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NEUROMOTOR BASES OF THE ESCAPE BEHAVIOUR OF *NASSA MUTABILIS*

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Summary

The complex sequence of movements in the escape behaviour of the snail *Nassa mutabilis* (L.) was described in detail and the neuromotor activity underlying the behaviour was investigated by extra- and intracellular recording. The escape reaction is triggered by a chemical stimulus to the animal's foot, in these experiments either application of KCl solution or contact with a starfish. It consists of a preliminary phase in which the shell tilts to its side, the actual locomotor phase, and a final righting movement. The snail performs leaps, in which the foot and the shell are repeatedly rotated with respect to one another. EMGs recorded from the columellar muscle during the escape reaction showed that bursts of potentials are coupled to the shell rotations. In the intact animal this burst activity ordinarily began $0{\cdot}6 \pm 0{\cdot}3$ s after stimulation with KCl. In an animal dissected for recording from the columellar nerve (which supplies the columellar muscle), KCl stimulation of the dorsum of the foot induced burstlike neuronal activity with a latency of $0{\cdot}5 \pm 0{\cdot}3$ s. The dorsal foot region, the site at which the escape reaction can be triggered, was found to be supplied by the posterior pedal nerves; electrical stimulation of these nerves elicited bursts in the columellar nerve. The left pleural ganglion, which is known to contain neurones that project into the columellar nerve, was also found to contain neurones responsive to KCl stimulation of the foot. These findings suggest that the left pleural ganglion contains a motor centre which is involved in control of activity of the columellar nerve, and is also active during the escape reaction.

Key words: marine gastropod, escape behaviour, neuromotor activity.

Introduction

The prosobranch marine snail *Nassa mutabilis* (L.) exhibits a striking, complex sequence of movements when certain echinoderms (e.g. the starfish *Marthasterias glacialis* L.) come into contact with the posterior part of its foot (Weber, 1924). This escape behaviour can be subdivided into three phases. In the initial phase the snail, in its normal upright position on the substratum, swings its shell to the side one or more times, detaches the sole of its foot from the substratum and tilts sideways, falling on the shell. Next, in the actual locomotor phase, the animal works itself away from the dangerous area by vigorous contortions of the foot. During this process, the foot and shell are again rotated in opposite directions. In the concluding phase the snail regains its normal upright position.

The stimulus that triggers this behaviour is chemical. Hoffmann (1930) showed that the secretion from the skin of starfish or sea urchins can elicit an escape reaction, as does application of various salt solutions (e.g. KCl). The stimulus must be applied to the dorsal surface of the foot; stimulation of other parts of the body causes only a withdrawal of the local skin region (Hoffman, 1930).

The movements of the shell during the escape reaction suggest that the columellar muscle is involved. The upper, free part of this muscle is attached to the columella of the shell, and the ventral end is incorporated into the visceral sac, where it radiates into the head and foot in several layers (Weber, 1925). In this paper the activity of the columellar muscle during the escape reaction is documented and evidence is presented of the central nervous events by which the muscle is activated.

Materials and methods

Specimens of *Nassa mutabilis* (L.) (Gastropoda, Prosobranchia) collected from the Gulf of Naples were kept for some time preceding the experiments in tanks filled with artificial sea water. In some experiments starfish of the species *Marthasterias glacialis* (L.), also from the Gulf of Naples, were used to trigger the escape reaction.

The individual phases of the escape behaviour were analysed by examination of video and photographic recordings of reactions triggered by application of $0{\cdot}5\,\mathrm{mol\,l^{-1}}$ KCl solution to the dorsal foot surface or by contact with starfish.

For recording of an electromyogram (EMG) from the columellar muscle of a freely moving animal, holes were drilled in the shell at two places. A steel wire (60 μm diameter), insulated with lacquer except at the tip, was inserted through each hole into the free part of the columellar muscle. The two wires, anchored to the shell with dental cement and connected to a Grass preamplifier (type P15), were used for differential recording of the electrical activity of the muscle. In these experiments, escape behaviour was elicited with $0{\cdot}5\,\mathrm{mol\,l^{-1}}$ KCl solution.

The snails were prepared for recording of motoneuronal activity by dissection under $MgCl_2$ anaesthesia; the dorsal surface was opened to expose the oesophageal-ring complex, including the columellar and pedal nerves. Two hoo

electrodes were used for differential recording from the nerves; activity within the ganglion was recorded intracellularly with Lucifer Yellow- and LiCl-filled microelectrodes. The escape behaviour was elicited either by dripping 200 μl of 0·5 mol l^{-1} KCl solution from a height of approx. 5 mm onto the foot (to which a modified Wheatstone bridge was attached as a stimulus detector) or by electrical stimulation of posterior pedal nerves transected distal to the site of the (hook) electrodes. The motoneuronal activity was displayed on a storage oscilloscope (Tektronix), photographed (Tönnies Recordine camera) and stored on magnetic tape (Racal recorder).

The CNS neurones were stained by backfilling with cobalt lysine (modified method of Altrup & Peters, 1982), and the subsequent intensification was carried out with whole-mount preparations.

