The respiratory quotient in the newborn pig

By L. E. MOUNT

ARC Institute of Animal Physiology, Babraham, Cambridge

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1. Rates of oxygen consumption and carbon dioxide production were measured in pigs from birth to 3 days of age in an open-circuit system.

2. The mean respiratory quotient (RQ) during the first 6 h following birth was 0·95 in fasted pigs and 0·91 in pigs which were allowed to feed.

3. The RQ fell during the remainder of the first postnatal day to mean values close to 0·85, whether the pigs were allowed to feed from birth or were fasted.

4. From 1 to 3 days of age the RQ had a mean value of 0·79.

5. There was little difference in the RQ of pigs exposed to environmental temperatures of either 32 or 16°.

6. It is concluded that the baby pig is not exclusively dependent on carbohydrate for its energy metabolism.

Several lines of evidence suggest that glucose, and not fat, is the important source of energy in the newborn pig. First, the glycogen content is much higher in this animal than it is in the newborn of some other mammals, for which quantitative comparisons are given in Table 1. Second, an induced fall in the level of blood sugar is associated with a decreased heart rate and a fall in body temperature (Goodwin, 1957), suggesting that metabolic rate declines when the blood sugar falls. Third, when the newborn pig is fasted the blood sugar falls, and the animal eventually dies in hypoglycaemia. The duration of fasting which is required to produce hypoglycaemia depends in part on the environmental temperature; the lower the temperature, then the higher is the metabolic rate and the more rapid the consumption of the carbohydrate stores. The consequence is that hypoglycaemia occurs earlier in the cold than it does under warm conditions (Morrill, 1952; McCance & Widdowson, 1959). The onset of hypoglycaemia is also influenced by age; in pigs of more than about 1 week of age it becomes difficult to induce hypoglycaemia by fasting (Hanawalt & Sampson, 1947).

Table 1. *Contents of fat and carbohydrate in various newborn mammals*
(From Dawes & Shelley, 1968)

Species	Body-wt (g)	Total lipid, (g/kg body-wt)	Carbohydrate or glycogen (g/kg body-wt) Muscle	Liver	Total	Reference
Rat	5	11	1·8	5·8	7·6	Widdowson (1950)
Rabbit	50	58	2·3	2·7	5·0	Dawkins & Hull (1964)
Rhesus monkey	450	—	7·5	2·5	10·0	—
Man	3500	161	—	—	11·3	Widdowson (1950)
Sheep	4500	30	8·8	2·2	11·0	Alexander (1962)
Pig	1000	11	20·9	2·1	23·0	Widdowson (1950)

For these reasons it may be expected that the respiratory quotient (RQ) in the newborn pig would be close to unity, at least in the first few days following birth. The content of fat in the body of the animal rises from about 1% at birth (Widdowson, 1950) to about 10% at 1 week of age (Brooks, Fontenot, Vipperman, Thomas & Graham, 1964). If it is assumed that the ability to store fat denotes a capacity to metabolize it, the RQ in the normally fed piglet would be expected to fall after the initial postnatal period. Similarly, it might also be expected that if an animal were fasted from birth the fat metabolism would not increase and therefore that the RQ would remain at unity.

In order to test these possibilities, a series of simultaneous measurements of the rates of oxygen consumption and of the production of carbon dioxide has been made in a number of newborn pigs under conditions which permitted the variation of RQ with age, feeding and environmental temperature to be determined. Earlier relevant work on metabolic rate and environment in the pig has been discussed elsewhere (Mount, 1968).

EXPERIMENTAL

Animals and their management

Observations were made on forty-one occasions on a total of thirty-seven pigs aged from 0·5 h to 3 days, with a range of body-weight from 0·84 to 2·10 kg (Fig. 1). The animals were taken from successive litters of healthy pigs without any attempt at selection. Some animals were removed from the sow, and, after body-weight and rectal temperature (by thermocouple 2 cm deep to the anus) had been recorded, were placed individually in the metabolism chamber, in size 46 cm by 33 cm by 32 cm high. Other pigs were removed from the sow and housed in cages with water, but without food, at an environmental temperature of 32° for periods up to but not exceeding 1 day. Observations were made on these animals either after the period of fasting, or both before and after. Metabolic measurements were made at chamber temperatures close to either 32 or 16°.

