THE CORTICAL AREA CONCERNED WITH COORDINATED WALKING IN THE RAT

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ONE FIGURE

INTRODUCTION

Buytendijk ('31, '32) reported that, although lesions to the cerebral cortex of the rat produced no paralysis, they did affect the coordination of movements. The incoordination became obvious when the animals were required to run on narrow pathways or to jump from one platform to another. He described the defect as permanent and present in all cases with considerable destruction. Maier ('32 a, '32 b) reported similar disturbances in coordination in rats when walking on narrow pathways, but found the disturbance to be associated with cortical lesions in the anterior half of the brain. Peterson ('31) found that unilateral destruction of the stimulable cortex on the side opposite the preferred hand resulted in a change in hand preference. No motor coordination, however, was noted.

The motor disturbances when present in the rat are not obvious when the rat runs in a maze or about its cage, but becomes very apparent when it runs an elevated pathway 2 inches or less in width. Pathways as narrow as 1 inch cannot be traversed by some cases, although casual observation on the floor would not detect any handicap. The incoordination observed when the animals run on narrow paths may express itself as follows:

1. Hind legs miss footing and pathway is straddled or both hind legs miss the same side of the pole.

2. On turning corners inside legs miss footing.

3. Attempts to regain footing result in many ineffective movements. The animal tends to cling tightly to the pole with its front legs, holding the body tight to the pole. Footing is best regained when the animal pulls itself along with its front legs for a stretch. The hind legs then drag and footing may be regained.

4. An animal hung from the pathway from its front legs sweeps its hind legs upward, but has difficulty in catching footing with them. A bad case invariably drops to the floor under such circumstances. A normal rat catches its footing under such circumstances with one sweep of its hind leg.

5. When the disturbance is slight and footing is not lost, it can be observed that the hind legs do not track properly.

The purpose of the present study is to determine whether the destruction of any particular part of the cortical surface causes the motor incoordination described.

METHOD AND PROCEDURE

A group of sixty-six adult albino and pigmented rats were trained to run for food from one table to another over elevated pathways 2 inches wide and 7 feet long. They soon became accustomed to the pathways and ran rapidly without loss of footing. After 5 minutes' daily practice for more than 3 weeks the animals were subjected to cortical lesions of various sizes and pattern. The lesion pattern was varied by destroying tissue through one, two and three pairs of trephine openings. In this manner the distribution of the lesions was not concentrated in any particular region.

From 6 to 9 days after the operation, the rats remained in their cages. During the next 6 days they were exposed to the pathways and fed in the test situation. It was assumed that this period of from 12 to 15 days was sufficient to allow for recovery from operative shock. After the preliminary recovery period the rats were required to run for food over the pathways, and were observed on the 18 days following, while making six trips from one table to another.

Loss in footing and inability to regain footing were recorded. After all records were obtained the rats were rated according to the degree of disturbance in locomotion. If behavior was normal, in that the rat ran rapidly and accurately on the narrow pathway, the rating was 0. If disturbance was present, but not obvious on each day of observation, or if the disturbance did not remain throughout the period of observation, the rating was 1. If locomotion was accompanied by loss of footing occurring each day, and the animal somewhat handicapped in its running speed, the rating was 2. If locomotion was greatly impaired, so that the hind legs often dragged when the pole was straddled, or if the rat frequently fell from the pathway, the rating was 3. Handicaps rated 3 alone were characterized by great difficulty in locomotion. In all cases there was improvement, but in cases rated 2 and 3 the handicap was always present.

TABLE 1

Distribution of cases according to the degree of motor disturbance

MOTOR HANDICAP RATING	NUMBER OF CASES	NUMBER OF TREPHINE OPENINGS THROUGH WHICH TISSUE WAS DESTROYED		
		1 pair	2 pairs	3 pairs
0	28	12	10	6
1	16	2	9	5
2	13	3	4	6
3	9	6	2	1
Total	66	23	25	18

At the end of the period of observation the rats were killed and the brains removed for histological examination. The locus and amount of destruction were then determined by methods described by Lashley ('29).

RESULTS

The distribution of the degree of disturbance of the various cases and the number of pairs of trephine openings through which tissue was destroyed are shown in table 1.

An examination of the lesions in the cases rated 3 in motor disturbance showed that they had a common area destroyed in both hemispheres. This common area is shown in figure 1, and constitutes 5.1 per cent of the cortical surface. It will be seen that it lies partly in areas j, f and n of Lashley's ('29) modification of Fortuyn's mapping. The first of these areas has been designated as somesthetic and the other two as motor.