Results

Movement patterns

The complex movement sequence of an escape response is illustrated in Fig. 1, which shows the behaviour of a snail that had contact with a starfish. At the beginning, the snail is in an upright position, with the sole of its foot totally attached to the ground (Fig. 1B 1). Then the shell is rotated to the left (Fig. 1B 1–6) and the foot is detached from the substratum (Fig. 1B 6–14). The snail leaps away from the starfish and finally rights itself (Fig. 1B 14–52). Two leaps together make up a complete movement cycle which can be divided into four subunits.

(1) Lying on its left side with foot curved, the animal swings its shell forward and to the right; at the same time it extends and twists the foot (Fig. 1B 14–16).

(2) The shell is rotated back into alignment with the body, so that the snail is lying on its right side. The foot is curved upwards, turning around the shell somewhat and shifting it slightly (Fig. 1B 16–20).

(3) The shell is swung forward and to the left and the foot is extended again, this time being twisted in the opposite direction (Fig. 1B 20–23).

(4) The shell is realigned with the body and the foot curves upwards again. Now the animal is lying on the left side, as in the starting position (Fig. 1B 23–28).

Subunits 1 and 2 (Fig. 1B 14–20) make up the first leap of the movement cycle, subunits 3 and 4 (Fig. 1B 20–28) the second.

There was some variability in the way in which leaps were performed (Fig. 2). Fig. 2A,B both show leaps in which the starting postures and the end postures are the same. At the beginning the snail lies on its left side in both cases. In Fig. 2A (corresponding to Fig. 1B 14–20) the shell is swung forward and to the right while the foot stretches out. Then the shell rotates around its longitudinal axis and the foot curves upwards again. The snail finally lies on its right side (movement type *A*). In Fig. 2B (corresponding to Fig. 1B 28–36) the shell is swung forward and to the right and the foot is stretched out. But, while curving upwards, the foot moves over the shell and rotates it around its longitudinal axis in the opposite direction to that in Fig. 2A (movement type *B*). The snail's end position is the same as in type

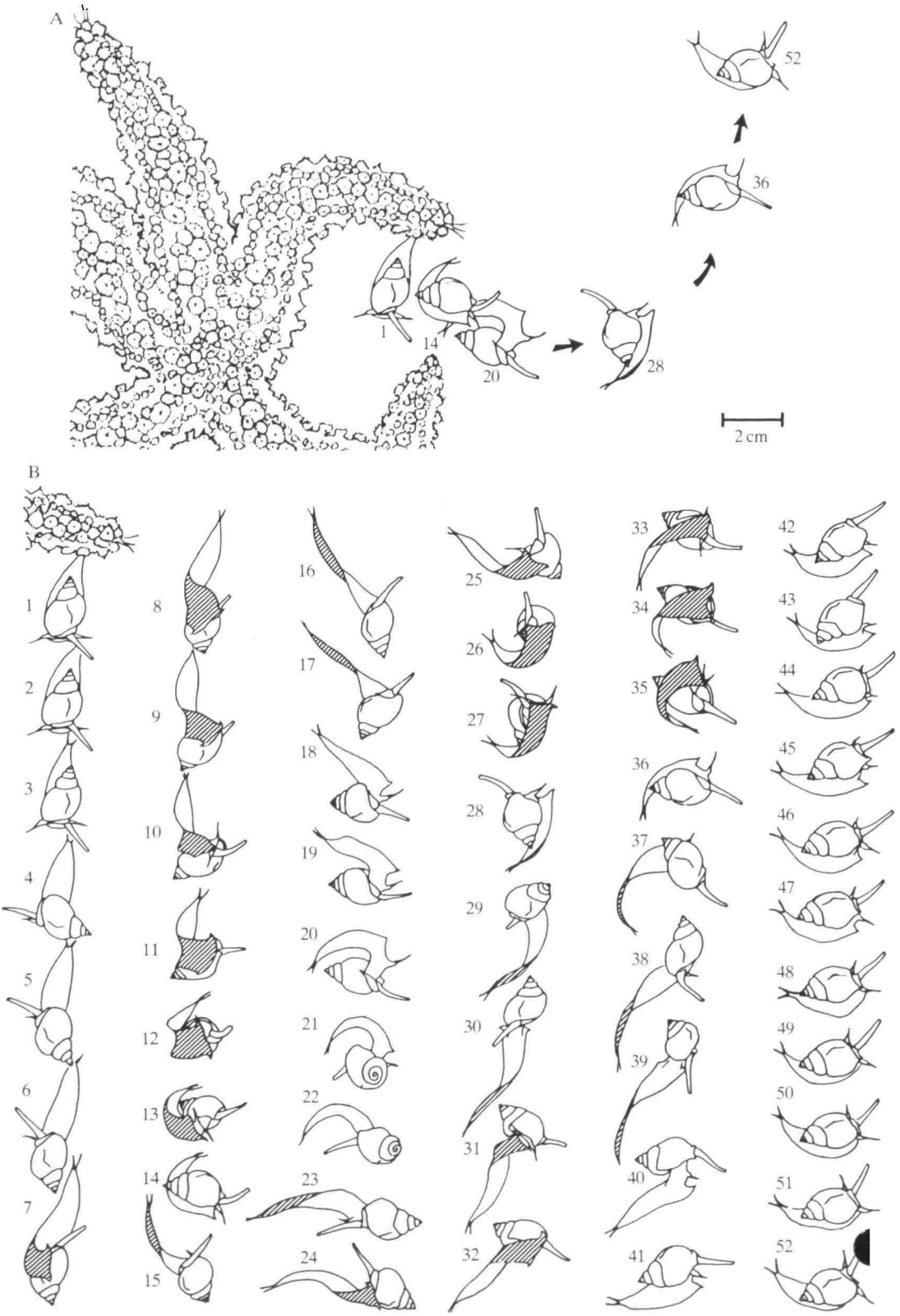
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Fig. 1

