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CONTROL OF LOCOMOTION IN THE FRESHWATER SNAIL *PLANORBIS CORNEUS*

I. LOCOMOTORY REPERTOIRE OF THE SNAIL

BY T. G. DELIAGINA* AND G. N. ORLOVSKY
A. N. Belozersky Interfaculty Laboratory, Corpus A, Moscow State University, Moscow 119899, USSR

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Summary

The freshwater snail *Planorbis corneus* moves as a result of the beating of cilia covering the sole of the foot. The tracks of snails crawling on the walls and on the bottom of an aquarium were recorded visually under various conditions of snail feeding. The following results were obtained.

1. In the absence of food, the snails exhibited diurnal changes in locomotor activity, with a maximum during the day. Horizontal tracks on the aquarium walls were commonest during the day and vertical ones at night. When crawling on the aquarium wall, the snail actively stabilized its horizontal or vertical orientation: when encountering an obstacle or after a forced turn, the snail re-established the initial direction of locomotion.
2. When fed on the water surface, the snail decreased its locomotor speed if food particles entered its mouth. The decrease in speed resulted from the slowing down of ciliary beating in the anterior part of the sole of the foot. This finding demonstrates that motor activity in different parts of the ciliated epithelium can be controlled independently by the nervous system.
3. When searching for food particles, the snail exhibited very sinuous tracks, the turns occurring spontaneously at irregular intervals. This finding shows that there is a programme of 'looping' in the nervous system.
4. When the snail was fed on the bottom near a vertical wall, it used the wall to climb to the water surface for lung ventilation. After ventilation, the snail performed a standard 180° turn and then returned to the food along the original outward track. Motion along a track was performed with high accuracy.
5. The locomotor apparatus of a snail allowed it to crawl not only on a flat surface but also along the very thin mucus thread that it makes.

Introduction

The present paper is the first in a series devoted to the control of locomotion in

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* Present address: Karolinska Institute, The Nobel Institute for Neurophysiology, Box 60 400, S-10401 Stockholm, Sweden.

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the freshwater snail *Planorbis corneus*. Like many other freshwater and marine gastropod molluscs, *Planorbis* uses the ciliated epithelium covering the sole of the foot for locomotion (for references, see Jones, 1975; Trueman, 1983). Ciliary beating in the narrow space between the sole and the substratum generates a force enabling the animal to move forward.

In this investigation of the system controlling locomotion in *Planorbis*, we aimed to resolve the following two problems. First, we sought to understand how the nervous system regulates the beating of cilia on the sole of the foot. Second, we sought to understand how the locomotor apparatus is used in those types of behaviour in which locomotion is associated with other activities. For example, during feeding, copulation, egg-laying and defensive reactions, the snail switches its locomotor apparatus on and off, regulates the intensity of its work and changes its direction of movement.

In the present paper, the locomotion of *Planorbis* will be described in relation to feeding and respiration. In spite of numerous studies of the behaviour of gastropod molluscs during feeding and respiration (for references see Geraerts and Joosse, 1983; Ghiretti, 1966; Kohn, 1983), we could not find, in the available literature, a detailed description of the influences of a mollusc's behaviour upon locomotion, except for some particular cases (Dawkins, 1974; Jager *et al.* 1979). It is necessary to emphasise that the present study is not a comprehensive investigation of snail behaviour in relation to feeding and respiration. Our goal was much more modest: to describe those peculiarities of the behaviour that are important for understanding the operation of the locomotor system. In our opinion, such a description is necessary in any attempt to analyse the nervous mechanisms of locomotor control.

Brief communications on some results of this study have been published (Deliagina, 1988; Deliagina and Orlovsky, 1988).

Materials and methods

Visual recording of the tracks of crawling snails was the main method used in the present study. In most experiments, 10 young snails bred in the laboratory (2.5–3 months old, shell diameter about 12 mm) were used. In a few experiments, adult snails collected in the local pond (age about 1 year, shell diameter about 25 mm) were used. For young snails, a small cylindrical aquarium with a clean wall was used (see Fig. 1A). For visual recording of tracks, a 'scene' (i.e. a sheet of half-transparent paper) was applied to the aquarium wall (see Fig. 1A). An experimenter traced with pencil the path of the crawling snail on the scene. All the scenes presented in this paper (except for a few cases indicated in the text) show the tracks of all the animals that crossed the scene during the time of observation (30 min). Recording sessions were repeated at intervals of 2–3 h during the day; in a few cases, the recordings were also performed at night under dim illumination. For adult snails, a rectangular aquarium (see Fig. 1B) was used. Recording of tracks was performed in the same way as for young snails.

Recordings of tracks were made under various conditions of feeding: (1) in the absence of food, (2) when the animals were fed dry *Daphnia* powder put on the water surface, and (3) when they were fed lettuce leaves fixed on the aquarium bottom. The experiments were carried out in July–August of 1986–1988, under natural light and at ambient temperature. Some additional details of the methods will be given below.

Results

Locomotion of snails in the absence of food

When watching the behaviour of snails one could easily perceive that some of them were in a state of 'rest', i.e. motionless and attached to the wall or to the bottom of the aquarium. During the day there were few snails in a state of rest, but at night one could observe simultaneously many (up to 70 %) animals attached to the walls or to the bottom. The state of rest could last from 10–20 min to several hours. The decrease in total locomotor activity at night was also caused by a decrease in the speed of locomotion. During the day, in most cases (80 %) locomotor speed was within the range 0.9–1.6 mm s^{-1}, but at night half the animals moved at less than 0.8 mm s^{-1}.

