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METABOLIC ACTIVITY OF THE SMALL INTESTINE OF THE RAT AND GOLDEN HAMSTER (*MESOCRICETUS AURATUS*)

BY T. H. WILSON* AND G. WISEMAN

From the Medical Research Council Unit for Research in Cell Metabolism, Department of Biochemistry, and the Department of Physiology, University of Sheffield

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A method of preparing small sacs of everted small intestine for the study of active movement of substances across the wall has been described in a previous paper (Wilson & Wiseman, 1954). This technique has been used in the study of the respiration and glycolysis of the various regions of the small intestine of the rat and golden hamster.

EXPERIMENTAL

The preparation of sacs of everted small intestine and the general experimental procedure are described by Wilson & Wiseman (1954). The intestinal sacs were placed into 25 ml. Warburg flasks and shaken at 90 oscillations/min (4 cm amplitude). At this rate of shaking there was very little disintegration of the tissue of either rat or hamster, although at faster rates there was often pronounced tissue disintegration, the rat intestine being more fragile than that of the hamster.

The thickness of the wall of intestinal sacs as used in the metabolic experiments was measured. In the case of the rat 0·2 ml. of fluid was introduced for each 1 cm length of intestine, while in the hamster 0·3 ml./cm was used. The thickness of the sac wall was calculated (assuming a specific gravity of 1·0) from the wet weight of the tissue and the length and circumference of the sac.

The lactic acid produced under aerobic conditions was measured by the colorimetric method of Barker & Summerson (1941), while the anaerobic lactic acid production was estimated manometrically.

RESULTS

Thickness of sac wall. The thickness of the wall of sacs made from various regions of the small intestine of the rat and hamster was estimated and the results are shown in Table 1. Since the length of the rat intestine is about twice that of the hamster more sacs were obtained from the intestine of the former. The thickness of the rat intestine was about 0·30 mm in the upper region of the jejunum while only about 0·15 mm in the lower ileum; that of the hamster intestine increased from about 0·23 mm in the duodenum to about 0·28 mm in the jejunum, and then decreased to a value of about 0·17 mm in the lower ileum.

* Exchange Fellow of the American Cancer Society.

Under the experimental conditions, with 100% O_2 as gas phase and a Q_{O_2} of -20 (μl./mg dry wt./hr), the limiting thickness for oxygenation of the tissue is 0·44 mm as calculated from the formula of Warburg (1923). Since the average thickness of the wall of the sacs varies from about 0·17 to about 0·30 mm, adequate oxygenation may be assumed, especially as the villiform structure of the mucosal surface greatly facilitates diffusion.

TABLE 1. Thickness of the wall of sacs made at various locations along rat and hamster small intestine

(The sac was distended by injection of 0·2 ml./cm length of intestine for the rat and 0·3 ml./cm for the hamster.)

	Golden hamster			Rat	
Location	Animal 1, thickness (mm)	Animal 2, thickness (mm)	Location	Animal 1, thickness (mm)	Animal 2, thickness (mm)
Duodenum	0·25	0·22	Duodenum	0·30	0·30
Upper jejunum	0·26	0·22	Upper jejunum	0·31	0·26
	0·29	0·28		0·26	0·28
	0·24	0·21		0·29	0·28
	0·20	0·19		0·25	0·23
Lower ileum	0·17	0·17		0·29	0·24
				0·24	0·22
				0·23	0·23
				0·22	0·21
				0·14	0·18
			Lower ileum	—	0·17

TABLE 2. Q_{O_2} of sacs made at various locations along the rat and hamster small intestine

(Each Warburg flask contained 3 ml. phosphate-saline containing 0·3% glucose, 0·2 ml. 2N-NaOH and filter-paper in centre-well, and was gassed with 100% O_2. Experimental period 1 hr. 37° C.)

	Q_{O_2} (μl./mg dry wt./hr)	
Location	Hamster	Rat
Duodenum	−22·7	−23·0
Upper jejunum	−14·3	−21·5
	−13·1	−23·5
	−12·8	−20·5
	−12·0	−19·6
	−12·6	−17·8
	−13·0	−17·2
	−10·0	−15·5
Lower ileum	—	−13·5

Oxygen uptake. Table 2 shows Q_{O_2} values for sacs made at different locations along the small intestine of the rat and hamster. In the hamster the Q_{O_2} decreased from -23 in the duodenum to -10 in the lower ileum; in the rat the value in the duodenum was -23 and that in the lower ileum was -14. In all experiments the rate of oxygen uptake of the sacs was constant for the 1 hr period studied. Three other experiments with each species were performed and similar results obtained.

Glycolysis. The rates of aerobic and anaerobic lactic acid production of sacs made at various locations along the small intestine of the hamster are shown

in Table 3. Anaerobically the rate of lactic acid production (μl./mg dry wt./hr) of the hamster intestine increased from 11 in the duodenum to 19 in the middle jejunum and then decreased to about 10 in the lower ileum. Aerobically the rate of lactic acid production decreased on passing from the upper to the lower

TABLE 3. Aerobic and anaerobic lactic acid production of sacs made at various locations along the hamster small intestine

(Warburg flasks contained the sac and 3 ml. bicarbonate-saline with 0·3% glucose; gas phase aerobically 5% CO_2 in O_2, anaerobically 5% CO_2 in N_2. Experimental period 1 hr. 37° C.)

