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Control of sequences of movements in crayfish escape behavior

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Summary. Crayfish escape from predators by a series of rapid tailflips. The production of this seemingly simple behavior involves the interaction of multiple neural control mechanisms. The rapid flexion phase of the first tailflip is a fixed action pattern that is always organized by giant command neurons. Subsequent reextension is a chain reflex mediated by sensory feedback from the initial flexion. All following tailflips are produced by a non-giant system which is activated in parallel with the giant system by the escape-initiating stimulus. Proper integration of the giant system and the non-giant system is mediated by a reaction time mechanism.

Key words. Command neurons; crayfish neuroethology; chain reflexes; escape behavior; fixed action patterns; motor control mechanisms; sensory feedback.

Introduction

A number of neuronal organizational principles have been postulated to explain simple stereotypic actions. Two opposite extremes in a continuum are the reflex on the one hand and the fixed action pattern on the other (fig. 1 A, B). In a reflex, central relay mechanisms transform a sensory stimulus into a motor response in a temporally and spatially graded manner. In a fixed action pattern, the sensory stimulus simply serves as a trigger to activate central circuits, which then produce a motor response in an all-or-nothing manner. Such simple organizational principles can be compounded to produce behavioral reactions of intermediate complexity[7]. Thus in the chain reflex mechanism initially proposed by Sherrington[26] (fig. 1 C) the first sensory stimulus produces a first motor response. This response is then detected by the animal and serves as a second sensory stimulus; this second stimulus then produces a second motor response, and so forth. In contrast, as first suggested by Brown[1], central neuronal circuits can be appropriately combined to produce a neuronal oscillator which, once activated by a sensory input, can then produce repetitive motor output (fig. 1 D). Such neuronal oscillators, often referred to as central pattern generators, are thought to underly most rhythmic behavioral responses[3,8]. All four of these neural mechanisms – reflex, fixed action pattern, chain reflex and neuronal oscillator – are integrated into a seemingly unitary act in the production of one simple and stereotyped behavior, the escape behavior of the crayfish.

Crayfish escape from predators by a series of tailflips which rapidly move the animal away from danger. The first tailflip in such a series can be initiated at very short latency. In such a case it always involves the action of giant neurons[9,10,27]. These giant neurons are often referred to as command neurons, a term which implies that their activation is both necessary and sufficient for the initiation of a given behavior[15,19]. Following this initial tailflip, a series of multiple tailflips is usually produced. To a casual observer, the overall sequence of tailflips involved in an escape reaction might appear to be a simple and homogeneously structured behavioral response. Yet this apparent simplicity is misleading. Crayfish escape behavior is actually quite complex. It involves numerous coordinating mechanisms which act at the levels of synaptic potentials, single neurons, neuronal circuits and motor subsystems[31,34].

In this review I shall discuss three aspects of the multiple coordinating mechanisms which underly the escape response of the crayfish. 1) The central role of the giant command neurons in triggering the initial short latency response. 2) the importance of sensory feedback in organizing the following phase of the behavior. 3) The mechanisms involved in integrating the first and the subsequent tailflips into a temporally coordinated response. An appreciation of some of the multiple mechanisms involved in the generation of crayfish escape behavior will reveal that although the giant command neurons do have important coordinating effects, their overall 'command' role in the organization of escape behavior is restricted.