Fig. 1C shows seven scenes obtained in the cylindrical aquarium with 10 young snails. The recordings were made at various times of the day and night, on the day after the animals had been deprived of food. One can see that, in all the scenes, most of the tracks were either nearly horizontal or nearly vertical; however, inclined and intricately shaped tracks were also present. At dawn (06:00 h) locomotor activity was low, and the snails crawled mainly in two parts of the scene: near the bottom and near the water surface. At 08:00 h the activity of the snails increased considerably, and they crawled mainly near the bottom along horizontal tracks directed to the right (there are 16 'right' tracks compared with one 'left' track). At 10:00 h the locomotor activity of the snails remained high, and their tracks were still concentrated near the bottom. But, compared with the preceding scene, the number of snails entering the scene from the bottom and soon returning to the bottom increased considerably. At 12:00 h, activity remained high. Horizontal tracks predominated, and these tracks were distributed over the whole depth of the tank rather than concentrated near the bottom (as at 10:00 h and 12:00 h). At 16:00 h, locomotor activity decreased to some extent, and the numbers of horizontal, vertical and curvilinear tracks were approximately the same. In the evening (at 20:00 h), locomotor activity increased again, especially near the bottom. Finally, at 24:00 h the scene showed a dramatic change: the locomotor activity decreased, and vertical tracks predominated. The next morning (at 08:00 h) the snails exhibited increased activity again, with horizontal tracks near the tank bottom predominating. We did not record the bottom tracks systematically, but in a few recorded scenes (one of them is presented in Fig. 1D) we could not detect any directional bias among the tracks.

For the scenes presented in Fig. 1C, a quantitative analysis of the directionality of tracks was performed. For this purpose the tracks were divided into three groups: horizontal, vertical and indefinite. We described horizontal tracks as those that crossed the left and right boundaries of the scene with a difference in height of less than 20 mm. With the scene width of 200 mm, this corresponded to a 10 % vertical 'drift' of a snail. Similarly, tracks with a horizontal drift of less than 10 % were considered to be vertical ones. In each of the scenes (Fig. 1C) the length of tracks was measured by means of a curvimeter, and these lengths were summarized separately for each group. The total length of all the tracks was then computed; this value characterizes the total locomotor activity of snails in each

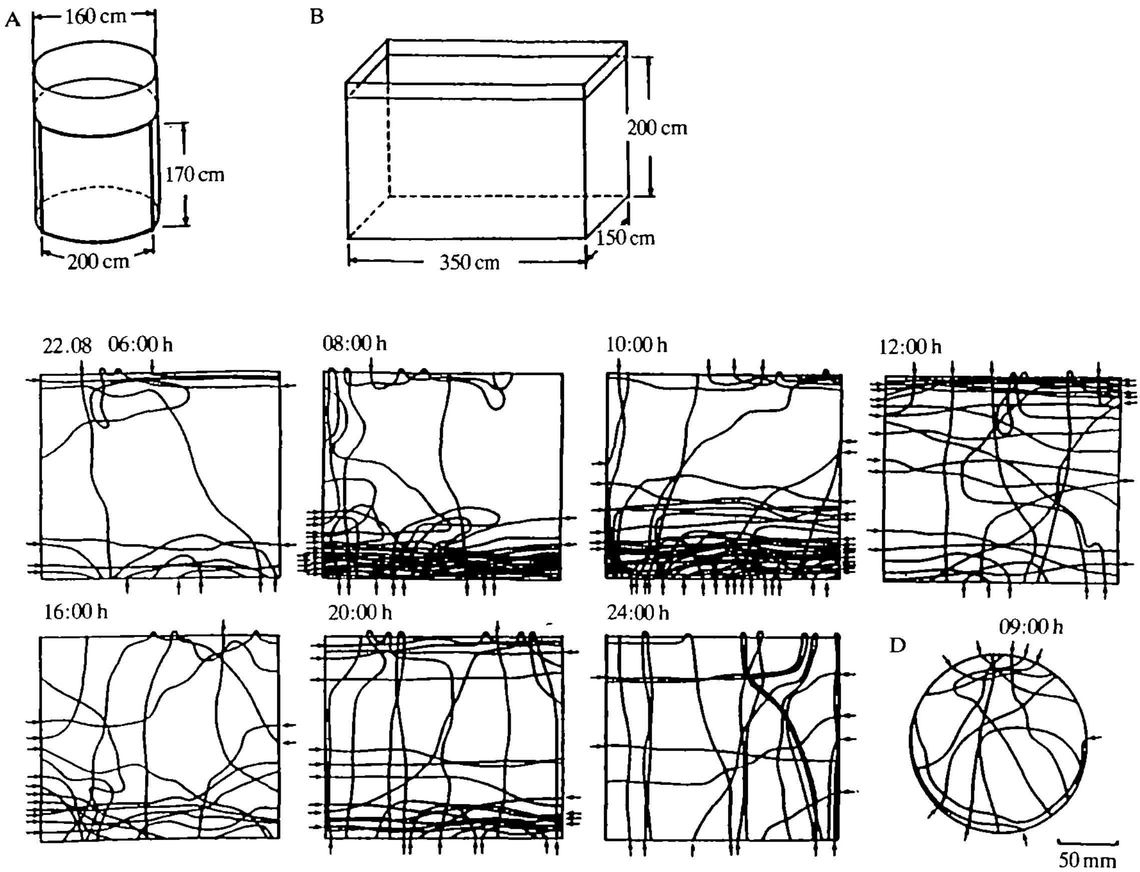

Fig. 1. (A,B) Methods of recording locomotor activity in snails. (A) Aquarium for young snails; the heavy line shows a 'scene', i.e. a sheet of half-transparent paper attached to the aquarium wall. (B) Aquarium for adult snails. (C) Creeping tracks of young snails ($N=10$) recorded at various times of day (on 22 August 1987). Scenes were obtained on the vertical wall of the aquarium. (D) A scene obtained on the bottom. For each of the scenes, the time (Moscow) of the beginning of recording is indicated; the duration of each recording session was 30 min. The beginning of each track is marked by an arrowhead. A short appearance of the snail on the water surface for lung ventilation is shown as a loop in the track.

