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Multifunctional interneurons in behavioral circuits of the medicinal leech

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Summary. We are using the medicinal leech to study the neuronal basis of behavioral choice. In particular, we are recording from neurons, both extracellularly and intracellularly, in preparations that can express three different behaviors: the shortening reflex, crawling and swimming. We have found that particular mechanosensory neurons can elicit any of the behaviors, and that the movements are produced by just four sets of muscles, each controlled by a small number of motor neurons. Hence, there must be three different pattern-generating neuronal circuits, each of which can be activated by the same set of sensory neurons. We are studying how the choice is made among the three behaviors by recording, while one behavior is being performed, from neurons known to be involved in the initiation of the other two. We have found that an interneuron, cell 204, which is known to initiate and maintain swimming, is also active during shortening and crawling. The activity level in this interneuron can influence whether a mechanosensory stimulus produces shortening or swimming. The neuronal mechanisms by which this choice is normally effected awaits further elucidation of the circuits that elicit and generate shortening and crawling.
Key words. Behavioral state; command neuron; gating neuron; leech; mechanosensory neuron; motor neuron; pattern-generating neuron; rhythmic motor pattern; shortening reflex; trigger neuron.

Introduction

It is commonly observed that an individual animal can respond very differently to a well-defined and controlled stimulus when it is presented on two different occasions. This variability has been attributed to such factors as the animal's motivational state, its ontogenetic development, or the environmental context in which the stimulus is presented. For instance, a dog's response to a meaty bone may depend on whether it is hungry or sated, whether it is newborn or mature, and whether or not there is a receptive mate nearby. A variety of terms have been used to describe these variations in behavioral state: "mood", "motivation" (Eibl-Eibesfeld[9]), "behavioral set" (Evarts et al.[10]), or "drive" (von Holst[27]). Such states are deduced from experiments monitoring an animal's response to a particular stimulus under different conditions (McFarland & Sibly[20]) or at different times (von Holst[27]), or to simultaneous presentation of two different stimuli that when presented individually evoke different behaviors (Davis[5,7,8]). Behavioral threshold can be

measured by finding the lowest stimulus intensity needed to elicit a given behavior. If the test stimuli can elicit more than one behavior, as in our studies, a choice among the possible behaviors must be made. The behavioral choice can be quantified as the fraction of trials that elicits each of the possible behaviors. Although we will discuss behavioral choice exclusively, it should be noted that measures of behavioral threshold are also measuring a choice – that between a response and a lack of response.

The neuronal basis of behavioral choice must involve interactions between the neuronal circuits that produce different behaviors. To date, two types of neuronal interactions have been described that could mediate these interactions:

1. Mutual inhibition. In the simplest case, inhibition would occur between two distinct circuits, each of which is dedicated to one behavior. This interaction would be clearest at the level of the "command neuron" for each behavior, i.e., an interneuron that triggers or gates a behavior (Kovac & Davis[14,15]). Mutual inhibition could also occur at the level of sensory integration, with neurons in the sensory pathways leading to the command neurons inhibiting one another (Reichert et al.[24]). In either case, if one of the mutually inhibitory neurons becomes more active than the others, it inhibits the others and thereby removes some of the inhibitory input onto itself. The overall effect of this disinhibition would be to ensure that only one of these circuits could be active at a time and that it would remain active until either the initial driving excitation disappeared or the inhibitory interactions fatigued. In such a system, small differences in the levels of initial activity in the interacting circuits would result in an absolute choice of behavior. This would result from the progressive loss of negative feedback (that is, the removal of inhibition onto the more active pathway from the less active of the two mutually inhibitory pathways) that would drive the system into a meta-stable state. Behavioral choice in this type of system would, therefore, depend upon the relative strengths of inhibitory interactions.

2. Differential sensory access to the pattern-generating systems. In one example of this mechanism, two pattern-generating circuits would share some neurons, with different levels of sensory input activating different elements of their command and pattern-generating circuits, thereby producing two different behaviors (Getting & Dekin[13], and this review). Behavioral choice in this case would depend upon the relative strengths of inputs onto the two parts of the circuit.

It should be emphasized that these possibilities are not mutually exclusive, nor are they the only ones that could explain behavioral choice. It is logically possible, for example, that a particular sensory pathway feeds onto several distinct pattern-generating circuits that have different thresholds, and that the higher-threshold circuit inhibits the lower-threshold one. In this arrangement, behavioral choice would depend upon behavioral thresholds, but would be produced by a one-way inhibitory interaction.