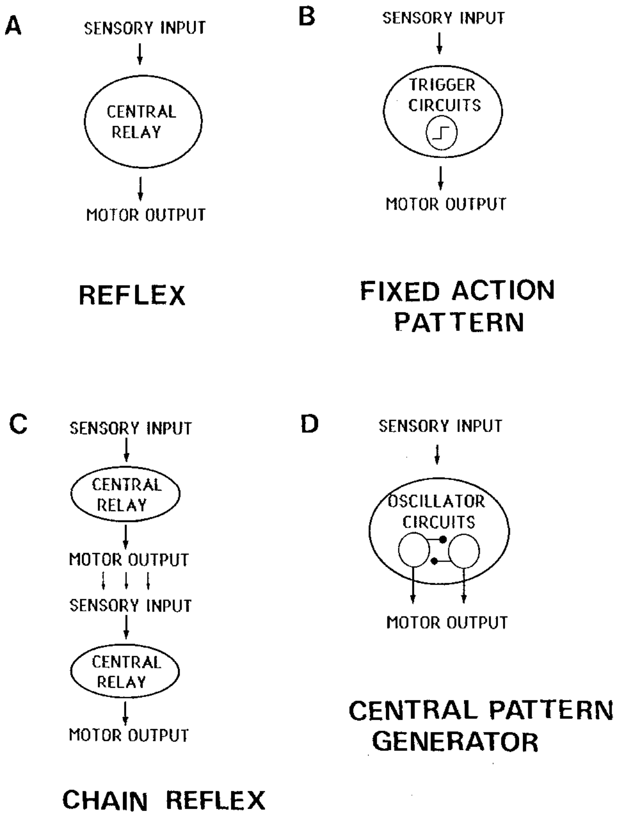

Figure 1. Simple stereotyped motor acts can be produced by reflex mechanisms (*A*) or fixed action pattern mechanisms (*B*). More complex serially ordered motor activity can be the result of chain reflexes (*C*) or central pattern generators (*D*).

Initial flexion is a fixed action pattern

From the work of Wine and Krasne[33] it is known that the initial short latency tailflip in an escape sequence always involves the activation of one of two pairs of giant neurons. These are the medial giant (MG) neurons and lateral giant (LG) neurons. Both have by far the largest-diameter axons in the ventral nerve cord. One can selectively record from these giant axons and thus show that they always fire immediately before a short latency tailflip. One can also selectively stimulate the giant axons and demonstrate that one action potential in these cells will always lead to a fast abdominal flexion response. Such experiments have shown that these giant neurons are at the heart of a fixed action pattern which rapidly transforms an appropriate, escape-initiating stimulus into phasic flexion of the animal's abdomen[36,37].

The giant axon systems initiate the fast-start escape response. Moreover, the spatial organization of this fast start response is built into these systems (fig. 2 A). The MG system responds to rostral sensory inputs and it organizes a motor response which causes the animal to dart backward. The LG sysem responds to caudal sensory inputs and it organizes a motor response which pitches the animal forward. The different orientation of the initial escape movements is explained by the differential connectivity patterns of the giant command neurons with large hemisegmental motor units called the motor giants[4,17,18,25]. The MG neurons make direct rectifying electrical synapses with the motor giants in all segments of the abdomen. The LG neurons make such synapses only with the motor giant neurons in the first three abdominal segments. When the MG neurons fire, all motor giants are excited, all segments flex, and the abdomen curls and propels the animal backward. When the LG neurons fire, there is no output to the caudal segments, which remain straight and so cause the thrust to be directed downwards, pitching the animal forward.

The giant command neurons are not only crucially involved in spatial coordination of the initial escape sequence, they also carry out much of the temporal coordination. This has been extensively studied in the LG neuron system (fig. 2 B). LG neurons activate the phasic flexor circuitry[16,36] and they also organize the delayed inhibition of this flexor circuitry both centrally and peripherally[28,35]. Moreover, the