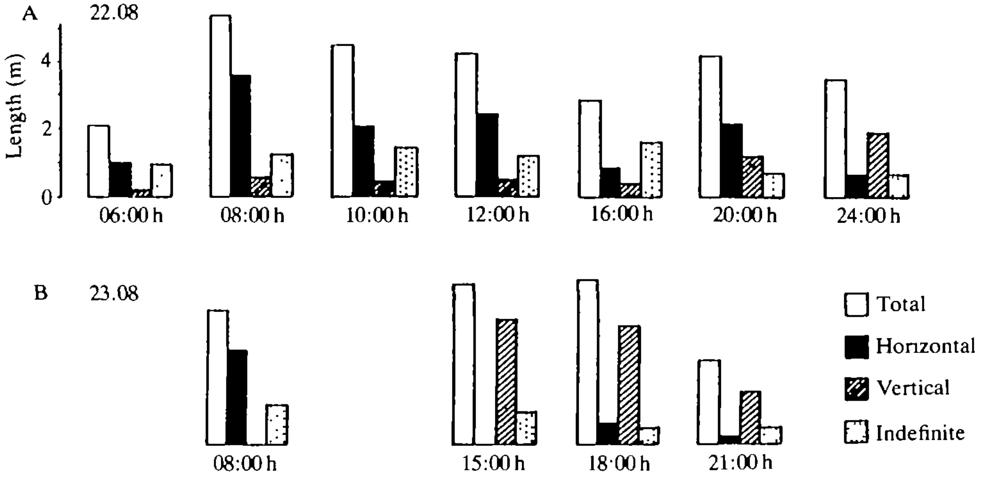

Fig. 2. Summary of the lengths of tracks of various types. (A) The scenes of Fig. 1C. (B) The scenes of Fig. 5A.

scene. The results are presented in Fig. 2A, from which one can see that in all the scenes (except for 06:00 h and 16:00 h) the length of the horizontal and vertical tracks accounts for the majority (60–80 %) of the total length. During the day, horizontal movement was commoner than vertical (06:00–20:00 h), but, at night, vertical movement predominated (24:00 h).

Both horizontal and vertical locomotion, which are so frequently observed in snails, are actively stabilized; they do not result from the absence of external obstacles. This is indirectly supported by the observation that, in many cases, the accuracy of maintaining the direction was very high. Fig. 3A shows the tracks of a snail that performed three turns around the aquarium during the observation time. The tracks of sequential crossings of the scene by the snail are numbered 1–4. Taking into account that the aquarium circumference was 500 mm, one can calculate that the vertical drifts of the snail in the first, second and third turns were 1, 2.5 and 2 %, respectively. The durations of these turns were 320, 325 and 330 s. These data demonstrate very high accuracy of maintaining both the direction and the velocity of locomotion. We did not succeed in observing more than four successive turns for any snail, since, after 2–3 turns, they usually crawled to the water surface (to ventilate the lung) or to the bottom.

Active stabilization of the horizontal and vertical orientation of a snail during locomotion was demonstrated directly in experiments with external obstacles (Fig. 3B). An obstacle (the end of a thin rod, or another snail) was placed in the path of the snail crawling along a horizontal (or vertical) trajectory. In most cases the snail, after it had touched the obstacle with a tentacle, turned to the right or to the left (depending on the tentacle stimulated) but soon returned to its initial direction (horizontal or vertical) and continued to crawl along a trajectory parallel to the initial one. The same result was obtained if a crawling snail was rapidly but

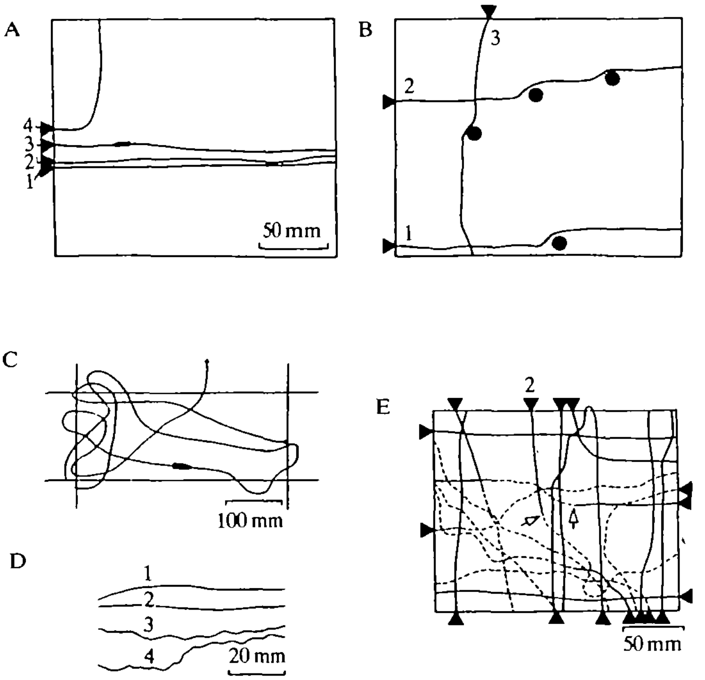

Fig. 3. (A,B) Stabilized directions of locomotion of young snails. (A) Sequential creeping tracks (1–4) of one snail which performed three turns around the aquarium. (B) Passing around obstacles while the snail crawled horizontally (1, 2) and vertically (3). (C) Stabilization of the position on the bottom (adult snail). The aquarium bottom is shown as well as the lower parts of the side walls (projected upon the bottom plane). During observation (30 min), the snail appeared seven times on the walls, but immediately returned to the bottom. (D) Creeping tracks of a non-grazing young snail (1, 2) and of a grazing one (3, 4). (E) Creeping tracks of young snails on the vertical algae-covered wall. Solid lines, non grazing snails; interrupted lines, grazing ones. On tracks 1 and 2, the arrows indicate the beginning of grazing.

carefully turned by its shell by 90°. If the snail did not exhibit a defensive reaction, it turned (in 5–10 s) by 90° in the opposite direction, and then continued to crawl along a trajectory parallel to the initial one.