Procedure

The rates of oxygen consumption and carbon dioxide production were measured by a Noyons type diaferometer (Kipp and Zonen, Holland) in an open-circuit metabolism apparatus. The principle of operation is that the differences between the oxygen and carbon dioxide concentrations in the air entering and leaving the metabolism chamber are determined from the thermal conductivity values of air samples; the values were printed continuously on a recorder. The mean differences between the ingoing and outgoing concentrations of oxygen and carbon dioxide were determined from the area under each trace plotted on the recorder chart during each run. The products of these differences and the known volume rates of air flow (standardized in the diaferometer) gave respectively the rates of oxygen consumption and carbon dioxide production.

Calibration. The diaferometer was calibrated both by the manufacturer's method of introducing gas samples of known composition, and by burning ethyl alcohol in the metabolism chamber at rates corresponding to the rates at which oxygen was consumed by the young pigs used in the experiments.

Alcohol checks were carried out at intervals during the course of the experiments.

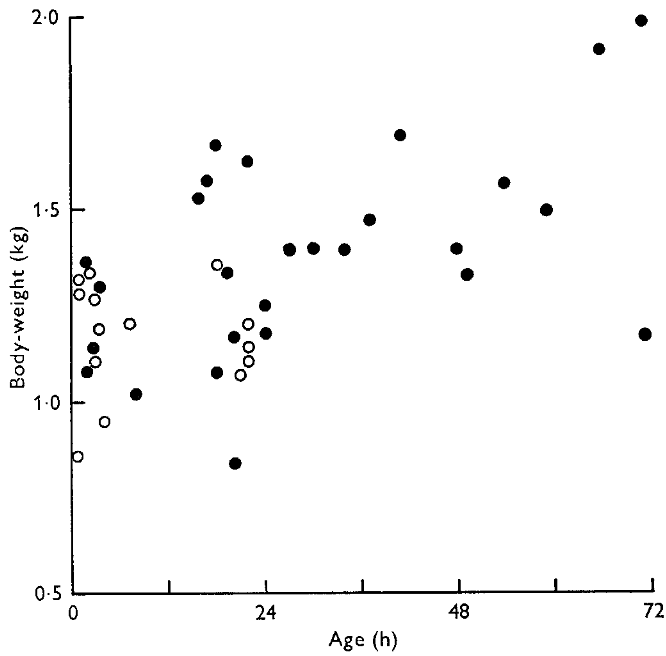

Fig. 1. Body-weights and ages of both the fasted and fed pigs at the times of measurement of rectal temperature, oxygen consumption and carbon dioxide production. ●, animals feeding normally from the sow since birth; ○, animals fasted from birth and kept at an environmental temperature of 32°.

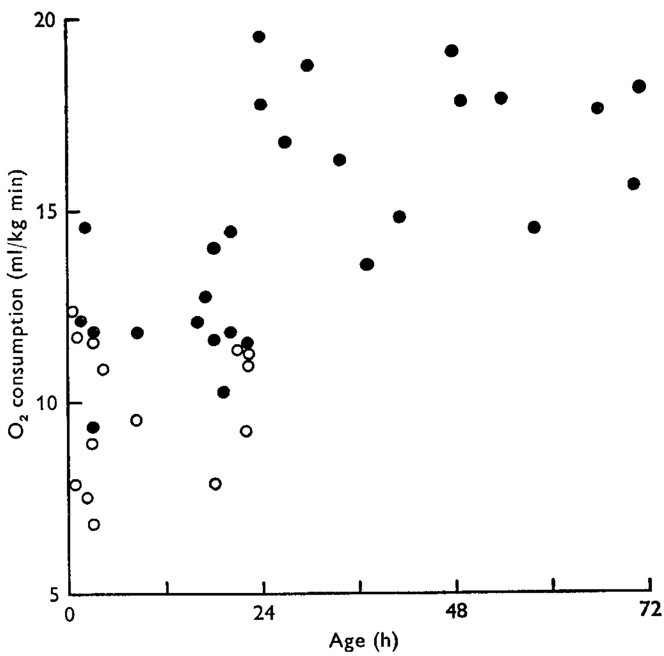

Fig. 2. Rates of oxygen consumption of pigs up to 3 days of age at an environmental temperature of 32°. ●, fed; ○, fasted from birth.