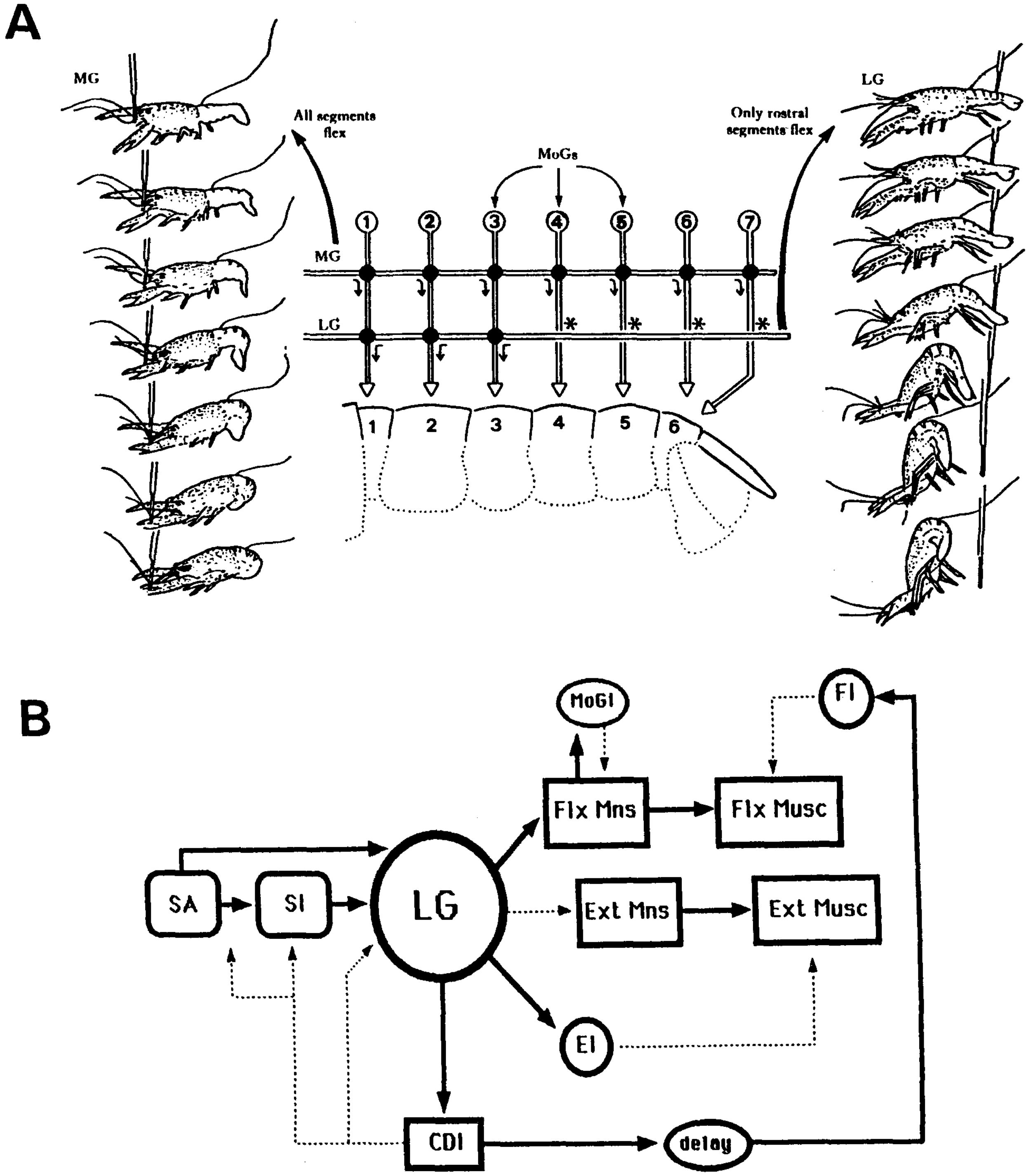

Figure 2. *A* Connectivity pattern of the giant command neurons with the abdominal flexor motor giants explain the orientation of the initial escape movement. MG command neurons make synapses with all motor giants. LG command neurons make synapses with motor giants only in the rostral three segments. Side panels show filmed responses to tapping the head, which fires the MG command neurons, and to tapping the abdomen, which fires the LG command neurons. When the MGs fire, there is output to all motor giants and the resulting tailflip propels the animal backward. When the LGs fire, there is only output to the motor giants in the rostral segments and the resulting tailflip propels the animal upward (modified after Dumont and Wine[4]). *B* Schematic representation of the information flow, which occurs during a LG mediated fast flexion response. The LG command neurons occupy a central role in the organization of the response. Solid lines indicate excitatory interactions, dotted lines indicate inhibitory interactions. No attempt has been made to distinguish between monosynaptic and polysynaptic pathways. Abbreviations: SA, sensory afferents; SI, sensory interneurons; LG, lateral giant command neuron; CDI, corollary discharge interneurons; MoGI, motor gliant inhibitor; Flx Mns, flexor motoneurons; Ext Mns, extensor motoneurons; EI, extensor inhibitor; FI, flexor inhibitor; Flx Musc, flexor muscles; Ext Musc, extensor muscles (modified after Wine[30]).

command neurons mediate antagonist inhibition, by means of central and peripheral inhibitory action on the phasic extensor circuitry[29]. Finally they also feed back pre- and postsynaptic inhibition onto neurons in the sensory processor network[2, 12, 13, 23]. Thus the giant neurons both trigger the initial phasic flexion and organize the spatio-temporal coordination of this reaction.