These findings clearly demonstrate that a snail, crawling on a vertical plane, can orient its body in the gravitational field. It seems likely that the corresponding mechanism is used for ‘holding’ a snail on the bottom or on the water surface. Fig. 3C shows the track of an adult snail crawling on the bottom of a rectangular aquarium for 30 min. During this period the snail crawled upon the vertical walls seven times, but soon returned to the bottom (where there was a deposit of food). A similar pattern for young snails can be seen in Fig. 1C (10:00 h), in which there are many short tracks near the bottom, i.e. a snail immediately returned to the bottom when it crawled onto the vertical wall. It will also be demonstrated (see below) that, while feeding on the water surface, a snail that leaves the surface soon returns to it (see Fig. 5A, 09:00 h).

The data presented show that a snail can orient itself, relative to the direction of gravity, in several discrete ways. These orientations determine the horizontal and vertical trajectories of crawling as well as the prolonged stay of an animal on the bottom or at the water surface.

Locomotion of snails during feeding on an algae-covered surface

Usually, in a carefully washed aquarium, in the complete absence of food, even a hungry snail seldom exhibited feeding movements during crawling. However, if the aquarium walls became green, i.e. were covered with algae, rhythmic feeding movements occurred. (For a description of feeding movements in freshwater pulmonate molluscs, see Arshavsky *et al.* 1988; Kater, 1974; Smith, 1987.)

While feeding, a snail did not change the speed of locomotion but changed the shape of its trajectory. Fig. 3D shows (on a large scale) two tracks of a non-grazing snail (1 and 2) and two tracks of a grazing snail (3 and 4). One can see small oscillations on tracks 3 and 4 caused by periodic lateral movements of the head of the animal during eating. The scene presented in Fig. 3E was obtained in an aquarium with algae on the wall. One can see that the tracks of grazing snails are more sinuous. In tracks 1 and 2 one can also see that, with the beginning of grazing (marked by an arrow), the rectilinearity of the movements ceased.

Movements of snails during feeding on the water surface

We distinguished three types of behaviour in snails fed on the water surface. In the first type of behaviour (Fig. 4A,B), a snail fastened itself to the aquarium wall near the water surface and deflected the head dorsally. In this position it performed rhythmic movements with the mouth and buccal apparatus which resulted in the suction of water with food particles. The rhythmic feeding cycle lasted about 1 s in young snails and 1.5 s in adults.

In the second type of feeding behaviour (Fig. 3C), almost the whole sole was flattened under the water surface, and only the posterior part of it ('tail') was fastened to the wall. As in the first type of behaviour, the snail performed rhythmic movements of the mouth and buccal apparatus. The pulsatory flow of floating particles, evoked by these movements, can be seen at a distance of up to 10 mm; it is shown in Fig. 4C by simple arrows. Besides this flow, there was also another one, much stronger, evoked by the beating of cilia on the sole of the foot. This flow was not pulsating and could be seen at a distance of up to 30 mm from the snail; in Fig. 4C this flow is shown by heavy arrows. In front of the snail, the effects of both flows are added, whereas they are subtracted from one another in the area somewhat caudal to the mouth (Fig. 4C). The particles that did not enter the mouth could perform a few oscillations near the mouth in the rostrocaudal direction (in accordance with the feeding rhythm), and then they either entered the mouth or were transported backwards along the sole and stored near the tail in the form of a lump of particles glued by mucus. This type of feeding behaviour was often accompanied by lateral movements of the snail. With all the available floating food particles gathered, the snail flexed its foot and started eating the lump

