SPINAL CONDUCTION AND KINESTHETIC SENSITIVITY IN THE MAZE HABIT[1]

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The importance of kinesthetic and organic sensations has been much emphasized in recent psychological speculation, both behavioristic and otherwise. Our most widely taught theory of the emotions is based upon a doctrine of sensory reverberations from visceral activity, the doctrine of "current control" of the speed and accuracy of movement still has many adherents, and the theory of implicit movements as the organic basis of thinking extends the same concepts to the psychology of thinking. In general, these developments represent a tendency, fostered by recent studies of nerve conduction, to seek the immediate completion of the conditioned-reflex circuit in motor activity and to substitute the conception of chain reflexes for that of continued intraneural activity.

Toward the development of this point of view the analysis of the sensory control of the maze habit has contributed no small part. Watson ('07) successively and simultaneously eliminated all of the important distance receptors of the rat without serious interference with the animal's ability to learn and execute accurately the maze habit. This seemingly left kinesthetic and organic sensitivity as the sole remaining basis for the habit. As Watson pointed out, these first studies, by the method of sensory elimination, gave only negative evidence without indication of the nature of the intraorganic processes which control the maze running.

In their study of behavior in a maze with alleys adjustable in length, Carr and Watson ('08) obtained further evidence that the movement series is internally conditioned and that after distraction the animal regained orientation from the kinesthetic pattern

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aroused by running some segment of the maze. They then clearly enunciated the theory that, "the 'movement to come' is released at the proper time by the afferent (kinesthetic) impulses aroused by the movement which has just been made," and this interpretation has been followed in almost all succeeding discussions of the maze habit. One of the most definite recent statements of this chain-reflex hypothesis is that of Washburn ('16). "When one is playing a piece of music for the first or second time, each movement has to have the stimulus of the notes on the page; when a piece has been long practiced, each movement sets up the next one 'automatically.' This really means that, as one movement is performed, the sensory processes occasioned by the contraction of the muscles involved excite the motor paths for the next movement. The stimulus for one movement is the kinesthetic excitations received from the preceding movement."

Vincent's later work ('15) showed the occasional importance of visual, olfactory and tactile cues, but did not question the essential conclusions from Watson's studies.

We were first led to doubt the validity of this interpretation of the maze habit by observations on the maze-running of rats after cerebellar injuries (Lashley and McCarthy, '27). Marked changes in the motor pattern were seen to have no effect upon accuracy of orientation in the maze, even in blind animals under conditions where other than supposedly kinesthetic cues seemed to be eliminated. This raised the question as to whether the habit is controlled by kinesthetic sensitivity or by some wholly intraneural mechanism, once orientation has been obtained. Are automatized sequences of movement the result of a mechanism by which each movement arouses sensory cues to initiate the next, or of some mechanism in which a central organization, once aroused, discharges successive motor impulses constituting the series, with comparative independence of the sensory consequences of the movements?

The experiments with lesions to the cerebellum are inconclusive because we know neither the important components of the movement system nor the afferent impulses which may be essential to the habit. Perhaps the only crucial experiment for the question would be one with animals having section of all the somatic sensory fibers. This seems technically impossible and the question may therefore be one which can be answered only in terms of relative probabilities deduced from indirect evidence. Loss of ability to run the maze after partial destruction of kinesthetic sensitivity might serve to establish the chain reflex theory. Survival of the habit after even severe disturbance of kinesthetic sensitivity may always be interpreted as due to failure to eliminate the significant afferent impulses. Nevertheless, the probability of the chain-reflex hypothesis is reduced in proportion to the extent of anesthesia and the absence of effects of anesthesia upon the performance of the habit.

With these limitations, it seemed to us that some significant data might still be obtained by a study of the effects of extensive destruction of the spinal afferent tracts upon the accuracy of maze running. We have, therefore, carried out a series of experiments in which animals trained in the maze were subjected to spinal lesions and subsequently tested for retention of the habit. The senior author alone is responsible for the surgical and histological part of the work. The training and tests of performance have been carried out by both of us independently on different sets of animals, with essentially similar results.