In addition to such neuronal interactions occurring after a stimulus is presented, it is clear that behavior elicited by a defined stimulus can be modified by influences that vary over time, such as learning or reproductive state (Davis et al.[6]). These influences are thought to affect neuronal properties through hormones or other neuromodulatory substances (see Selverston, this review). However, to explain how neuromodulators bring about long-term changes, the neuronal basis of the individual behaviors must first be known in some detail. We have started to approach the issue of behavioral choice using the medicinal leech, because its behavior is remarkably sophisticated, given the simplicity of its nervous system.

Behavioral choice in the leech

Leeches produce a variety of behavioral responses to mechanosensory stimulation (Kristan et al.[17]). Three that we have studied are shortening, crawling, and swimming (fig. 1). Each of these involves a coordinated movement of the 21 essentially identical midbody segments. Movement in each segment is caused by contractions of four sets of muscles. Three sets form the bulk of the body wall; these are: 1. longitudinal muscles, which are parallel to the long axis; 2. circular muscles, which ring the long axis; and 3. oblique muscles, which make up a thin layer at 45° angles to the first two. The fourth set, the dorsoventral muscles, bridge the internal space from dorsal to ventral surfaces. Longitudinal muscle contractions shorten a segment, circular muscle contractions reduce its diameter, and dorsoventral muscle contractions flatten it; these latter muscles are, therefore, also called "flatteners". Because the internal space is a closed volume, contractions of either the circular or flattener muscles cause the segment to lengthen.

The muscles in each segment are controlled by a small number of identified motor neurons, whose somata are located in the segmental ganglion. Shortening, crawling, and swimming all draw upon this limited set of motor neurons and require that their activity be coordinated in different ways, so the three behaviors are generally incompatible. In fact,

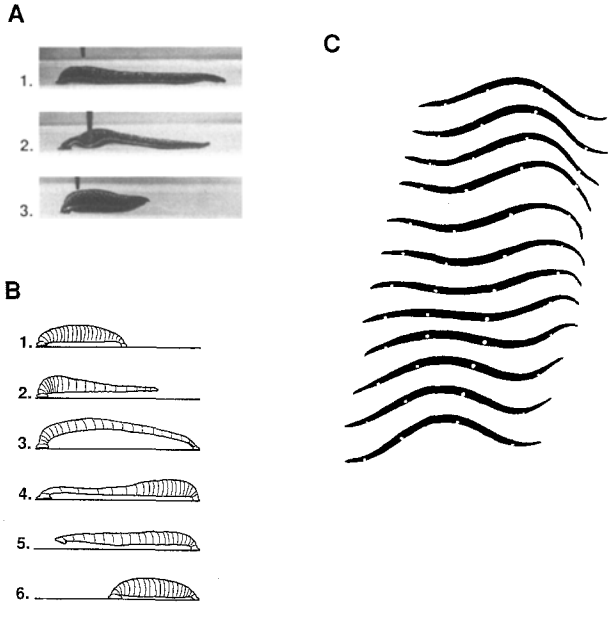

Figure 1. Three behaviors being studied in the leech, *Hirudo medicinalis*. The animals used in these experiments measured 4–6 inches when fully extended. *A* The shortening response. *A1* The leech is lying motionless on the bottom of a plexiglass chamber; a probe (the back end of a small paint brush) is poised just above its dorsal surface, near the posterior end of the leech. *A2* The leech's response after having been touched with the probe on its dorsal surface: the animal is shorter, largely due to a longitudinal contraction in several segments around the site of stimulation. *A3* Another type of shortening response sometimes obtained, in which there is a vigorous shortening of all the segments. *B* Crawling. Panels 1–6 are drawings of successive movements during one step cycle of a leech crawling under water along the bottom of a plexiglass chamber. Drawings 2 and 3 show the extension phase of the step and drawings 4 and 5 show the contraction phase. The duration of the step cycle is variable, ranging from 3 to more than 20 s. *C* Swimming. The images from top to bottom are successive frames of a film, taken at 40 ms intervals, of a leech swimming from right to left. This sequence illustrates one complete cycle of the swimming movements. White beads were sewn onto the lateral edge of the body to mark the location of segments 1, 5, 10 and 15. The period of swim cycles in freely-swimming leeches varies from about 0.4–1.5 s.