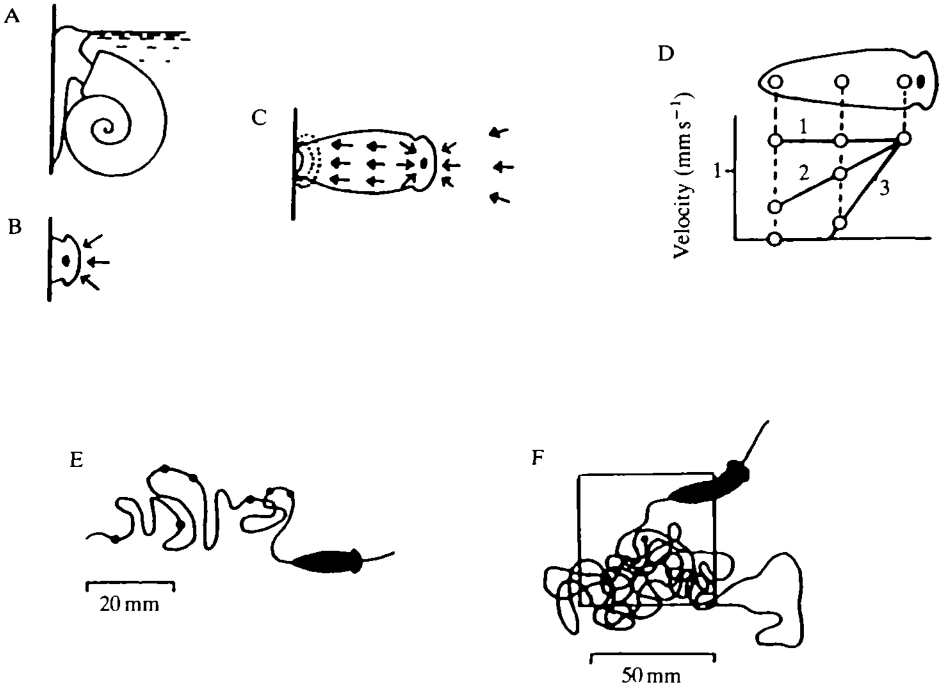

Fig. 4. (A–E) Behaviour of adult snails during feeding on the water surface. (A,B) The first type of feeding behaviour. The snail is fastened to the side wall and performs rhythmic suction movements with the mouth. The arrows show the flow of food particles produced by these movements. (C) The second type of feeding behaviour. The snail is fastened to the wall by its 'tail'. The flow of food particles is evoked by both suction mouth movements (simple arrows) and ciliary beating (heavy arrows). The dotted line shows the lump of food particles stored near the tail. (D,E) The third type of feeding behaviour. The snail moves under the water surface; the graph (D) shows the speed of small particles, moving along the foot sole, at three points on the sole, during normal locomotion (1), and after the contact with a small amount (2) or a large amount (3) of food. (E) Trajectory of the snail during feeding on the water surface. Time intervals between dots are 2 min. (F) 'Searching' movements of a snail. The snail was transferred from the water surface to the bottom during feeding. Total duration of trace, 20 min.

of food particles stored near the tail. Sometimes the snail unfastened itself from the aquarium wall and fell to the bottom, together with the food lump. On the bottom it ate the lump.

In the third type of feeding behaviour, the whole sole was flattened under the water surface (Fig. 4D), the cilia beat intensively, and the snail moved under the water surface at the normal locomotor velocity (about 1.5 mm s^{-1}). During locomotion, the snail performed rhythmic feeding movements. Until the first food particles entered the mouth or touched the lip, locomotion was not disturbed, and the intensity of ciliary beating was the same throughout the sole. This was demonstrated by the observation that small particles on the sole surface moved evenly backwards along the whole foot length (they were almost motionless in relation to the aquarium). In the graph (Fig. 4D, 1) we show schematically that the speed of particles in the anterior, middle and posterior parts of the sole was the same.

When a food particle touched the lip or entered the mouth, the beating of cilia on the middle and posterior parts of the foot sole became less intense. This was clearly visible to the naked eye: the moving particles decelerated in the course of their transport along the sole (Fig. 4D, 2). When more food particles touched the lips or got into the mouth, the beating of cilia on the posterior part of the sole stopped completely (Fig. 4D, 3), which resulted in a sharp decrease in the locomotor speed of the snail (from 1.5 to 0.1–0.3 mm s^{-1}). The picture described for the second type of feeding behaviour (Fig. 4C) could then be observed: the nearly motionless snail produced two flows of particles, one of them caused by rhythmic suction of water into the mouth, the second by the beating of cilia on the anterior part of the sole. The particles that passed by the mouth were transported to the tail, stored there, and then eaten. In the third type of feeding behaviour the snail moved under the water surface in a complex trajectory (Fig. 4E). Contacts with food particles resulted in deceleration; after eating them the speed increased again. This is why the movement of a snail along the trajectory was very uneven, as seen in Fig. 4E, where time intervals between black circles on the track were equal to 1 min. One can see in Fig. 4E that the intervals between successive turns of the snail (i.e. between sharp bends in the track) varied from 30 to 120 s.

As noted above, a snail with a lump of food particles not unfrequently fell to the bottom of the tank. Such a situation could also be induced artificially. In these experiments an adult snail moving under the water surface and searching for food was rapidly transferred to the bottom. The snail soon returned to the water surface and began searching for food again. Then the food (*Daphnia* powder) was put on the water surface, and the snail was allowed to eat for 10 min. After this, the snail was again transferred to the bottom, where it moved in a very sinuous trajectory (Fig. 4F); it crawled at the normal speed (about 1 mm s^{-1}) but changed the direction of locomotion repeatedly. The intervals between turns were 10–30 s. As a result, the track of the snail was extremely tangled; in a 20-min period the snail remained within the limits of the 50 mm × 50 mm square nearly all the time. But after 20 min of 'looping', the track changed sharply, and the snail soon reached the water surface. This experiment was repeated eight times with five snails, and in all cases tracks similar to those in Fig. 4F were observed. After even a short period of feeding on the water surface (15 s), the snail moved in a sinuous trajectory when put on the bottom, although the looping time (about 5 min) was shorter than after prolonged feeding.

Feeding on the water surface also caused long-term changes in the pattern of movement. Fig. 5A shows five scenes obtained on the day of feeding. (The snails had been fasted for 36 h; their tracks obtained the day before are presented in Fig. 1C.) At 08:00 h, the snails exhibited high locomotor activity with most of the horizontal near-bottom tracks directed to the right, as had been observed at the

