FUNCTIONAL SIGNIFICANCE OF THE VENTRAL AND LATERAL FUNICULI IN THE FROG'S SPINAL CORD

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Abstract. The spinal cord was transected at the level of calamus scriptorius either completely (spinal preparation) or partially (funicular preparation). In the operated frogs and in normal controls cranial and peripheral receptive fields were stimulated by natural stimuli. Results indicated that the information necessary for somatic activation of the protective flight ascends in the dorsolateral funiculus, which can be characterized as an ascending part of the reflex arc of somatotopically guided avoidance behavior. The tectal region is apparently a center of responses. The information necessary for activating different patterns of locomotion adequate to environmental conditions goes unilaterally through the ventral and ventrolateral funiculus. A diminished specificity of these motor patterns observed after injury of the ventrolateral funiculus seems to be related to a reduced feedback from the periphery. Lacking of aquatic pattern of limb movements (even when terrestrial patterns of locomotion were undisturbed), and drowning in water seem to be related to an injury of a vestibulo-spinal system in the ventral funiculus. It is concluded that the ventrolateral area of the frog spinal cord, i.e., the area between median fissure and dorsal root, forms a closed system providing afferent and efferent information sufficient to evoke normal behavior.

INTRODUCTION

A high autonomy of the spinal cord function in lower vertebrates has been repeatedly stressed since the last century. However, even in the most primitive forms, a supraspinal control over body movement has
been reported. It is generally accepted that centers localized in cerebral peduncles, area statica and the rhombencephalic reticular formation influence the reflex activity of the spinal cord in anurans (1, 4, 5, 28, 37, 41). The tectal region is thought to mediate visually guided approach-avoidance responses (11, 33, 43). The exact origin, course and termination of supraspinal pathways have been studied principally in recent experimental studies (7, 12–15, 35, 36, 38, 39, 44, 45, 53). However, a functional significance of different funicular pathways in the spinal cord has not been determined experimentally (5, 28, 42, 54).

The aim of this study was to assess the functions of the frog’s spinal cord connected to the brain by discrete funiculi (“funicular preparations”).

The white matter of the spinal cord of the frog is divided into dorsal, lateral and ventral funiculi, their border being formed by dorsal and ventral roots (22). The uniform structure of the whole ventrolateral area and the lack of structural differentiation within this system have been stressed repeatedly (34, 50, 55). In our material the white matter just below the dorsal root entrance was considered as the dorsolateral funiculus, and the whole region in which motoneuron axons enter the white matter as the ventrolateral funiculus. The term “funicular preparation” served to denote an animal in which the spinal cord and the brain are connected exclusively by a particular funiculi. This investigation involved a systematic exploration of the behavior of various funicular preparations. The observations of these animals compared with normal and spinal animals was the test used.

MATERIAL AND METHODS

The experiments were carried out on approximately 100 frogs (Rana esculenta). Some of these were tested before the operation and will be referred to as normal control group. The spinal preparations were used as the another control group. The large group of experimental animals consisted of a number of various funicular preparations.

The spinal cord was completely or partially transected at the level of calamus scriptorius or 1 mm below (Fig. 2A) by a modification of Franzisket’s method (19).

The funicular preparation can be divided into various groups according to the localization of white matter spared at the level of transection:

1. V preparation, in which one or both of the ventral funiculi were left (8 animals, Figs. 1A and 2B);
2. V-VL preparation, in which ventral and ventrolateral funiculi were spared uni- or bilaterally (22 animals, Fig. 1B);

3. V-VL-L preparation, in which, besides the ventral and ventrolateral funiculi, the lateral part of the lateral funicules was spared unilaterally (10 animals, Fig. 1C);

4. V-VL-L-DL preparation, in which dorsolateral, lateral and ven-

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Fig. 1. Schematic representation of different types of spinal preparations: A, V preparation; B, V-VL preparation; C, V-VL-L preparation; D, V-VL-L-DL preparation; E, iV-VL-L-DL preparation; F, L preparation; G, V-coVL preparation. The dashed area, extent of damage. For further explanation see text.
trolateral funiculi were spared unilaterally and in which (i) two ventral funiculi were left, so that the ventrolateral area of white matter was preserved unilaterally (V-VL-L-DL preparation) (5 animals, Figs. 1D and 2C), or in which (ii) the left ventral funiculus was partly injured, i.e., their medial part was damaged (IV-VL-L-DL) (3 animals, Fig. 1E);

5. In several frogs other parts of the ventral and lateral funiculi were spared. Two preparations with spared lateral funiculi on both sides were examined (L preparation) (Fig. 1F). In some preparations the ventral funiculus of one side and the ventrolateral funiculus of the other were preserved (V-coVL) (Fig. 1G).

