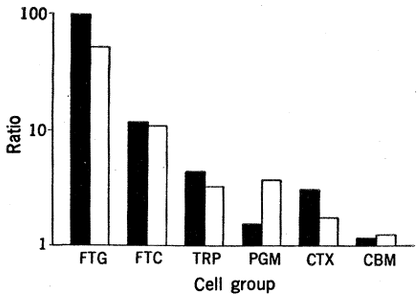

Fig. 3. Ratio of geometric mean discharge rates in D sleep to those in W (filled bars) and to those in S (open bars) for neurons observed in FTG, the tegmental fields adajacent to FTG (*FTC*), the tegmental reticular nucleus (*TRP*), pontine gray matter (*PGM*), posterolateral neocortex (*CTX*), and cerebellar Purkinje cell simple spikes (*CBM*).

as high as 14:1. In view of the unusually large spike amplitudes, most of the neurons recorded in the FTG are likely to have been "giant cells"; thus the observations described are likely to have been made on those cells. Most FTG neurons either showed very low discharge rates (< 1 impulse per second) or were silent during W and S, while during D discharge rates increased to large multiples of those during W and S (Figs. 1B and 2). To determine the ratio of D discharge rates to those in W and S, we calculated first the geometric means of discharge rates in W, S, and D for the population of 34 FTG neurons. Then we calculated the medians and arithmetic means for the same data (Table 1). All of the measures are much higher in D than in W or S. Use of the geometric mean, as contrasted with the median or arithmetic mean, preserves the ratio scale for computation of population ratios of discharge rates (*7*). For FTG neurons these ratios were D/W, 98.5, and D/S, 51.1; in other words, the group geometric mean discharge rate of the 34 FTG neurons in D was 98.5 times that in W and 51.1 times that in S.

Such concentration of neuronal activity in D (when compared with W and S) has not been found in any other brain site. The magnitude of the ratios for FTG neurons is compared with that of neurons observed at other sites (Fig. 3). Of particular importance in terms of the selectivity criterion is the progressive decrease of the ratios at recording sites increasingly distant from the FTG; the ratios are five to ten times lower in adjacent tegmental reticular structures, while at distant recording sites (posterolateral neocortex and Purkinje cells in cerebellar vermis) and in the tegmental reticular nucleus and pontine gray (sites thought to have strong cerebellar connections), ratios are 25 to 30 times lower than in FTG.

The data from FTG neurons satisfy the selectivity criterion discussed earlier better than any other group of cells yet encountered. The large ratios of discharge rates in D to those in W and in S seen in FTG neurons are what might be expected in recordings from neurons whose activity is most intimately related to the events of D. The lower ratios in adjacent reticular regions demonstrate that rate increases of this magnitude during D are not a property of all pontine reticular cells; rather, there appears to be a decreasing gradient of activity ratios with recording sites increasingly distant from FTG. Our findings are therefore consistent with the hypothesis that neurons in the FTG may be involved in the generation of D sleep phenomena.

Our data are suggestive of, rather than proof of, a critical role for FTG neurons in generating desynchronized sleep phenomena. It is possible that the FTG neurons are themselves "follower" neurons under the control of other, still unrecorded cells in the brain. We believe that the method of recording and the approach to data analysis described will permit assessment of this alternative. By these methods, additional physiological evidence bearing on the central control question can be derived from an analysis of the temporal relationship of FTG neuronal activity to the tonic and phasic events of D sleep. More definitive tests of pacemaker activity in neurons such as these by intracellular recording techniques may also be possible.