Location	$Q^{O_2}_{\text{lactic acid}}$ (μl./mg dry wt./hr)	Location	$Q^{N_2}_{CO_2}$ (μl./mg dry wt./hr)
Duodenum	9·7	Duodenum	11·1
Upper jejunum	10·6	Upper jejunum	14·7
	7·8		15·6
	5·7		19·0
	2·8		17·3
Lower ileum	3·3		15·8
			15·5
		Lower ileum	10·4

TABLE 4. Aerobic and anaerobic lactic acid production of sacs made at various locations along the rat small intestine

(Warburg flasks contained the sac and 3 ml. bicarbonate-saline with 0·3% glucose; gas phase aerobically 5% CO_2 in O_2, anaerobically 5% CO_2 in N_2. Experimental period 1 hr. 37° C.)

Location	$Q^{O_2}_{\text{lactic acid}}$ (μl./mg dry wt./hr)	Location	$Q^{N_2}_{CO_2}$ (μl./mg dry wt./hr)
Duodenum	24·0	Duodenum	26·7
Upper jejunum	34·1	Upper jejunum	29·0
	24·6		30·4
	12·3		25·4
	9·8		16·8
Lower ileum	3·4		16·5
			16·5
		Lower ileum	12·9

end of the intestine but the values were lower than those obtained anaerobically. This Pasteur effect (increased lactic acid production in the absence of oxygen) was greater in the ileal than in the jejunal region. In the rat, as in the hamster, both the aerobic and anaerobic lactic acid production increased from duodenum to jejunum and then decreased towards the ileo-caecal valve (Table 4). An appreciable Pasteur effect was observed only in the lower half of the intestine. The anaerobic glycolysis decreased in most experiments during the experimental period of 1 hr, the rate in the second half hour being 15–30% lower than that in the first. The results shown in Tables 3 and 4 were typical of three experiments for each animal.

Effect of lowering the temperature. A few experiments were performed at 32° C with jejunal sacs of the rat to determine whether the high rate of aerobic glycolysis would continue under conditions less likely to produce anoxia. The average Q_{O_2} was −12·5 (8 sacs), the average $Q^{O_2}_{\text{lactic acid}}$ was 14·2 (7 sacs), and

the average $Q^{N_2}_{CO_2}$ was 13·0 (4 sacs). Decreasing the temperature of incubation lowered the Q_{O_2} of the rat jejunal sacs from about −20 at 37° C to about −12·5 at 32° C, which is the order of change expected if the tissues were adequately oxygenated at both temperatures. At this lower temperature, as at 37° C, no appreciable Pasteur effect was obtained in jejunal segments, suggesting that the high rate of aerobic glycolysis by the rat small intestine is not due to anoxia under the conditions of the aerobic experiments at 37° C.

DISCUSSION

Weil-Malherbe (1938) and Dickens & Weil-Malherbe (1941) have previously measured the respiration and glycolysis of the isolated mucosa of rat small intestine and noted as a special feature of this tissue a high aerobic glycolysis. Lundsgaard (1940) has also found aerobic lactic acid production in perfused small intestine of the cat. The high rate of aerobic glycolysis of rat small intestine has been confirmed with the present technique; lower rates were obtained with the intestine of the golden hamster.

Metabolic gradients underlying various phases of intestinal activity were suggested as long ago as 1918 (Alvarez & Starkweather), but only in relatively recent years has clear evidence been presented. Differences of metabolic activity have been observed for the isolated mucosa of the rat by Dickens & Weil-Malherbe (1941) and also for the isolated smooth muscle of the cat by Evans (1923) when these tissues were taken from the various regions of the small intestine. On the other hand, the jejunum of the rat has a thicker mucosa (Dickens & Weil-Malherbe, 1941) and also a greater mucosal area/cm of serosal length (Wood, 1944; Fisher & Parsons, 1950) than the ileum. The decrease in the activity on passing down the intestine, therefore, may be due to a fall in ratio of mucosa to smooth muscle in addition to a fall in activity of the mucosa itself.

The main species variation is in the rate of aerobic lactic acid production by the small intestine. The rat and mouse (Dickens & Weil-Malherbe, 1941) and cat (Lundsgaard, 1940) show a higher rate than the rabbit (Rosenthal, 1947) and the hamster.

SUMMARY

1. Small sacs of everted small intestine of rat and golden hamster have been used for the *in vitro* study of oxygen uptake and aerobic and anaerobic lactic acid production.

2. The Q_{O_2} of rat intestine varies from −23 in the duodenum to −14 in the lower ileum, that of the hamster from −23 to −10.

3. The $Q^{N_2}_{CO_2}$ in the rat increased from 27 in the duodenum to 30 in the upper jejunum and then fell to 13 in the lower ileum; in the hamster the $Q^{N_2}_{CO_2}$ rose from 11 in the duodenum to 19 in the upper jejunum followed by a fall to 10 in the lower ileum.

4. The Pasteur effect was small in the duodenum and jejunum of both animals but increased towards the lower ileum.

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