All preparations in which even a small part of a certain funiculus was intact were classified as belonging to a group with that funiculus intact. The estimation of tissue spared was relatively easy in preparations in which the transection was made half-way between the II and III dorsal root entrance. Preparations sectioned at the level of calamus scriptorius, where such estimation was impossible, have been rejected. Altogether 56 above-described funicular preparations could be classified.

Postoperative care was the same as in spinal animals (19). The examination of reflex activity of the operated frogs was made 10, 20, 30, 50 and sometimes 100 days after the operation. In 20 operated animals the reflexes were also tested 12 and 15 mo after the surgery.

The following spinal reflexes were examined in all the frogs:

1. Shake-off of the foreleg (wiping, Abwischreflex (19, 20, 30));
2. Non-sexual and sexual clasping reflex (Adductions-, Umarmungs- und Umklamerungreflexe (6, 18, 32));
3. Protraction of the shoulder with extension of the whole limb and spreading of the toes or retraction of the shoulder with extension of the remaining joints, i.e., stretching of the limb onto the back (2, 6, 21, 58);
4. Ipsilateral reciprocal flexion-extension reflexes of the fore and hindlimb with the frog lying on its back or half-restrained, so that the extremities have no support, and left stretched in exactly the same position (59);
5. Shake-off of the hindlimb (wiping, Abwischreflex (8, 17, 19, 20));
6. Flexion reflex of the hindlimb passively extended by its own weight (49, 56);
7. Uni- and bilateral extension of the hindlimbs and jumping examined in the sitting animal (3, 10).

The following reflexes elicited from cranial receptive fields were investigated in all our animals:

1. “Face wiping” movements performed by both forelegs in response to light tactile stimulation of the mouth and nostrils with Frey’s hair;
Fig. 2. A: Division of the white matter of the frog spinal cord into: V, ventral; VL, ventrolateral; L, lateral; DL, dorsolateral funiculi. Microphotograph from Klüver-Barrera stained slides at calamus scriptorius level (cal. scr.), half-way between calamus scriptorius and III dorsal root, and at the level of III dorsal root entrance (III DR).
Fig. 2. B: Sections of lesioned spinal cord segment in V preparation (frog 7A). C: Sections of lesioned spinal cord segment in V-VL-L-DL preparation (frog 12F).
2. Flight\(^1\) or passive defence reaction evoked by nociceptive stimulation of the head;
3. Flight or passive defence reaction evoked by large moving objects in the visual field (16, 31).

The behavior under different environmental conditions was examined in all the normal, 10 spinal and in 25 various funicular preparations. Frogs were:
1. Tested in a closed box (50 \times 50 \times 15 \text{ cm});
2. Put in an open box surrounded by 5 or 15 cm high walls;
3. Tested in an open field situation;
4. Put in a small aquarium with water at room temperature;
5. Left alone on a dry islet in the middle of a spacious water-filled tank made of perforated bricks, where the frogs could hide (modification of the open field situation test).

The majority of preparations were sacrificed 3 mo after the operation. Twenty of them were kept alive for 12 and 15 mo. The spinal cords were fixed in 10\% neutral formalin, removed and photographed for verification of the level of section. Histological control was performed in the majority of cases. Serial sections 10 \mu m thick were made in the frontal or the horizontal plane and stained with Klüver-Barrera method. Some of the preparations, in particular those in which a relatively large part of the funiculi was left undamaged, were studied macroscopically.

RESULTS

The reflex activity of operated animals differed depending on the level of transection. Stimulation of the dorsal part of the body evoked a greater variety of reflexes in the preparations sectioned at the calamus scriptorius level than in similar preparations sectioned in the vicinity of the III dorsal root (about 1 mm below the spino-bulbar junction) (Fig. 3). The relatively low threshold of extension, jumping and alteration/displacement of receptive fields of the hindlimbs reflexes was observed in animals with the "low" transection. The flexion reflex of the foreleg and all the related functions such as clasping, wiping and face-wiping reflexes were absent in these frogs. The ambulatory and swimming patterns were disturbed, if at all present. The preparations transected at the intermediary level differed from each other. However, extension and all related functions have a relative low threshold in all

\(^1\) Active behavior elicited by visual releasers of avoidance and somatic releasers of escape responses is referred to here as flight.
these animals, and the flexion reflex could sometimes be obtained in preparations sectioned half-way between II and III roots.