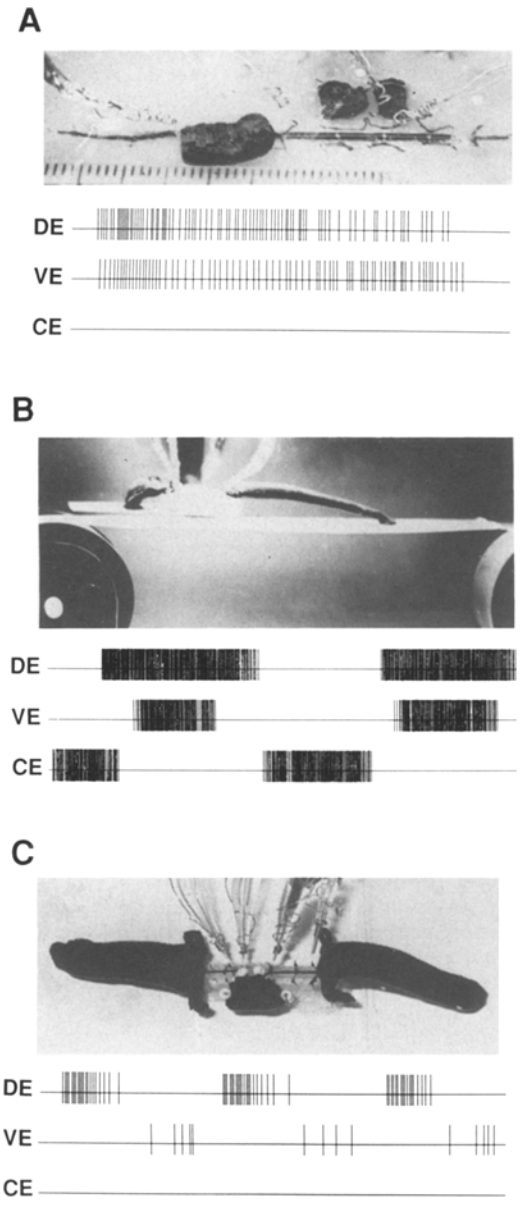

Figure 2. Semi-intact preparations used to study leech behavior. *A* Shortening response. The nerve cord from segments 3 through 19 was exposed. The right portions of segments 10 through 12 were left attached to their ganglia by all their nerves, to allow the shortening reflex to be monitored. The body wall from the left side of segments 15 and 16 was left attached by a single nerve, to allow the activation of mechanosensory neurons in a controlled manner. The nerve cord and pieces of body wall were pinned to wax in the bottom of a saline-filled chamber, and suction electrodes recorded from segmental nerves and stimulated small patches of skin in the body wall. Below the picture of the preparation are tracings of the impulse activity generated by dorsal longitudinal muscle excitors (DE) and ventral longitudinal muscle excitors (VE), obtained from extracellular recordings that contained the axons of several motor neurons. Such responses last 5–10 s. *B* Crawling. The body wall from segments 10 through 14 was dissected away, leaving only the nerve cord connecting the intact front and back parts of the animal. The denervated, intact ends of segments 10 and 14 and the exposed nervous system were pinned to a wax platform suspended above a treadmill, which consists of a plastic belt wrapped around two plexiglass wheels. In this device, the front sucker is free to grasp the treadmill belt whereas the back sucker attaches to a stationary extension at the back of the wax platform. The animal begins to crawl by extending its front end, grasping the belt with its front sucker, then shortens, thus pulling the treadmill backward. The back sucker then lifts off its platform and reattaches, whereupon the front sucker releases and the front of the animal extends to start another step. Suction electrodes record the activity of motor neurons from the exposed nerves. The activity of dorsal longitudinal muscle excitors (DE), ventral longitudinal muscle excitors (VE), and circular muscle excitors (CE) are indicated in the traced recordings shown below the picture of the preparation. The steps produced by such a preparation are much more variable and last longer than those in intact, freely-moving animals, taking from 20 s to over a minute to complete. *C* Swimming. As in the crawling semi-intact preparation, five ganglia in the middle of the leech were exposed for recording and the animal was pinned to the bottom of a saline-filled chamber. The anterior and posterior brains, in the head and tail segments, were removed. In addition, a piece of body wall was left attached to the middle exposed ganglion, to monitor the dorsal and ventral longitudinal muscle contractions. The tracings of extracellular recordings below show the activity of DE, VE and CE motor neurons. The cycle period for these impulse bursts was about 1 s. Note the two microelectrodes, directed at the middle exposed ganglion, which are used to obtain the sorts of intracellular recordings shown in figs 4, 5 and 6.

they never occur simultaneously; the system can produce only one of the three behaviors at a time.