Fig. 1. The escape response of *Nassa mutabilis*. (A) Spatial course: a snail in the upright position (1) makes contact with the arm of a starfish which is attached to the ground and shown from above. The snail tilts to the side (14), moves away from the starfish (20, 28 and 36) and finally rights itself (52). The frame numbers correspond to those in the lower picture. (B) Temporal course: the escape response of the snail in the upper picture is shown in 52 frames, numbered consecutively. The time interval between frames is 100 ms.

A. There are two corresponding types of movement when the snail lies on its right side in the starting position (Fig. 2C,D). Irrespective of the starting posture, movement type *A* could be seen in escape responses a little more often than type *B*. The ratio was 27:22 (type *A*: type *B*; from 82 leaps in 22 escape responses). Swinging the shell forward was a very fast process in both type *A* and type *B* movements (mean time = 0·27 s, S.D. = 0·07 s, $N = 20$) which took less time than its realignment with the body (type *A*: mean time = 0·44 s, S.D. = 0·14 s, $N = 11$; type *B*: mean time = 0·65 s, S.D. = 0·11 s, $N = 9$).

The number of leaps in each escape response differed widely. There could be a single leap in response to stimulation by starfish but we also observed an escape reaction with 12 leaps. The snail could perform more leaps (even more than 25) when it contacted the starfish again during the escape response. Usually the escape reaction did not end until the snail had moved out of reach of the predator. As a rule, the direction of locomotion changed during the reaction, so sometimes the snail could move back towards the predator and renew contact. In fact, the escape reaction was sometimes stopped just when the snail returned to the immediate vicinity of the starfish. If the two then touched one another, within less than 1 s the snail began a second escape reaction.

It should be pointed out that contact with a starfish did not always lead to an escape reaction even when the starfish touched the dorsal surface of the snail's foot. Sometimes the snail simply crawled away. When 0·5 mol l^{-1} KCl solution was used as the stimulus, a complete escape reaction was elicited in 47 % of the trials. In 15 %, the only response was turning of the shell while the animal kept the sole of its foot in contact with the substratum, and in the remaining 38 % there was no visible response (a total of 100 trials with 20 animals). In one case the reaction did not begin until 7·5 s after the stimulus onset. In all other trials in which either a complete reaction or shell rotation was elicited, the latency to the beginning of movement was 0·6 s (S.D. = 0·3 s). With 1 mol l^{-1} KCl the mean number of leaps was 7·5 (S.D. = 3·5; 10 trials with 10 animals).

The initial phase of the escape response was variable in the following respects, too. The first shell rotation could be to the left or to the right side. There could be one shell rotation or a few shell rotations before the snail detached the sole of its foot from the ground. The escape reaction could even be triggered when the snail was not adhering to the substratum by its foot, but was lying on its shell with the foot either on its side or on top.