In asymmetrical transections the spinal reflexes elicited on the two sides of the body were different. These preparations and those transected just above the third root entrance were therefore rejected.

Fig. 3. Scheme of the receptive fields of some spinal reflexes in frog lesioned at the level of calamus scriptorius (I) and just above the III dorsal root entrance (I). Dotted area, receptive field of the shake-off of the foreleg; dashed area, receptive field of the shake-off of the hindlimb; vertically lined area, receptive field of the bilateral extension of the hindlimbs and jumping.

Stimulation of the trunk and extremities

The whole assembly of spinal reflexes (see Methods) was obtained in all the V, V-VL and L preparations (34 frogs). In these animals the threshold of flexion and extension in particular joints was lower than the threshold of flexion and extension of the whole limb. In the passively suspended animal, increased intensity of stimulation activated “chain reflexes” (59). In the sitting animal, a jumping reflex was evoked by a strong pinching of the lateral part of the toes of the fore- and hindlimb. A sporadic stimulation of the trunk and extremities did not evoke
the ambulatory rhythm of progression. However, in some of the V-VL preparations walking could be elicited, the response having a long latency. It was found that this diagonal pattern of limb movements depended upon head movements and not upon body stimulation, since it could be observed after passively moving the anterior part of the body. The question whether or not the threshold of the reflexes observed in the spinal animal differed from the threshold of the reactions described above cannot be answered on the basis of this experiment.

The V-VL-L preparation did not respond to light tactile stimuli. Sometimes the flight reaction or spinal reflexes were obtained in response to strong and repetitive stimulation of the body trunk. In normal animals and in the V-VL-L-DL preparations group the tactile and nociceptive stimulation at different receptive fields of the body and extremities induced flight or passive defence responses. Nevertheless, stimulation of the back evoked the shake-off response of the hindlimb, if the animal was kept in a small closed box. Similarly the embracing reflex was obtained when the frog was held in the experimenter's hand. Generally even light tactile stimuli evoked flight.

Of particular interest was the fact that in the V-VL-L-DL preparations, in which the ventral funiculi (ventral commisure?) were damaged, light stimulation of all receptive fields of the trunk and extremities evoked local reflexes on the "fully transected" side whereas the flight reaction was observed on the "funicular" side.

The possibility that at least part of the reflexes obtained in the V-VL-L-DL preparations was evoked from cranial receptive fields, i.e., from the visual or acoustic systems, was excluded in control experiments, employing special screens.

_Simulation of cranial receptive fields_

Light tactile stimulation of the head usually evoked the flight reaction in normal frogs, sometimes the shake-off of the foreleg or closing and retraction of the eyes (27). The last reaction was the single one observed in the spinal and L preparations. In all the remaining funicular frogs the alternate shake-off of the forelegs (although the hands did not touch the skin) were elicited by tactile stimulation of the skin around the mouth and nostrils. Acceleration of the respiratory rate and turning of the body towards the visual stimulus was observed in some preparations, when Frey's hair came into the visual field of the animal.

In normal frogs there were seen two types of responses to nociceptive stimulation of any place on the head as well as to the sight of large advancing objects. The animals ran from the stimulus (flight) or squatted down and closed their eyes (passive defence reaction). The last reac-
tion was observed in 7 various funicular preparations. Generally the active behavior (flight) appeared under these conditions.

A more detailed study of this “flight” reaction revealed differences between various preparations. The V-VL-L-DL and V-VL-L groups jumped in the open field and walked in the small closed box as normal frogs (all the 15 preparations examined). In same cases the withdrawal reaction was observed. The V-VL preparations could respond similarly (5 out of 17 examined preparations) or employed the diagonal pattern of limb movements in both situations (8 frogs out of 17 examined). A mixed reaction (walking and jumping alternatively) was sometimes observed in these animals. Three V-VL preparations used mixed or abnormal motor patterns. This last behavior was usually evoked in the V preparations group. Nine out of 10 animals examined alternatively exhibited walking and shake-off of the forelegs or walking, jumping and shake-off of the fore and hindlimbs. Preparations moved at random to and from the stimulus. In some of these frogs tremors of extended forelimb and long latencies of individual components of diagonal and in phase locomotor movements were observed. These abnormalities disappeared subsequently. A strong tendency to move without any definite pattern was occurred in one V preparation and in a preparation where one ventral and one contralateral ventrolateral funiculus was spared (V-coVL). These preparations moved each limb separately in response to adequate stimulation of the cranial receptive fields.