These widespread effects of the giant neurons, mediated by their extensive synaptic connectivity within the abdominal ganglia, are the reason why the term command neuron seems an appropriate designation for their behavioral role. The term command neuron should not, however, be taken to indicate that the giant neurons produce the entire escape response. They organize the first, short latency flexion phase but they do not produce the rest of the escape sequence.

Reextension is a chain reflex

In intact animals under normal behavioral conditions the initial phasic abdominal flexion is followed by a phasic reextension of the abdomen. Intracellular recordings from deafferented preparations show that this phasic reextension is not based on central synaptic effects caused by giant neuron firing. Activation of the command neurons in such a preparation results in inhibition of the extensor motoneurons not in excitation[29, 30, 32]. For extensor excitation to occur after the initial flexion, sensory feedback from the flexion phase of the behavior is crucial[22]. Any manipulation which interferes with the normal production of waterborne sensory feedback from the initial abdominal flexion, for example any type of mechanical restraint of the animal, will virtually abolish the reextension response. Thus sensory feedback is necessary for the reextension response. Moreover, it is also sufficient for the reextension response.

This can be directly demonstrated in a quiescent animal by simulating the waterborne sensory feedback that would be produced during phasic flexion of the abdomen. This type of sensory input can result in extensor activation in the quiescent animal which is similar in amplitude and in time-course to that seen in the behaving animal during the normal reextension response[22]. Thus since giant command neuron activity is neither necessary nor sufficient and since sensory feedback from the initial flexion is both necessary and sufficient for the reextension response, this component of the escape response is a (rare) example of a behavioral reaction of the chain reflex type[20].

A reaction time mechanism produces serial order

Given that the flexion phase of the initial tailflip is a fixed action pattern and that the reextension phase is a chain reflex, how are the subsequent repetitive tailflips (fig. 3 a) organized? A detailed analysis of the characteristics of these subsequent tailflips show that they are not simply repetitions of the initial tailflip[22, 24]. For example, in such tailflips extensor bursts precede flexor bursts. These tailflips are thus composed of an extension-flexion motor sequence, different from the flexion-reextension sequence of the initial tailflip (fig. 3 B). Moreover, the non-giant system that produces the repetitive tailflips actually inhibits both the giant command neurons and the reextension reflex[14]. Current experimental evidence indicates that, like most other iterated rhythmical motor sequences, the repetitive non-giant tailflips are the product of neural oscillator circuitry.

Since the non-giant tailflips follow the initial giant triggered tailflip in an orderly manner, a mechanism for the coordinated activation of the non-giant system must exist (fig. 3 C). Three possibilities for such an ordered activation of the non-giant system can be envisaged. First, the non-giant system might be activated by sensory feedback from the initial giant-mediated tailflip. Second, the giant axons themselves might trigger the non-giant system centrally through appro-

