. IV. Central origin of a fixed action pattern. *J. Neurobiol.* **4**, 287-300 (1973)
- Fourtner, C.R., Drewes, C.D., Pax, R.A.: Rhythmic outputs coordinating the respiratory movement of the gill plates of *Limulus polyphemus*. *Comp. Biochem. Physiol.* **38A**, 751-762 (1971)
- Grillner, S.: Locomotion in vertebrates: central mechanisms and reflex interactions. *Physiol. Rev.* **55**, 304-347 (1975)
- Hyde, I.H.: The nervous mechanism of respiratory movements in *Limulus polyphemus*. *J. Morphol.* **9**, 431-448 (1893)
- Hyman, L.H.: The invertebrates: Platyhelminthes and Rhynchocoela. The acoelomate bilateria, Vol. II. New York: McGraw-Hill 1951
- Jennings, J.B.: Symbiosis in the Turbellaria and their implications in studies on the evolution of parasitism. In: Symbiosis in the sea. Vernberg, W.B. (ed.). Columbia: South Carolina Press 1974
- Koester, J., Mayeri, E., Liebeswar, G., Kandel, E.R.: Neural control of circulation in *Aplysia*. II. Interneurons. *J. Neurophysiol.* **37**, 476-496 (1974)
- Lankester, E.R., Benham, W.B.S., Beck, E.J.: On the muscular and endoskeletal systems of *Limulus* and *Scorpio*, with some notes on the generic characteristics of scorpions. II. Description of the muscular and endoskeletal systems of *Limulus*. *Trans. Zool. Soc. (London)* **11**, 314-338 (1885)
- Moffett, S.: Neuronal events underlying rhythmic behavior in invertebrates. *Comp. Biochem. Physiol.* **57A**, 187-195 (1977)
- Patten, W.: The evolution of vertebrates and their kin. Philadelphia: Blakiston 1912
- Patten, W., Redenbaugh, W.A.: Studies on *Limulus*. II. The nervous system of *Limulus polyphemus*, with observations upon the general anatomy. *J. Morphol.* **16**, 91-180 (1900)
- Stein, P.S.: Intersegmental coordination of swimmeret motoneuron activity in crayfish. *J. Neurophysiol.* **34**, 310-318 (1971)
- Truman, J.W., Sokolove, P.G.: Silk moth eclosion: hormonal triggering of a centrally programmed pattern of behavior. *Science* **175**, 1491-1493 (1972)
- Watson, W.H. III: Long-term patterns of gill cleaning, ventilation and swimming in *Limulus*. *J. Comp. Physiol.* **141**, 77-85 (1980)
- Watson, W.H. III, Wyse, G.A.: Coordination of heart and gill rhythms in *Limulus*. *J. Comp. Physiol.* **124**, 267-275 (1978)
- Willows, A.O.D., Dorsett, D.A., Hoyle, G.: The neuronal basis of behavior in *Tritonia*. III. Neuronal mechanism of a fixed action pattern. *J. Neurobiol.* **4**, 255-285 (1973)
- Wyse, G.A.: Intracellular and extracellular motor neuron activity underlying rhythmic respiration in *Limulus*. *J. Comp. Physiol.* **81**, 259-276 (1972)
- Wyse, G.A., Page, C.H.: Sensory and central nervous control of gill ventilation in *Limulus*. *Fed. Proc.* **35**, 2007-2012 (1976)
- Wyse, G.A., Sanes, D.H., Watson, W.H. III: Central neural motor programs underlying short- and long-term patterns of *Limulus* respiratory activity. *J. Comp. Physiol.* **141**, 87-92 (1980)