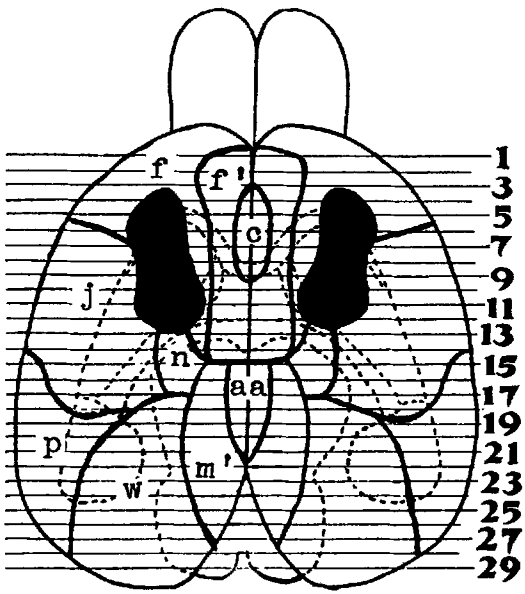

Fig. 1 Black portion of diagram designates the symmetrical cortical area which was completely destroyed in all rats having marked motor incoordination. The letters designate areas isolated by Fortuyn as modified to fit Lashley's brain charts.

If our isolated area is a critical area for coordinated walking, rats with lesser disturbance should have this area involved to a lesser extent. To determine this, cases with motor disturbances rated 0, 1 and 2 were examined and the extent of the critical area destroyed, measured.

Columns 2 and 3 of tables 2, 3, 4 and 5 give the total extent of destruction and the per cent of destruction of the critical area, respectively.

TABLE 2 [1]

Description of cases with motor disturbance rated 0 (no disturbance)

RAT'S NUMBER AND SEX	TOTAL PER CENT OF DESTRUCTION	PER CENT OF DESTRUCTION OF CRITICAL AREA	NUMBER OF TREPHINE OPENINGS USED	LOCUS OF MAJOR PART OF LESION	SUBCORTICAL DESTRUCTION IN	
					Anterior half	Posterior half
3F	5.9	10.0	3	AP	0	0
45F	9.0	75.6	2	A	0	0
31M	10.5	28.0	3	P	0	0
51M	13.1	26.8	2	AP	0	0
65F	13.2	90.2	1	A	+	0
6F	14.9	59.8	3	AP	0	0
43F	15.4	73.2	2	AP	0	0
30M	16.1	59.8	3	AP	0	0
71M	16.7	17.1	1	P	0	0
25M	16.8	48.8	3	AP	0	0
66F	17.6	9.9	1	P	0	+
47F	17.6	58.5	2	AP	+	0
24M	17.7	53.7	3	AP	0	0
54M	18.2	73.2	2	AP	0	0
61F	18.7	7.3	1	P	0	+
64F	20.8	7.4	1	P	0	+
53M	21.3	58.5	2	AP	+	0
55M	21.4	41.5	2	P	0	0
73M	23.3	39.0	1	P	0	+
70M	23.5	68.3	2	AP	0	0
96F	23.9	12.2	1	P	0	0
52M	23.9	41.5	2	AP	0	0
74M	24.5	24.4	1	P	0	0
92F	25.2	43.9	1	P	0	+
46F	25.5	58.5	2	AP	+	0
84M	27.7	24.4	1	P	0	+
82M	28.3	61.0	1	P	0	+
86M	29.7	41.5	1	P	0	+
28	540.4	1214.0		{2 A, 13 AP, 13 P}	4	8
Average	19.30	43.36			(14.3%)	(28.6%)

[1] M and F of column 1 indicate male and female, respectively. The numerals of column 4 indicate the number of pairs of trephine openings through which tissue was destroyed. A and P of column 5 designate that the lesion was primarily confined to the anterior or posterior halves of the brain surface, respectively; and AP that the lesion was spread over both halves. The 0 and + of columns 6 and 7 indicate the absence or presence of subcortical destruction in the anterior and posterior halves of the brain, respectively.

It will be seen that rats with a motor disturbance rated 0 have an average of 43.36 per cent of the critical area destroyed; those with the rating of 1, 70.03 per cent of the area; and those with the rating of 2, 86.55 per cent of the area. Rats with disturbance rated 3, of course, have all of the area destroyed. The composite lesion of each group included the whole of the critical area.