Ethyl alcohol was burnt in a small lamp with a glass-fibre wick, designed for the purpose. The periods of alcohol combustion extended from 20 to 80 min; the alcohol burnt was estimated from the weight of the lamp before and after each period, with a small correction applied for loss of alcohol by evaporation. The correction was determined from the difference in weight during a corresponding period in which the alcohol check routine was followed, with the exception that the lamp was not lit and the wick was covered. The lamp was lit *in situ* by an electrically heated filament, and snuffed by a cover manipulated from outside the chamber. The mean recovery rates from six successive alcohol checks were 108% (range 103–113%) for oxygen, and 104% (range 100–107%) for carbon dioxide, calculated on the basis of the standard figures given with the instrument. By the manufacturer's method of calibration using known gas mixtures, the corresponding recoveries were 109·5% for oxygen and 100% for carbon dioxide, measured on only one occasion. The figures derived from the alcohol checks were used as the reference bases for the calculation of metabolic rate and RQ.

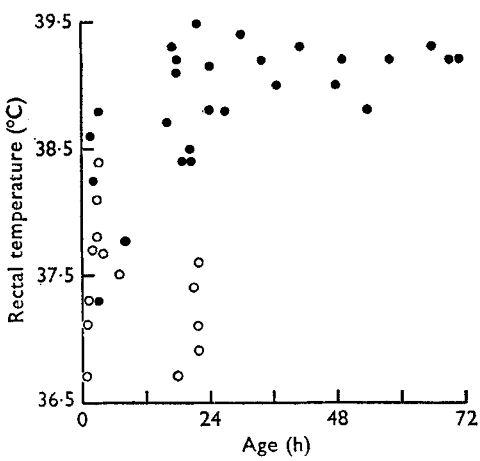

Fig. 3

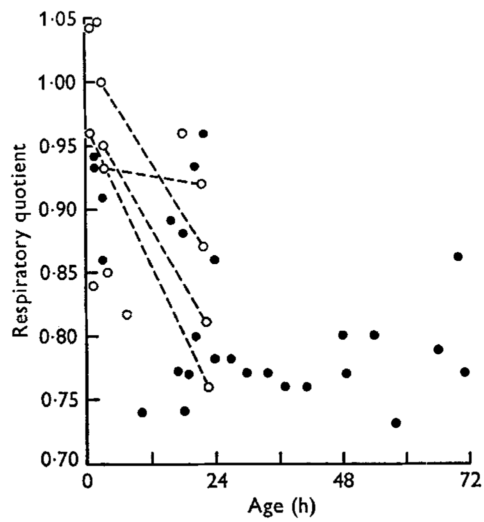

Fig. 4

Fig. 3. Rectal temperatures of pigs at the times of measurement of oxygen consumption. ●, fed; ○, fasted from birth.

Fig. 4. Calculated respiratory quotients for pigs at 32° environmental temperature. ●, fed; ○, fasted from birth.

RESULTS

Metabolic rate and body temperature. The rates of oxygen consumption at 32° environmental temperature by newborn pigs in these experiments are given in Fig. 2, both for those which were allowed to feed from birth and for those which were fasted. The results for the fed pigs show the characteristic rise in metabolic rate during the postnatal period (Mount, 1959); the rise was not apparent in the fasted animals, but a proper comparison cannot be made since the fasting period was limited to 24 h. Rectal temperatures measured at the same time showed the expected rise during the 1st day after birth in the normally fed pigs, but this rise did not occur in the fasted animals (Fig. 3).

RQ. The calculated RQs at a mean environmental temperature of 32° are given in Fig. 4, and means and standard errors at different ages in Table 2.

Table 2. *Respiratory quotients for pigs up to 3 days of age, at a mean environmental temperature of 32°, either fasted or fed from birth*

(The values are means with their standard errors, with numbers of observations in parentheses)

Age (h)	Fasted	Fed
< 6	0·95 ± 0·03 (8)	0·91 ± 0·02 (4)
6–24	0·86 ± 0·03 (6)	0·83 ± 0·03 (9)
24–72	—	0·79 ± 0·01 (14)

Comparison of fasted pigs of less than 6 h with those of 6–24 h old shows a significant decline in RQ with age ($P < 0·05$). Four pairs of points in Fig. 4 are linked by interrupted lines, each pair of values being obtained with one pig; a paired-variate test shows a significant fall in the mean value ($P = 0·05$) from about 2 to about 20 h of age. Comparison of values for fed pigs of under 6 h and of 6–24 h of age also shows a significant fall ($P < 0·05$) during the 1st day after birth.