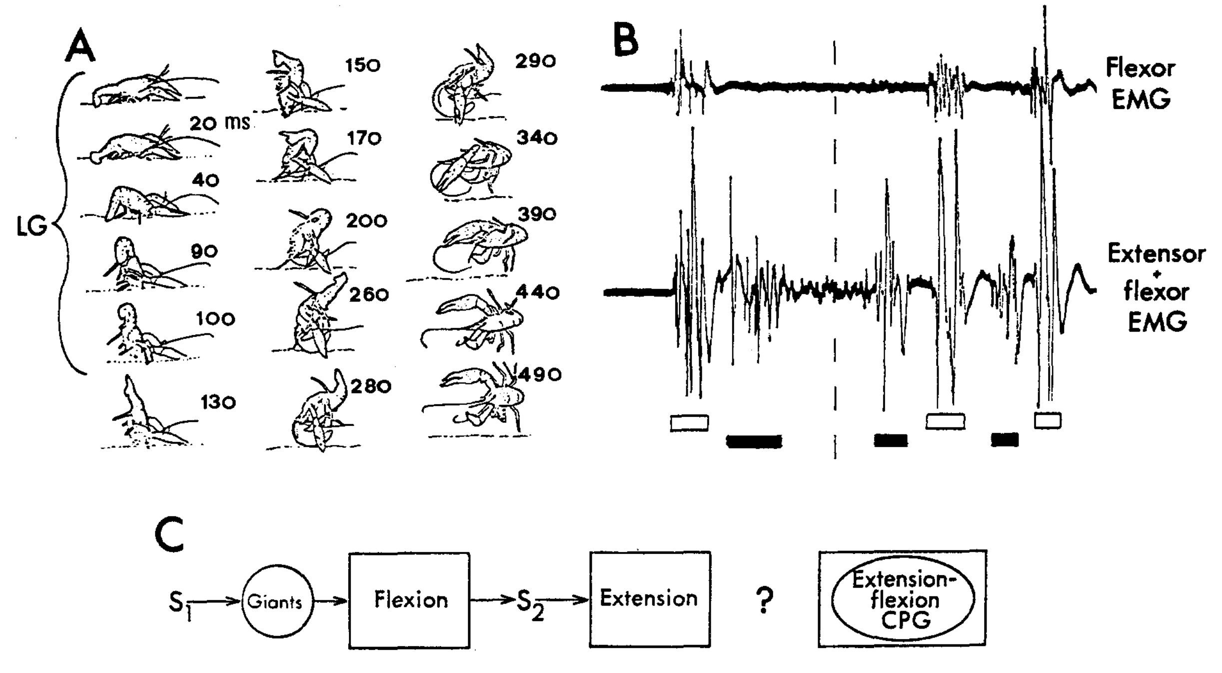

Figure 3. Characteristics of compound tailflip escape behavior. *A* Tracings from a series of three tailflips, the first (bracket) initiated by the LGs and subsequent tailflip mediated by the non-giant system (modified after Wine and Krasne[33]). *B* Flexor and extensor EMG recordings from a similar escape sequence. The phase relation between extension and flexion is reversed after the first flip (modified after Reichert et al.[22]). *C* Three motor components of escape behavior. Escape initiating tactile stimulation (S_1) results in an initial giant mediated fast flexion phase, a second reextension phase which is a consequence of sensory feedback (S_2) from the flexion, and following repetitive tailflips mediated by the non-giant system. How is the non-giant (CPG) system activated? Three alternatives could be responsible for the ordered activation of the non-giant system (see text) (modified after Reichert et al.[22]).