TABLE 3[1]

Description of cases with motor disturbance rated 1 (slight disturbance)

RAT'S NUMBER AND SEX	TOTAL PER CENT OF DESTRUCTION	PER CENT OF DESTRUCTION OF CRITICAL AREA	NUMBER OF TREPHINE OPENINGS USED	LOCUS OF MAJOR PART OF LESION	SUBCORTICAL DESTRUCTION IN	
					Anterior half	Posterior half
76M	13.8	90.2	1	A	+	0
88M	17.7	82.9	1	A	+	0
57M	18.2	51.2	2	AP	+	0
5F	19.7	56.1	3	AP	+	0
37F	21.5	40.2	3	AP	+	0
62F	21.8	76.6	2	AP	+	+
35M	22.4	65.9	3	AP	0	0
59M	23.3	53.7	2	AP	+	+
68F	23.8	63.4	2	AP	+	+
48F	25.1	68.3	2	AP	+	+
2F	25.2	69.5	3	AP	+	+
44F	26.2	73.2	2	AP	+	0
1F	28.0	95.1	3	AP	0	0
56M	28.8	89.0	2	AP	+	+
89M	29.7	70.7	2	AP	+	+
81M	30.0	74.4	2	AP	+	+
16	375.2	1120.4		2 A, 14 AP, 0 P	14	8
Average	23.45	70.03			(87.5%)	(50.0%)

[1] See footnote for table 2.

These findings suggest that the degree of disturbance is a function of the extent to which our critical area is destroyed. Results of Mr. S. A. Kirk, working in our laboratory, indicate that when a unilateral lesion to the side opposite the dominant hand reverses the handedness, the lesion always involves most of the critical area. When less than half of the area is involved, no change in hand preference results. These data corroborate the relationship between destruction of our critical area and the disturbance in motor function. However, when individual cases in table 1 are examined, it is found that animals with no motor disturbance often have a very large part of the critical area destroyed. Thus four of the cases have more than 70 per cent of the area destroyed without showing any disturbance in coordinated walking.

TABLE 4 [1]

Description of cases with motor disturbance rated 2 (moderate disturbance)

RAT'S NUMBER AND SEX	TOTAL PER CENT OF DESTRUCTION	PER CENT OF DESTRUCTION OF CRITICAL AREA	NUMBER OF TREPHINE OPENINGS USED	LOCUS OF MAJOR PART OF LESION	SUBCORTICAL DESTRUCTION IN	
					Anterior half	Posterior half
69M	14.9	97.6	1	A	0	0
75M	16.3	98.8	1	A	0	0
22M	20.3	89.0	3	AP	0	0
21M	21.2	91.5	3	AP	0	0
36F	21.4	57.4	3	AP	0	0
33M	21.9	65.9	3	AP	+	+
41F	23.6	93.9	2	AP	+	+
23M	23.9	84.1	3	AP	+	+
40F	24.9	80.5	2	AP	+	+
95F	25.0	97.6	1	AP	0	+
93F	26.1	95.1	2	AP	0	0
32M	29.2	79.3	3	AP	+	+
42F	29.9	94.4	2	AP	0	+
13	298.6	1125.1		{2 A, 11 AP, 0 P}	5	7
Average	22.97	86.55			(38.5%)	(53.8%)

[1] See footnote for table 2.

Exceptional cases of this sort suggest that the extent of motor disturbance is not entirely due to destruction of our critical area. It is possible that the total amount destroyed may play a part in determining the degree of disturbance. Tables 2, 3, 4 and 5 show that rats with disturbances rated 0 have an average lesion of 19.30 per cent; those rated 1, 23.45 per cent; those rated 2, 22.97 per cent; and those rated 3, 23.81 per cent. As the last three values are about equal, it cannot be argued that the extent of destruction as such determines the amount of disturbance. However, as rats with no disturbance have a somewhat smaller average lesion, it seems possible that the extent of destruction may have something to do with the presence or absence of a disturbance. It might be supposed that if little other destruction is present, large destruction of the critical area might be ineffective. To

TABLE 5 [1]

Description of cases with motor disturbance rated 3 (marked disturbance)

RAT'S NUMBER AND SEX	TOTAL PER CENT OF DESTRUCTION	PER CENT OF DESTRUCTION OF CRITICAL AREA	NUMBER OF TREPHINE OPENINGS USED	LOCUS OF MAJOR PART OF LESION	SUBCORTICAL DESTRUCTION IN	
					Anterior half	Posterior half
63F	13.1	100	1	A	0	0
67F	18.5	100	1	A	0	0
50F	21.1	100	2	AP	+	0
85M	23.5	100	1	A	0	0
72M	26.6	100	2	AP	0	+
83M	26.7	100	1	A	+	+
94F	26.7	100	1	A	+	0
91F	28.1	100	1	A	+	+
4F	30.0	100	3	AP	+	+
9	214.3	900		6 A, 3 AP, 0 P	5	4
Average	23.81	100			(55.6%)	(44.4%)

[1] See footnote for table 2.

determine this, the first fourteen cases and the second fourteen cases of table 2 have been averaged separately. The first fourteen cases have an average lesion of 14.48 per cent as compared with the second fourteen, the average of which is 24.12 per cent. However, the extent of the critical area destroyed for these two divisions is 49.00 per cent and 37.81 per cent, respectively. Similar treatment of the other tables does not yield such differences. In their cases the inverse relationship between the total extent of the lesion and the extent of the critical area destroyed is not present. This suggests that small lesions may have larger amounts of the critical area destroyed without impairing motor abilities.