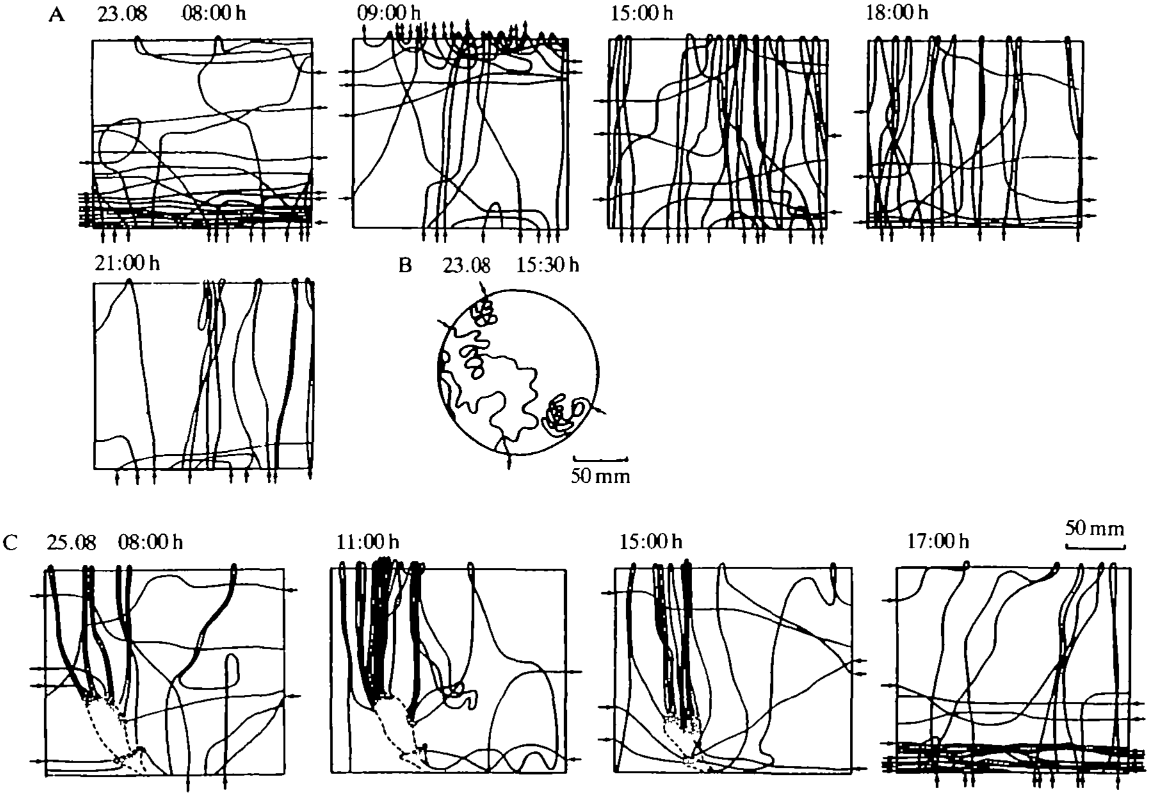

Fig. 5. (A,B) Creeping tracks of young snails which were fed on the water surface. The food was given at 08:30 h. Prolonged halts of snails near (on) the water surface for feeding are marked by dots. Other conventions, as in Fig. 1C. (C) Creeping tracks of young snails which were fed on the lettuce leaves fixed at the aquarium bottom near the wall. The leaves are shown by interrupted lines; the parts of leaves contacting the wall are stippled. Other conventions as in Fig. 1C.

same time the day before (Fig. 1C, 08:00 h). At 08:30 h, food powder was strewn upon the water surface. 15 min later most of the snails appeared near the water surface and started eating. Their tracks at the height of the eating are shown in Fig. 5A (09:00 h). One can see that most snails gathered near the water surface. If a snail appeared on the vertical wall, it immediately turned upwards again. There were also long vertical tracks from the bottom to the water surface. This was because, in the process of feeding, a snail sometimes fell to the bottom, with a lump of food particles attached to its foot (see above). After the snail had eaten these particles, it returned to the water surface. By 11:00 h, all the food on the water surface had been eaten and the snails left the water surface. From this time until the evening, their locomotor activity was high (15:00 h, 18:00 h), decreasing only later in the evening (21:00 h). All this time the snails crawled mainly in vertical trajectories, which comprised 80 % of the total length of track (Fig. 2B, 15:00–21:00 h). The bottom trajectories were much more sinuous (Fig. 5B) than before feeding (compare Fig. 1D).

Locomotion of snails during feeding on the bottom

1–2 h after lettuce leaves had been fixed on the aquarium bottom, nearly all the snails clustered together on the leaves and began eating them. If the leaves contacted the aquarium walls, the snails used the walls to come up to the water surface for ventilating the lung. Fig. 5C shows four scenes obtained on a day when snails fed on lettuce leaves (the top parts of the leaves that touched the wall are stippled). By 08:00 h not all the snails had found the leaves, but they gradually gathered there. The snails used the aquarium wall to reach the water surface to ventilate the lung. At 11:00 h most snails were feeding on the leaves. One can see numerous vertical tracks directed upwards (for lung ventilation) and downwards (for returning to the food). At 15:00 h, most of the leaves had been eaten, and excursions to the water surface became less frequent. At 17:00 h, the leftover lettuce was removed from the aquarium, and many near-bottom horizontal tracks appeared in the scene.

In most cases, a snail that had ascended to the water surface to ventilate the lung returned along its own trace or along the traces of other snails. As a result, the snail returned to the previous place of feeding. This is shown in Fig. 6, where the ascent and descent tracks of four snails are presented (Fig. 6A) as well as the way