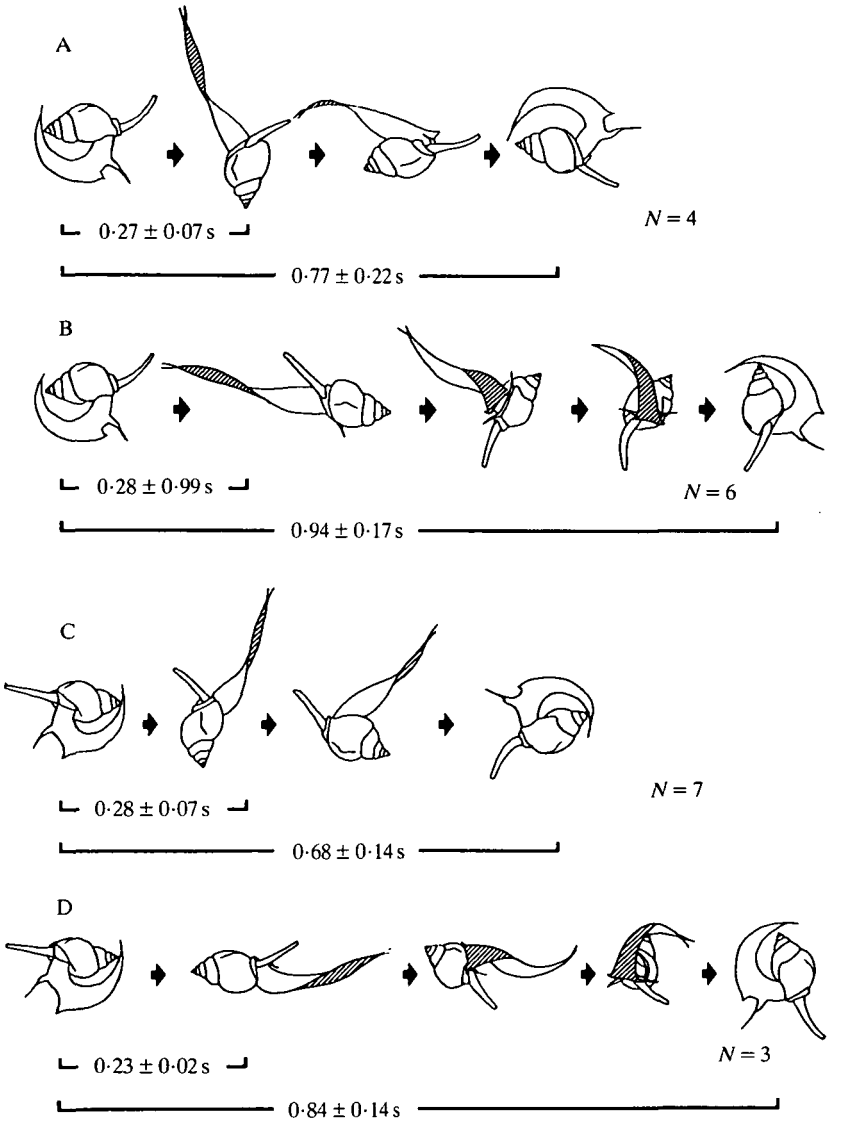

Fig. 2. Different types of leaps. Each row (A–D) shows a particular kind of leap. The leaps of A and C are designated as type *A*, those of B and D as type *B*. Temporal consecutive body postures are shown from left to right. The time intervals between the frames are not equal. In A and B the shell is swung to the right side of the body, in C and D to the left side. The data below each row denote the time for which the shell is swung towards the side of the body (upper data) and the total time of the leap (lower data). Means and standard deviations are given. The data are from 20 leaps. They result from 10 escape responses of 10 animals (two leaps from each escape response). *N* is the number of leaps of a particular type. Each type of leap can be seen in Fig. 1B: A corresponds to the frame sequence 14–20, B to 28–36, C to 36–42 (combined with the onset of a righting movement) and D to 20–28.

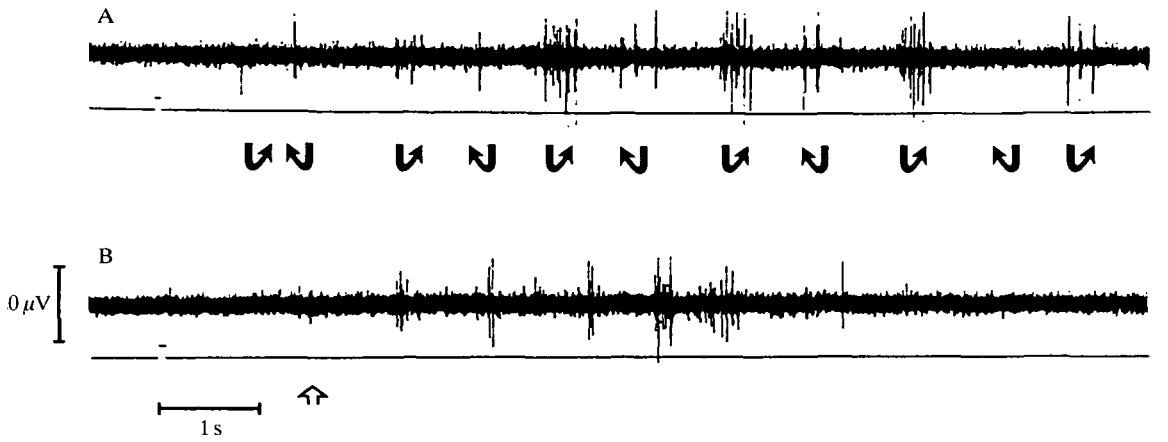

Fig. 3. Electromyograms from the columellar muscle (upper trace). The escape behaviour was triggered by KCl stimulation of the dorsal foot surface (lower trace). (A) Snail prevented from turning onto its side; the curved arrows mark the alternating leftward and rightward rotations of the shell. (B) Snail moving freely; the short arrow marks the first shell rotation.

Muscle activity

During the escape reaction there were bursts of activity in the EMG from the columellar muscle. In many cases there was a temporal correlation between these bursts and the following rapid rotations of the shell, during either the initial or the locomotor phase of the reaction. For example, in the experiment from which the recording shown in Fig. 3A was taken, the animal was prevented from turning over onto the side of the shell; as a result, it rotated the shell vigorously many times to the right and left. Each of these rotations was preceded by a burst of potentials in the columellar muscle. Fig. 3B shows the rhythmic pattern of activity recorded from the columellar muscle during a normal escape reaction. The first burst was followed by a leftward rotation of the shell.

Occasionally, in response to KCl stimulation the animal merely lifted its propodium or pressed its shell close to the foot. Also, in these cases bursts could be recorded from the columellar muscle.

Motoneuronal activity

The columellar nerve emerges from the dorsocaudal surface of the left pleural ganglion and innervates the columellar muscle near its insertion on the columella. The nerve contains spontaneously active fibres. Two groups of spikes (impulse units) could be distinguished on the basis of their relative amplitude. The large-amplitude units (50–100 μV in Fig. 4) were grouped into bursts 1–2 s in duration that accompanied visible contractions of the columellar muscle; the small-amplitude units (approx. 20 μV in Fig. 4) usually appeared independently of visible muscle movement (Fig. 4). Transections of the nerve, either near the

muscle or near the ganglion (see Fig. 6), showed that this activity was entirely efferent.