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16 August 1971

Central and Peripheral Control of Gill Movements in Aplysia

Abstract. *Two types of gill contraction in* Aplysia *were used to study the relation of peripheral and central pathways in controlling behavioral responses in a mollusk. A weak or moderate tactile stimulus to the mantle elicits gill contraction (gill-withdrawal reflex) as a component of a more extensive withdrawal response; a stimulus applied directly to the gill elicits a localized response of the gill pinnule (pinnule response). Central pathways through the abdominal ganglion are both necessary and sufficient for the gill-withdrawal reflex, and motor neuron L7 makes direct connections with gill muscles, without engaging the peripheral plexus. Peripheral pathways are necessary and sufficient for the pinnule response. As a result of the independence of peripheral and central pathways, habituation by repeated tactile stimulation of one pathway does not affect the responsiveness of the other pathway.*

The nervous system of higher animals varies in the proportions of central ganglionic masses and peripheral nerve plexuses. In vertebrates, peripheral nerve plexuses are restricted to certain viscera, such as stomach and intestine, but in higher invertebrates, nerve plexuses (*1*) are often more extensive, innervating skin and muscles of locomotion. For example, mollusks and annelids have well-developed central nervous systems, yet peripheral path-

ways that course through the subepithelial plexus of the skin can mediate behavioral responses in the absence of central ganglia (*2–5*). The analysis of the neural control of behavior in these animals therefore requires a detailed understanding of the relative contributions of the peripheral plexus and the central nervous system.

As early as 1906, Bethe (*4*), studying the marine mollusk *Aplysia*, suggested that the nerve plexus serves to mediate slow local responses over short distances, whereas the central nervous system mediates rapid action over great distances. Although supported by several studies (*6*) Bethe's notion leaves open the question of whether a given reflex is mediated exclusively by central or peripheral pathways or whether all reflex responses involve concomitant activation of both pathways. Furthermore, it is not known whether the central pathways innervate effector organs directly or via the peripheral plexus. To answer these questions it is necessary to record from the appropriate central neurons and from the muscles they innervate. Our recordings were designed to isolate and interact the central and peripheral components controlling gill movements in *Aplysia*. We find that the peripheral pathways mediate local gill pinnule responses, whereas independent central pathways mediate a defensive gill-withdrawal reflex.

The gill of *Aplysia* is a large external respiratory organ composed of afferent and efferent veins and about 16 individual elements (pinnules). A weak tactile stimulus (*7*) applied to the siphon or the mantle shelf elicits a defensive withdrawal reflex consisting of a withdrawal of the gill into the mantle cavity (gill-withdrawal reflex) and contraction of the siphon and the mantle shelf (Fig. 1A). Comparable stimuli applied directly to the gill do not elicit the total defensive reflex (Fig. 1, A and B) but produce small local contractions limited to the stimulated pinnule (Fig. 1B) or part of the pinnule [the pinnule response, see (*8*)]. The receptive fields of the two responses also differ (Fig. 1, A and B). The gill-withdrawal reflex can be elicited by a stimulus applied to the siphon and the mantle shelf (*9*), a wide area of the skin adjacent to the gill (Fig. 1A). By contrast, the receptive field for the pinnule response is centered on the pinnule itself, with the strongest contraction occurring under the site of stimulation (Fig. 1B). The differences in the receptive fields, as well as in the nature of the contractions, are consistent with data which indicated that the pinnule response is mediated by peripheral pathways (*5*), whereas the gill-withdrawal reflex is mediated by central pathways (*9*). To examine the relative independence of these two types of pathways we performed a number of experiments to determine whether the central pathways were necessary and sufficient to mediate the gill-withdrawal reflex and whether the peripheral pathways were necessary and sufficient to mediate the pinnule response.

The abdominal ganglion contains four motor neurons whose firing causes gill contraction (*9, 10*). These motor cells receive excitatory synaptic input from the siphon and mantle shelf, the sensory receptive field of the gill-withdrawal reflex (*9*). To determine whether this central component was sufficient to produce the gill-withdrawal reflex we surgically isolated a part of the receptive field (the siphon) from the rest of the animal, leaving it attached to the abdominal ganglion by only the siphon nerve (Fig. 1C). In this preparation, devoid of any possible parallel peripheral pathways through the skin, tactile stimulation of the siphon still produced a brisk gill-withdrawal reflex. Intracellular recordings from gill motor neurons showed that in this preparation, as in the more intact animal, siphon stimulation produced large excitatory postsynaptic potentials that mediated the reflex response by causing discharge of the motor neurons.

