XCIV. METABOLISM OF NORMAL AND TUMOUR TISSUE.

XV. THE RESPIRATORY QUOTIENT OF BRAIN CORTEX.

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ELLIOTT AND BAKER [1935] have repeated a number of observations made by ourselves on respiratory quotients of various isolated tissues [Dickens and Simer, 1930, 2; 1931, 2; Dickens and Greville, 1933, 1, 2; 1935]. While duplicating many of our results they state that in some cases "important differences from their findings have been observed". On these differences they base a fundamental criticism of our work on metabolism.

The most striking difference reported was in the case of rat-brain cortex, where Elliott and Baker report a mean R.Q. 0.86 (extremes 0.93–0.78). Our results were much higher being in the region of unity, thus supporting the view held by nearly all workers that in brain the oxidation of carbohydrate preponderates [Gayda, 1914; Loebel, 1925; Meyerhof and Lohmann, 1926, 1, 2; Himwich and Nahum, 1929; 1930; Himwich and Fazikas, 1932; Himwich, 1932; Ashford and Holmes, 1931; Gerard and Schachter, 1932; Weil-Malherbe, unpublished].

Despite the fact that their results were in opposition to this prevailing view and that their experiments were based on a single technique for determination of R.Q. and on a comparatively small number of experiments, Elliott and Baker suggest that their own results should be accepted as correct.

In view of the fact that by the use of our three independent methods of R.Q. determination we have never observed values of the order claimed by Elliott and Baker, we now report (Table I) all successfully completed experiments on rat-brain cortex made during the last five years. Fig. 1 shows the graphical representations of these results. They are quite clearly those to be expected on statistical grounds for a tissue of R.Q. 1, using a method subject to an error of a few per cent.¹

Elliott and Baker's complete results on rat-brain cortex are included in Fig. 2: the difference between these results and our own is far outside any possible error of our experiments. It will be noted that whilst the results in our experiments follow the statistical law, those of Elliott and Baker show no peak but rather a wide plateau indicating a lack of uniformity in their results.

Elliott and Baker attempt to explain their low results by a complicated theory based on the action of salt solutions on tissues. They suppose, too, that our experiments lasted for 5 hours which was not the case (see Table I), and they also assume wrongly that the R.Q. rose during this period. A simpler explanation of this supposed increased R.Q. will be suggested later.

¹ Since the R.Q. of medulla [Himwich and Fazikas, 1932] and of peripheral nerve [Meyerhof and Schmidt, 1929] which consist largely of white matter is low, it is possible that a slight contamination with white matter may account for a few results being low.

Table I. *Respiratory quotient of rat-brain cortex; measurements of Dickens and co-workers.*

Date	Exp. no.	Respiratory quotient	Time of exp. (min.)	Medium	Method
3. iv. 30	1	1.00	120	PG	D & S 1
29. iv. 30	2	1.02	180	"	"
	3	1.00	180	"	"
	4	1.03	180	"	"
30. iv. 30	5	0.96	150	"	"
	6	0.98	150	"	"
	7	1.00	120	"	"
7. vi. 30	8	0.94	75	"	"
	9	1.00	105	"	"
8. vi. 30	10	0.96	165	"	"
	11	0.98	135	"	"
10. vi. 30	12	0.98	180	"	"
	13	0.97	180	"	"
—, iii. 31	14	1.00	75	BG	D & S 2
—, iii. 31	15	0.99	90	"	"
—, iv. 31	16	1.00	100	"	"
—, iv. 31	17	0.99	180	"	"
	18	0.99	180	"	"
30. vi. 31	19	0.94	180	"	"
	20	0.96	180	"	"
—, v. 31	21	1.04	180	BG (serum)	"
—, v. 31	22	0.95	180	BG	"
	23	0.95	180	"	"
15. xii. 31	24	0.96	150	BL	"
16. xii. 31	25	1.00	150	"	"
17. xii. 31	26	1.01	180	BG	"
11. i. 32	27	0.97	180	"	"
	28	1.02	180	"	"
13. i. 32	29	0.97	160	BF	"
14. i. 32	30	1.01	210	BL	"
13. iv. 32	31	1.01	160	BF	"
28. ii. 33	32	1.00	200	BG	"
	33	1.01	200	BF	"
2. iii. 33	34	0.91	180	BG	"
	35	0.95	180	BF	"
3. iii. 33	36	1.01	120	PG	"
	37	1.03	120	PF	"
19. vii. 33	38	1.03	90	BG	D & G
24. vii. 33	39	0.99	120	"	"
30. i. 34	40	0.98	120	"	"
3. ii. 35	41	1.02	90	PG	D & S 1
	42	1.01	90	"	"
5. ii. 35	43	1.03	120	BG	D & S 2
25. iv. 35	44	1.00	80	PG	D & S 1
	45	1.02	80	"	"
4. vi. 35	46	0.96	180	"	"
5. vi. 35	47	1.02	120	"	"
	48	1.01	120	"	"
3. v. 34	49	0.99	175	BG	D & S 2
4. ix. 34	50	0.96	180	"	"
23. xi. 34	51	0.97	150	"	"
26. xi. 34	52	0.92	180	"	"
17. xi. 33	53	0.96	185	BL	"
26. xi. 33	54	0.97	165	"	"

