THE WHOLE-BODY WITHDRAWAL RESPONSE OF 
LYMNAEA STAGNALIS

II. ACTIVATION OF CENTRAL MOTONEURONES AND MUSCLES BY 
SENSORY INPUT

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Summary

The role of centrally located motoneurones in producing the whole-body withdrawal response of Lymnaea stagnalis (L.) was investigated. The motoneurones innervating the muscles used during whole-body withdrawal, the columellar muscle (CM) and the dorsal longitudinal muscle (DLM) were cells with a high resting potential (−60 to −70 mV) and thus a high threshold for spike initiation. In both semi-intact and isolated brain preparations these motoneurones showed very little spontaneous spike activity. When spontaneous firing was seen it could be correlated with the occurrence of two types of spontaneous excitatory postsynaptic potential (EPSP). One was a unitary EPSP that occasionally caused the initiation of single action potentials. The second was a larger-amplitude, long-duration (presumably compound) EPSP that caused the motoneurones to fire a burst of high-frequency action potentials. This second type of EPSP activity was associated with spontaneous longitudinal contractions of the body in semi-intact preparations. Tactile stimulation of the skin of Lymnaea evoked EPSPs in the CM and DLM motoneurones and in some other identified cells. These EPSPs summated and usually caused the motoneurone to fire action potentials, thus activating the withdrawal response muscles and causing longitudinal contraction of the semi-intact animal. Stimulating different areas of the body wall demonstrated that there was considerable sensory convergence on the side of the body ipsilateral to stimulation, but less on the contralateral side. Photic (light off) stimulation of the skin of Lymnaea also initiated EPSPs in CM and DLM motoneurones and in some other identified cells in the central nervous system (CNS). Cutting central nerves demonstrated that the reception of this sensory input was mediated by dermal photoreceptors distributed throughout the epidermis. The activation of the CM and DLM motoneurones by sensory input of the modalities that normally cause the whole-body withdrawal of the intact animal demonstrates that these motoneurones have the appropriate electrophysiological properties for the role of mediating whole-body withdrawal.

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Introduction

The effect of sensory input on gastropod behaviour has been investigated in several species. Most of these studies have examined the role of mechanosensory and chemosensory input on feeding (Rosen et al. 1979, 1982; Audesirk, 1979; Audesirk and Audesirk, 1979, 1980a,b; Kemenes et al. 1986) or the effect of sensory input on the production of withdrawal responses.

In *Aplysia californica*, sensory neurones involved in local withdrawal responses of the anterior tentacles (Fredman and Jahan-Parwar, 1977, 1980), gill (Kupfermann and Kandel, 1969; Kupferman et al. 1971, 1974; reviewed by Kandel, 1976, 1979) and tail (Walters et al. 1983a,b) have been identified and their interactions with interneurones and motoneurones investigated. Similarly, the role of sensory neurones in inducing escape swimming in *Tritonia diomedea* has been examined (reviewed by Getting, 1983).

In *Lymnaea*, ultrastructural studies have identified six different types of epidermal sensory cell (Zylstra, 1972; Zaitseva and Bocharova, 1981) and demonstrated that these are most abundant on the tentacles, lips, front edge of the foot, pneumostome, mantle edge and dorsal and lateral surfaces of the foot (Zylstra, 1972). The peripheral nerve pathways involved in transmission of tactile information to the CNS have been mapped electrophysiologically (De Vlieger, 1968; Janse, 1974, 1976; Janse and Van Swigchem, 1975) and it has been shown that peripheral nerves have overlapping receptive fields. In *Lymnaea*, two types of primary touch-sensitive neurones as well as primary stretch-sensitive neurones and higher-order sensory neurones sensitive to touch, pressure and stroke or stretch have been identified (Janse, 1974). Nerve recordings made during tactile stimulation of the skin demonstrated that, with the exception of one type of primary touch-sensitive neurone (which is only involved in peripheral reflexes), the cell bodies of these sensory neurones are located within the CNS. Among the higher-order sensory neurones, integration occurred in peripheral ganglia prior to the sensory information being relayed to the CNS (Janse, 1974). More recently, Janse and co-workers have examined the control of respiratory behaviour in *Lymnaea* and, by intracellular recording, have shown that statocyst cells (Janse et al. 1988) and other central neurones (Janse et al. 1985; Van Der Wilt et al. 1987) receive sensory input in response to changes in $P_{O_2}$ and after tactile stimulation of the skin or pneumostome.