KCl stimuli to the dorsal surface of the foot elicited bursts of the larger units in the columellar nerve (Fig. 5A) with a latency of 0·5 s (S.D. = 0·3 s). The bursts varied greatly in duration; as a rule, the series was begun with a burst lasting several seconds, in which the spike frequency was around 10 impulses s^{-1}.

In most of such tests (70 %), this initial burst was followed by others, consisting of 2–10 impulses and lasting at most 2 s, which were repeated at intervals of 1–3 s. In 15 % of the trials only the initial burst appeared, and in the others the responses were either nearly continuous or quite weak (35 trials, 19 animals). In most of these recordings about 10 large-amplitude units could be distinguished on the basis of relative impulse amplitude. The small-amplitude units responded to KCl stimulation with about the same latency as the larger units, increasing their discharge rate to an average of approx. 25 impulses s^{-1}. During the return to the baseline discharge rate of 3–10 impulses s^{-1}, their activity level often varied in the rhythm of the bursts of the larger units. The responses were unchanged after transection of the nerve near the muscle (Fig. 6).

The increase in neuronal discharge rate produced by KCl stimulation of the foot could last as long as 70 s, gradually declining from a maximum near the beginning of the response (Fig. 5B).

The response to chemical stimulation recorded from the columellar nerve remained nearly unaltered after transection of all the pedal nerves except for the posterior ones (numbers 6–11 according to Herbst, 1983). When these posterior nerves were cut, the burst activity in the columellar nerve was reduced; the reduction was progressively greater as fewer of the posterior pedal nerves remained intact.

A response of the motoneurones in the columellar nerve could also be elicited by electrical stimulation of posterior pedal nerves. The most effective stimuli were found to be single pulses (width 0·8–1 ms, amplitude 1–3 V) and brief pulse trains (duration about 100 ms, frequency about 100 Hz). During such stimuli, large-amplitude units in the columellar nerve discharged at rates of more than 5 impulses s^{-1}. In 88 % of these trials one or two special components of the response could be discerned (Fig. 7). The first component appeared only 10–20 ms

Fig. 4. Spontaneous activity in the columellar nerve. The recording shows both impulses with a relatively small amplitude and those with a relatively large amplitude. The latter are grouped into distinct bursts, which are always accompanied by a visible contraction of the muscle.

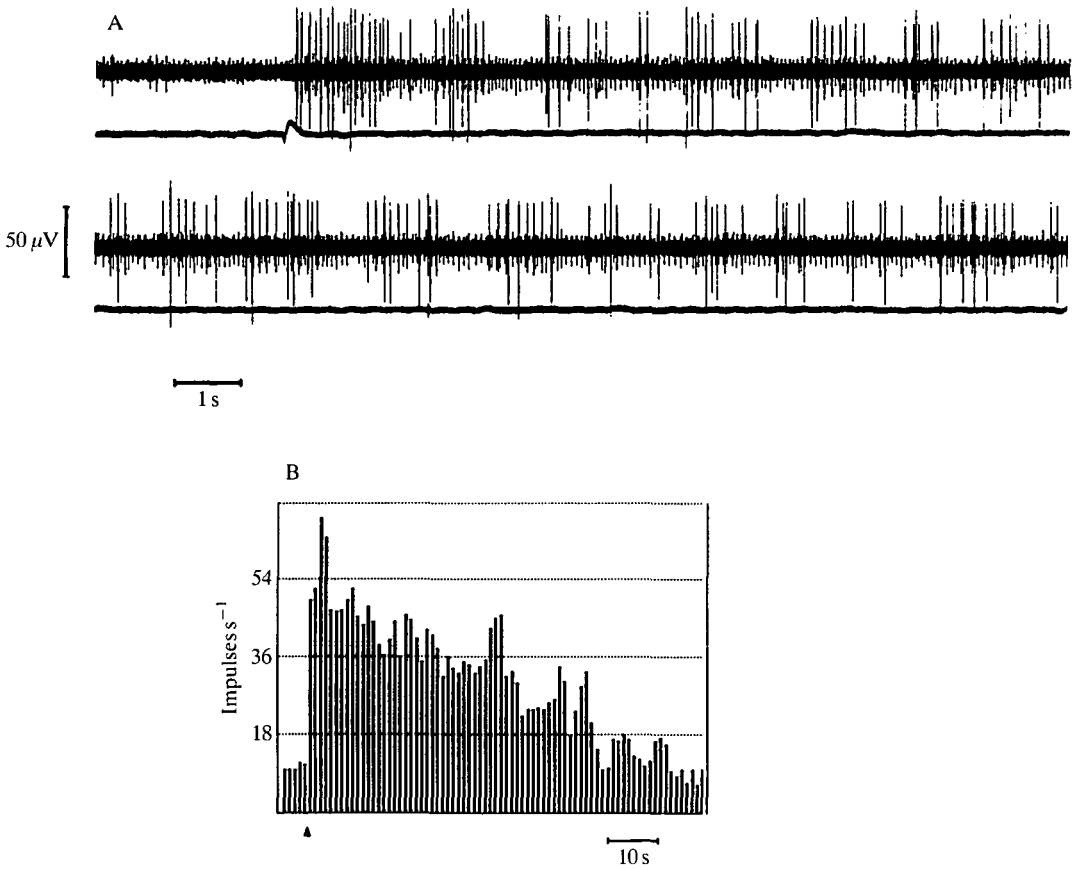

Fig. 5. Activity in the columellar nerve in response to stimulation of the dorsal foot surface with 0·5 mol l^{-1} KCl solution. (A) Upper trace: original recording, showing burst activity; the initial burst is followed by others varying in duration and frequency, at intervals of several seconds. Lower trace: KCl stimulus mark. (B) Histogram (impulse frequency in consecutive seconds) constructed by summation of the frequency histograms for seven different responses. Arrowhead, KCl stimulus mark.