Abbreviations. Medium: B = bicarbonate saline

P = phosphate saline

G = medium contained 0.2% glucose

F = medium contained 0.2% fructose

L = medium contained 0.2% lactate

Methods: D & S 1 = Dickens and Simer (1930, 1)

D & S 2 = Dickens and Simer (1931, 1)

D & G = Dickens & Greville (1933, 2)

Fig. 1. Respiratory quotient of rat-brain cortex [Dickens and co-workers].

Fig. 2. Respiratory quotient of rat-brain cortex [Elliott and Baker, 1935].

Table II. *Rat-brain cortex; results of Elliott and Baker [1935], Table II, p. 2434.*

Exp. no.*	Rate of respiration (μ l. O ₂ per hour)	"Respiratory quotient"
15	150	1.00
14	160	0.93
7	182	0.93
4	183	0.93
8	213	0.90
3	217	0.91
1	272	0.81
12	300	0.83
2	302	0.88
13	316	0.89
5	328	0.86
11	333	0.85
10	342	0.84
6	366	0.78
9	380	0.87

Mean 0.93

Mean 0.84(5)

* These numbers refer to the 15 individual estimations of Elliott and Baker, Table II, samples 1 to 10; numbering from the top downwards.

It appeared to us probable that there was some unsuspected error in the technique used by Elliott and Baker.

Inspection of their results [Elliott and Baker, 1935, Table II] revealed a possible source of such an error. The quantities of tissues used by Elliott and Baker are very large and consequently the rate of gas exchange is much higher than in our experiments. In Table II Elliott and Baker's results for rat-brain cortex are recorded in order of increasing gas exchange calculated from their figures for respiration and tissue weight.

It is evident from inspection of this table that there is a general fall in the observed "respiratory quotient" with increasing rate of gas exchange. In six experiments out of fifteen where the gas exchange is below 220 μ l. O₂ per hour, the "R.Q." is never below 0.90 and the average is 0.93. In the remaining nine observations where the gas exchange exceeds 250 μ l. per hour there is not one "R.Q." of 0.90 or above and the average is 0.845.

The one value of R.Q. 1.0 in Elliott and Baker's table is explained by them as being due to the prolonged action of salt solution. It seems to us more probable that the correct explanation is that this was the only experiment in which adequate gas equilibrium occurred, the gas exchange being in this particular experiment at the more reasonable level of 150 μ l. O₂ per hour.

The need for caution in this respect was emphasised in our earlier papers [Dickens and Šimer, 1931, 1, 2] where we pointed out that with our method gas exchanges above a certain magnitude were liable to introduce serious error. It is of course impossible for us to say what limit of gas exchange is permissible for the particular apparatus and rate of shaking used by Elliott and Baker, but the critical survey of their results suggests that it may be of the same order as in our vessels, *viz.* 100–150 μ l. per hour. The errors introduced by ignoring this precaution are not susceptible to quantitative treatment. They could perhaps account also for some of Elliott and Baker's results on highly glycolysing tissues, where it appears probable that the gas exchange due to very large glycolysis might easily lead to quite indeterminate irregularities in these results.

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