METHODS

Training. The animals were trained with food as incentive and five trials per day in a maze with 8 *culs de sac* (fig. 1) until 10 consecutive runs without error were made. This maze had been constructed to record errors automatically so that animals could be tested in it in total darkness. The recording platforms were arranged symmetrically on each side of the openings from alley to alley so that they gave no directive tactile cues. Two groups of rats were trained with somewhat different subsequent procedures. The first consisted of young rats purchased from a local dealer. They were rested for seven days after training, were then retrained until 10 consecutive errorless trials were obtained (preliminary retention tests) and subjected to operation. Seven days after operation they were again retrained to 10 successive errorless trials (post-operative retention tests). During all the work with them these animals were very unstable, easily distracted during the period in the maze and rarely eager for food. They are number 1, 2, 3, and 6 of the protocols. Their records were difficult to interpret because of their erratic behavior, so the experiment was repeated with another group.

These were older animals, reared in the laboratory. They were were given 50 trials of overtraining after reaching the criterion of 10 errorless trials. They were then rested for ten days, given preliminary retention tests and also ten trials with the maze in darkness. (This was accomplished by covering the maze with

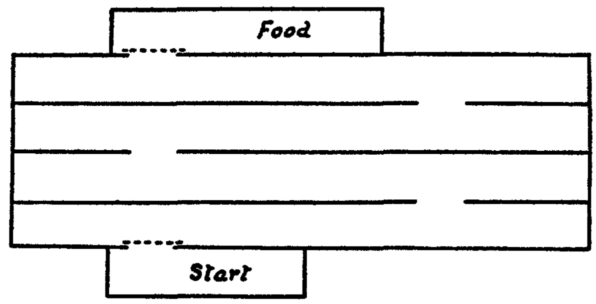

FIG. 1. GROUND-PLAN OF MAZE

Start, starting compartment; *Food*, food compartment. The broken lines represent swinging doors serving to prevent back-tracking from the maze and food compartment.

black cloth and several layers of heavy paper. Observation through a peephole failed to reveal light leakage after thirty seconds adaptation for our eyes.) The animals were then operated and from six to ten days later, depending upon the rate of recovery, were given postoperative retention tests.

Surgical. Under ether anesthesia the third cervical neural arch was removed and the cord exposed by a transverse incision of the dura. The point of a thin-bladed iridectomy knife was passed through the cord at the depth to which we wished the lesion to penetrate and the overlying fibers then cut through with the edge. This insured that all fibers peripheral to the line of penetration of the knife were cut and not merely pushed aside.

The injuries involved either section of the dorsal funiculus, section of both lateral funiculi, or section of the ventral funiculus. The last injury involved lifting the cord from the canal with consequent compression and shock and only one animal, and that with a partial lesion, survived. After the injury to the cord the muscles and skin were united above the cord by interrupted sutures and the wound dressed with collodion.

Histological. At necropsy the brain and cord were removed and prepared in serial sections by the Marchi method. For most cases complete serial sections were preserved from below the level of the lesion to the superior colliculi. The figures of plates 1 and 2 are made from camera outlines. Solid lines are used to represent general regions and contours; stippling in all cases represents degenerated fibers; solid black areas represent unabsorbed clots. For the plates one section was sketched at the level of maximum injury (*a*) and one (*b*) at a sufficiently higher level to avoid the degeneration of the shorter ground bundles and present only tracts which could be traced into the medulla.

There are few data available on the spinal tracts of the rat so we have been compelled to work out their position as well as possible from our material. A certain fallacy may arise here since our knowledge of the tracts is limited to what we have destroyed and our estimates of the character of the lesions are based upon that knowledge. However, the lesions cover every part of the cord except the median ventral columns so we may be sure that in one or another animal we have severed every organized tract in the cord and that the demonstration of the tracts is limited only by the level of the lesions and the defects of the Marchi technique as a method for the rat.

THE SPINAL TRACTS OF THE RAT

The conduction paths of the spinal cord of the rat have not been described in detail. Interest has centered chiefly in the pyramidal tracts because of their deviation from the usual lateral position. They have been described and figured by Lenhossek ('89), Bechterew ('90), Goldstein ('04), Van Der Vloet ('06), King ('10), Ranson ('14), and Linowecki ('14).