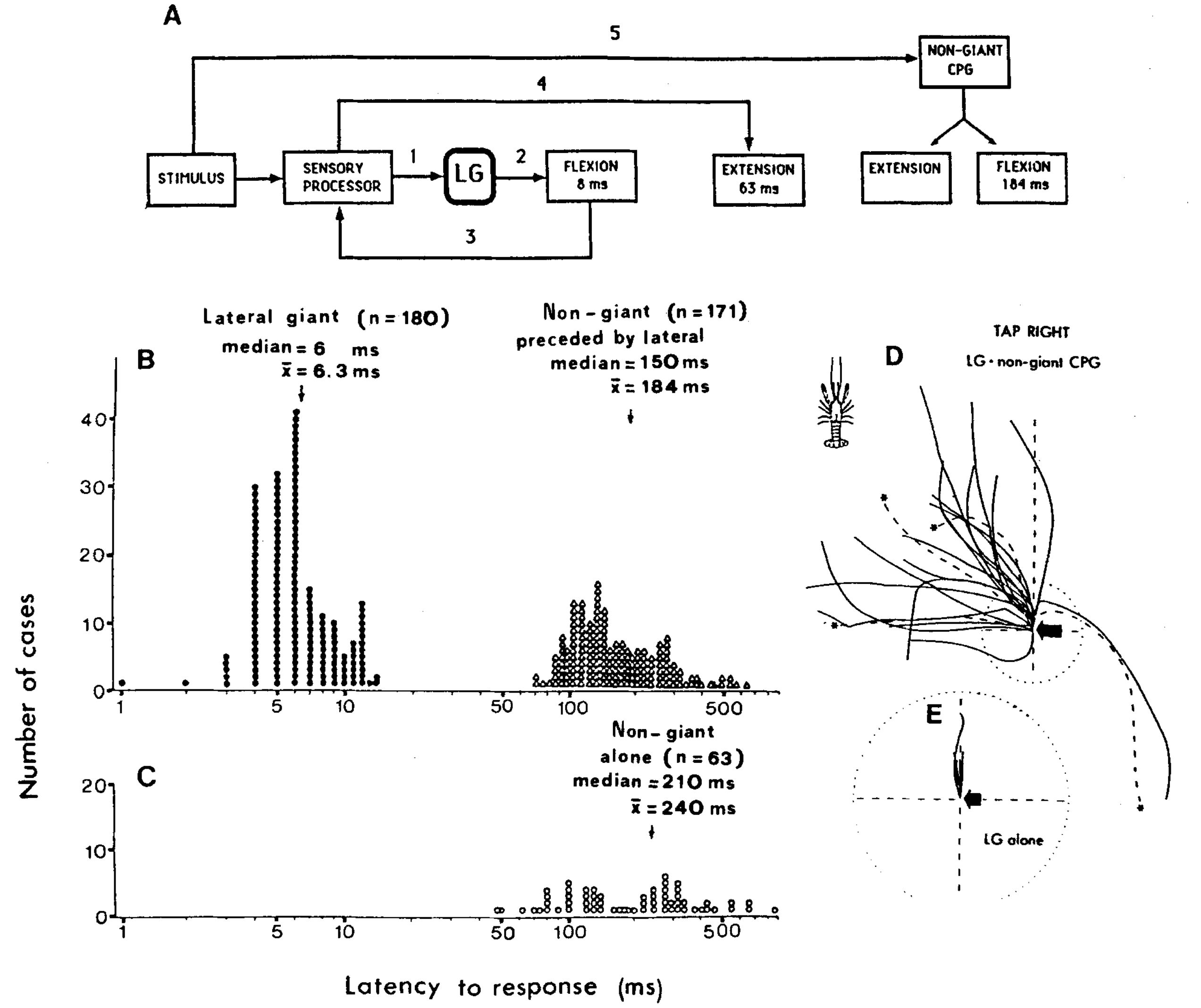

Figure 4. *A* Causality of components of the compound tailflip escape behavior. The sequential order of the different components is indicated by numbers. The escape initiating stimulus is processed and excites the LG command neuron. Phasic abdominal flexion is then triggered by the LG command neuron. Sensory feedback from this flexion triggers reextension. The initial escape initiating stimulus which activates the giant neuron system also causes delayed activation of the non-giant system in parallel. *B* The response latency of the non-giant system is long enough to insure an orderly transition from giant to non-giant tailflips. The LG system has a mean reaction time of about 6 ms. This is an order of magnitude faster than the reaction times of the subsequently activated non-giant system. *C* The latencies of the non-giant tailflips when they are produced in isolation are similar to the latencies seen when the non-giant tailflips follow a giant mediated tailflip. *D* Orientation during non-giant tailflips involves a lateral component that, on average, removes the animal from the stimulus source. Taps were delivered to the right side of the animals. The path taken by an animal is shown as a solid line, except for responses that began without giant axon activity which are shown as dashed lines and marked with asterisks. Size and orientation of the animal is shown in the inset. Diameter of the dotted circle is 6 cm. *E* In contrast to non-giant tailflips, LG command neuron mediated tailflips (shown at enlarged scale) are laterally symmetrical and do not move the animal very far. Diameter of the dotted circle is 6 cm (*B*–*E* modified after Reichert et al.[22]).

priate delay circuitry. Third, the non-giant system might be activated in parallel with the giant system by the escape-initiating stimulus. To decide among these alternatives, the giant axons were selectively and electrically stimulated in unrestrained animals. In over 99% of the cases the resulting behavior was a single giant mediated flexion and reextension response without subsequent non-giant tailflips[20, 21]. This would not be expected if the non-giant system were triggered either by sensory feedback or by the giant command neurons. It indicates that the escape-initiating stimulus is necessary for activation of the non-giant system.

