THE SURVIVAL OF THE MAZE HABIT AFTER CEREBELLAR INJURIES

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The close anatomical relation of the cerebellum to the proprioceptive systems and the importance of the latter for the maze habit suggest that, if the cerebellum is ever concerned in learning or retention, this function will be revealed by a study of the effects of cerebellar lesions upon the activities of animals in the maze. The supposed relations of the cerebellum to the vestibular reflex paths suggest further that the cerebellum may be involved, not only in postural adjustments to gravity, but also in the more remote orientation of the body in space, as in the maintenance of the sense of direction. Although the clinical literature on man lends little support either to the mnemonic or orienting function of the cerebellum, systematic observations on these points are not numerous, and it has seemed worth while to test their possibility by an acute experiment with the maze. An immediate necessity for such tests arose also in work by the senior author on cerebral localization of the maze habit, in which the effects of possible slight lesions to the cerebellum could not be disregarded.

METHODS

Rats were trained in a rectangular maze, having eight *culs de sac*, for five trials per day until ten consecutive errorless trials were obtained. After ten days without practice retention was tested by retraining until ten successive errorless trials were again obtained (preliminary retention tests). The cerebellum was then destroyed more or less completely by cauterization through a small median trephine opening just back of the parieto-occipital suture. Ten days after operation, or longer, in case

the animals were still unable to walk at the end of this time, retention was again tested (post-operative retention tests) by the same method as before operation. The data given on time and trials in learning and retention tests include the ten error-

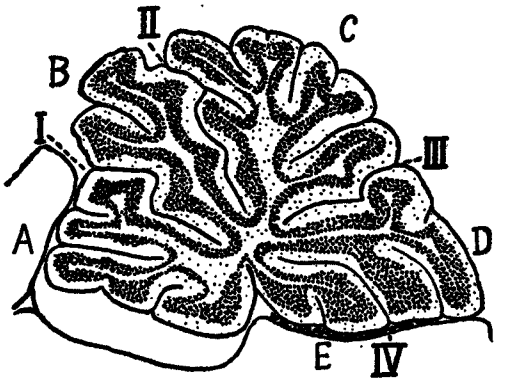

FIG. 1. MEDIAN SAGITTAL SECTION OF THE CEREBELLUM
Bradley's nomenclature of lobes and fissures is indicated

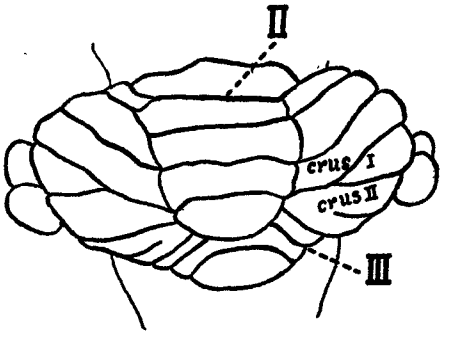

FIG. 2. DORSAL VIEW OF CEREBELLUM

less trials. With the completion of these tests the animals were brought to necropsy and serial sagittal sections of the cerebellum and brain stem were prepared with a general cell stain. From these, reconstructions of the lesions were made by the graphic method.

ANATOMY OF THE CEREBELLUM OF THE RAT

Figure 1 shows a median sagittal section of the cerebellum. It is divided, according to Bradley's embryological studies (1913) into five chief lobes, lettered A to E in his descriptions. These are separated by the principle fissures I to IV. Of these, fissure II corresponds to the Sulcus primarius, III to Fissura