Studies of the processing of photic information have demonstrated that behavioural responses to shadows are mediated by dermal photoreceptors, rather than the eyes (Stoll, 1972), that only responses to light being switched on are recorded from the optic nerves (Stoll, 1973) and that a dermal light-sensitive system is responsible for non-ocular orientation behaviour (Van Duivenboden, 1982).

In the previous paper (Ferguson and Benjamin, 1991) the muscles mediating whole-body withdrawal of *Lymnaea* and their innervation by a network of motoneurones were described. This paper examines the effects of the sensory modalities that induce withdrawal behaviour (photic light off and tactile sensory
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stimuli) on the activity of these motoneurones. In semi-intact preparations, it is shown that these sensory inputs cause activation of the CM and DLM motoneurones and a contraction of the muscles used during withdrawal (the CM and the DLM). This demonstrates that the CM and DLM motoneurones have the appropriate electrophysiology to mediate whole-body withdrawal. Preliminary reports of some of these results have appeared elsewhere (Benjamin et al. 1985; Ferguson and Benjamin, 1985).

Materials and methods

Animals were obtained as described in the previous paper (Ferguson and Benjamin, 1991). They were maintained under a 12h:12h light:dark cycle for a minimum of 1 week prior to experiments and given the minimum disturbance compatible with being fed regularly.

Light off and tactile stimuli were presented to the semi-intact animal by switching off the light source illuminating the preparation or prodding the epidermis with a rounded glass probe or a cat’s whisker. The whisker had a diameter of 0.3 mm and delivered a pressure of approximately 2.5 g mm\(^{-2}\) to the area of skin stimulated (calibrated using a pan balance). In some experiments this hair was mounted on a piezoelectric crystal. The voltage change caused by deformation of the crystal when the animal was stimulated was fed directly into an oscilloscope, allowing the latency of the response to be measured. Electrophysiological experiments were conducted in Hepes (Sigma) buffered saline, using conventional recording techniques, isolated brains and a semi-intact preparation similar to that described in the previous paper (see Fig. 1, Ferguson and Benjamin, 1991). The semi-intact preparation consisted of a deshelled snail bisected by longitudinal cuts along the dorsal and ventral midlines of the head-foot. The CNS was pinned out between the two halves of the body wall. All nerves were left intact.

Results

Spontaneous inputs received by CM and DLM motoneurones

The electrophysiology of all the electrotonically coupled CM and DLM motoneurones (and of the visceral and right parietal ganglion cells described in the previous paper, but whose motoneuronal role is unknown) was very similar. They showed no obvious spontaneous activity, had resting potentials between \(-60\) and \(-70\) mV and were normally silent. Two types of excitatory postsynaptic potential (EPSP) were recorded both in isolated brains (Fig. 1A) and in semi-intact preparations (Fig. 1B, C). The most frequently recorded input (100% of preparations) was a unitary EPSP which varied in amplitude from 2 to 15 mV, and in which individual potentials were often summated. When this input occurred it was usually recorded synchronously in motoneurones in different ganglia of the brain. An example of this is given in Fig. 1A (arrows), where a right cerebral A cluster
Fig. 1. Spontaneous inputs received by the CM and DLM motoneurones were of two types. A unitary excitatory postsynaptic potential (EPSP) (arrows, A) which rarely caused spike initiation and a large-amplitude EPSP which always caused a burst of action potentials. The large-amplitude EPSP was received synchronously by all CM and DLM motoneurones and was present in isolated (A) and semi-intact (B and C) preparations. In semi-intact preparations the bursts of spikes in the CM and DLM motoneurones was accompanied by high-frequency excitatory junctional potentials (EJPs) in the CM and DLM and a longitudinal contraction of the head-foot (visual observation).
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DLM motoneurone and the left parietal DLM motoneurone were recorded simultaneously. This input was usually not strong enough to depolarize the cell to the threshold for action potential initiation.