These experiments indicate that the central pathways are sufficient to mediate the gill-withdrawal reflex, but they cannot exclude a contribution of parallel peripheral pathways in the intact animal. We therefore reversibly removed from the reflex pathway in a relatively intact animal (*11*) first individual motor neurons and then the whole abdominal ganglion.

To estimate the contribution of individual motor neurons to the total reflex we impaled a given motor neuron with a double-barreled microelectrode (for recording and passing current), and monitored gill contractions by means of a photocell (*9, 11*). We elicited the gill-withdrawal reflex by identical tactile stimuli to the siphon, and we examined the amplitude of the gill contraction with the motor neuron at its resting potential and firing normally, and then with the motor neuron selectively removed from the reflex pathway by hyperpolarizing it to prevent spike generation (Fig. 2A). In this way we estimated that the average contribution of motor neuron L7 to the gill-withdrawal reflex was 40 percent [11 experimental runs, three cells, see (*12*)]; the contribution of LD-G was estimated to be 35 percent (four experimental runs, two cells). Since the contractions produced by L7 and LD-G have been found to be additive, these

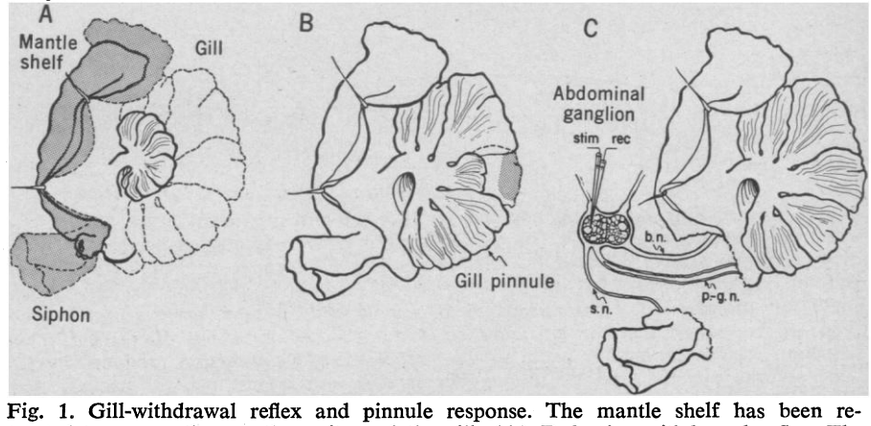

Fig. 1. Gill-withdrawal reflex and pinnule response. The mantle shelf has been retracted to expose the mantle cavity and the gill. (A) Defensive withdrawal reflex. The reflex is elicited by tactile stimulation within a receptive field (shaded area) consisting of the siphon and the mantle shelf, and involves contraction of the whole gill as well as the siphon and mantle shelf. Relaxed position (dashed lines); contracted position (solid line). (B) Pinnule response. The response is elicited by a tactile stimulus applied to a gill pinnule. With a moderate stimulus, only a single pinnule contracts, and the receptive field (shaded) is limited to the contracting pinnule. (C) Isolated siphon preparation. To eliminate possible peripheral pathways between the siphon and the gill, we isolated the siphon, except for its connection to the abdominal ganglion via the siphon nerve (*s.n.*). The abdominal ganglion remained connected to the gill via the branchial (*b.n.*) and pericardial-genital (*p.-g.n.*) nerves.

two cells account for a major portion of the total reflex. This finding is consistent with data which indicated that L7 and LD-G are particularly effective in eliciting gill movement and that the other motor neurons (for example, L9-1 and L9-2) produce much weaker effects (*9*).

