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PARTITION OF HEAT PRODUCTION IN THE RAT

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RESUMO

Partição da Produção de calor no rato

Realizou-se um exame da literatura científica sobre a produção de calor através do metabolismo aeróbico ao nível do organismo como um todo e ao nível de órgãos individuais. Pôde-se com isso obter uma estimativa da partição da produção de calor no rato.

UNITERMOS: Produção de calor, metabolismo celular, rato.

ABSTRACT

The literature on metabolic heat production at the level of the whole organism and at the level of individual organs is examined. An estimate of the partition of heat production in the rat is presented.

KEY WORDS: Heat production, tissue metabolism, rat.

INTRODUCTION

Over two centuries ago, Lavoisier and Laplace conducted the first scientific measurement of the heat produced by the animal body (Lavoisier & Laplace, 1780). The two famous Frenchmen also suggested that animal heat was the result of the common phenomenon of combustion, that is, a process in which a nutrient reacts with oxygen to produce water, carbon dioxide, and heat. Originally, it was thought that combustion took place in the lungs (Lavoisier, 1777). For several decades, evidence was accumulated for the idea that combustion occurs at the tissue level (Schutzenberger, 1874), and when it was demonstrated that the process takes place in the mitochondria of billions of cells everywhere in the body (Keilin, 1925), the question arose about the partition of heat production among different organs. If respiration (the gradual combustion observed in the organism) takes place in several parts of the body, can we assume that all organs are equally effective in producing heat? And is the distribution the same during rest and exercise, in the cold and at thermoneutrality? These questions have been dealt with in an unsystematic manner during the last 50 years, and the objective of this paper is to summarize the empirical evidence currently available concerning the most widely used laboratory animal, the rat.

WHOLE ORGANISM METABOLISM

A 300 g rat resting quietly in a thermally neutral environment (T_a = 25°C) consumes approximately five milliliters of oxygen per minute (Boyle *et al.*, 1981; Field *et al.*, 1939; Gordon, 1988; Nakatsuka *et al.*, 1983; Page & Chenier, 1953). Assuming that the animals are eating a regular balanced rodent chow, and also assuming that anaerobic metabolic activity is negligible, the comsumption of each milliliter of oxygen indicates the production of 20.3 joules of heat (Eckert & Randall, 1983; Schmidt-Nielsen, 1983). Consequently, the resting heat production (RHP) of the rat is about 5.8 W/kg.

The RHP of the rat can be increased several fold by an increase in activity level (Gordon, 1988; Morrison, 1968; Poole & Stephenson, 1977) or by a decreased ambient temperature (Gordon, 1987; Herrington, 1940; Refinetti & Carlisle, 1986; Swift & Forbes, 1939). Smaller but still significant changes in RHP are produced by endogenous circadian oscillations (Shido et al., 1986) and by changes in the nutritional state of the animals (Boyle et al., 1981; Rothwell & Stock, 1981). Finally, larger rats usually have correspondingly higher rates of heat production expressed in a per animal basis, but slightly lower rates when expressed per unit of body masss (Refinetti et al., in press; Spiers & Adair, 1986; Taylor, 1960).

TISSUE METABOLISM

Most studies on tissue metabolism are conducted in vitro. Slices of tissue or whole organs are extracted from the animal and tested in metabolic chambers. Ideally, such studies should be conducted in vivo, so that all physiological conditions prevailing in the intact animal can be preserved. In practice, however, it is usually impossible to measure the oxygen concentration in the blood flowing to and from each organ. In most cases, therefore, some uncertainty remains regarding the accuracy of the experimental results, althought there is some evidence that in vitro measurements are good indicators of in vivo activity (Field et al., 1939; Krebs, 1950; Martin & Fuhrman, 1941).

Determinations of the resting metabolic rate of different tissues (expressed in terms of volume of oxygen consumed per minute per unit of fresh tissue mass) by different authors are shown in Table 1. As metabolic rate is not reported in the same units by all authors, some conversions were necessary. These involved the assumptions that the consumption of 1 liter of oxygen STPD releases 20.3 kJ of heat, that 1 liter of oxygen STPD contains 44.6 mmol of substance, and that the dry weight of an organ corresponds to 25% of its wet weight.

TABLE 1 - Metabolic Rate of Different Tissues.