The contribution made by particular motor neurons to each of the behaviors has been studied in semi-intact preparations (fig. 2). Shortening is produced by the co-activation of excitatory motor neurons to dorsal and ventral longitudinal muscles along the entire body, while the circular motor neurons remain silent (fig. 2A). (All muscles in the leech are innervated by both excitatory and inhibitory motor neurons. In this discussion, only the contribution of the excitatory motor neurons will be mentioned. For all behaviors, the activity of the inhibitors is opposite to that of the corresponding excitors.) Note that sometimes the contraction is localized, with the strongest contractions seen near the site of stimulation (fig. 1 A2), whereas other times the whole body contracts maximally (fig. 1 A3). Intermediate levels of shortening can also be observed.

Crawling consists of two distinct phases: extension, with the back sucker attached (Fig. 1 B2,3) and contraction, with the front sucker attached (Fig. 1 B4,5). The extension phase is caused by activity in the circular motor neurons, and the contraction phase, as in the shortening reflex, results from co-activation of dorsal and ventral longitudinal excitors, although the timing and strength of the dorsal and ventral excitor activity is somewhat different from the pattern that produces shortening behavior (fig. 2B). Front sucker attachment at the end of an extension movement appears to trigger the detachment of the posterior sucker, followed by a front-to-back wave of contraction; likewise, posterior sucker reattachment at the end of the contraction wave triggers a detachment of the anterior sucker and a front-to-back wave of extension (Stern-Tomlinson et al. [26]).

Swimming is characterized by alternating bursts of impulses in the dorsal and ventral longitudinal excitors (Kristan et al. [18]) (fig. 2C). Throughout the swim, the circular motor neurons are silent and the dorsoventral motor neurons are active, causing the animal to elongate and flatten. (In fact, swimming is the only known behavior of the leech that uses the dorsoventral muscles in an obvious fashion.) The front-to-back undulation that propels the leech forward results as the longitudinal excitor burst pattern is repeated slightly later in successively more posterior segments.

The neuronal circuit for swimming

As the result of research in three laboratories over the last 15 years (Stent et al.[25]; Weeks[28,29]; Kristan & Weeks[19]; Brodfuehrer & Friesen[1,2,3,4]; Nusbaum[21]; Nusbaum et al.[22]; Friesen[11,12]), we now can trace the pathway that controls swimming from mechanosensory neurons to motor neurons entirely through monosynaptic connections among identified interneurons (fig. 3). These studies were performed by recording from pairs of neurons in semi-intact preparations or in isolated nerve cords; both preparations produce essentially the same rhythmic neuronal activity (Kristan & Calabrese[16]). All of these neurons can be identified by physiological and morphological criteria. The circuit is largely hierarchical: sensory neurons connect to trigger neurons, which activate gating neurons; a constant level of firing in the trigger or gating neurons activate the pattern-generating neurons, which produce oscillatory activity and connect to motor neurons in such a way as to produce the rhythmic motor neuron bursts that constitute the motor program for swimming. (Because of their ability to elicit swimming, the trigger and gating interneurons are also referred to as "swim-initiating interneurons", or, more loosely, "command neurons".)

Study of this elaborate network has provided insight into how behavioral choice is likely to occur. A critical neuron in this circuit is cell 204 (Weeks & Kristan[30]; Weeks[28]). The type of experiments supporting this conclusion are exemplified in figure 4. Mechanosensory stimulation that elicits swimming always activates cell 204 (fig. 4A), and stimulation of a single cell 204 in a semi-intact preparation or in an isolated nerve cord generates the rhythmic swimming activity pattern in the whole nervous sysem (fig. 4B). In order to generate swimming by passing current into one cell 204, the cell must be depolarized more than is seen when swimming is elicited by sensory stimulation. The reason seems to be that mechanosensory stimulation always activates the cells 204 in several segmental ganglia as well as the other identified swim-initiating interneurons, cells 21 and 61. When two of these swim-initiators are depolarized simultaneously to firing levels similar to those seen in response to mechanosensory stimulation, swimming results (Weeks & Kristan[30]; Nusbaum & Kristan[23]). Thus the identified swim-initiating interneurons appear to be sufficient to account for the decision to swim.

The close correlation observed between the firing level in cell 204 and swimming behavior suggested that this neuron might be committed to swimming behavior, i.e., that its one and only function might be to decide whether or not the leech will swim. It was somewhat of a surprise, therefore, to find that this neuron is also active during other behaviors and that it may play a role in their production.

Cell 204 activity during crawling and shortening

The activity of cell 204 was recorded during both crawling and shortening, in the semi-intact preparations shown in figs 2A and 2B. In crawling (fig. 5), cell 204 receives neither excitatory nor inhibitory input during the contraction phase. In contrast, during the extension phase of crawling, cell 204 is excited, although not as strongly as it is during swimming. The role played by cell 204 in crawling is not yet known. It may serve to activate the dorsoventral motor neurons (see fig. 3), thereby helping to elongate the body. Alternatively, its activity may poise the animal to initiate a swim. Leeches do sometimes start swimming in the midst of a step, and whenever they do so, they take off during an extension, the phase in which cell 204 is excited.