The second type of EPSP was always received synchronously by all electrotonically coupled cells. This compound EPSP input caused a rapid depolarization of up to 40 mV in amplitude and a high-frequency burst of 20–40 action potentials, lasting 1–2 s. Within the burst, there was no absolute synchrony of action potentials in particular pairs of cells (Fig. 1A) and different cells were often excited for slightly different periods (Fig. 1B). In semi-intact preparations, activation of CM and DLM motoneurones by this synaptic input was correlated with a rapid longitudinal contraction of the body, and a burst of large-amplitude, high-frequency excitatory junctional potentials (EJPs) was recorded from the CM and DLM simultaneously with the activity in the motoneurones (Fig. 1B,C). This input was observed in less than 5% of isolated brains and reduced preparations and, when present, had no fixed periodicity, occurring between once every 10 s and once or twice an hour. The reason for the variability in the frequency of occurrence of this strong EPSP input and its behavioural significance are unclear. However, the fact that this input occurred in the isolated nervous system indicates that there are centrally located interneurones capable of producing these strong bursts of spikes in the CM and DLM motoneurones independently of sensory input to the snail. Whether this second type of EPSP input comes from the same interneurone(s) as the first is not clear because in neither case have the neurones responsible been identified.

Sensory inputs received by CM and DLM motoneurones

Effects of tactile stimuli

The most effective tactile stimuli for activating CM and DLM motoneurones were repeated gentle proddings of the skin of the animal. These stimuli were normally presented by touching the skin with a flexible cat’s whisker as this provided a standard stimulus to the animal (although it should be noted that the area of skin being stimulated could show slightly different levels of contraction during repeated stimulation). Each prod evoked a burst of summating EPSPs within the motoneurones, which usually depolarized them sufficiently to produce action potentials (Fig. 2). The maximum amplitude of the compound EPSP varied in different cells, but was usually between 5 and 35 mV. The response to each prod was phasic and usually only lasted for 1 or 2 s. Successive stimuli caused reactivation of the motoneurones (e.g. Fig. 2A).

All motoneurones showed similar excitatory responses to tactile stimulation of the skin. Fig. 2 shows the general features of the effect of tactile stimulation of the ipsilateral lip on CM and DLM motoneurones and on the activity of the CM and DLM. These three recordings (from different preparations) show that after tactile stimulation synchronous synaptic inputs were evoked in two left cerebral A cluster DLM motoneurones (Fig. 2A), in left cerebral A cluster DLM and CM moto-
Fig. 2
neurones (Fig. 2B) and in a left pedal G cluster CM motoneurone and a left cerebral A cluster DLM motoneurone (Fig. 2C). (For locations of motoneurones see Fig. 4, Ferguson and Benjamin, 1991.) In all three examples, tactile stimulation of the lip caused a depolarization of the motoneurones, usually resulting in action potential initiation. High-frequency compound EJPs recorded extracellularly from the DLM and CM coincided with spike activity in the motoneurones and the duration of this activity was very similar in muscles and motoneurones. Even when a prod failed to produce an action potential in a particular motoneurone EJP activity was still recorded in the muscle, suggesting that other motoneurones were active at the same time. An example of this is most clearly given in Fig. 3A. Here, the largest cerebral A cluster DLM motoneurone was recorded with a smaller cerebral A cluster DLM motoneurone. Both cells received synchronous EPSP input, but only the smaller cell was depolarized sufficiently to produce action potentials. This suggests that the threshold for activation may be higher for the larger cerebral A cluster cells than for the smaller ones. Some of the EPSPs received by the larger cell had a large amplitude and were probably electrotonic EPSPs produced by action potentials in other cells (arrowed, Fig. 3A).

A different type of experiment is shown in Fig. 3B. Here the latency of the mechanoreceptor response was measured. The tactile stimulus was applied to the left lip of the snail using a cat's whisker attached to a piezoelectric crystal. This allowed the latency of the response in the cerebral A cluster neurone to be measured more accurately than using the hand-held probe. The top trace of Fig. 3B shows the voltage change recorded from the piezoelectric crystal upon tactile stimulation of the animal, and the bottom trace shows an action potential evoked in a left cerebral A cluster DLM motoneurone. The record indicates a delay of about 140 ms from the start of the mechanical stimulus to the start of the action potential in the motoneurone. This value was typical of all motoneurones tested.