To ascertain whether any remaining contraction, not accounted for by the action of L7 and LD-G, involved central or peripheral pathways we reversibly blocked all central pathways by bathing the abdominal ganglion (and not the rest of the animal) in a solution of isotonic $MgCl_2$. To insure that blockade was occurring (*13*), we monitored a motor neuron intracellularly. The reflex response to a moderate tactile stimulus was reversibly reduced to an average of 5 percent of control by high magnesium solution (eight runs, four preparations). In six out of eight runs the reflex was totally abolished (Fig. 2B). In the two remaining cases the high magnesium solution reduced the reflex contraction to about 15 percent of control despite the fact that in one of these preparations central synaptic transmission was not fully blocked. These experiments indicate that the central pathways mediate at least 85 percent and probably all of the gill-withdrawal reflex elicited by weak and moderate stimuli. The central pathways are therefore necessary as well as sufficient for mediation of the gill-withdrawal reflex.

Although the gill-withdrawal reflex does not require peripheral pathways in parallel with central ones, it is possible that the central pathways converge on the peripheral ones at the gill muscle. For example, the gill motor neurons may not innervate the gill muscle directly, but only via a peripheral plexus. Therefore, we obtained simultaneous intracellular recordings from gill muscle fibers (*14*) and motor neuron L7. Cell L7 produces gill movement by contracting the efferent vein and the pinnules (*9, 10*). We obtained intracellular recordings from muscle fibers in the efferent vein and found that action potentials in L7 produced excitatory junctional potentials (EJP's) in these gill muscle fibers (Fig. 3A). The EJP's followed firing in L7, with constant latency, even in a seawater solution with high calcium content (ten times normal concentration), which presumably would raise the threshold of neural elements that might be interposed between L7 and the gill muscle. These experiments support conclusions based on less direct data (*9*) and indicate that L7 makes direct connections with the gill musculature. More recent experiments indicate that the other major gill motor neuron, LD-G, also makes direct connections to gill muscle (*14*).

We next examined the pinnule response and confirmed Peretz's finding (*5*) that the pinnule response persists when all central ganglia are removed. This shows that peripheral pathways are sufficient to mediate the pinnule response, but it does not eliminate the possible role of a central component in the intact animal, since a tactile stimulus to the gill might result in excitatory synaptic input to gill motor neurons. We therefore recorded from L7 while directly stimulating the gill and found that tactile stimuli that produce pinnule responses, evoked little or no excitatory synaptic input (*15*) in motor neuron L7 (Fig. 3B). Thus the peripheral pathways are also both necessary and sufficient for the pinnule response. It therefore appears that the two types of gill responses are mediated by two types of pathways that are essentially independent functionally.

Both the gill-withdrawal reflex (*16*) and the pinnule response (*5, 17*) undergo habituation or response decrement with repeated tactile stimulation. Since our data indicated an independence of the central and peripheral pathways we predicted there would be no spread (or generalization) of habituation from one pathway to the other.