after the stimulus pulse and consisted of 2–10 impulses at a frequency of about 200 impulses s^{-1}. The second component, observed in 74 % of the trials was a burst lasting 1–2 s at a frequency of 10–20 impulses s^{-1} with a latency of about 1 s. In 21 % of the trials such bursts recurred at intervals of several seconds, producing a pattern like that following chemical stimulation. In only 12 % of all the experiments with electrical stimulation was there little or no change in neuronal discharge rate (78 experiments, 22 animals).

Motoneuronal activity was also observed in posterior pedal nerves 6–11 in response to KCl stimulation of the foot, but in most experiments (8 out of 11) it was a more continuous discharge than that in the columellar nerve. The latency in the pedal nerve was about 100 ms.

Recordings were taken from the pleural ganglion on 12 occasions, and in three

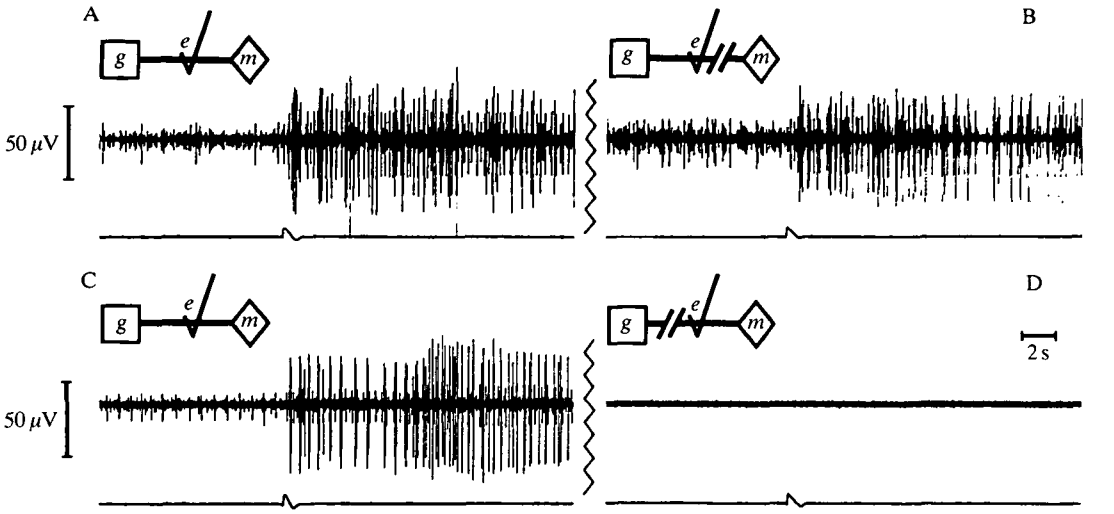

Fig. 6. Neuronal responses from the columellar nerve (upper traces) to KCl stimulation (lower traces) before and after nerve transection. (A) Activity in the intact nerve. (B) Nerve transected between the hook electrodes and the columellar muscle; the activity resembles that before the transection. (C) Same as in A (another animal). (D) Nerve transected between the left pleural ganglion and the electrodes; all activity is absent now. *e*, electrodes; *g*, ganglion; *m*, muscle.

cases a response to chemical stimulation of the foot was observed. Because of the violent muscle contractions that were elicited at the same time, the intracellular recording was lost within a few seconds (4 s at most) after stimulus onset. Fig. 8 shows the activity recorded from the soma of a neurone in the left pleural ganglion. Prior to the KCl stimulus it discharged 1–2 impulses s^{-1} and about 120 ms after the stimulus the discharge rate rose to 4–5 impulses s^{-1}. In the simultaneous recording from the columellar nerve (approx. 1 mm posterior to the ganglion) an impulse appeared about 1 ms after each soma spike; that is, there was a direct 1:1 relationship between the intracellular activity and one of the extracellularly recorded units.

Fig. 7. Example of activity in the columellar nerve in response to electrical stimulation of the posterior pedal nerve 7. The motoneuronal response (upper trace) resembles that to chemical stimulation, consisting of a number of bursts (II, the second component); a few impulses appear after only approximately 20 ms (I, first component). Stimulus mark (lower trace): 1 ms, 1 V.