Ranson ('14) has described the position of Clarke's column and the tract of Lissauer. The rubro-spinal tract has been traced by Held ('90) and by Papez ('23), but briefly and without figures so that its exact position in the cord is not clear. We have not found descriptions of other tracts.

The series of cases studied in the present experiment has involved the interruption of all the tracts of the cord in one or another animal and we have been able to trace these in so far as they are revealed by the Marchi technique. The pyramidal tract does not stain readily by the Marchi method, as Ranson and others have pointed out, because of the thinness of its medullation. The same seems true of other long descending tracts, for in only a few of our specimens have we been able to trace degeneration below the lesions. In contrast, many ascending tracts show clearly, with well defined limits.

Descending tracts

Cortico-spinal. The descending fibers from the cortex occupy the median ventral position in the dorsal funiculus (plate 1, fig. C). Decussation of the pyramidal tracts to this position seems to be complete and Ranson ('13, '14) reported no other descending degeneration after hemidecerebration.

Rubro-spinal. This has been described in a preliminary note by Papez ('23). He does not figure it and states its position in the cord only as corresponding to that in other mammals. We find a large clearly limited bundle ventro-lateral to the dorsal horns (plate 1, figs. B and C) which is probably the rubro-spinal tract.

Schultz's comma. After section of the dorsal funiculus the comma appears as a small, well defined descending bundle lying between the fasciculus gracilis and fasciculus cuneatus on each side (plate 1, fig. B).

No other clearly defined descending tracts are visible in our preparations. After lesions to the lateral and ventral funiculi many degenerated fibers may be traced caudad in these regions, but they appear rather uniformly scattered and as our preparations do not include lesions above the cervical cord it is impossible to distinguish the source of the various scattered fibers.

Ascending tracts

Fasciculus gracilis. In degeneration of the dorsal funiculus this tract appears as a clearly defined bundle which can be traced to its complete termination in the nucleus gracilis (plate 1, fig. 4b).

Fasciculus cuneatus. This bundle lies lateral to the fasciculus gracilis (plate 1, fig. 4b). It gives off fibers to the gray matter throughout its length and receives additions from the dorsal cervical roots (plate 2, fig. 6b).

After destruction of the lateral funiculus, degeneration appears throughout an extensive zone in the ventro-lateral region of the cord (plate 2, fig. 8 and 9b). Traced into the medulla these ascending fibers are seen to break up into four principal groups (plate 1, fig. A). It has not been possible to determine with certainty the origin of these bundles in the cord, but their most probable positions in the cervical cord, judged by tracing downward from the medulla, are indicated below.

Fasciculus spino-cerebellaris dorsalis. The fibers lying in the more dorsal portions of the lateral funiculus may be traced forward to the medulla where they separate from the remainder of the degenerated mass to pass laterad to the posterior cerebellar peduncles (plate 1, fig. A, *s.c.d.*).

Fasciculus spino-cerebellaris ventralis. The more ventral fibers of the lateral funiculus may be distinguished in the medulla as a broad band of fibers which ultimately turn laterad to reach the anterior cerebellar peduncle (plate 1, fig. A, *s.c.v.*).

Spino-quadrigeminal system (?). After destruction of the lateral funiculus a large number of degenerated fibers appear scattered in the ventral region of the reticulated substance of the medulla (plate 1, fig. A, *s.q.*). Traced forward they ascend and are lost, in our material, in the region of the inferior colliculi. Traced caudad, they could be followed to the most ventral portions of the lateral funiculus and to scattered fibers of the ventral funiculus.

Fibers to the median longitudinal bundle. After lesions to the ventral portion of the lateral funiculus or to the ventral funiculus a few degenerated fibers appeared in the fasciculus longitudinalis medialis of the medulla, (plate 1, fig. A). These could not be traced to their termination because of defective fixation of our material. They seemed to be derived chiefly from the scattered fibers of the ventral funiculus. Some of the fibers of this and the preceding systems may reach the thalamus.