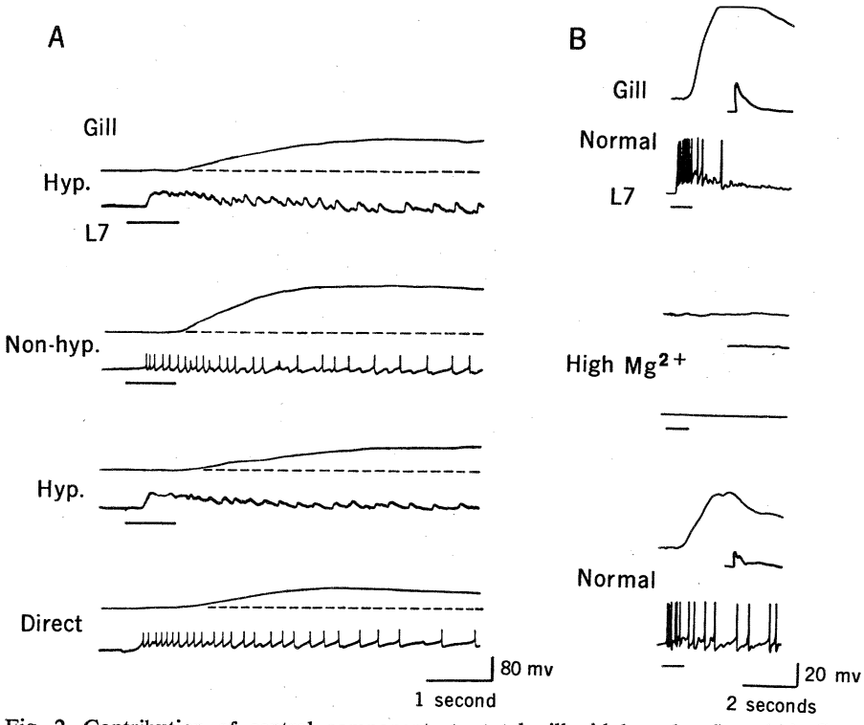

Fig. 2. Contribution of central components to total gill-withdrawal reflex. (A) Contribution of motor neuron L7. The gill-withdrawal reflex was elicited every 5 minutes by a jet of seawater (indicated by solid line, under L7 record) applied to the siphon and, on alternate trials, L7 was hyperpolarized (*Hyp.*) so that the excitory input could not discharge it. Comparisons of hyperpolarized to nonhyperpolarized (*Non-hyp.*) trials showed that the gill contraction was reduced by about 40 percent. This reduction was approximately equal to the size of the gill contraction produced by L7 when it was directly fired by a long depolarizing pulse (last pair of traces), that caused L7 to fire in a pattern comparable to that produced by the normal excitatory input. (B) Contribution of the total central pathway. With the abdominal ganglion in normal seawater a jet of seawater applied to the siphon produced a large excitatory input to L7, and a large gill contraction. With the abdominal ganglion bathed in high magnesium solution, and with all synaptic input eliminated to L7 and presumably to other cells in the ganglion, the gill-withdrawal reflex was totally abolished. When the ganglion was returned to normal seawater, synaptic input and the gill contraction partially recovered. Since on some trials the high-gain record of the gill response is blocked, a low-gain record is included just below the high-gain record (paper speed 15 times slower, gain 0.25 of upper record). In (A) and (B) the lower traces are the intracellular records from L7, and the upper traces are the output of a photocell placed under the gill to monitor contraction.