The convergence of sensory input from different areas of the body surface onto particular motoneurones is demonstrated in Fig. 4. Different parts of the body were stimulated whilst recording DLM motoneurone activity. The effects of stimulating the left lip or the left mantle edge whilst recording from a left cerebral A cluster DLM motoneurone and the left parietal DLM motoneurone are shown. Stimulating both body areas produced synchronized excitation of both motoneurones. When the lip was stimulated (Fig. 4Ai) the cerebral cell fired action potentials before the parietal cell became active. Stimulation of the mantle edge
Fig. 3. Details of the tactile response. The largest cerebral A cluster DLM motoneurones were less excitable than other cells in the cluster (A). Tactile stimulation of the left lips rarely caused them to fire action potentials. However, they received EPSPs synchronously with other motoneurones in the cluster and EJPs in the DLM. Some of these EPSPs were probably electrotonically conducted spikes from other active motoneurones (arrows). When the cat’s whisker used for tactile stimulation was mounted on a piezoelectric stylus (B), touching the skin produced a voltage change (top trace) from which the latency to action potential initiation could be measured. The latency in B was 140 ms.

(Fig. 4Aii) caused synchronous activation of both cells. These two different body areas are innervated by different nerves, the lips by the lip and superior cervical nerves and the mantle edge by the parietal nerves (Janse, 1974). Thus, there must be considerable sensory convergence onto the DLM motoneurones from different parts of the body, as the two cells were excited after stimulation of both the lip and the mantle edge.

There was widespread reception of tactile input by cells ipsilateral to the site of stimulation and, within these cells, the input evoked similar EPSP and spike activity. However, responses on the contralateral side were much weaker. This is shown in Fig. 4B where simultaneous recordings were made from a left and right cerebral A cluster DLM motoneurone and the left CM. Tactile stimuli were delivered in turn to the left lip and then the right lip. More spike activity and a larger underlying EPSP were evoked within the cerebral A cluster motoneurone when the stimulus was delivered to the ipsilateral side of the body compared with that applied to the contralateral side, although stimulation of the contralateral side
Fig. 4. Effect of the site of tactile stimulation on CM and DLM motoneurones. Touching lip and mantle skin areas known to be innervated by several different nerves (Janse, 1974) caused simultaneous excitation of ipsilateral motoneurones in parietal and cerebral ganglia (Ai and Aii, same cells), suggesting that tactile inputs are widely distributed throughout the CNS. When both sides of the body were stimulated separately (B), the response was stronger on the ipsilateral side than on the contralateral side.
of the body did cause some EPSPs and spikes in the left cerebral A cluster motoneurone. Therefore, it would seem that there is some asymmetry in the sensory convergence of tactile input, with the predominant response being produced on the ipsilateral side of the body.

**Effects of photic (light off) stimuli**

When the light incident on semi-intact preparations was switched off (to mimic the effect of passing a shadow over the animal) synchronous excitatory synaptic input was evoked in all motoneurones (Fig. 5). In each case the input consisted of a fast-rising compound EPSP which rapidly waned and often led to spikes (Fig. 5A) or had lower-amplitude fast potentials superimposed on the depolarizing waveform. These latter potentials could have been either blocked spikes or electrotonic EPSPs caused by spike activity in other, more active, motoneurones. Muscle activity occurred after light off, even when the motoneurone being recorded did not show full-sized action potentials (Fig. 5B), suggesting that some other cells of the motoneurone population were, indeed, active. Cells in different ganglia of the CNS received the sensory input synchronously (Fig. 5C). In different preparations the latency between light off and the onset of the depolarizing wave was consistently about 400 ms, the resultant compound EPSP lasted for about 2 s and had an amplitude between 10 and 25 mV. Light off stimulation was always followed by extracellular muscle activity (Fig. 5B) and longitudinal shortening of the body similar to that occurring in the intact animal.

The eyes were not responsible for mediating the sensory input after light off, as cutting the optic nerves had no effect on the input received by CM and DLM motoneurones (Fig. 6A). However, the CNS had to be connected to the skin by peripheral nerves for the input to be received (Fig. 6B). No EPSP input was observed following the presentation of light off stimuli to isolated brain preparations, demonstrating that the response to light off was not merely due to the direct activation of central neurones. These results suggest that dermal receptors are involved in the reception of light off stimuli and are consistent with previous findings (Stoll, 1972, 1973, 1976; Stoll and Bijlsma, 1973) of dermal light off responses from the skin nerves but no activity within the optic nerve of *Lymnaea* in response to either light off or shadow stimuli.