The number of animals in different groups of preparations in which designate pattern of behavior was observed is given in Table I. The effects of specific stimulation of somatic and cranial receptive fields are given in Table II.

**Table 1**

Motor patterns evoked in various funicular preparations by aversive stimuli in different conditions (the number of animals in brackets)

<table>
<thead>
<tr>
<th>Conditions</th>
<th>Motor pattern</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Jumping</td>
</tr>
<tr>
<td>Open field situation</td>
<td>V-VL-L-DL (5)</td>
</tr>
<tr>
<td></td>
<td>V-VL-L (10)</td>
</tr>
<tr>
<td></td>
<td>V-VL (5)</td>
</tr>
<tr>
<td>Small closed box</td>
<td>Not present</td>
</tr>
<tr>
<td></td>
<td>V-VL-L (10)</td>
</tr>
<tr>
<td></td>
<td>V-VL (13)</td>
</tr>
<tr>
<td>Group</td>
<td>Number of animals</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>------------------</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>Normal</td>
<td>20</td>
</tr>
<tr>
<td>V-VL-L-DL preparation</td>
<td>5</td>
</tr>
<tr>
<td>iV-VL-L-DL preparation</td>
<td>3</td>
</tr>
<tr>
<td>V-VL-L preparation</td>
<td>10</td>
</tr>
<tr>
<td>V-VL preparation</td>
<td>22</td>
</tr>
<tr>
<td>V preparation</td>
<td>8</td>
</tr>
<tr>
<td>V-coVL preparation</td>
<td>3</td>
</tr>
<tr>
<td>L preparation</td>
<td>2</td>
</tr>
<tr>
<td>Spinal</td>
<td>20</td>
</tr>
</tbody>
</table>
It is important to note that disturbances observed in the flight reaction cannot be due to an impairment of effectors, since the preparations were able to move their limbs in a normal way. For example, in a V preparation in which no pattern of moving was observed in response to the sight of large moving objects strong stimulation of the hindlimb evoked a well-coordinated jumping movement.

Behavioral responses under different environmental conditions

In this series of experiments simple tests were used for eliciting natural behavioral responses of the animal.

Preparations in which only the lateral part of the lateral funiculi was left intact (L preparations), similarly to spinal animals did not respond to distant stimuli and drowned passively when put into water.

In the open field situation the flight reaction and effective attempts to reach a hiding place in dark corners were observed in all normal frogs and in three V-VL-L-DL preparations. In most funicular animals, however, the attempts to hide were ineffective and usually the animal ceased to move entirely before reaching the hiding place (12 preparations out of the 25 examined). The V preparations were less active. Three of the 5 animals examined sat practically motionless when the ground was moist. The unilateral V-VL preparations frequently made 2–3 steps. Usually a diagonal pattern of limb movements was observed in this animals.

In the second experiment normal frogs as well as various funicular preparations jumped out of the small open box (15 frogs out of the 25 examined, both V-VL-L-DL and V preparations). Some of the V-VL-L and V-VL preparations got out of this box after a distinct walking reaction (5 animals). Some of the V-VL and V preparations moved inside the box and could not surmount even a wall, as low as 5 cm (5 animals). Progressive changes, however, occurred in three V-VL preparations: at the first attempt, it took the animal some time to leave the box (3–5 min); after 10 days it got out almost immediately and during the third experimental session, i.e., after 3–5 trials, it jumped out immediately.

The preservation of the ventral funiculus enabled the animal to float and not to drown, as was the case with spinal animals or L preparations. However, in the V preparations' swimming movements were not observed. On the contrary all the V-VL preparations could swim regularly as a rule (20 preparations examined). Nevertheless, in the unilateral V-VL preparations a distinct tendency to remain motionless was observed, whereas the bilateral ones were relatively agile. The V-VL-L and V-VL-L-DL preparations with ventral funiculi spared did not differ
from normal frogs, whereas the V-VL-L-DL preparations in which the left ventral funiculus was partly injured could be drowned, although a high degree of motor excitability was observed and animals "swam" with chaotic movements, each limb operating separately. After a tactile stimulation of the planta or a contact with the aquarium floor, the animals made movements which resembled walking or jumping.