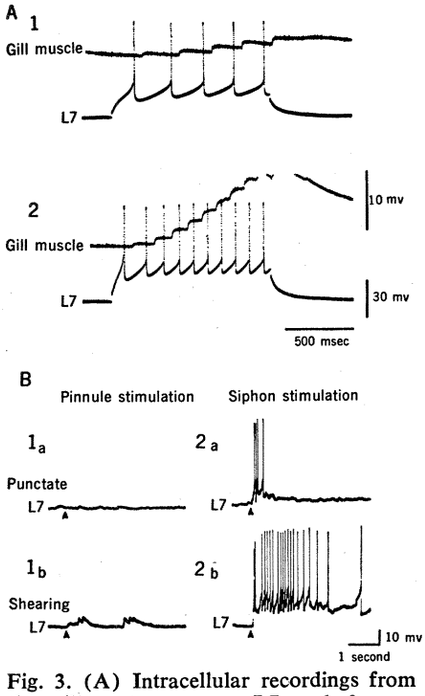

Fig. 3. (A) Intracellular recordings from the gill motor neuron L7 and from a gill muscle cell on the inner surface of the efferent branchial vein. The spikes in L7 were elicited by depolarizing pulses of different intensities. The EJP's in the gill followed L7 spikes one for one with a fixed latency at both low frequencies (5 per second, part 1) and higher frequencies (10 per second, part 2). At the higher frequency considerable potentiation of the EJP's was present. (B) Synaptic input to gill motor neuron (L7) from the gill and the siphon. L7 was hyperpolarized to prevent background spike activity. A brief punctate stimulus (sable brush) applied to a pinnule, resulted in no synaptic input to L7 (B 1_a). The same stimulus applied to the siphon produced a moderate synaptic input (B 2_a). A shearing stimulus (brush stroke) to the gill resulted in a small synaptic input to L7 (B 1_b). The same stimulus applied to the siphon resulted in a massive synaptic input eliciting several spikes in L7 (B 2_b).

We habituated one response or the other (12 runs, six animals) by means of repeated tactile stimuli presented to either the receptive field of the gill-withdrawal reflex (siphon or mantle shelf, Fig. 1A) or the gill pinnules (Fig. 1B) and tested the nonhabituated response for generalization of habituation (Fig. 4). We found that 10 to 20 tactile stimuli to the siphon (or mantle shelf) produced marked habituation of the gill-withdrawal reflex (to a mean of 7 percent of the initial control), but produced no significant change in the magnitude of a pinnule response to direct tactile stimulation of the gill (108 percent of control). Conversely, repeated stimulation of the gill produced habituation of the pinnule response (to 50 percent of control) but produced no significant change in the magnitude of the gill-withdrawal reflex elicited by siphon stimulation (106 percent of control). Failure of generalization of habituation of one pathway to the other provides further support for the independence of the central and peripheral pathways.

Although the peripheral and central pathways that act on the gill can be independently activated when weak or moderate intensity tactile stimuli are applied to specific areas, it is sometimes possible to activate both pathways concurrently by using strong or noxious stimuli. For example, strong or prolonged mechanical stimulation of a single pinnule can result in the spread of contraction to neighboring pinnules, leading at times to contraction of the whole gill. Although this type of contraction can be peripherally mediated and occurs even when central transmission is blocked, very strong stimuli presented directly to the gill also produce excitatory synaptic potentials in gill motor neurons, capable of discharging them and bringing in a central action in addition to the peripheral one. In addition, a strong or noxious stimulus applied to the siphon or the mantle shelf can sometimes produce gill contraction, even when the ganglion is removed or when transmission through the ganglion is blocked with a high Mg^{2+} solution. The peripheral action could amplify the central action to strong stimuli in the intact animal.

Our results clarify the functional organization of the central pathways that mediate the gill-withdrawal reflex to weak and moderate intensity tactile stimuli and indicate that, in *Aplysia*, central pathways controlling gill contraction exist in parallel with peripheral pathways, and that the two types of pathways have different properties. They do not, however, specify the functional organization of the peripheral nerve plexus that mediates gill pinnule responses. Nerve plexuses usually consist of finely distributed neurite processes intermingled with nerve cells or peripheral ganglia. The gill of *Aplysia* contains a peripheral (branchial) ganglion, and one or two other nests of cells at various points along the peripheral nerve (*4, 5, 18*). It is not known whether the pinnule response involves any of these peripheral neurons, or whether it is due to axon reflexes of