By taking advantage of the greater sensitivity of the non-giant system as compared to the giant system one can further show that the escape-initiating stimulus is also sufficient for the activation of the non-giant system. If the escape-initiating tactile stimulus is reduced to threshold intensity, about 40% of the resulting escape responses are mediated exclusively by the non-giant system[21]. Since the giant command neurons are neither necessary nor sufficient for activation of the non-giant system and since the escape-initiating stimulus is both necessary and sufficient, the non-giant system is turned on in parallel with the giant neuron system by the initial escape eliciting stimulus (fig. 4a).

Parallel activation of two motor control systems which converge onto the same neuromuscular system poses problems of appropriate timing. This is especially important in the control of escape responses such as in crayfish tailflip behavior, since almost any kind of conflicting motor control could be life threatening. Thus in crayfish escape, interference between the giant and the non-giant system must be avoided at

all costs. The mechanism which is used to ensure proper serial order in the crayfish is one that is extremely reliable. It is a reaction-time mechanism which is based on the different activation times of the giant versus non-giant systems[20].
The giant neuron system is optimized for speed. It consists of some of the largest neurons in the animal, many of which are interconnected by electrical synapses to minimize synaptic delay[5,36,37]. Mean latencies of the LG neuron system are around 6 ms (fig. 4B). In contrast, activation of the non-giant system takes much longer (fig. 4 B, C). Mean latencies for the appearance of the first non-giant mediated flexion response are around 180 ms[20,21]. This means that by the time the non-giant system becomes activated, the first giant-mediated flexion phase is already over. Parallel activation of two separate motor control systems with different intrinsic reaction times thus assures the proper integration of the initial fixed act and chain reflex response and the subsequent non-giant oscillator responses into what appears to be a homogeneous behavioral sequence.

It may seem unclear why the escape response of the crayfish should be controlled by two separately activated motor systems. Perhaps the fast acting command neuron system ignores features of the escape-eliciting stimulus that the slower non-giant system might have time to process, and use for a better oriented response. As in other fast start behaviors[5], the giant command neuron system would 'get the animal going' quickly in a stereotyped, preprogrammed way, thus giving the more flexible non-giant system more time to 'think about things'. Indeed, the giant neuron system ignores the laterality of the initial stimulus. The LG system always causes a tailflip forwards regardless of whether the stimulus comes from the right or from the left[21,33]. In contrast the non-giant system reacts to the laterality of the stimulus. Non-giant escape orientations discriminate at least the quadrant from which the stimulus originates and guide escape on the average to the opposite quadrant[21]. Moreover, the longer latency non-giant response actually moves the animal a considerable distance away from the site of stimulus origin (fig. 4D). The LG reaction is very fast, but it does not get the animal far away from potential danger (fig. 4E). In this sense the role of the command neurons in escape behavior is also restricted.

Conclusion

The enormous selection pressure that must act on escape behavior has produced in the crayfish a response that is fast, effective and reasonably failsafe. To fulfill these behavioral criteria, the underlying nervous system has integrated multiple motor control mechanisms into the production of a smoothly orchestrated response. The command neuron concept is quite useful in describing the action of the giant neurons during the first short latency flexion phase of the behavior. During this fast-start phase of the behavior, the giant axons have widespread and powerful effects on a large assortment of neural processes. After this phase, however, the role of the giant axons in movement control is terminated and other central and peripheral control mechanisms take over.