In our preparations, which included section of every part of the cord, no other definite degenerated tracts could be detected. There is no assurance that other important ascending tracts may not have remained unstained owing to conditions of medullation similar to that of the pyramidal tract. This is, however, of little importance for our experiments since, whether stained or not, there is no question but that they were cut in some of our animals.

In general, the tracts of the rat's cord present no fundamental differences from those of higher mammals, to which we can ascribe the results obtained in our studies of behavior. The ascending tracts of the dorsal funiculus and the spino-cerebellar tracts are large and sharply defined. The pyramidal tract is restricted to definite area and this seems true also of the rubro-spinal. On anatomical grounds there seems no more reason to predict a diffuseness of function in the cord of the rat than in that of the monkey or man.

The path of the proprioceptive impulses is perhaps not yet certainly established, but the weight of evidence from clinical material indicates that sensitivity to movements and bodily posture is disturbed only by lesions within the posterior columns. Head ('20) states that, " . . . . the impulses associated with passive position and movement and with tactile discrimination do not, within the limits of the spinal cord, reach the point where they are recombined, but continue uncrossed to pass along the fibers of primary afferent systems in the posterior columns. It is not until they reach the posterior column nuclei (nucleus gracilis and nucleus cuneatus) that they pass from a primary to a secondary sensory system" (p. 401), and again, "We therefore find, that the only definite consequence of destruction of the posterior columns is to produce loss of tactile discrimination (compass test) and of the sense of passive position and movement on the same side as the lesion" (p. 402).

GENERAL EFFECTS OF LESIONS

For each of the regions of the cord involved in the experimental destructions the animals showed definite syndromes. The picture after section of the dorsal funiculi seemed primarily one of reduced sensitivity to bodly position. In walking the animals had a sprawling gait, with feet rather widespread. They tended to walk on the dorsal surface of the fore feet, less frequently of the hind feet. There was occasional incoördination, especially a lack of syncronization of the fore and hind legs. In rapid walking or running, the hind legs tended to drag in recovery from the backward step, and in turning to one side the opposite fore leg was often dragged stiffly behind. In running rapidly in the maze all legs were recovered too slowly from the backward step so that the animals seemed to run ahead of their feet and fall forward. When tested at the edge of a table with one leg unsupported this leg was often allowed to hang flaccid until movements of progression were initiated (a condition noted in many animals after section of the dorsal roots of a limb). When the animals were placed on a board which was tipped at various angles their posture in maintaining balance seemed practically normal. Only crude tests for cutaneous sensitivity could be used. They gave no indication of abnormality, but were unreliable for any but the grossest changes.

Section of the lateral funiculi gave a picture suggestive of cerebellar ataxia. The gait was staggering with exaggerated balancing movements of the tail. The animals frequently fell to one side, especially in making the turns of the maze. Tested at the edge of the table, the unsupported limbs were recovered as promptly as by a normal animal. On a tipping board, adjustments to change of position were sometimes slow or defective, but often normal in all animals. There were suggestions of disturbances of cutaneous sensitivity, a slight analgesia and a tendency to bite at the fore feet during the first few days after operation.

In the one case with lesion in the ventral funiculus the behavior was almost normal, with perhaps a slight hyperextension of the legs for the first few days after operation.

PROTOCOLS

Destruction of fasciculi gracilis and cuneatus and of the pyramidal tract

No. 1. Young male, somewhat unstable during training. Training record: Time, 1463 seconds; errors, 67; trials, 45. Preliminary retention tests: Trials, 10; time, 53 seconds; errors, 0.

Dorsal funiculus sectioned at third cervical segment. On the following days there was some incöordination in walking, with a tendency to walk on the dorsum of the fore feet. The hind limbs were dragged occasionally in walking and in turning toward either side the fore leg of the other side was dragged. There seemed to be some analgesia.