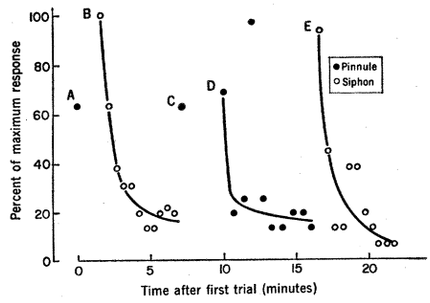

Fig. 4. Independence of habituation of gill-withdrawal reflex and pinnule response. Gill or pinnule contractions were measured by a photocell. At *A*, a single shearing stimulus was presented to several pinnules. At *B* the gill-withdrawal reflex was habituated by presenting a series of stimuli to the siphon, every 30 seconds. After habituation of the gill-withdrawal reflex, a stimulus to the pinnules similar to that given at *A* resulted in a contraction (point *C*) that was identical to that of *A* before habituation of the gill-withdrawal reflex. At *D* the pinnule response was habituated. A test stimulus presented to the siphon (point *E*) showed that during habituation of the pinnule response, the gill-withdrawal reflex had recovered almost completely. The gill-withdrawal reflex was again habituated. Siphon stimuli consisted of jets of water from a Water Pik. The pinnule stimuli consisted of brush strokes across the gill. This stimulus produced a relatively large contraction involving several pinnules. Similar results were obtained with a weak Water Pik stimulus applied directly to the pinnules. Response magnitudes are represented as a percent of the maximum response obtained (point *B*, 100 percent).

central cells, or even direct stimulation of muscle (*19*). By studying the peripheral neurons and muscle by means of intracellular techniques, it should be possible to specify to what degree these neurons participate in the local pinnule responses.

Gastropod molluscs are useful for cellular studies of behavior because of the size and accessibility of their central neurons. Our results indicate that the existence of an extensive peripheral nerve plexus need not complicate the analysis of the central control of behavior. By using selective stimuli applied at a distance from the effector organ it is possible to study reflexes exclusively controlled by the central nervous system.

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7. Weak and medium strength tactile stimuli (jets of seawater) were produced by the low (3 g) and medium (6 g) settings of a Water Pik apparatus or by a poke with No. 2 red sable brush (1 g). Strong stimuli were produced by the maximum setting (25 g) on the Water Pik, by vigorous brushing, or by poking with a glass or wooden rod (12 g). The force of the jet of seawater was measured by directing it under water, at a 2.54-cm-diameter target, 1.9 cm away from the nozzle. The target was attached to a force transducer by a 5-cm arm. The same system was used to estimate the force of the brush, by pressing the brush against the target.
8. The less committal term "pinnule response" is preferable to pinnule reflex. A response that remains after the central nervous system has been removed should not be considered a reflex until it can be shown that sensory and motor neuronal elements are involved. It is not known whether the pinnule response is mediated by peripheral ganglia; by a peripheral nerve plexus; or by direct responsiveness of, and conduction through, muscle fibers.
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12. The value of 40 percent is based on 11 experimental runs each consisting of two trials in which the gill contraction elicited when L7 was hyperpolarized was compared to the contraction when L7 was not hyperpolarized. In the relatively intact preparation the size of the reflex response tends to decrease throughout the course of an experiment. Therefore, an alternate estimate of the L7 contribution to the reflex was obtained by comparing the reduced response with L7 hyperpolarized to the average amplitude of the two gill responses taken during the trials immediately before and after L7 was hyperpolarized. This procedure yielded values of 36, 38, 47, and 83 percent for the contribution of L7. A similar procedure on one LD-G cell yielded a value of 36 percent.
13. These experiments utilized a relatively intact preparation with a slit made in the neck region to externalize the abdominal ganglion (*11*). The stage on which the ganglion was pinned was modified into a small chamber that could be filled with 1 or 2 ml of a given solution with little leakage into the large chamber (3 liters) that held the animal. The level of the seawater in the main chamber was maintained slightly above the ganglion chamber, so that leakage consisted primarily of flow into the ganglion chamber. Probably because of leakage, synaptic transmission through the ganglion was not invariably blocked completely; even with a solution of pure isotonic $MgCl_2$, postsynaptic potentials, although always reduced, were not always completely abolished. In two additional experiments utilizing extracellular recordings from the genital, pericardial, and branchial nerves, we found that raising the magnesium concentration to four times normal blocked all efferent spike activity evoked by a tactile stimulus to the siphon. Since this concentration of magnesium did not block spike activity, it appears likely that all central afferent pathways from tactile receptors make chemical synaptic connections in the abdominal ganglion.
14. The gill was removed from the animal and remained attached to the abdominal ganglion by means of the branchial nerve, which enters the efferent vein of the gill at its anterior insertion. The efferent vein was opened to allow visualization of the muscle fibers whose contractions contribute a significant part of the total gill-withdrawal reflex. K. Rubinson (personal communication) has some anatomical evidence that the region of the efferent vein from which intracellular recordings were obtained is rich in muscle cells and is devoid of any neuronal cell bodies. These experiments on L7 and parallel experiments on LD-G will be described in detail elsewhere (H. Pinsker, T. Carew, K. Rubinson, I. Kupfermann, E. R. Kandel, in preparation).
15. In some cases stimulation of the gill seemed to trigger interneuron II (as evidenced by a burst of inhibitory postsynaptic potentials in L7) and led to a triggered or late "spontaneous" contraction of the gill (*9*, *10*) clearly distinguishable from either the pinnule response or the gill-withdrawal reflex. It is thus possible that the gill sends an excitatory input to interneuron II.
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19 July 1971; revised 30 August 1971 ■