During the shortening reflex, cell 204 is also excited, although not as strongly as during swimming (fig. 6A). Again, its role is as yet uncertain. It may contribute to the shortening response through its effects on already-identified interneurons. For instance, cell 204 is known to excite cell 208, which in turn excites dorsal longitudinal muscle excitors in posterior segments. Alternatively, the sensory stimulus that elicits shortening may activate two different command networks: an as-yet unknown one that elicits shortening, as well

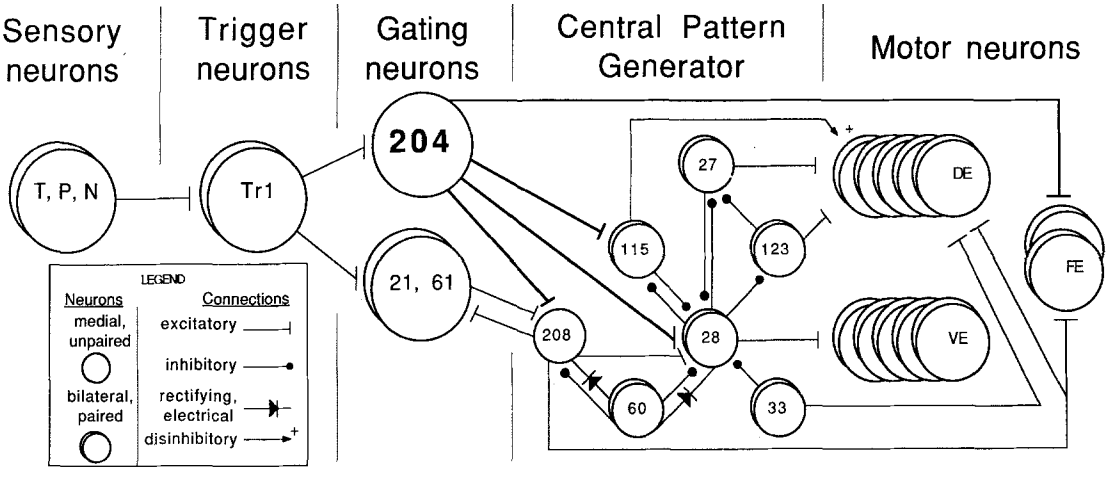

Figure 3. The neuronal circuit for leech swimming. The connections shown are a simplified summary of the connections found within each segmental ganglion and between neurons in different ganglia. Cell numbers are assigned by location within the ganglion, whereas 'T, P, N' refers to touch, pressure, and nocioceptive mechanosensory neurons. Dorsal longitudinal muscle excitors (DE), ventral excitors (VE), and flattener muscle excitors (FE) are sets of identified neurons which innervate distinct regions of the continuous sheet of longitudinal muscles and dorsoventral (flattener) muscles, respectively. Most of the neurons shown are found in bilateral pairs in every ganglion. Some exceptions are: (1) the trigger neurons, represented by Tr1, which are found in bilateral pairs only in the subesophageal ganglion; (2) cell 208, which is present in each ganglion as an unpaired medial cell; and (3) cell 204, which is found as an unpaired medial cell located only in segmental ganglia 10 through 18. The paired interneurons have weak electrical connections between them. The connections shown are those made by the sensory neurons and interneurons onto interneurons within their own ganglion. They also contact neurons in other ganglia. Interganglionic connections are usually similar to intraganglionic ones, but in some cases they are different, and there are some interganglionic connections that are not found intraganglionically. Interneurons connect with motor neurons within the same ganglion and in other ganglia; for simplicity, only the excitatory connections onto motor neurons are shown, but many inhibitory connections also occur.