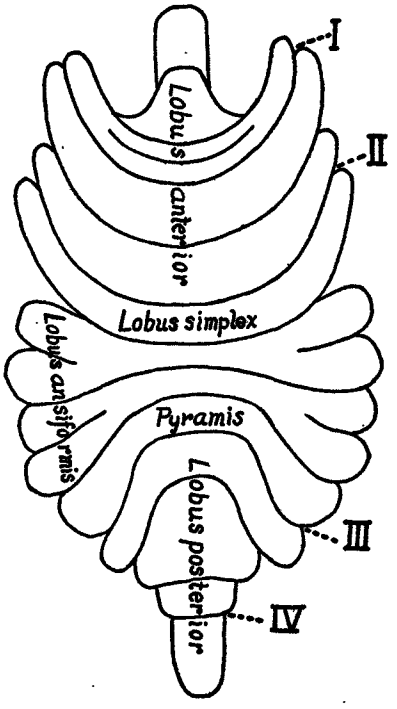

FIG. 3. DIAGRAM INCLUDING VENTRAL AND DORSAL SURFACES OF THE CEREBELLUM

The lettering of fissures corresponds to that in figure 1

secunda, and IV to the Sulcus uvulo-nodularis of Bolk. Lobes A and B correspond to Bolk's Lobus anterior, the anterior half of C to his Lobus simplex. The caudal half of lobe C together with lobes D and E make up his Lobus medianus posterior. On the dorsal surface (fig. 2) only the fissures II and III are visible. The vermis is not well marked off from the hemispheres. The

ansiform and paramedian lobes may be distinguished as separated from it by slight longitudinal depressions. Flocculus and paraflocculus are distinguishable and there appears to be also a small pars petrosus.

The dentate nuclei lie rather far laterad beneath the ansiform lobes. We have not attempted to distinguish the various roof nuclei, since all remained intact except in one case, in which all were destroyed.

GRAPHIC METHODS

For representation of the lesions the following method was devised. Sagittal sections at equal distances throughout the cerebellum were sketched under the camera lucida. All gyri were identified throughout the series and the surface width of each was measured for each section. These dimensions were then plotted on coördinate paper from a curved base line drawn to represent the Sulcus primarius. Connecting the points so determined gave the diagram shown in figure 3. Since only sagittal sections were used the diagram is foreshortened laterally and fails to represent the full area of the ansiform lobes. Flocculus and paraflocculus are not represented. Their condition in the operated cases is stated in the protocols.

In figure 3 the parts are lettered to correspond with Bradley's nomenclature, for identification with the actual visual appearance shown in figure 2. In making the reconstructions of the lesions sagittal sections of the operated brains were compared with camera sketches of the normal sections from which the diagram had been prepared, the gyri remaining intact identified and the lesions then blocked out on the diagrams. In addition to the diagram a camera sketch of a median sagittal section of each operated brain is given (figures *a* in plate 1). Comparison of these with figure 1 may serve to give a clearer notion of the extent of injury.

SENSORY CONTROLS

Watson (1907) has shown conclusively that vision, olfaction and other forms of exterostimulation are, singly, not essential

to accurate running of the maze. It has not been shown, however, that, in case of disturbance of the kinaesthetic mechanisms, they may not supply substitute cues for the normal internal ones. Without some control of exteroceptive stimuli the survival of the maze habit after cerebellar destruction can not be interpreted, since it might be due either to the normal failure of the cerebellum to participate in the habit or to the use of other sensorimotor integrations when the cerebellar mechanisms are rendered nonfunctional. The maze employed in these experiments offered practically no possibility of differential tactile or olfactory cues which could guide the animal over the true path. Vision was ruled out in two animals (nos. 6 and 7) by enucleation of the eyes after training but before lesion to the cerebellum.

PROTOCOLS

No. 1. Adult female. Inactive and very erratic during training, making frequent errorless trials after the fourteenth of practice but tending to reexplore the maze after brief periods of correct running. Her learning record was:

Time 27,918 seconds. Errors 139. Trials 106

Preliminary retention tests were not given.

After operation the only clear motor symptoms were tremor and spasticity of the hind legs, which cleared up completely within ten days. In the postoperative retention tests the animal showed the same erratic behavior as in initial learning. The following is a record of the errors in the first trials of these tests:

Trial	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Errors	1	1	0	0	0	3	0	0	0	0	3	1	0	0	0

This gives clear evidence of the animal's retention of the habit as well as of her previous reaction tendencies in the maze situation.

Lesion: The extent of destruction is shown in plate 1, figures 1*a* and 1*b*. The lesion embraces the greater part of lobes B and C but leaves their lateral portions (Crus secundum, Bolk) intact. The dentate and roof nuclei are uninjured.