The behavior of different frogs when left alone on a small islet in a spacious water container can be summarized as follows: the V-VL-L-DL and V-VL-L preparations jumped into the water, swam to the bricks and hide there (12 preparations examined). To some extent the V-VL preparations acted similarly. They were able to hide, although it took them longer. They made swimming movements with intervals. In some of these preparations abnormal body positions were observed which disappeared after several trials. Some of the V and V-VL preparations slid into the water from the islet after various periods of time, but most remained motionless on the surface of the water.

The iV-VL-L-DL preparations were not examined in these conditions. The behavior of different preparations in different environmental conditions is summarized in Table III.

**Table III**

Behavior in different environmental conditions

<table>
<thead>
<tr>
<th>Group</th>
<th>Number of animals</th>
<th>Open box</th>
<th>Closed box</th>
<th>Open space</th>
<th>Water container</th>
<th>Water container</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Small</td>
<td>Small</td>
</tr>
<tr>
<td>Normal</td>
<td>20</td>
<td>Jumping</td>
<td>Walking</td>
<td>Jumping</td>
<td>Swimming floating</td>
<td>Swimming swimming</td>
</tr>
<tr>
<td>V-VL-L-DL preparation</td>
<td>5</td>
<td>Jumping</td>
<td>Walking</td>
<td>Jumping walking</td>
<td>Swimming floating</td>
<td>Swimming swimming</td>
</tr>
<tr>
<td>iv-VL-L-DL preparation</td>
<td>3</td>
<td>Jumping</td>
<td>Walking</td>
<td>Jumping walking</td>
<td>Drowned (motor excitat-</td>
<td>Floating</td>
</tr>
<tr>
<td>V-VL-L preparation</td>
<td>10</td>
<td>Walking</td>
<td>Walking</td>
<td>Walking</td>
<td>Swimming floating</td>
<td>Swimming</td>
</tr>
<tr>
<td>V-VL preparation</td>
<td>22</td>
<td>Walking</td>
<td>Walking</td>
<td>Walking</td>
<td>Floating</td>
<td>Swimming at intervals</td>
</tr>
<tr>
<td>V preparation</td>
<td>8</td>
<td>Walking</td>
<td>Undefined behavior</td>
<td>No effect or walking (?)</td>
<td>Floating</td>
<td>Floating</td>
</tr>
<tr>
<td>L preparation</td>
<td>2</td>
<td>No effect</td>
<td>No effect</td>
<td>No effect</td>
<td>Drowned (passively)</td>
<td>Drowned (passively)</td>
</tr>
<tr>
<td>Spinal</td>
<td>20</td>
<td>No effect</td>
<td>No effect</td>
<td>No effect</td>
<td>Drowned (passively)</td>
<td>Drowned (passively)</td>
</tr>
</tbody>
</table>
DISCUSSION

The II root (hyomandibularis) partially innervates the foreleg in the frog (22). In our preparations the spinal cord was sectioned between the II and III dorsal root entry zone. Thus in the operated animals somatic information from the ventral part of the shoulder entered the CNS cranially to the level of lesion or was eliminated. Other information from the trunk and extremities entered CNS caudally to the lesion. Large anterior horn cells are present in the frog at the level of calamus scriptorius. Flexor motoneurons are situated more cranially than the motoneurons supplying extensor muscles of the same region of the limb (with the exception of motoneurons of the toes) (54). It is possible therefore, that the efferents were injured to a different extent in various funicular animals. The flexor motoneurons to the foreleg could be excluded in preparations transected at a relatively low level. This hypothesis is confirmed by the following observations: (i) the flexion reflex of the foreleg and all the more complex functions connected with this movement were absent in preparations sectioned just above the III dorsal root; (ii) in preparations transected at the level of calamus scriptorius these functions were unaffected; (iii) the preparations cut half-way between dorsal root II and III exhibited intermediate properties. As aforesaid preparations with efferent deficiencies were rejected.