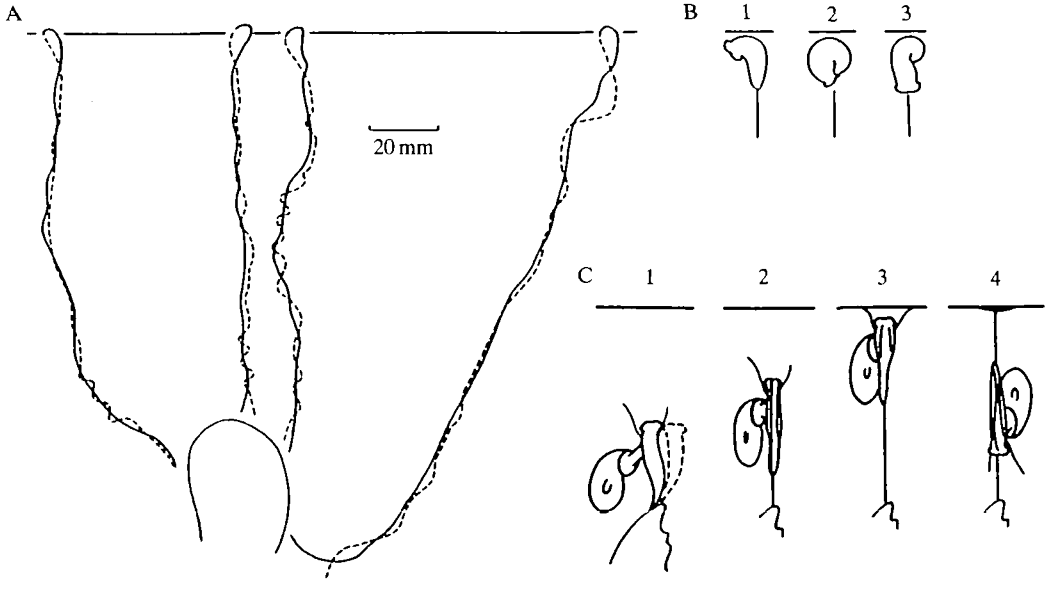

Fig. 6. (A,B) Crawling of snails along the mucus trace; (A) some of the tracks (at higher magnification) presented in Fig. 5C. Solid lines show ascending tracks, interrupted lines show descending ones. (B) How a snail turns after lung ventilation. (C) Building the mucus thread (1–3) and crawling along it (4) (see text for explanation).

the snails turned near the water surface (Fig. 6B). After a snail had reached the water surface and ventilated (during 10–20 s) the lung, it turned 180° to the right, so that its head appeared exactly on its own trace (Fig. 6B). The descending trajectories (interrupted lines in Fig. 6A) were very close to the ascending ones, except that the snail, during the descent, not unfrequently performed lateral oscillations with an amplitude of several millimetres ('searching' movements).

If the lettuce leaves placed on the bottom did not touch the vertical wall of the aquarium, the snails used another way of ascending to the water surface: they made a thread of mucus (Fig. 6C). Initially, a snail fastened itself by its tail to the top of a leaf and, for a long period, performed waving movements with its foot (Fig. 6C, 1). Then it unfastened itself from the leaf and started floating, leaving an ever longer thread behind the tail, the distal end of the thread being fastened to the top of the leaf (Fig. 6C, 2,3). When the snail had reached the surface and ventilated the lung, it turned down and crawled along the thread; the upper end of the thread appeared to be fastened to the water surface (Fig. 6C, 4). Later, this thread was used by other snails which ascended and descended along it.

Discussion

Influences upon the locomotor activity

We observed diurnal changes of locomotor activity in the snails, with a minimum at night (Fig. 2A). Similar changes were observed in a closely related species of freshwater pulmonate, *Helisoma trivolvis* (Kavaliers, 1981). In *Planorbis*, not only did total locomotor activity exhibit a diurnal rhythm but the relationship between horizontal and vertical motion also changed with time: horizontal tracks predominated during the day, and vertical ones at night (Fig. 2A). In addition, the zone of activity of snails shifted from the bottom [in the morning, Fig. 1C (08:00 h, 10:00 h)] to the water surface [during the day, Fig. 1C (12:00 h)].

The relationship between locomotor activity and feeding behaviour depends upon the type of food. A snail did not decelerate when it began eating the algae covering the aquarium walls. This seems reasonable: since the algal layer is very thin, repetitive scraping of the same place would be pointless. In contrast, while feeding on lettuce leaves or while eating the dry *Daphnia* powder on the water surface, a snail decelerated or even stopped moving. Whilst eating *Daphnia*, the snails decelerated gradually depending on the amount of food they got into their mouths (Fig. 4E). This also seems reasonable: it would be pointless to leave the source of food until it was exhausted. It is interesting that inhibition of the locomotor apparatus (i.e. termination ciliary beating) can be restricted in the posterior part of the sole of the foot, while the cilia on the anterior part of the sole continue beating; this part of the ciliated epithelium is thus converted from a locomotor organ to an organ transporting food particles. The ciliated epithelium can also be used for transporting the mucus in the caudal direction when a snail is building a mucus thread for coming up to the water surface (Fig. 6C). The foot cilia, therefore, can perform various functions. Neuronal mechanisms of differential control of various zones of ciliated epithelium are described in the second paper of this series (Deliagina and Orlovsky, 1990).

Inhibition of locomotion was also observed in *Planorbis* during reproductive behaviour, i.e. during mating and egg-laying (T. G. Deliagina and G. N. Orlovsky, unpublished data), as has been demonstrated for some other gastropod species (Geraerts and Joosse, 1983; Goldschmeding *et al.* 1983; Pinsker and Dudek, 1977). It is also well known that locomotion of freshwater snails is inhibited during defensive reactions. The locomotory system of *Planorbis* is activated when they start to move up from the bottom to the water surface for lung ventilation (Fig. 6A). Some of these inputs to the locomotion control system have been investigated electrophysiologically and are described in the second paper of this series (Deliagina and Orlovsky, 1990).

Fixed directions and planes of snail locomotion

In many of the scenes presented in this paper, horizontal and vertical tracks predominated, and their length, in a number of cases, reached 80 % of the total length of all tracks [see Fig. 1C (08:00 h, 10:00 h) and Fig. 5A (15:00 h, 18:00 h)]. We also show that both vertical and horizontal directions of locomotion are stabilized; that is, they are resistant to external disturbances (Fig. 3B). We have not been able to show that a snail can stabilize its direction of locomotion in anything other than the horizontal and vertical directions, except when it is crawling along a mucus trace (Fig. 6A). Since a snail, crawling on a clean aquarium wall, has no indications of the vertical (or horizontal) direction except for the force of gravity, it is evident that, during locomotion, the animal must: (1) measure the direction of the force of gravity, and (2) orient its body in relation to this direction in a specific way.