No. 2. Adult female. The initial learning record was:

Time 1338 seconds. Errors 81. Trials 29

Preliminary retention tests gave the following records:

Time 169. Errors 4. Trials 11

After operation the animal showed slight action tremors and spasticity of the hind legs, which cleared up within six days. In postoperative retention tests she gave from the first clear evidence of retention of the habit, making an errorless record on the second trial and again on the fourth. The requirements for complete relearning were the following:

Time 657 seconds. Errors 14. Trials 19

Lesion: The extent of destruction is shown in plate 1, figures 2*a* and 2*b*. It is very similar to that in no. 1, but extends into the dorsal margin of lobe D and leaves the greater part of the ansiform lobes intact. The flocculus, paraflocculus and cerebellar nuclei are uninjured.

No. 3. Adult female. She was very inactive and somewhat erratic during training. Her learning records were:

Time 11,132 seconds. Errors 60. Trials 61

Only one error was made in the first five trials of the preliminary retention tests but the record thereafter was irregular.

Time 434 seconds. Errors 7. Trials 19

After operation the animal showed gross tremors of the whole body, particularly marked in the hind limbs which were extended laterally and spastic. There was a tendency to rotate to the left and frequent backward somersaulting. This condition persisted for four or five days. After ten days there was great improvement; rapid progression in spite of gross tremors and staggering gait. Retention tests gave the following results:

Time 1403 seconds. Errors 9. Trials 15

There is clear evidence of retention from the first, with the same unsteadiness of performance which marked the preliminary retention tests.

Lesion: The extent of destruction is shown in plate 1, figures 3*a* and 3*b*. The dorsal half of lobe A together with lobes B and C are almost entirely destroyed. The anterior half of the ansiform lobes is involved. Both dentate nuclei are partially destroyed. Flocculi and paraflocculi are intact.

No. 4. Adult female. The performance in initial learning was:

Time 2388 seconds. Errors 33. Trials 35

Preliminary retention tests gave errors in only the first two trials.

Time 229 seconds. Errors 7. Trials 12

After operation there was extreme contraction of the left hind leg and extension of the right. In walking there was rotation to the left and frequent backward somersaulting. When picked up the animal clutched wildly at anything within reach and gave indications of vertigo. For the first four days she was force-fed, then began to eat spontaneously but showed little improvement in motor symptoms. Thirty days after operation the motor symptoms were still pronounced. She walked as if drawing a heavy weight, with fore and hing legs extended forward and dragging her along in a series of lunges. At this time she was tested in the maze and made a perfect retention record.

Time 801 seconds. Errors 0. Trials 10

Lesion: The extent of destruction is shown in plate 1, figures 4*a* and 4*b*. Practically all of lobes A, B and C, the flocculi and paraflocculi and both dentate nuclei are destroyed. Lobes D and E and the roof nuclei remain intact.

No. 5. Adult female. The training record follows:

Time 1179 seconds. Errors 43. Trials 48

In preliminary retention tests the animal was erratic and slow, although giving clear evidence of retention.

Time 2464 seconds. Errors 52. Trials 48

For the first five days after operation the animal showed only a slight general tremor, then gave signs of collapse with stupor. This improved but the animal was unable to walk during the succeeding twenty days. On the twenty-fifth day after operation she was able to progress slowly but still showed marked incoördination and tremor. Retraining was begun at this time. Thirteen days later additional symptoms developed, involving rapid rolling to the left on any attempt to walk. Two days later this phase had passed and retraining was resumed. Training was completed three days later with 10 consecutive errorless trials. The record for the postoperative tests was:

Time 5337 seconds. Errors 97. Trials 78

This gives no evidence of retention of the habit but clear proof of ability to reacquire it.

Lesion: At necropsy the position of the cerebellum was found to be occupied by a large cyst. On removal of this, no trace of the cerebellum could be discovered. The dorsal surface of the medulla was exposed, the medulla was much compressed and the peduncles were completely atrophied.

The animal presents a case of normal orientation in the maze in the complete absence of the cerebellum. The apparent loss of the habit subsequent to operation cannot be ascribed directly to the cerebellar destruction, for we have records of equal deterioration of the maze habit in animals in which infection was limited to the scalp.