Effects of stimulation of the body receptive fields

In a normal frog the stimulation of the body and extremities evokes a passive defence or a biologically effective flight reaction. Some of the local spinal reflexes appear under special conditions. For example, the shake-off of the hind limb was found after closing the avenues of escape and the embracing reflex after “immobilizing” the animal in a supine position (43). In the spinal frog, stimulation of the body and limbs evokes reflexes related to the receptive field, the type and intensity of the stimulation and to the position of the examined limb. The relatively local reactions include uni- and bilateral flexion and extension, shake-off, streck, stretch and clasping reflexes. The number of rather chaotic movements is observed in response to a strong and repetitive stimulation. A strong mechanical stimulation of the toes can induce jumping even in the acute spinal frog. It was noted that all patterns of rhythmic movements of progression in anurans are of spinal origin (3, 6, 9). Thus in both groups of animals similar response patterns are present, but a given set of them characterizes the given group.

The V-VL-L-DL preparations resembled normal animals and to stimulation of the trunk and extremities reacted adequately by flight, pas-
sive defence reaction or local reflexes. On the other hand, this stimulation did not evoke flight in the V and V-VL preparations. In that respect the animals resembled spinal preparations. In the V-VL-L preparations an extremely high threshold of all responses was observed, although a flight reaction could sometimes be elicited. *Thus the dorsolateral and to some extent the lateral funiculus can be characterized as an ascending part of the reflex arc of somatotopically guided avoidance behavior.* All preparations in which one dorsolateral funiculus was preserved were able to perform the flight reaction to the stimulation of the ipsilateral half of the body: the information runs ipsilaterally. The medial part of the ventral funiculus at the level of calamus scriptorius (the role of commissura anterior was not investigated) mediates information from the contralateral half of the body. The afferent influx from the fully transected side was not observed in the described experiment after damage of these structure.

**Effects of the stimulation of cranial receptive fields**

In this group of reflexes the reflexogenic zones are on the head, while the effectors are in the spinal cord. They cannot be elicited in spinal animals or in the L preparations. This seems to indicate that, in the frog, a supraspinal control over body movements is not mediated via the lateral part of the lateral funiculus.

In the normal frog an alternative shake-off of both of the forelegs is observed if food touches the skin around the mouth. Light tactile stimulation of that skin area, as well as stimulation of the nostrils elicited such a reaction in all our funicular animals, with the exception of L preparations. It is thus not possible to determine which supraspinal system is involved in this function. Besides, the feedback from the foreleg could partially pass along the II dorsal root above the transection, partially through the supraspinal ascending tracts spared at the level of section. It is noted that in some frogs other elements of prey-catching behavior were found, e.g., at the sight of a small moving object — Frey’s hair (visually guided approach behavior; 11, 16, 30, 33, 51, 52).

Nociceptive stimulation of the head evokes a passive defence or active flight reaction in normal frogs (43). This protective flight reaction can be elicited not only by an adequate stimulation of the head, but also by the sight of large moving objects (visually-guided avoidance behavior; 11, 31, 33). With the exception of the L preparations, aversive visual stimuli elicited active behavior in all our funicular animals; nevertheless, there were differences between individual group. The V-VL-L-DL and V-VL-L preparations fled like normal animals. The V-VL preparations were most variable from the point of view of motor acti-
vity. Some of the preparations resembled normal frogs, but in most cases it was observed that an impaired motor pattern alternated with one that was normal under the circumstances. An impairment was most obvious in the V preparations where abnormal motor patterns usually alternated with each other. According to the classification used the ventrolateral funiculus was spared in the first group, it was damaged to a varying extent in individual frogs in the second group and it was eliminated in the third group. Thus disturbances of flight on land correspond to the extent of damage to the ventrolateral funiculus. It would be interesting to know if the feedback from the periphery or specific descending influences are responsible for the result obtained and whether or not another ascending tract is mediating this function.

**Natural behavior of the frog**

The motor behavior observed in an open space qualitatively resembled that evoking aversive responses. However, cessation of movements and not abnormal motor patterns were usually observed in preparations with a small portion of the white matter spared at the level of section. There can be little doubt that the result depended on the level of general arousal of the animal in the two experimental situations.

The most interesting aspect of the free behavior tests was that the level of motor activity of different types of funicular preparations was relatively stable, to some extent independent of the experimental situation. The V preparations exhibited relatively little "spontaneous" and evoked activity, the bilateral V-VL preparations were more active than the unilateral ones and some of the V-VL-L-DL preparations closely resembled normal animals. In general it appeared that the amount of white matter (descending fibers) preserved corresponded to the extent of motor activity exhibited by the animal both on land and in water. It is possible that this activity depends on the level of facilitating influences upon the entire motor system of the spinal cord.