Retention was tested ten days after operation. The record for 15 trials was the following:

Time	*Errors*	*Time*	*Errors*
18	0	8	0
34	0	10	0
83	3	10	0
92	3	22	1
43	0	10	0
9	0	9	0
7	0	8	0
6	0		

Locomotion was slowed considerably in the maze, owing largely to the motor incoördination, but the first two trials were made without error and the total record gave clear evidence that the maze pattern was retained

Lesion: Section through the site of injury showed that practically all of the cord above the level of the central canal had been destroyed (plate 1, fig. 1a). The f. gracilis, cuneatus and the pyramidal tract together with the dorsal horns of the gray matter were destroyed. Section at the level of the first cervical segment showed complete degeneration of the f. gracilis and cuneatus except for the lateral areas representing the fibers of the first and second cervical nerves (plate 1, fig. 1b). Scattered degenerate fibers in the lateral and ventral funiculi probably originate from injury to the third pair of nerves and to the dorsal horns of the gray matter.

No. 2. Young male. Training marked by periods of refusal to run the maze. Training record: Time, 5409 seconds; errors, 153; trials, 20. Preliminary retention tests: Time, 63 seconds; errors, 0; trials, 10.

On the first day of preliminary retention tests he would not run in the maze and did not eat when placed in the food compartment.

Dorsal funiculi sectioned at third cervical segment. On the following days he tended to drag his legs and walk on the dorsum of the feet, like number 1. Retention was tested ten days after operation. On the first day he showed little evidence of hunger and behaved much as on the first day of the preliminary retention tests, making the following record:

Time	*Errors*
330	8
360	8
142	4
63	1

He was not fed after these tests and on the next day made the following record:

Time	*Errors*	*Time*	*Errors*
21	0	17	0
10	0	15	0
17	0	15	0
27	0	9	0
13	0	6	0
14	0		

The record does not show perfect retention but is far better than that for initial learning. In view of his earlier records, we are justified in concluding that this case does not give conclusive evidence for loss of the habit after spinal lesion.

Lesion: Section at the third cervical segment (plate 1, fig. 2a) shows destruction of the greater part of the cord above the level of the central canal. The f. gracilis, cuneatus, and practically all of the pyramidal tract were interrupted. A section below the first cervical roots (2b) shows complete degeneration of the f. gracilis and cuneatus, except for the portions supplied by the second cervical nerve, and extensive degeneration in the right spino-cerebellar tracts corresponding to the degeneration in the right lateral funiculus, shown at the level of injury.

No. 3. Young male. Behavior normal during initial training. Training record: Time, 1669 seconds; errors, 97; trials, 20. No preliminary retention tests given.

The dorsal funiculus was sectioned deeply. On the following days there was marked incoördination in walking. The fore feet were usually flexed with the dorsum on the ground. Hind feet were frequently dragged in walking and were not drawn up when placed over the edge of a support. When making coördinated steps the feet were widespread, so that the belly touched the ground. There was probably some positive disturbance of sensitivity, as on the eighth day he amputated his left fore paw. Retention was tested fourteen days after operation. On the first day he would not eat in the maze and his behavior was erratic. The record for the first day was the following:

Time	*Errors*
24	2
46	4
38	2
689	20

He was not fed and on the next day made the following record:

Time	*Errors*	*Time*	*Errors*
17	0	27	0
60	0	26	4
14	2	9	0
7	0	8	0
8	1	7	0
7	1	8	0
8	0	12	1

The behavior on the first day did not resemble that of an untrained animal and there was indifference to food. On the following day, when the incentive to run was increased, errorless trials were obtained from the first. Like the record of number 2, this is somewhat ambiguous. It indicates some retention, but is impossible to interpret.

Lesion: At the third cervical level the position of the lesion was clearly marked by scar tissue and clots (plate 1, fig. 3a). It involved all of the dorsal funiculus, the greater part of the gray matter on the right, and the dorsal third of the lateral funiculus, including the rubrospinal tract. At the second cervical segment (plate 1, fig. 3b) there was complete degeneration of the f. gracilis and cuneatus and considerable degeneration in both lateral columns.

No. 4. Large adult male. Given 50 trials overtraining. Training record: Time, 1676 seconds; errors, 49; trials, 29. Overtraining: Time, 279 seconds; errors, 1; trials, 50. Preliminary retention tests: Time, 106 seconds; errors, 3; trials, 16.