ORGAN	ANIMAL	ml/min/kg	SOURCE
Brain	dog	99	Gayda, 1914
	rat	50	Caldwell & Wittenberg, 1974
	rat	100	Silva <u>et al</u>., 1983
	rat	31	Field <u>et al</u>., 1939
Kidney	rat	90	Caldwell & Wittenberg, 1974
	rat	49	Freed <u>et al</u>., 1973
	rat	100	Jansky & Hart, 1963
	rat	69	Field <u>et al</u>., 1939
Heart	rat	60	Caldwell & Wittenberg, 1974
	dog	48	Evans & Starling, 1913
	rat	32	Field <u>et al</u>., 1939
Liver	rat	55	Caldwell & Wittenberg, 1974
	rabbit	10	Harken <u>et al</u>., 1977
	rat	34	Field <u>et al</u>., 1939
Lung	rat	10	Caldwell & Wittenberg, 1974
	dog	10	Evans & Starling, 1913
	dog	10	Weber & Visscher, 1969
	rat	21	Field <u>et al</u>., 1939
Muscle[1]	dog	5	Stainsby & Otis, 1964
	rat	9	Kolar & Jansky, 1984
	rat	12	Dubois-Ferriere & Chinet, 1981
	mouse	18	Wickler, 1981
	rat	6	Jansky & Hart, 1963
	rat	15	Field <u>et al</u>., 1939
Diaphragm	rat	30	Caldwell & Wittenberg, 1974
	rat	30	Field <u>et al</u>., 1939
WAT[2]	rat	20	Hallgren <u>et al</u>., 1986
	human	20	Sorbris <u>et al</u>., 1979
BAT[3]	rat	43	De Castro & Hill, 1988
	rat	21	Foster & Frydman, 1978
	hamster	34	Nedergaard & Lindberg, 1979
Splenn	rat	22	Field <u>et al</u>., 1939
	rat	13	Krebs, 1950
Testis	rat	17	Field <u>et al</u>., 1939
Gut	rat	17	Field <u>et al</u>., 1939
Skeleton	rat	3	Field <u>et al</u>., 1939
Skin	rat	7	Field <u>et al</u>., 1939
Artery	pig	2	Scott <u>et al</u>., 1970

[1]Skeletal muscle

[2]White adipose tissue

[3]Brown adipose tissue

PARTITION OF HEAT PRODUCTION

Based on the experimental data shown in Table 1 and on the results of measurements of organ weight in the rat (Field et al., 1939; Foster & Frydman, 1978; Turton, 1979), it is possible to calculate the partition of heat production in the body of the resting rat. All values shown in Table 1 were increased by 30% to compensate for in vitro inactivity (Field et al., 1939; Martin & Fuhrman, 1941), converted to units of heat, and displayed in Table 2.

TABLE 2 - Partition of Heat Production During Rest.

Organ	Mass (g)	Metabolism (W/kg)	Heat (W)	%
Brain	2.1	31	0.07	4
Kidneys	2.4	34	0.08	4
Heart	1.0	21	0.02	1
Liver	15.2	14	0.21	11
Lungs	1.6	5	0.01	1
Muscle	129.5	5	0.65	34
Diaphragm	1.0	13	0.01	1
Gut	17.[illegible]	8	0.14	7
Spleen	0.7	8	0.01	1
WAT	33.0	0.9	0.03	2
BAT	2.5	14	0.04	2
Testes	2.8	8	0.02	1
Skeleton	22.0	1	0.02	1
Skin	39.4	3	0.12	6
Remainder	59.3	8	0.47	24
WHOLE RAT	330.0	5.57	1.90	100

It can be noticed in Table 2 that organs such as the brain, kidneys, and heart have a very high metabolic rate (21-34 W/kg), whereas white adipose tissue and the skeleton have a very low metabolic rate (1 W/kg). The average (whole animal) metabolic rate is about 6 W/kg. It should be pointed out that skeletal muscle has a relatively low metabolic rate (5 W/kg) but constitutes such a large part of the body (130 g in a 300 g rat) that its total heat production is very high (34% of the total heat produced by the animal).

During exercise, the activity of the skeletal muscles, the heart, and some other organs increases dramatically. The skeletal muscles are specially important because of their large mass. Active muscles can increase their metabolic rate 5-8 times above resting levels (Spriet et al., 1985; Stainsby & Otis, 1964). Since whole organism metabolism also increases about 5-8 times, at least in humans (Nielsen, 1970), the partition of heat production does not seem to be affected by exercise. Further research on rat exercise is clearly necessary to elucidate this question.

Cold exposure causes an elevation of metabolic rate, especially in cold adapted animals. Based on the data on blood flow rate to different organs, it has been suggested that 60% of the increase in heat production is due to brown adipose tissue (Foster & Frydman, 1978). Assuming a twofold increase in whole animal metabolism, brown adipose tissue could be responsible for 23% of total body heat production in a cold environment rather than the meager 2% in thermal neutrality. This would be a significant change in the partition of heat production.

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