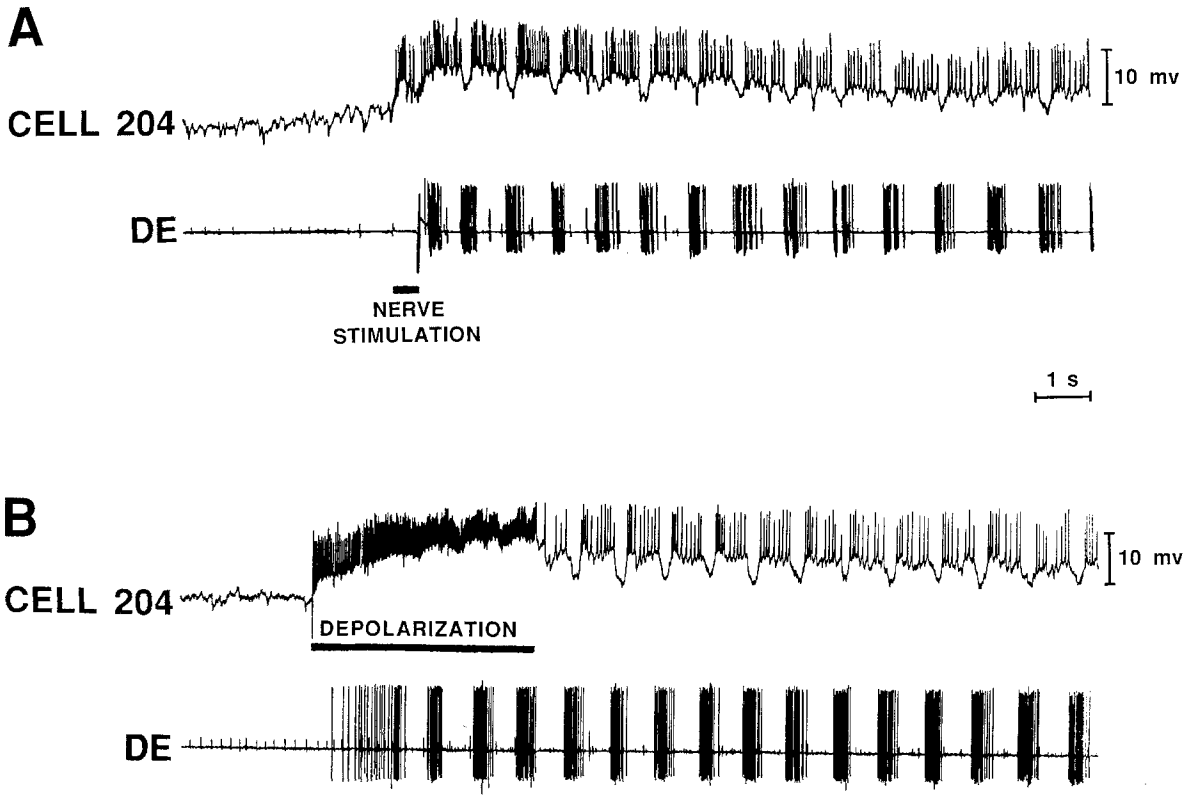

Figure 4. Evidence that cell 204 is a swim-initiating neuron. *A* Cell 204 is active before and during all induced swim episodes. The top trace is an intracellular recording from cell 204 in a midbody ganglion, and the bottom trace is an extracellular recording showing the bursts of impulses produced in a DE motor neuron in an adjacent ganglion during a swim episode. During the time indicated by the bar below the bottom trace, the segmental nerve was stimulated electrically. We have found that any stimulus, electrical or mechanical, that elicits swimming behavior also produces a depolarization of cell 204 throughout the swim episode. *B* Stimulation of cell 204 elicits swimming. The recordings are the same as in A. Passing depolarizing current into cell 204 produced a swim motor pattern, as recorded in the DE, that is indistinguishable from the pattern seen when swimming is produced by touching the skin or stimulating a nerve electrically.

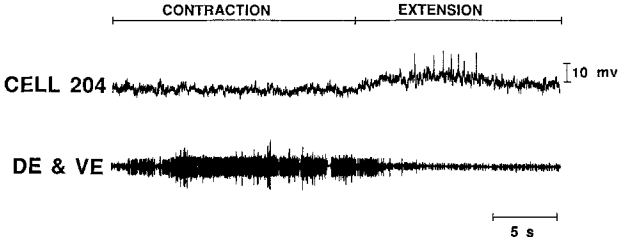

Figure 5. Activity of cell 204 during crawling. The upper trace is an intracellular recording from cell 204 during a single step of crawling, obtained from a semi-intact preparation, as shown in fig. 2B. The lower trace is a simultaneous extracellular recording from a nerve which contains axons of both the DE and VE motor neurons, both of which contribute to the contraction phase. The cycle has been divided into extension and contraction phases, as determined from the behavior of the intact front and back portions of the animal. The steps taken by such a preparation are highly variable in length and manner of execution, so that a detailed description of the motor neuron activity with the behavior requires correlating the filmed or videotaped movements with electrophysiological recordings.

as the one that includes cell 204 and that would elicit swimming if its activity were strong enough. This latter possibility is suggested by the observation that an increase in one cell 204's activity, produced by passing depolarizing current into its soma, caused the preparation to swim rather than to shorten in response to the same sensory stimulus (fig. 6C). This low level of depolarization of cell 204 by itself produced only a weak burst of motor neuron activity (fig. 6B).