The dorsal funiculus was deeply incised at the third cervical segment. On the following days he walked with a sprawling gait, falling occasionally in making turns and frequently stepping on the dorsum of the feet. Retention was tested five days after operation. The record was the following:

Time	*Errors*	*Time*	*Errors*
7	0	6	0
6	0	8	0
12	0	6	0
7	0	8	0
5	0	8	0

The record shows perfect retention and a speed in traversing the maze only slightly inferior to the preoperative record. The maze was covered and performance tested in darkness. The record was the following:

Time	*Errors*	*Time*	*Errors*
28	2	7	0
22	0	7	0
8	0	8	0
8	0	6	0
10	0	8	0

After the exploration of the covered top of the maze in the first trial no further errors were made when moving in total darkness.

Lesion: Section at the third cervical level showed complete interruption of the dorsal funiculus, destruction of the posterior horns and a considerable amount of degeneration in the right lateral funiculus (plate 1, fig. 4a). Section above the first cervical level (plate 1, fig. 4b) showed complete degeneration of the f. gracilis and cuneatus with considerable degeneration in the region of the dorsal spino-cerebellar tract.

These four cases all show complete interruption of the fasciculus gracilis, fasciculus cuneatus and pyramidal tracts, with more or less degeneration in the regions of the rubro-spinal tracts and of the dorsal spino-cerebellar bundles. Two cases, numbers 2 and 3, showed somewhat erratic behavior in preoperative tests and similar behavior after operation so that their records are not clear cut. They do, however, show some indication of retention. The other two, with equally extensive destruction give unequivocal evidence for *perfect retention of the maze habit. Destruction of the dorsal funiculus did not in the least affect their ability to make the correct turns of the maze.*

Destruction of fasciculus gracilis and fasciculus cuneatus without extensive injury to the pyramidal tracts

No. 5. Large male, more than usually stable. Initial training: Time, 957 seconds; errors, 32; trials, 14. Preliminary retention tests: Time, 35 seconds; errors, 0; trials, 10. Overtraining: Time, 182 seconds; errors, 1; trials, 50.

Ten trials with the maze darkened were given before operation.

Time	*Errors*	*Time*	*Errors*
25	2	4	0
18	3	7	0
5	0	6	0
4	0	5	0
4	0	4	0

The dorsal funiculus was sectioned at the third cervical segment. For the first few days the animal tended to circle to the right in walking. This condition cleared up quickly, leaving the usual picture of reduced sensitivity to posture. Retention was tested eight days after operation, with the following record.

Time	*Errors*	*Time*	*Errors*
8	0	13	0
5	0	4	0
16	0	8	1
10	0	6	0
7	0	12	0

On the following day, with the maze darkened, he made the following record:

Time	*Errors*	*Time*	*Errors*
38	2	8	0
36	2	7	0
10	0	6	0
8	0	6	0
18	1	12	0

The post operative tests show some slowing in locomotion but no loss of ability to traverse the maze correctly. With vision eliminated the record was as good as that made under similar conditions before the spinal lesion.

Lesion: Section above the third cervical level showed complete destruction of the f. gracilis and f. cuneatus with little if any involvement of the pyramidal tracts (plate 1, fig. 5a). Section at the first cervical level showed degeneration restricted almost entirely to the two ascending fasciculi (plate 1, fig. 5b).

No. 6. Young male, very unstable throughout the experiment. Initial training: Time, 710 seconds; errors, 53; trials, 50. Preliminary retention tests were not given.

The dorsal funiculus was transsected at the third cervical segment. On the following days little abnormality of behavior was noted beyond a tendency to walk on the dorsum of the paws and drag them slightly. Retention was tested seven days after operation, with the following record, made in three consecutive days:

Time	*Errors*	*Time*	*Errors*	*Time*	*Errors*
322	12	23	2	8	0
201	11	15	0	13	2
80	3	15	0	12	0
33	1	10	0	7	0
34	1	8	0	11	1
16	1	8	0	8	0
9	0	11	1	5	0
12	1	11	0	5	0
7	0	22	2	6	0
15	2	92	6	5	0

This record is not significantly better than the initial training record. The behavior during retention tests was characterized throughout by prolonged periods of quiescense in the starting compartment and by failure to eat after the food had been reached.