To identify the peripheral afferent pathways sending light off sensory information to the CNS, nerves connecting the skin to the CNS were cut. These experiments were complicated by the finding that the amplitude of the EPSP evoked by light off varied in different cells (see Fig. 5) and by the technical difficulty of maintaining the penetration of a given cell whilst cutting nerves. In general, cutting a single nerve made little difference to the amplitude of the EPSP evoked in the motoneurone or to the activity in the DLM. This can be seen in Fig. 7A (same preparation, left and right parietal nerves, Fig. 7Aii, and left and right medial lip nerves, Fig. 7Aiii, were lesioned in turn and light off stimuli were presented to the animal 5 min after each lesion). The main exception to this general rule followed cutting of the left and right tentacle nerves. This produced a
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Fig. 5. Excitatory effects of photic (light off) stimulation. After light off, excitatory input was received by CM and DLM motoneurones. This input often caused cells to fire action potentials (A). In cells that did not fire action potentials there were usually electrotonic EPSPs in the depolarizing waveform (B) which were presumably due to activity in coupled cells. The input was received synchronously by DLM motoneurones in the same (B) and different (C) ganglia and was accompanied by a burst of EJPs in the CM and DLM (B) and a longitudinal contraction of the foot.

noticeable decrease in both the amplitude of the EPSP evoked in the DLM motoneurone and the muscle activity in the DLM after the light off stimulus (compare Fig. 7Bi, before, with Fig. 7Bii, light off stimulus presented 5 min after bilateral tentacle nerve cuts). These findings suggest that there are many afferent pathways by which photic light off information is fed into the CNS from the skin, but that the tentacle nerves are particularly important routes for carrying this sensory information. This is compatible with the ultrastructural studies of Zylstra
Fig. 6. Reception of light off stimuli is mediated by the skin, not the eyes. (A) A similar excitatory input was received by cerebral A cluster DLM motoneurones before (Ai) and after (Aii) both optic nerves from the eyes had been cut (i and ii are from different cells). (B) Isolating the CNS from the skin, by cutting all nerves, abolished the excitatory synaptic input (Bii) normally received by the DLM motoneurones (Bi).

(1972), who found that ciliated receptor cells (which may be photosensitive) are located throughout the epidermis of the head-foot and are most concentrated in the tentacles.

Although the responses of CM and DLM motoneurones to tactile and photic sensory stimuli have been described separately, all motoneurones tested received sensory input of both modalities. An example of this is given in Fig. 8. The same left cerebral A cluster DLM motoneurone was stimulated first with light off (Fig. 8A), and then with two tactile stimuli delivered to the left lip (Fig. 8B). In response to both types of stimuli the motoneurone fired action potentials, electrical activity was recorded from the left CM, and the semi-intact preparation underwent a longitudinal contraction.

Sensory inputs received by other identified neurones

In addition to the CM and DLM motoneurones, some other previously identified Lymnaea neurones also received input after sensory stimulation of the body wall of the animal (for the positions of these cells see Benjamin et al. 1985). Three examples of this are given in Fig. 9. In the first of these (Fig. 9A) the giant cell RPD1 (identified by Benjamin and Winlow, 1981) was recorded together with a left cerebral A cluster DLM motoneurone. Tactile stimulation of the left anterior foot caused simultaneous excitation of both the DLM motoneurone and RPD1,
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Fig. 7. Effect of cutting nerves on the amplitude of excitatory synaptic input received by left cerebral A cluster DLM motoneurones in response to light off stimuli. (Ai–iii) Same preparation, suction electrode maintained in constant position on left DLM (top trace). Different cerebral A cluster cells recorded in Ai, Aii and Aiii. (Ai) Light off, all nerves intact. (Aii) Light off 5 min after cutting left and right parietal nerves. (Aiii) Light off 5 min after also cutting left and right medial lip nerves. Note slight reduction in amplitude of compound EPSP in Aiii. EJPs in left DLM are presumably due to activity of other motoneurones. (B) Different preparation. (Bi) All nerves intact, light off evokes a spike within the left cerebral A cluster DLM motoneurone (top trace) and EJPs in the DLM (bottom trace). (Bii) Light off 5 min after cutting both tentacle nerves. No spike in motoneurone (different cells in Bi and Bii) and reduced activity in the DLM.
Fig. 8. CM and DLM motoneurones receive both modalities of sensory input. Light off (A) and touching the left lip (B) evoked action potentials in a left cerebral A cluster DLM motoneurone and EJPs in the left CM.