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Escape behavior in the cockroach: Distributed neural processing

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Summary. Escape reactions are often considered to be among the simplest behaviors. The nerve circuits guiding these reactions are also generally thought to be simple. For instance, in several species a single interneuron is sufficient to trigger normal escape. The evasive response of the cockroach, however, appears to be more complex both behaviorally and physiologically. In this review, several complications of the behavior are pointed out, based on a recent computer-graphic analysis of the leg movements. Next described is the cooperative role of several interneurons – not just one – in evoking an escape turn away from the stimulus. A model of this multicellular code for stimulus direction is then presented that correctly predicts the turning behavior under many different experimental conditions. Finally, an overall scheme of the information processing for escape behavior is presented.

Key words. Escape behavior; giant interneurons; cockroach; *Periplaneta americana;* feedback.

Introduction

One of the major reasons for selecting an invertebrate animal for neuroethological study is the possibility of working at the level of individually identified neurons. Among the behaviors whose controlling neurons are easiest to identify are escape reactions. Here the rapid conduction of impulses that is essential for quick evasion from a predator is produced by axons of especially large diameter. The 'giant neurons' sporting such axons have well repaid investigation in crayfish [21], earthworms [17], crickets [20, 23], cockroaches [3] and other invertebrates. One of the few vertebrate systems in which individual interneurons have been identified and studied is also an escape system, that of teleost fish [18].

It is generally accepted that escape behaviors are simple and highly stereotyped, at least with regard to the initial movements [18, 39]. It is also held that neuronal circuits for escape are quite simple. For example, rather than the numerous small interneurons that characterize many other types of circuit, there is often a limited number of giant interneurons. Some of these are even able, individually, to trigger a normal escape movement, as in crayfish [21], teleost fish [18] and flying crickets [26]. Moreover, a given 'lateral giant interneuron' of the crayfish not only triggers escape, but also carries out by itself three other behavioral functions: 1) making the decision whether or not to escape from a given stimulus [27], 2) silencing competing behaviors by sending inhibitory signals to their control circuits [40], and 3) serving as the focus for certain modulatory influences on the escape behavior [19, 40].

Through recent studies of the cockroach escape system a different, more complex, picture is beginning to emerge. The behavior involves aspects of information processing not previously known for this system, some of which are described below. Also, though there are giant interneurons, there are many of them, and responsibility is widely shared among them. In this review I address primarily these selected aspects of the escape system, focussing substantially on our own work, much of which is still in progress. An excellent comprehensive review [30], and two more general reviews [2, 3] have appeared in recent years.

The behavior

The escape response of the cockroach to an approaching predator is usually a turn in the opposite direction followed by a run [7, 8]. The major or only sensory cue used by the cockroach to detect the predator's approach and determine its direction is the wind gust that precedes the predator's moving body [8].

Recent computer-graphical analysis of high speed films [5] (J. M. Camhi and A. Levy, unpublished observations), together with earlier analyses [7, 13] reveal the details of movement during the turn. For instance, a wind puff from the left front elicits a sharp right turn that consists, at least initially, of a pivot about the most posterior point on the body. Later, forward translatory movement is added to the pivot, followed by purely foward movement (fig. 1). The pivot to the right begins with the left hind leg in a swing phase (leg lifted off the ground and brought forward), in roughly half the trials, and in a stance phase (leg remaining on the ground) in the other half of the trials. The remaining legs virtually always begin the turn with a stance phase. The stance phase of the right hind leg is particularly prolonged, often outlasting

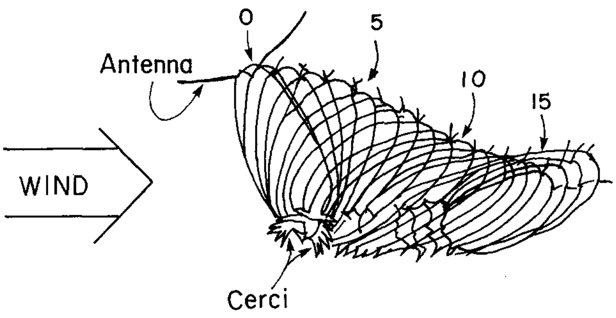

Figure 1. Turning response of a cockroach away from a wind puff. The body's silhouette is shown at successive 4-ms intervals, as drawn from cine frames. The body's position prior to the response (0), and on frames 5, 10 and 15 is indicated by the numbers. The initial pivot about the cerci is typical.