No. 6. Adult male. Initial training in the maze required:

Time 2846 seconds. Errors 30. Trials 33

Preliminary retention tests required:

Time 340 seconds. Errors 7. Trials 20

The eye balls were then enucleated, with retention tests two days later.

Time 107 seconds. Errors 1. Trials 11

The cerebellum was next partially destroyed. Recovery was rapid and at the end of ten days there remained only a slight action tremor. Retention was tested at this time and found to be perfect.

Time 188 seconds. Errors 0. Trials 10

Lesion: The extent of destruction is shown in plate 1, figures 6*a* and 6*b*. All of the dorsal convexity of lobes B and C is destroyed. The lesion extends deep into the substantia alba so that probably large areas in addition are rendered non-functional. The cerebellar nuclei seem intact.

No. 7. Adult male. Initial training gave the following record:

Time 560 seconds. Errors 12. Trials 20

Preliminary retention tests:

Time 356 seconds. Errors 5. Trials 14

The eyes were enucleated with retention tests two days later.

Time 129 seconds. Errors 0. Trials 10

The cerebellum was then partially destroyed. Postoperative symptoms were slight and cleared up entirely within ten days. Postoperative tests showed perfect retention.

Time 182 seconds. Errors 0. Trials 10

Lesion: The extent of injury is shown in plate 1, figures 7*a* and 7*b*. The lesion

is very similar to that in number 6 but extends farther laterad in lobe B and invades the white matter to a lesser extent. Basal nuclei are intact.

DISCUSSION

The records of the animals reported individually above are summarized in table 1. Exclusive of no. 5, which suffered from infection, the average constants for learning and retention before and after operation were:

	TIME	ERRORS	TRIALS
	seconds		
Initial learning	7,697	59.2	47.3
Preliminary retention tests	178	3.8	12.4
Postoperative retention tests	608	6.3	16.5

The averages for the postoperative tests are not significantly higher than those of the preliminary tests. The fact that the animal with the most extensive operative destruction (no. 4) made no errors after operation indicates that the slight decrease in efficiency of the others in these tests was not due to any mnemonic disturbance directly resultant from cerebellar lesion. The averages of these cases and the record of no. 5, with complete absence of the cerebellum, show that this structure is not necessary for the learning or retention of the maze habit.

TABLE 1

Summary of training and retention tests for all cases described in the text

NUMBER	TIME	LEARNING		PRELIMINARY RETENTION TESTS			POSTOPERATIVE RETENTION TESTS		
		Errors	Trials	Time	Errors	Trials	Time	Errors	Trials
	seconds			*seconds*			*seconds*		
1	27,918	139	106				417	15	35
2	1,338	81	29	169	4	11	657	14	19
3	11,132	60	61	434	7	19	1,403	9	15
4	2,388	33	35	229	7	11	801	0	10
5	1,179	43	45	2,464	52	48	5,337	97	78
6	2,846	30	33	107*	1*	11*	188	0	10
7	560	12	20	129*	0*	0*	182	0	10

* After enucleation of eyeballs.

The results with nos. 6 and 7, in which the cerebellar lesion was preceded by enucleation of the eyes, together with the control of olfaction and differential tactile stimuli provided by the maze itself show that after cerebellar lesions the animals did not fall back upon exteroceptive cues but continued to react on the basis either of kinaesthetic stimuli, or of some centrally organized mechanism. Their behavior in the absence of differential exteroceptive stimuli was not essentially different from that found by Watson with normal rats.

In no. 5 the entire cerebellum including the basal nuclei was absent when the animal was running the maze without error. This demonstrates beyond question that the cerebellum is not necessary for the acquisition of the maze habit. The case was complicated by infection, so that the loss of the habit following operation cannot be interpreted. In the other animals not all of the cerebellum was destroyed, yet there seems no reason to believe that the parts remaining intact are any more likely to contain mechanisms functional in orientation than are those destroyed. In no. 4, which showed perfect retention of the habit after operation, only lobes D and E (Lobus medianus posterior) escaped destruction. Van Rynberk (1908) obtained no symptoms from destruction of this area alone and only an exaggeration of the symptoms following destruction of the Crura prima when the area was destroyed along with the latter. Such meager data on the function of the area are scarcely helpful for the present problem. But previous extirpation experiments do indicate rather clearly that, although gross localization of function exists within the cerebellum, there is so great an overlapping and interdependence in the functions of its parts that the restriction of mnemonic or orienting functions to so small an area is virtually ruled out. Moreover, the parts remaining intact belong almost altogether to the primitive cerebellar system (Edinger, 1910) in which there is the least likelihood of the localization of these more complex functions.