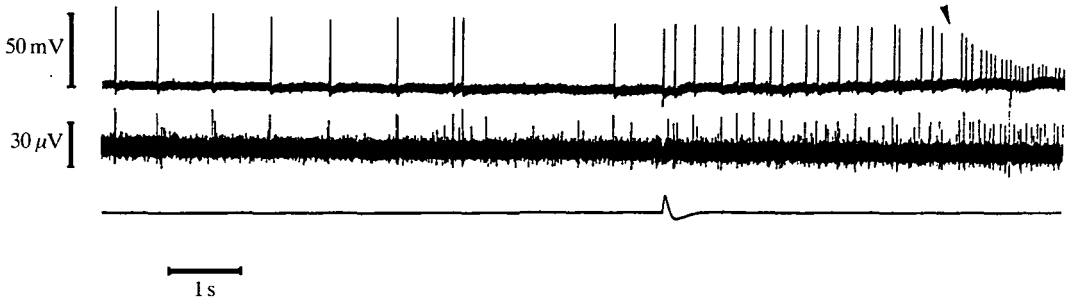

Fig. 8. Simultaneous recordings from the CNS and from the columellar nerve, showing a response to chemical stimulation of the foot. Top trace: intracellular recording from the soma of a neurone in the left pleural ganglion; approximately 4 s after the stimulus the electrode was displaced by increasingly vigorous muscle movements (arrowhead). Middle trace: recording from the columellar nerve about 1 mm away from the ganglion; one of these units is correlated in time with the intracellularly recorded action potentials. Bottom trace: KCl stimulus mark.

Neuroanatomy

More than 50 cell bodies and many fibres in the CNS were stained by cobalt lysine backfilling of the columellar nerve. The results are summarized in Fig. 9, which includes only those neurones that were marked in at least two of the 11 backfills. In the left pleural ganglion there were 42 stained somata, 12 of them with a diameter of over 50 μm. A large group of these fibres in the columellar nerve formed a median tract that passed diagonally through the ganglion and branched repeatedly in the anterodorsal region. In parts of several other ganglia adjacent to the pleural ganglion, some cell bodies were also stained: eight in the left pedal ganglion, five in the subintestinal ganglion and three in the cerebral ganglion. Backfills of left posterior pedal nerves 7–10 revealed a cell body region in the posterior part of the left pedal ganglion and a fibre tract terminating in the region of the pedal ganglion that also contained stained motoneurones of the columellar nerve. In one of the pedal nerve backfills a group of eight cell bodies in the left pleural ganglion was also stained (not shown in Fig. 9).

Discussion

The escape response of *Nassa* is triggered by chemical stimuli (Weber, 1924; Hoffmann, 1930), and the only region sensitive to these stimuli is the dorsal surface of the foot (Hoffmann, 1930). Weber (1924) points out that the snail moves away from a predator by means of this response only if the predator has approached from behind, so that it first contacts the dorsal part of the foot. The results of our neurophysiological experiments reflect the specialization of this region. Stimulation of the posterior pedal nerves (nos 6–11), shown by Herbst (1983) to innervate the dorsal skin of the foot, produced a marked increase in the discharge of columellar nerve fibres. The columellar nerve supplies the columellar

muscle, which our EMG recordings have shown to play an important role in the escape behaviour. The anterior pedal nerves innervate the anterior region of the foot but not its anterior surface; accordingly, stimulation of these anterior nerves had essentially no effect on the spike activity in the columellar nerve.

It is not clear whether the motor programme initiated in our experiments by KCl stimulation of the foot or by electrical stimulation of the posterior pedal nerves is the same as that controlling the escape behaviour under natural conditions. The timing of the bursts in the columellar nerve is not an adequate criterion, because even in the intact animal the intervals between the successive components of the escape reaction vary greatly. The only parameter that is somewhat informative is the latency of the response in the columellar nerve. When the stimulus was application of KCl to the foot, this latency corresponded approximately to the time that elapsed between stimulation and the onset of the behavioural response in the intact animal ($0{\cdot}5 \pm 0{\cdot}3$ s compared with $0{\cdot}6 \pm 0{\cdot}3$ s). When the posterior pedal nerves were stimulated electrically, there was an additional brief discharge in the columellar nerve after only 10–20 ms. These initial impulses were probably an effect of the simultaneous activation of a larger population of pedal nerve fibres with this form of stimulus.

As we have pointed out, even a single chemical or electrical stimulus elicits

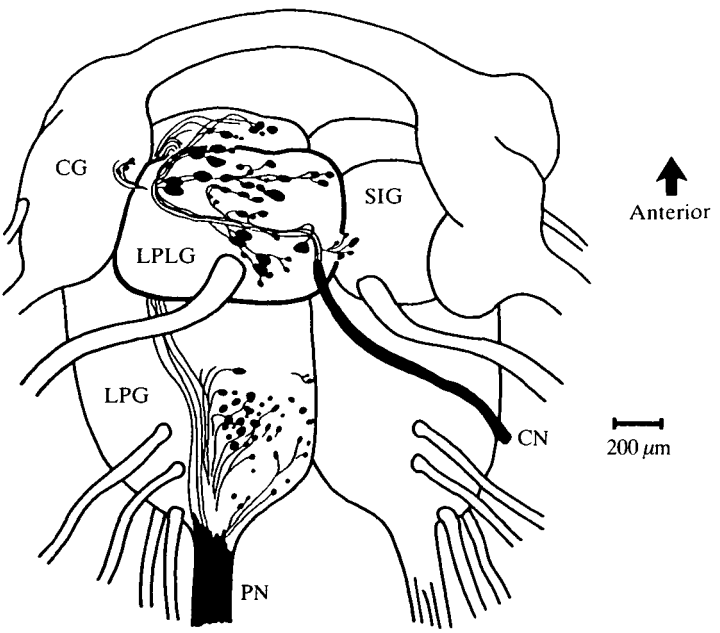

Fig. 9. Stained neurones in the left pleural ganglion (LPLG) and in the left pedal ganglion (LPG). The sketch includes only the neurones that were stained in at least two of the 11 cobalt backfills of the columellar nerve (CN) or left pedal nerves (PN) 7–10. The fibres passing to the anterior part of the left pedal ganglion are not shown where they run below the pleural ganglion. CG, cerebral ganglion; SIG, subintestinal ganglion.