Lesion: There was active infection of the wound, inflammation of the cord with necrosis of the dorsal horns at the third cervical level (plate 2, fig. 6a). Section at a higher level showed extensive degeneration of the f. gracilis and cuneatus with some degenerated fibers in the spinocerebellar tracts, chiefly on the left (plate 2, fig. 6b).

Of these two cases the first alone can be considered. The infection rules out the negative evidence of the second and leaves only as significant the fact that, in spite of the infection and destruction of tissue, he was able ultimately to traverse the maze without error. Number 6, with greater actual destruction showed perfect retention of the maze habit and ability to traverse the maze in darkness as well after as before the spinal injury.

Partial destruction of the dorsal and of one lateral funiculus

No. 7. Large male, about 200 days old. Initial training: Time, 1077 seconds; errors, 38; trials, 21. Overtraining: Time, 247 seconds; errors, 0; trials, 50. Preliminary retention tests: Time, 41 seconds; errors, 0; trials, 10.

Preliminary tests with the maze darkened gave the following:

Time	*Errors*	*Time*	*Errors*
85	5	7	1
8	1	4	0
5	0	4	0
5	0	5	0
7	1	5	0

An attempt was made to divide the dorsal funiculus, but the knife was driven deeply into the left side of the cord. General behavior after operation was not markedly different from that of animals with only the dorsal funiculus cut, except that adjustments to tipping the substratum were made rather slowly and inaccurately. Retention was tested six days after operation with the following record.

Time	*Errors*	*Time*	*Errors*
11	0	10	0
22	1	10	0
11	0	7	0
12	0	8	0
10	0	8	0

Tests with the maze darkened gave the following record:

Time	*Errors*	*Time*	*Errors*
35	0	33	0
25	0	14	0
38	0	27	0
55	0	43	0
22	0	30	0

The prolonged time in these tests is due to the fact that the animal was disturbed by the cover of the maze and repeatedly stopped during every trial to push against it with his nose.

Lesion: The cut extended diagonally from the outer margin of the right f. cuneatus through the left dorsal horn to the lower margin of the left spino-cerebellar tract, interrupting all the fibers above this line (plate 2, fig. 7a). Section at a higher level shows almost complete degeneration of the f. gracilis and cuneatus of both sides, degeneration of the left spino-cerebellar tracts and many degenerate fibers in the region of the spino-tectile bundles (plate 2, fig. 7b).

This case, with nearly complete section of the f. gracilis and cuneatus and interruption of the spino-cerebellar tracts of one side gave clear evidence of ability to run the maze even in darkness.

Section of the lateral funiculi

No. 8. Large male, about 200 days old. Initial learning: Time, 5861 seconds; errors, 83; trials, 20. Overtraining: Time, 431 seconds; errors, 0; trials, 50. Preliminary retention tests: Time, 55 seconds; errors, 0; trials, 10.

Preliminary tests with the maze darkened gave the following results:

Time	*Errors*	*Time*	*Errors*
125	9	7	0
16	1	5	0
15	1	3	0
8	0	4	0
10	0	3	0

The lateral funiculus was divided on each side at the level of the third cervical segment. On the following days he showed tremor and hyperextension of the legs, staggering gait with a tendency to fall to the side, especially in turning, and constant balancing movements of the tail. There was some difficulty in adapting to inclination of the substratum. Retention was tested ten days after operation with the following record:

Time	*Errors*	*Time*	*Errors*
10	0	10	0
11	0	12	0
8	0	11	0
11	0	8	0
11	0	7	0

With the maze darkened, the record was the following:

Time	*Errors*	*Time*	*Errors*
115	4	22	0
46	1	18	0
15	0	20	0
15	0	100	2
18	1	13	0

This record is somewhat inferior to the preoperative one, but gives conclusive evidence of ability to traverse the maze in darkness.

Lesion: At the third cervical level the lesions of the two sides were separated longitudinally by about one millimeter, that on the right being the more cephalad (plate 2, fig. 8). On the left the knife had passed though the fasciculus cuneatus and diagonally downward to interrupt the entire lateral funiculus, involving the dorsal horn of the gray matter as well. On the right the lesion extended vertically from the lateral margin of the fasciculus cuneatus through the dorsal and ventral horns and involved the entire lateral funiculus (plate 2, fig. 8).