Studying the neuronal basis of behavioral choice

Our studies do not show conclusively the mechanisms by which leeches choose one behavior over another in response to the same mechanosensory stimulus. They do, however, eliminate mutual inhibition among key command cells as the major mechanism for choosing among swimming, shortening and crawling, because cell 204 is not inhibited during shortening or crawling. In addition, the pathway from sensory cells to Tr1 to cell 204 appears to be activated whether or not swimming is initiated (Brodfuehrer & Friesen[4]). Therefore, there seems to be little variation in at least one of the sensory pathways to the trigger and gating neurons for swimming.

Several possibilities for the role of cell 204 in making the choice between behaviors are now under consideration. They include:

1. A one-way inhibition from swim-related interneurons onto other pattern-generating circuits. In such a scheme, swim interneurons would inhibit the command neurons or pattern-generating circuits for shortening and crawling, but neither behavioral circuit would inhibit cell 204. Such a one-way inhibition would place swimming at the top of any behavioral hierarchy and would make the level of firing in cell 204 the factor which absolutely determines whether or not a leech will swim. This would commit cell 204 exclusively to swimming; i.e., its firing level would necessarily be too low

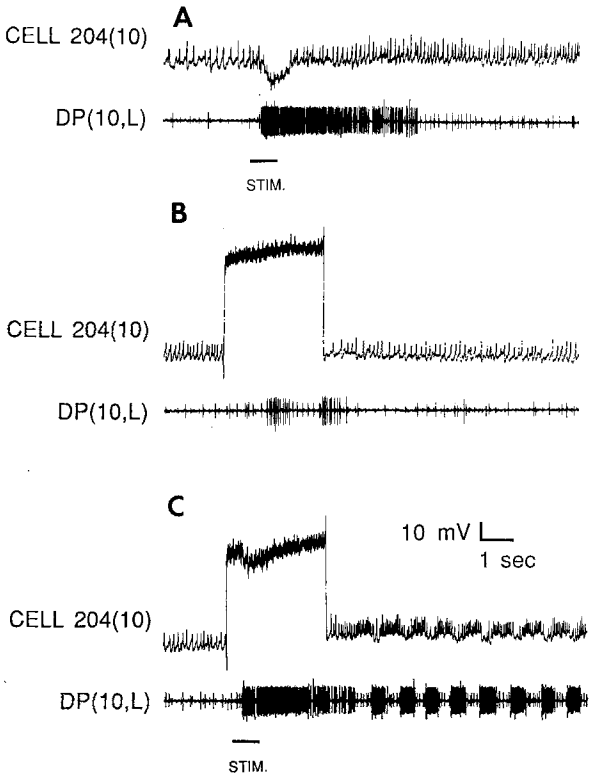

Figure 6. The influence of cell 204 on the choice between shortening and swimming. *A* The activity of cell 204 during a shortening response. The top trace is an intracellular recording from a cell 204 in segment 10 in an isolated nerve cord. The bottom trace is an extracellular recording from a segmental nerve on the left side of segment 10, which shows the response of DE motor neurons to stimulation of mechanosensory neurons in the body wall. Six impulses were initiated in two mechanosensory neurons during the time indicated by the bar below the bottom trace. *B* Depolarization of cell 204 alone elicits weak, unsustained motor neuron activity. Depolarizing current was injected into cell 204 through the recording electrode for 2 seconds, as indicated by the sharply rising and falling deflections in the recording. *C* Depolarization of cell 204 turns a shortening response into a swimming response. The same cell 204 and motor neurons were recorded as in A and B, and the stimuli given separately in A and B were delivered simultaneously. When presented during cell 204 depolarization, sensory stimulation consistently produced swimming rather than shortening.

during shortening or crawling to activate the swimming pattern generator, so its activity would produce no behavioral effect during these two behaviors.

2. Cell 204 participates in all three behaviors. At high firing rates, cell 204 elicits swimming and at lower activity levels, it contributes to shortening or to crawling. Fig. 7 shows that stimulation of cell 204 activates interneuronal pathways to all the longitudinal muscle excitors, which could help to produce shortening, as well as to the flattener muscle excitors, which could help to produce lengthening. Therefore, if the flattener excitors were inhibited in the shortening reflex, cell 204 activity would strengthen the shortening response. If, instead, the longitudinal muscle excitors were inhibited, cell 204 activity could contribute to the extension phase of crawling. Such a mechanism is similar to that proposed by Getting and his colleagues (Getting & Dekin[13], and this review) for producing either shortening or swimming from the same set of pattern-generating neurons in *Tritonia*.