Auxins in Citrus: A Reappraisal

Beginning with a report in 1963 (*1*), a group of scientists from the Citrus Research Center at Riverside, California, published a series of papers dealing with a new, natural growth-promoting substance that has been found in young citrus fruits. Results obtained through thin-layer and column chromatography, paper electrophoresis, and spectrofluorimetric determinations showed that the new compound could not be indoleacetic acid (IAA) and suggested that it was nonindolic. Being unable to find any indolic auxins in citrus fruits, Khalifah, Lewis, and Coggins called the new compound "citrus auxin" and considered it to be of physiological significance in citrus and probably also in additional plant species (*2*).

Accumulating physiological and chemical evidence seems to warrant a reappraisal. Bioassay determinations revealed the presence of considerable auxin activity in numerous citrus tissues (*3*). An IAA-oxidase system was detected in roots and aerial parts of citrus seedlings, showing specificity toward IAA (*4*). Vigorously growing Eureka lemon shoots contain a single auxin component which copartitions and cochromatographs with labeled IAA and migrates to the same R_F as synthetic IAA in eight solvent systems in paper chromatography (*5*). The difficulties in obtaining the chromogenic reactions typical to IAA were also overcome by employing solvent partition followed by a two-dimensional run on thin-layer chromatography (TLC), with up to 100 g of fresh material per TLC plate. Labeled IAA markers and biological auxin activity were recovered from the zones that responded to chromogenic sprays on parallel plates (*6*).

Flower parts, including ovaries, showed relatively high auxin activity, as determined by bioassay (*3*). Extracts from fruits at later developmental stages evinced, on purification, several zones with auxin activity, but did not seem to contain detectable amounts of IAA (*7*). However, Khalifah (who himself belonged originally to the "citrus auxin" team) showed that citrus fruitlets incorporated [^{14}C]tryptophan into IAA (*8*).

Direct and complete evidence for the existence of indolic auxins in citrus fruits has now been provided through extensive purification followed by chemical and physical identification. An extract from young fruitlets of *Citrus unshiu* (satsuma orange), a week after bloom, was purified by solvent partition followed by numerous steps of column, paper, and thin-layer chromatography and by countercurrent distribution, yielding several zones which respond to Ehrlich's reagent and show biological activity in the *Avena* curvature bioassay. The active components were identified by gas-liquid chromatography, and by ultraviolet, infrared, and mass spectra. The young fruitlets were shown to contain IAA [0.5 to 1.0 mg/kg (fresh weight)] and indoleacetamide [5.0 mg/kg (fresh weight)] (*9*). Only traces of IAA and indoleacetamide could be found in 2-month-old fruits, but neither fruitlets nor older fruits revealed the presence of biologically active auxins which had the properties ascribed to "citrus auxin" (*9*).

It seems, therefore, that the existence of indolic auxins in citrus tissues is now well documented, even though