No. 9. Large male, about 200 days old. Initial training: Time, 1297 seconds; errors, 57; trials, 18. Overtraining: Time, 338 seconds; errors, 0; trials, 50. Preliminary retention tests: Time, 47 seconds; errors, 0; trials, 10.

Preliminary tests with the maze darkened gave the following record:

Time	*Errors*	*Time*	*Errors*
175	11	5	0
6	0	4	0
5	0	5	0
5	0	5	0
5	0	5	0

The lateral funiculi of both sides were cut at the third cervical level. The subsequent behavior of the animal was much like that of number 8, but with a less steady gait and some indication of analgesia. In retention tests he fell almost every time in making a turn in the maze. Retention tests were given six days after operation, with the following record:

Time	*Errors*	*Time*	*Errors*
34	1	8	0
10	0	9	0
8	0	10	0
10	0	9	0
8	0	9	0

Tests with the maze darkened gave the following:

Time	*Errors*	*Time*	*Errors*
37	2	9	0
27	1	24	1
13	0	11	0
12	0	9	0
9	0	10	0

Lesion: Section at the level of the injury showed total destruction of both lateral funiculi with little or no injury to the dorsal or ventral funiculi. Section at the first cervical roots showed degeneration of the spino-cerebellar tracts of both sides and ascending degeneration of fibers from the third dorsal root in the right f. cuneatus. (Plate 2, figs. 9a and 9b.)

No. 10. Male, about 200 days old. Initial training: Time, 2022 seconds; errors, 80; trials, 45. Overtraining: Time, 322 seconds; errors, 3; trials, 50. Preliminary retention tests: Time, 85 seconds; errors, 1; trials, 14.

The lateral funiculus of each side was divided at the third cervical segment. On the following days he showed hyperextension of the legs, staggering gait with tendency to fall to the side, constant balancing movements of the tail and some tremor of the legs.

Retention was tested five days after operation with the following record:

Time	*Errors*	*Time*	*Errors*
14	0	8	0
12	0	10	0
45	2	29	0
12	0	10	0
9	0	8	0

Tests with the maze darkened gave the following:

Time	*Errors*	*Time*	*Errors*
56	1	18	0
82	2	11	0
29	0	17	0
52	1	10	0
20	0	10	0

In these tests the additional time was consumed in pushing at the cover of the maze.

Lesion: Section at the third cervical level showed lesions restricted to the dorsal halves of the lateral funiculi without invasion of the gray matter (plate 2, fig. 10a). At the first cervical level there was partial degeneration of the dorsal spino-cerebellar tract of each side with no other involvement.

These three cases, involving interruption of all the paths of the lateral *funiculi and considerable motor disturbance, resembling a cerebellar ataxia, showed perfect retention of the maze habit with ability to traverse the maze in the absence of visual cues.*

Injury to the ventral funiculus

No. 11. Large male, about 200 days old. Initial training: Time, 2491 seconds; errors, 71; trials, 23. Overtraining: Time, 647 seconds; errors, 7; trials, 50. Preliminary retention tests: Time, 83 seconds; errors, 1; trials, 11.

Preliminary tests with the maze darkened gave the following:

Time	*Errors*	*Time*	*Errors*
86	8	16	1
18	1	6	0
11	1	15	1
10	0	7	0
8	0	6	1

The cord was exposed, raised, and the knife passed through the ventral columns. Following the operation there was little disturbanace of behavior beyond a slight tendency to drag the hind feet in walking. Retention tests were given six days after operation.

Time	*Errors*	*Time*	*Errors*
9	0	13	0
15	0	25	0
15	0	14	0
13	0	12	0
10	0	11	0
58	1		

Tests with the maze darkened gave the following:

Time	*Errors*	*Time*	*Errors*
54	4	28	0
17	0	18	0
20	0	13	0
15	0	35	1
14	0	28	0

Lesion: In dividing the cord for fixation the segment containing the lesion was destroyed. A section immediately above the lesion shows extensive degeneration throughout the ventro-lateral column of the left side with little involvement of the right. It seems certain that the knife