Let us now consider whether the locus of the extra destruction plays a part. Columns 4 and 5 of tables 2, 3, 4 and 5 give a description of the lesions. Numerals 1, 2 and 3 in column 4 indicate whether the lesion was produced through one, two or three pairs of trephine openings. (The greater the number of trephine openings the greater the spread of the lesions.) A and P of column 5 indicate whether the mass of a lesion was primarily in the anterior or the posterior halves of the brain, respectively, and AP indicates that the lesion was spread rather uniformly over both anterior and posterior halves.

In cases with no motor defects (table 2) it is found that in only two cases (7.1 per cent) is the lesion primarily in the frontal half; and in each of these cases the lesion is small, but greatly invades the critical area. In thirteen cases (46.4 per cent) the lesions are well distributed and in thirteen cases (46.4 per cent) they are primarily posterior. Thus rats with no motor disturbance have the mass of their lesions away from the critical area; and in the larger lesions the mass of destruction is not in tissue surrounding the critical area even when the critical area is considerably invaded.

Similar examination of tables 3, 4 and 5 reveals that with greater motor disturbance, more and more of the lesion tends to be in the frontal half of the brain, i.e., in the region adjoining the critical area. With marked motor disturbance the lesion is primarily anterior. These data are brought together in table 6. This table shows strikingly that tissue adjoining the critical area contributes to the motor disturbance.

There remains only the possibility that subcortical destruction may contribute to the motor disturbance. In all cases such destruction was slight and often unilateral. Columns 6 and 7 of tables 2, 3, 4 and 5 indicate destruction of subcortical tissue in the anterior and posterior halves of the brain, respectively. In table 2 the subcortical destruction is least frequent, but in table 3 it is most frequent. Because subcortical destruction was not most frequent in cases with profound motor disturbance (table 5) and because only about half of these cases had either frontal or posterior subcortical destruction, it is highly unlikely that such destruction determined the nature of our results.

TABLE 6

Relation between degree of motor disturbance and locus of major part of lesion

DEGREE OF MOTOR DISTURBANCE	PER CENT OF CASES WITH LOCUS OF LESION IN		
	A	AP	P
0	7.1	46.4	46.4
1	12.5	87.5	00
2	15.4	84.6	00
3	66.7	33.3	00

SUMMARY

Cortical lesions in the rat do not produce paralysis, but they may greatly handicap its performance when running on narrow poles. To determine whether or not this handicap is due to the loss of some particular area, sixty-six rats were subjected to various patterns of lesions and then tested to determine their skill on narrow poles. The performance of each rat was rated with 0 (no handicap), 1, 2, or 3, according to the degree of disability in walking on the poles.

The results show that nine cases were markedly handicapped. These rats had a common area destroyed in both hemispheres which constitutes about 5 per cent of the total cortical surface. The area extends partly in Fortuyn's area j (somesthetic) and partly in his areas f and n (motor). Of the remaining rats, twenty-eight showed no loss in ability and these involved our critical area to an average extent of 43 per cent; sixteen rats had handicaps rated 1 and these involved the critical area to an average extent of 70 per cent; thirteen rats had handicaps rated 2 and these had an average of 87 per cent of the area destroyed. Examination of destruction outside the critical area revealed that tissue immediately in the vicinity of the critical area contributed to

disturbance in walking. For this reason, some cases with large destruction of the critical area, but slight destruction of surrounding tissue, showed little or no motor disturbance.

Subcortical destruction was associated with large lesions, but not with the disturbance in coordinated walking.

CONCLUSION

The results of this study indicate that coordinated walking in the rat is primarily dependent upon a particular area which is structurally partly motor and partly somesthetic. This area, therefore, appears to have a coordinating function. No particular part of the area seems to be more important than any other. (As tissue was destroyed from various points, various patterns of the critical area were involved in the various cases.) Tissue surrounding this area, when destroyed, contributes to the disturbance. We have thus found what seems to be a rather specifically localized area which nevertheless functions in accordance with the law of mass action. The tissue surrounding the critical area, although it contributes to the function of the area, is not equipotential with it. Tissue in the posterior part of the brain when destroyed does not contribute to the disturbance.

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