Similarly, tactile stimulation of the left anterior foot caused simultaneous activation of pleural D group cells (Haydon and Winlow, 1982), a cerebral A cluster DLM motoneurone and the left DLM and CM (Fig. 9B). Like the CM and DLM motoneurones, these cells also received sensory input after light off. This is shown for a pleural D group neurone and a right cerebral A cluster DLM motoneurone in Fig. 9C.

These data demonstrate that tactile and photic input, in addition to being widely distributed to the DLM and CM motoneurones (see Fig. 4), is also received by other cell types. At present, the function of these cells is unknown, and although both RPD1 and pleural D group neurones have axons in the nerves innervating the CM and DLM (Ferguson, 1985), they were not motoneurones for these muscles and were not involved in longitudinal shortening of the body. However, considering how similar their activity is to that of the CM and DLM motoneurones, it is possible that they play some other role during whole-body withdrawal.

Discussion

The role of the CM and DLM motoneurones

The results presented in this paper support the hypothesis that the previously
Fig. 9. Reception of sensory inputs by cells that are not CM and DLM motoneurones. Tactile stimulation of the left anterior foot evoked synchronous EPSPs in left cerebral A cluster DLM motoneurones, the giant cell RPD1 (A) and a pleural D group cell (B). This usually led to simultaneous spike activity. The pleural D group cell was also excited, synchronously with a DLM motoneurone, after light off (C).
identified CM and DLM motoneurones of *Lymnaea* (Ferguson and Benjamin, 1991) are involved in the whole-body withdrawal response. Contraction of these muscles and subsequent shortening of the body in the semi-intact preparation are always accompanied by spike activity in neurones of the CM and DLM motor pools. This can be induced by spontaneous excitatory synaptic inputs to the motoneurones (relatively rare) or by sensory inputs from the skin, which are known to initiate whole-body withdrawal responses in the intact snail. The behavioural role of the 'spontaneous' activity in the CM and DLM motoneurones is unclear, but it must be centrally generated as it occurs in isolated, as well as semi-intact, preparations. It may underlie the spontaneous withdrawal responses that are sometimes seen in the intact snail or play a role in locomotory activity that involves shell movements generated by endogenous central activity (Haydon and Winlow, 1986). In the absence of sensory input from the skin, the high resting potentials of the CM and DLM motoneurones ensure that they are silent. This is presumably important for the snail because strong withdrawal of the snail into its shell prevents other types of behaviour occurring.

Whether the centrally located motoneurones of *Lymnaea* are entirely responsible for the whole-body withdrawal response is unclear because the large number of neurones involved (see Fig. 4 of the previous paper) made it impossible to assess the contribution of particular neurones to the total response. Peripheral motoneurones are known to play a role in other defensive withdrawal responses (e.g. the gill withdrawal response of *Aplysia californica*, Peretz, 1970; Peretz et al. 1976), but normally these are localized responses occurring in one part of the body. The whole-body withdrawal response of *Lymnaea* requires the coordinated response of two muscles covering most of the body surface and it seems unlikely that this could be achieved by a peripheral neural network. This conclusion is supported by the work of Cook (1975), who showed that cutting the columellar and cervical nerves to the periphery, or the central pleuro-pedal connectives (all of which contain many of the axons of the CM and DLM motoneurones; Ferguson and Benjamin, 1991), abolishes most of the withdrawal response in *Lymnaea*.

**Sensory input to motoneurones**

Further evidence supporting the role of the motoneurones in the whole-body withdrawal response is that the sensory modalities that normally cause whole-body withdrawal also activate the CM and DLM motoneurones. In the semi-intact preparation, both photic (light off) and tactile stimulation of the skin were effective in causing activation of the CM and DLM motoneurones, strong EJP activity in the CM and DLM and a resultant longitudinal contraction of these muscles. It is the reception of these common inputs and the electrotonic coupling of the CM and DLM motoneurones (Ferguson and Benjamin, 1991) that are responsible for coordinating the activity of the motoneurones involved in the whole-body withdrawal response.