extended activity in the columellar nerve (up to 70 s). This can be caused by diverse mechanisms such as a continuous stimulation, a neuronal network or neurochemical processes in the CNS. Although the stimulus detector mounted directly above the foot surface (registering the electrical resistance) indicated that the KCl stimulation had a duration of less than 1 s, the possibility of a prolonged influence of ions must be considered. Nevertheless, even if chemical stimulation were to be continued for some time, there must be other causes for the extended reaction, because even a single electrical pulse applied to pedal nerves elicited a response of long duration in the columellar nerve.

The nerve response could also be prolonged by means of a possible neuronal network: every serial burst in the columellar nerve could result from a feedback of muscle activity elicited by the preceding burst. Another possible cause for the extended response is the occurrence of some neuromodulatory substance. It might be released locally in the CNS, causing postsynaptic neurones to generate the motoneuronal pattern.

Experiments on pulmonates have shown that the pedal ganglion is an important centre for control of columellar muscle activity. Neurones in the pedal ganglion of *Lymnaea* send axons to the columellar muscle, and the 1:1 relationship between the impulses in the nerve cells and the muscle potentials indicates that these are motoneurones (Jansen & ter Maat, 1985). In the same study it was shown that these neurones are involved in movement of the shell during egg deposition. According to Winlow & Haydon (1986), neurones in the pedal ganglion are responsible for the rhythmic movements of the shell, caused by contractions of the columellar musculature, that accompany locomotion in *Lymnaea*. Motoneurones in the pedal ganglia of *Helix* control the activity of the columellar muscle during the protective reflex (Samygin & Karpenko, 1980*a*).

That the left pedal ganglion is also involved in the control of shell movement during the escape response of *Nassa* is indicated by our finding that fibres in the posterior pedal nerves pass to a region on the left pedal ganglion in which cell bodies of neurones of the columellar nerve were stained.

However, *Nassa* differs from *Helix* (Samygin & Karpenko, 1980*b*) and *Lymnaea* (Jansen & ter Maat, 1985) in that the great majority of the columellar nerve neurones stained in *Nassa* have cell bodies in the left pleural ganglion. Twelve of these somata are considerably larger than the rest. It is obvious that about the same number (about 10) of large efferent impulse units have been recorded from the columellar nerve in response to stimulation of the foot. Nevertheless, up to now only one nerve cell of the left pleural ganglion could clearly be shown to be integrated into a neuronal pathway responsible for an increase in columellar nerve activity after KCl stimulation of the foot (Fig. 8). Furthermore, activation of neurones in the pleural ganglion by stimuli to the foot must occur by way of interneurones, because no afferents from the foot were found to project directly into the left pleural ganglion.

It follows that the pleural ganglion of *Nassa* contains an important motor centre by which the activity of the columellar muscle is controlled. This result is surprising

because in neither *Helix* (Samygin & Karpenko, 1980*b*) nor *Lymnaea* (Jansen & ter Maat, 1985) have the pleural ganglia been found to contain nerve cell bodies that send axons into the columellar nerves. The neurones stained by way of the columellar nerves in *Helix* have somata in the pedal, cerebral and parietal ganglia (Samygin & Karpenko, 1980*b*); cobalt staining through the three columellar nerves in *Lymnaea* has revealed somata in the pedal and cerebral ganglia (Jansen & ter Maat, 1985).

Neither *Helix* nor *Lymnaea* has behaviour patterns comparable to the escape response of *Nassa*, and it is only in *Nassa* that the left pleural ganglion contains neurones that control the columellar muscle, which is involved in the escape response. Taken together, these findings suggest that the neurones in the pleural ganglion control components of behaviour characteristic of the escape response, such as the rhythmically repeated, powerful turning of the shell.

The pedal musculature also contributes to the escape reaction, twisting and extending the foot as shown in Figs 1 and 2. Correspondingly, application of KCl to the dorsal foot surface increases the efferent activity in the pedal nerves, which innervate the muscles of the foot. Nearly all the cell bodies in the CNS stained by cobalt backfilling through the left posterior pedal nerves were found in the posterior part of the left pedal ganglion. In only one case did this procedure stain a few somata in the left pleural ganglion. Evidently, then, the efferent innervation of the posterior pedal musculature originates mainly in the pedal ganglia.

The changes in neuronal activity elicited by KCl stimulation of the foot imply that both the left pleural ganglion and the pedal ganglia participate in controlling the escape response of *Nassa*. That other ganglia could also be involved is indicated by the presence of stained somata in the cerebral and subintestinal ganglia after cobalt backfilling of the columellar nerve.

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