The RQ was clearly lower in pigs 1–3 days old than it was in animals during the 1st day: this is borne out by the highly significant difference found between the values for, on the one hand, all the 0–24 h old pigs taken together, and, on the other, all the 1–3 days old pigs ($P < 0·001$).

It was during the first few hours following birth that the highest RQs were found, and these occurred in pigs fasted from birth. There was no difference, however, between the mean values for fasted and fed pigs within the same age groups, that is either under 6 h or between 6 and 24 h.

In each of thirty pigs the RQ was estimated at both 32° and 16° environmental temperatures; some were exposed first to 32°, and others to 16°. At the lower temperature the rate of oxygen consumption was elevated above that found in the warm environment, as expected from previous experience (Mount, 1959, 1968). The mean RQ of fasted pigs 0–24 h old was 0·03 higher at 16° than at 32°, that for fed pigs 0–24 h old was 0·06 higher at 16°, and that for pigs 1–3 days old, fed, was 0·01 higher at 16°. Taken by themselves these differences were not significantly different from zero; however, the combined values for all the 0–24 h old pigs, both fasted and fed, gave a mean RQ that was 0·05 higher at 16°, and this was a significant difference ($P < 0·05$). The difference in RQ under cold and warm conditions was also higher for the 0–24 h old pigs than it was for the older animals ($P < 0·05$).

DISCUSSION

Under the conditions of these experiments, the respiratory quotient in the newborn pig was close to unity only in the first few hours after birth, and the highest values were found when the animals were fasted. The RQ fell during the 1st postnatal day, whether the animal was fed or not, indicating the metabolism of non-carbohydrate material. It does not appear, therefore, that the baby pig is exclusively dependent on carbohydrate for its energy metabolism. Further, the fact that the postnatal decline in RQ occurred in the fasted animal suggests that the intake of food is not essential to the change in metabolic pattern which was indicated by the fall in RQ; indeed, the RQ was not significantly affected by withholding food from birth. The mean RQ was above 0·9 during the first 6 h after birth, below 0·9 for the rest of the 1st day, and then in the region of 0·8 during the 2 succeeding days.

The RQ values do in fact suggest a mixed fat–carbohydrate substrate, with an expected contribution from protein metabolism (McCance & Widdowson, 1959). Widdowson (1950), however, found the fat content of the newborn pig to be very low, of the order of 1% of the body-weight. Even so, this quantity, relatively small when compared with other newborn mammals (see Table 1), could satisfy the animal's energy requirements to a considerable degree during a brief span of the neonatal period, as the following calculation shows. If half of the fat in a 1·2 kg pig were to be available for oxidation, the 6 g of fat so utilized would provide 54 kcal energy. At thermal neutrality, the rate of oxygen consumption by the newborn pig rises from a mean value of rather less than 10 ml/kg min following birth to about 15 ml/kg min after the 1st day, corresponding to rates of heat production of approximately 3–5 kcal/h for a pig weighing 1·2 kg. The small amount of assumed available fat would thus by itself provide these needs for up to about 12 h. The postnatal fall in RQ might therefore be explained on the assumption that the newborn pig is similar to the human infant in mobilizing its available fat during the neonatal period (Novak, Melichar & Hahn, 1966).

The rather higher RQ under cold conditions (16°) as compared with the warm (32°), in pigs less than 1 day old, suggests that a larger part of the increased metabolism due to cold exposure is derived from the metabolism of carbohydrate rather than from fat. In pigs more than 1 day old, however, there is no difference between RQs in the cold and the warm, although the elevation of metabolic rate in the cold is similar to that found in the younger pigs, suggesting that a larger part of the metabolic demand can then be met from the oxidation of fat.

Measurements of RQ are notoriously open to considerable error when made under non-equilibrium conditions, owing to retention or loss of carbon dioxide from the body fluids. In these experiments each animal was allowed to remain quietly, in the dark, in the metabolism chamber before the measurement period began, long enough for equilibrium to become established. The open-circuit system used has given results closely similar to those obtained earlier from longer runs, of 5–9 h, in a closed-circuit system (Mount, 1959). The mean value for RQ found on that occasion was 0·84, with a standard error of 0·01, from ten experiments, the mean age of the pigs at the beginning of the runs being 14 h.

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