In view of such considerations the conclusion seems justified that the cerebellum of the rat plays no significant part in the habit systems involved in maze running.

SUMMARY

The cerebellum was severely injured in a number of animals previously trained in the maze. In both seeing and blind animals perfect retention of the habit was demonstrated after the operations. One animal with the cerebellum completely destroyed learned to run the maze without error. There is no evidence that the cerebellum plays any part in the performance of the maze habit.

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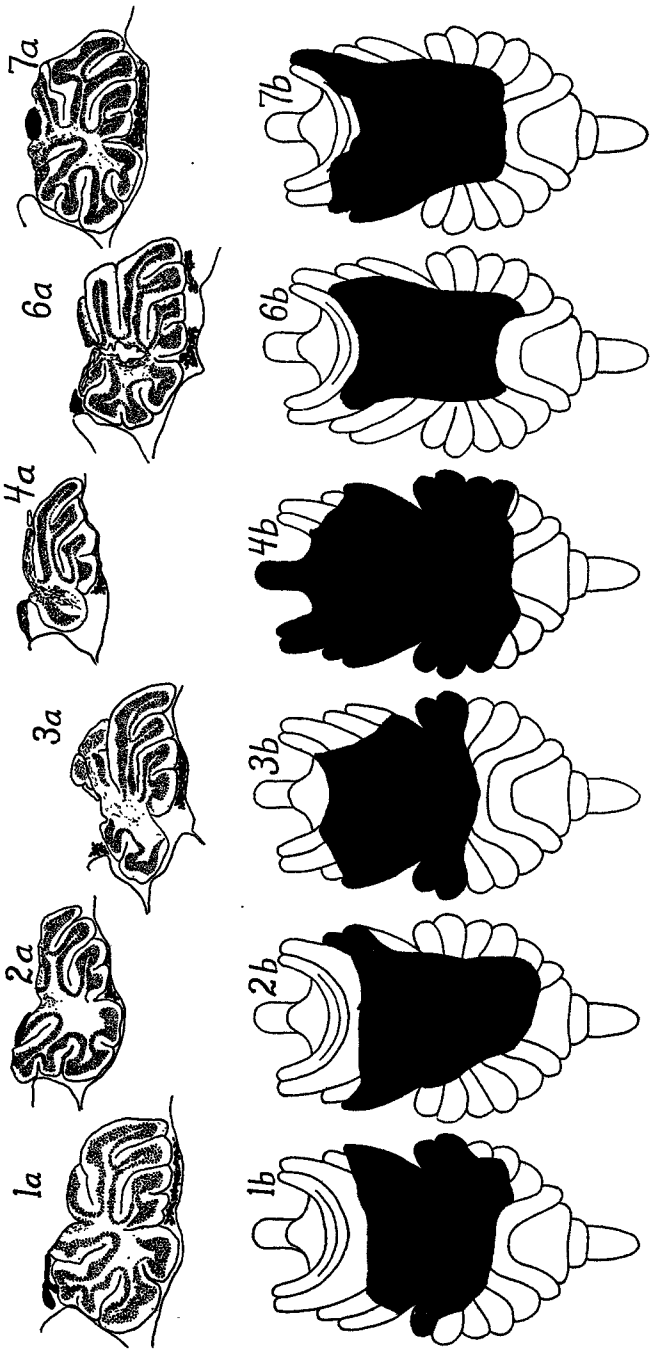
PLATE 1

RECONSTRUCTIONS OF THE LESIONS DESCRIBED IN THE PROTOCOLS

The numbering of the figures corresponds to the numbers assigned to the animals in the text.

a. Camera outlines of median sagittal sections.

b. Diagram showing the total extent of lesions.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