This coordination of motoneurone activity is important because the CM and DLM motoneurones are located in at least seven ganglia of the CNS (Ferguson and Benjamin, 1991).
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and Benjamin, 1991). During whole-body withdrawal these cells must be synchronously activated; the CM and DLM must contract together to pull the shell forward and shorten the ventral area of the head-foot. Much of this coordination of the response can be explained by the fact that once the sensory inputs reach the CNS they are widely distributed to the CM and DLM motoneurones. Thus, sensory inputs converge onto cells located in widely separated ganglia of the CNS, and they receive synchronous EPSP input from both photic (light off) and tactile stimulation from all parts of the skin of the head-foot. It should be noted that the sensory inputs received by CM and DLM motoneurones and by RPD1 and pleural D group neurones were not received by all neurones within the CNS. A neurone located in the right pedal F cluster (identified by Slade et al. 1981) and causing contraction of the circular muscle of the head-foot is one example of a cell that received no input after presentation of either modality of sensory stimulus (Ferguson, 1985).

The receptors responsible for both types of sensory activation of the withdrawal response are presumably located in the skin (Zylstra, 1972; Zaitseva and Bocharova, 1981). Direct evidence from nerve cutting showed that the eyes are not involved in the light off response and that this is probably mediated by light off receptors in the skin, as previously proposed by Stoll (1972, 1973, 1976). The degree of sensory convergence could not be tested directly with the photic stimulus used here (switching off the main source of light to the preparation) as the whole body surface was stimulated, but cutting particular nerves did not prevent the excitatory response in CM and DLM motoneurones. Given that the innervation of the skin from different nerves is discrete (although different nerves do have innervation areas that overlap to a limited extent; Janse, 1974), receptors responsible for the response presumably project along separate peripheral nerve pathways from different parts of the body surface. Thus, the convergence of light off stimuli onto many different motoneurones must mean that the sensory input is widely distributed once it reaches the CNS from particular nerve roots. This is also true for the tactile inputs to the CNS, as different areas of the body wall relay information about tactile stimulation to the CNS through particular nerves (Janse, 1974). Again, the tactile inputs initiated by touching particular parts of the body wall affected motoneurones in many different ganglia and thus the tactile input must be widely distributed once it reaches the CNS. With tactile stimulation, sensory convergence could be shown directly by probing different parts of the surface of the body and recording similar inputs to a particular cell. Some of this convergence may be facilitated by the presence of several afferent pathways to the CNS from a particular part of the body. For instance, whole-body withdrawal can be evoked by tactile stimulation of the lips. The sensory information is conveyed to the cerebral ganglia of the CNS via the lip nerves and to the pedal ganglia via the superior cervical nerves (Janse, 1974). However, the motoneurones causing contraction of the CM are located in the cerebral and pedal ganglia, and the motoneurones that cause contraction of the DLM are located in the cerebral, pedal, pleural and left parietal ganglia (Ferguson and Benjamin, 1991). For whole-
body withdrawal to be complete and coordinated, motoneurones in different ganglia must be excited synchronously by sensory input, thus requiring that the sensory information relayed via nerves to the cerebral and pedal ganglia also converges onto cells in other ganglia of the CNS.

Recording from the peripheral nerves of *Lymnaea*, Janse (1974, 1976) and Janse and Van Swigchem (1975) distinguished two major categories of touch-sensitive neurones that had cells bodies within the CNS: primary and higher-order cells. Primary sensory cells responded to touch or stretch and had receptive areas varying in size from small to large (up to half the body surface); higher-order sensory neurones responded to touch, pressure and stroke, or to stretch, and had large receptive fields. The type of stimuli applied during the present investigation probably activated the touch, pressure and stretch receptors described by Janse (1974, 1976) and Janse and Van Swigchem (1975). Therefore, more selective presentation of tactile stimuli to the animal is required to determine exactly which type of tactile sensory neurones normally evokes whole-body withdrawal behaviour. Similarly, further experiments are required to localise sensory neurone cell bodies within the CNS and to determine whether the connections between sensory cells and the CM and DLM motoneurones are mono- or polysynaptic.

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