3. Cell 204 is a general arousal cell that prepares the leech for any of several behaviors; which behavior actually occurs depends upon the activity in other pattern-generating networks. This possibility seems unlikely because direct stimulation of cell 204 produces swimming and never any other behaviors. However, it is possible that all natural sensory stimuli that activate cell 204 may also activate other pathways, so activation of cell 204 exclusively may never occur normally.

There are other possibilities, including a combination of any two or all three of the mechanisms above. It is clear from this discussion, however, that it is possible to formulate very specific and very testable hypotheses about general classes of neuronal mechanisms. For instance, possibilities #1 and #3 can be distinguished from #2 by recording from cell 204 and an identified motor neuron – the flattener excitor – during the three behaviors. Synaptic input from cell 204 should be weakened or masked during the shortening reflex if #2 is correct and unaffected if either of the others is correct. Other possibilities can be tested only after we know more about the pattern-generating circuits for crawling and shortening, work that is now in progress. The overall impression that we have so far is that production of behaviors and choice between them employs many kinds of neuronal interactions, and that behavioral choice is likely to result from some combination of these and other possibilities.

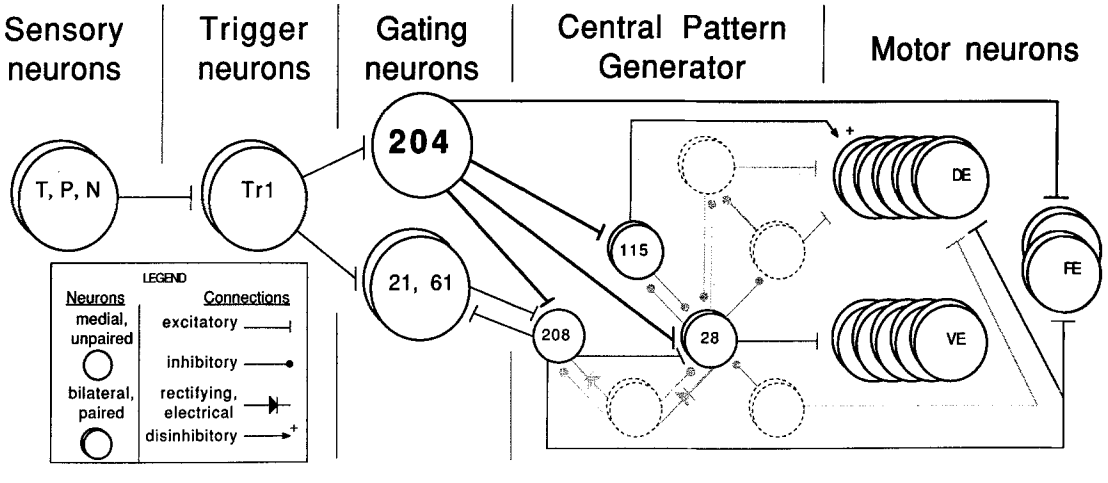

Figure 7. The pattern-generating interneurons in the swim circuit that are directly activated by cell 204. The cells shown in grey are those cells that are either not directly influenced by cell 204 or that are inhibited by cells activated by cell 204. In this network, there are pathways from cell 204 to the DE, VE and FE motor neurons that could produce either a sustained shortening or a sustained extension. These pathways could be selectively activated during different behaviors, as a result of summation with input from other neurons.

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Mechanisms of flight steering in locusts

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Summary. Steering in flight by locusts provides a well-studied example of the modulation of a rhythmic motor output by unpredictable inputs from outside to produce adaptive behaviour, in this case a form of locomotion. The simplest form, correctional steering, allows the animal to compensate for unintentional deviations from course. Its mechanisms are relatively well understood. The central nervous circuitry which makes this behaviour possible can be thought of as an autopilot. The entire process, from sensory input to the aerodynamic effects of changed motor outputs, is here reviewed. Intentional change of course, either spontaneous or induced by a change in the outside world, is more complex: it demands not only active steering, but also the temporary disablement of the autopilot. The mechanisms by which this could be achieved are discussed.
Key words. Flight; sensory modulation; feature detection; interneurons; sensorimotor integration; locust.

Introduction

Many behaviours are based on centrally generated rhythmic outputs [19]. In order that central circuitry can produce adaptive behaviour, its output must be modified by sensory information. This can derive from proprioceptive or exteroceptive inputs and can be phase-related or phase-unrelated. Insect flight provides an outstanding example of this process, and