A few examples have also been presented in this paper to demonstrate that a snail, while crawling, can stay for a long time within the limits of the aquarium bottom (Fig. 3C) or on the water surface (Fig. 5A, 09:00 h). In both cases, a snail crawling on a horizontal surface now and then came up against a vertical wall and crawled on it. But its stay on the wall appeared to be very short: the snail turned down (if it reached the wall from the bottom) or up (if it arrived from the water surface) and soon returned to the horizontal surface. We assume that in these cases a snail uses the same principle of orientation that was used in the task of horizontal (vertical) locomotion, i.e. it measures the direction of the force of gravity and orients its body in relation to this direction. As a result, the plane on which the snail is crawling – either the bottom or the water surface – becomes fixed.

To stabilize the direction of locomotion, the snail must correct the body orientation in accordance with deflections from the 'desirable' direction. Apparently, for these corrections the snail uses several standard 'rules', some of which have been described above. For example, when a snail crawling vertically (or horizontally) on a vertical wall was forced to deflect to the right or to the left from the 'desirable' direction, it returned to the initial direction by turning to the opposite side without any 'searching' movements (Fig. 3B). When a snail reached the water surface to ventilate the lung, it performed a standard 180° turn; by the end of this turn, the snail was oriented with the head down, which is necessary for returning to the bottom (Fig. 6B). A snail that 'wanted' to crawl only on the bottom, once on the vertical wall, would turn until it reached the vertical position with the head down so as to return to the bottom (Fig. 3C). Finally, in some scenes obtained in the morning (Fig. 1C, 08:00 h; Fig. 5A, 08:00 h), most horizontal near-bottom tracks were directed to the right, which suggests a standard manner used by snails to get into such a trajectory (a turn to the left with its initial movement directed downwards, and a turn to the right with its initial movement directed upwards).

The biological expedience of the fixation of some directions and planes of movement is obvious for a variety of reasons. Fixation of the vertical direction (positive and negative geotaxis), which is found in many gastropods (Janse, 1981; Wolff, 1975), makes for a rapid rise to the water surface for lung ventilations, as well as for a rapid return to food sources located on the bottom. But vertical trajectories are not only related to respiration: in Fig. 5A (09:00 h) there are several vertical tracks used by snails to move quickly to food located on the water surface.

Fixation of the plane of the water surface is expedient in cases when the food is on the water surface. Fixation of the bottom plane can be expedient for the same reason. Less obvious is the biological expedience of fixation of the horizontal direction, especially the very high accuracy of maintenance of this direction (Fig. 3A).

Changes in the mechanism of gravity orientation

We observed not infrequently that a snail, crawling on the vertical wall, changed the direction of locomotion from horizontal to vertical, or *vice versa* (see e.g. Fig. 3A, track 4), and both the horizontal and vertical orientation of the snail were stabilized, i.e. resistant to external disturbances. A snail which spent a lot of time on the bottom (and whose position on this plane was actively stabilized) could suddenly ascend to the water surface in a vertical trajectory (Fig. 5C), and the vertical orientation of the snail on this trajectory was also stabilized. Switching in the mechanism of gravity orientation takes place with every respiratory act: during the rise to the water surface the upward direction is fixed, and after lung ventilation the downward one is fixed (change of the sign of geotaxis). While feeding on the water surface, a snail never left the surface for long (fixation of a plane) but, soon after all the food had been eaten, the snail left the water surface and crawled to the bottom in a vertical trajectory. Finally, vertical tracks were commoner than horizontal ones at night, whereas during the day (especially in the morning) horizontal tracks predominated (Fig. 1C).

Thus, the behaviour of a snail is determined, to a large extent, by changes in the mechanism of orientation in the gravitational field. These changes occur under the effect of both external factors (for example, the presence of food in a certain part of the aquarium) and internal factors (necessity for lung ventilation, etc.). Long-term changes in the behaviour of a snail brought about by external causes and lasting – in some cases – for a long time after the disappearance of these causes are also determined by changes in the gravity orientation mechanism. For example, for several hours after feeding on the water surface, the snails exhibited mostly vertical tracks (Fig. 5A, 15:00 h, 18:00 h).

In many cases, however, the behaviour of the snails was not connected with the gravity orientation mechanism. This happened, for example, when a snail fed on the aquarium wall covered with algae. When the rhythmic mechanism of scraping and transporting the food ('grazing') was activated, the snail track became sinuous (Fig. 3E). Another example is the crawling of a snail along a mucus thread (Fig. 6A).

'Searching' movements

There is a mechanism in the system of locomotor control in *Planorbis* which, in the absence of any external stimuli, forces the snail to perform left and right turns at irregular intervals. This mechanism was switched on when a snail fed on the water surface (Fig. 4E), or when it fell to the bottom and lost its food (Fig. 4F). The biological expedience of this mechanism is obvious: it restricts the area of crawling and increases the probability of finding food. The operation of this mechanism, once it has been triggered, is much longer than the duration of the initial stimulus (of contact with food). The central origin of switches of motor activity from the left half of the sole to the right half, and *vice versa*, has been demonstrated in electrophysiological experiments (Deliagina and Orlovsky, 1990).

There is also another mechanism in the *Planorbis* nervous system which imparts periodic deflections (to the right and to the left) of the head during locomotion. These deflections can be observed when a snail feeds on the algae covering the aquarium walls (Fig. 3D) or when a snail is crawling along the mucus trace (Fig. 6A). These lateral head movements seem to be used for finding the mucus trace, or for finding the shortest way to a rich food source. Similar oscillations of the head were also observed in another pulmonate gastropod, *Lymnaea stagnalis*, during feeding on an algae-covered surface (Dawkins, 1974).

In the next paper of this series (Deliagina and Orlovsky, 1990), the organization of the efferent system of pedal ganglia controlling the ciliated epithelium on the sole of *Planorbis* will be described.

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