To some extent this simple hypothesis could explain why walking prevails in various experimental conditions. Usually the frog with a small part of the white matter spared at the level of the spino-bulbar junction, exhibited an ambulatory rhythm of progression in all situations. However, even a V preparation could jump out of a small open box. As we know, a lot of muscle energy goes to lift the body against gravity, while energy devoted to terrestrial progression is very low in the frog (25). It is therefore assumed that jumping was to some extent eliminated in preparations with a decreased "output" from the brain.

The frequency of swimming movements observed in various funiculal preparations seems to be related to the extent of damage to the
ventrolateral funiculus. Nevertheless, these movements were well-coordinated, if present. The lack of aquatic pattern of limb movements was observed after injury of the ventral funiculus, even when terrestrial patterns of locomotion were undisturbed. On the other hand, preparations with a damaged ventral funiculus drowned in water. Both types of impairment can be related to labyrinthine control of movement and they closely resembled the effects of removing the labyrinth (24, 25). Abnormal postural components of terrestrial locomotion, if at all present, could not be determined by the methods used in our experiments (see 25).

**Anatomical considerations**

Our results show that the ventrolateral area of the white matter of the frog spinal cord forms a closed system providing sensory, and motor information sufficient to evoke a normal behavior of the animal. The role of some of the funiculi constituting the investigated part of the nervous tissue was described above. The comparison of this role with anatomical data will be the aim of the last part of the discussion. It was demonstrated that sparing the ventral and ventrolateral funiculi at the level of calamus scriptorius produced a preparation reacting as an intact animal to all stimuli except those applied to the trunk and the extremities. The somesthetic information necessary for the activation of protective flight reaction ascends in the dorsolateral funiculus. The origin and destination of this information is unknown. It may be presumed that the tectal region which serves somatosensory functions mediated this avoidance behavior:

The gray matter of the amphibian spinal cord contains a number of secondary sensory elements, the so-called funicular and commissural cells (48). It is assumed that the ventral and lateral funiculi are largely made up of axons of these cells. Unilateral funicular cell axons ascend in the lateral funiculus and seem to be concerned with spino-cerebellar and cerebellum-spinal systems (4, 14, 22, 36, 39, 40, 42, 46, 47, 56). On the other hand, the spino-cerebellar and spino-tectal pathways are closely related in lower vertebrates. For example, at the level of medulla oblongata of the frog the spino-cerebellar and spino-tectal tract are intermingled (40) and in some urodela many of the fibers which cross the midline, forming a component of the comissura cerebelli, were observed to arise as collaterals of spino-tectal fibers (27, 40). A hypothesis may be put forward that the spino-tectal tract accompanies the spino-cerebellar tract through the spinal cord passing through the dorsal part of the lateral funiculus.

The V-VL preparations reacted as intact animals to changes in en-
vironmental conditions. If only the ventral funiculus was preserved, the preparation did not exhibit adequate reactions. A loss of information from the periphery seems to be responsible for nonspecific excitation of the spinal cord. Formerly it was believed that contralateral commissural cells’ axons carried through the ventrolateral funiculus information about pain, temperature, general tactile and primitive muscle sense to the motor tegmentum of the medulla oblongata and to the tectum mesencephali (5, 28). In our experiments the information detected through the ventrolateral funiculus appeared sufficient for a correct operation of spinal motor patterns, both local and locomotor. It is noted that in a normal frog a terrestrial or aquatic pattern of limb movements depends on the presence or absence of mechanical stimuli applied to the ventral surface of the body and the planter surface of the paw (25).

Thus the following mechanism of progression can be postulated in the frog: the “receptive field” for locomotion includes somesthetic and visual receptors. Stimulation of each of these receptors affects the impulses propagated to the tectum mesencephali, the somesthetic one acting through the dorsolateral funiculus. The mode of operation of the tectum (reflex center) is unknown, but in fact dispersed system facilitates the entire motor system of the spinal cord (1, 5, 23, 43). The feedback from the labyrinth enables the animal to float, whereas the feedback from the periphery seems to be necessary to “channel” those facilitating influences. It would be interesting to know the extent of redundancy in this system (26).

REFERENCES

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