Effects of Acute Cold Exposure and Age on Respiratory Quotients in Piglets[1] (34756)

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Age-dependent improvement in the piglet's cold resistance (1) apparently derives from increased ability to produce (2), not conserve (3), metabolic heat. Carbohydrate is the piglet's chief substrate (4–6), and it has been suggested (7) that during cold stress the piglet has an increased rate of carbohydrate, but not lipid, oxidation. Nevertheless, despite high depot and circulating carbohydrate levels, 8-hr-old piglets cannot maintain a constant body temperature in a 5° environment (8), whereas those a day older can (1). Plasma free fatty acids (FFA) levels are higher after norepinephrine injection or cold exposure in 2-day-old piglets than in young ones (9). It was suggested (9) that in older piglets sympathetically-induced lipid oxidation supplements and partially supplants glucose oxidation during acute cold exposure, so the piglet can meet the environmental thermal demand, whereas the younger piglet would be more dependent on the poorly regulated (8–11) utilization of carbohydrate.

The study reported here was intended to provide more information on the qualitative nature of the neonatal piglet's metabolic response to cold through observation of the piglet's respiratory quotient (RQ) at thermoneutrality and during cold stress.

Materials and Methods. Hampshire-Yorkshire piglets suckled freely until removed from dams to be studied at 12 or 84 hr of age. One piglet of each age from each of 4 litters was used. They were held at thermoneutrality (35°) unless being exposed to cold (5°).

Respiratory-gas exchange of each piglet was measured, first at 35° and then at 5°, using an open-circuit analytical system (12). During calorimetry a piglet was kept in a 20-liter light-metal container which had a window. Prior to each measurement period the container was allowed to adjust to the experimental thermal environment in the respective climatic chamber (13). Air was drawn (45 liters min^{-1}) from the chamber through the container. Partial pressures of O_2 and CO_2 in the effluent gas were monitored every 24 sec. A period of 12 min after introduction of the piglet into the system for each run was sufficient for equilibrium to be attained, both theoretically (14) and as indicated by plateauing of the rates of oxygen consumption ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$). After equilibration in the respective environment, respiratory-gas exchange was measured for 16 min at 35° and for 32 min at 5°. The $\dot{V}O_2$ and $\dot{V}CO_2$ at standard conditions were calculated for 16-min steady-state periods (one at 35° and two at 5°) in an attempt to preclude the question of the influence of loss or retention of Co_2 from body fluids on RQ (15). The RQ were calculated as $\dot{V}CO_2/\dot{V}O_2$.

Results and Discussion. The $\dot{V}O_2$ (ml $kg^{-3/4}$ min^{-1}) observed were: for the single 16-min steady-state period at 35°, 14 ± 3 for 12-hr-old piglets and 23 ± 5 for 84-hr-olds; for the first 16-min steady-state period at 5°, 29 ± 2 for 12-hr olds and 32 ± 3 for 84-hr-olds; and for the second 16-min steady-state period at 5°, 30 ± 2 for 12-hr-olds and 34 ± 3 for 84-hr-olds. An analysis of variance was conducted on $\dot{V}O_2$ for the single 16-min steady-state period at 35° and for the

[1] Contribution from the Missouri Agricultural Experiment Station, Journal Series No. 5549. Approved by the Director.

first such period at 5°. Age, environmental temperature, and their interaction were fixed sources of variation; litter sum of squares was removed from residual variance to yield the error term. The results indicated that $\dot{V}O_2$ was significantly higher at 5° than at 35° ($p<.05$) and at 84 hr than at 12 hr of age ($p<.10$), but the interaction of environmental temperature and age was not significant. Piglets of both ages were cold-stressed by the colder environment, as evidenced by higher $\dot{V}O_2$ at 5°. The higher $\dot{V}O_2$ per unit of metabolic body size (15) for 84-hr-old piglets in both environments agrees with general trends (16) and previous observations on piglets (2). The $\dot{V}O_2$ did not differ significantly between the first and second steady-state periods at 5° for either age.

The calculated RQ data are summarized in Table I. The RQ data were analyzed in the same way as were the $\dot{V}O_2$. Significant main effects of environmental temperature ($p<.01$) and age ($p<.05$) on RQ were observed. The interaction of environmental temperature and age was not significant; piglets of both ages had depressed RQ in the cold and older piglets had lower RQ at both environmental temperatures. A similar age effect on RQ has been reported for piglets (17), but the present results are at variance with reports that cold-induced depression of RQ was not found in piglets (17, 18). However, in at least one of these studies (17), all measurements were made below the piglet's minimal critical temperature, which is about 34° (2, 19, 20), and therefore comparison with the thermoneutral RQ was not possible.

TABLE I. Respiratory Quotients of Piglets Aged Either 12 or 84 hr During Equilibrium at Environmental Temperature of Either 35 or 5°.[a]

Age (hr)	No. of piglets[b]	Period[c] (min)	Environmental temp (°) 35	5
12	4	12–28	0.95 ± 0.02	0.89 ± 0.03
	4	28–44	—	0.90 ± 0.02
84	4	12–28	0.90 ± 0.01	0.84 ± 0.02
	4	28–44	—	0.85 ± 0.02

[a] Means and associated standard errors of steady-state measurements of 16-min duration. Analysis of variance, described in Results and Discussion, indicated significant main effects of both age ($p<.05$) and environmental temperature ($p<.01$) on RQ during the 12–28 min period. RQ at 5° did not differ significantly between periods at either age.

[b] One piglet of each age from each of 4 litters was used.

[c] Minutes after introduction of piglet into the analytical system. Twelve min were allowed for equilibration before steady-state measurements were begun.

The composite nature of the RQ precludes its exact interpretation. However, when calculated from measurements made at equilibrium and considered together with other metabolic information, the RQ gives an estimate of the proportionate rates of catabolism of the classes of substrate. Depression in RQ from unity indicates a relative increase in the proportionate oxidation rate of fat and/or protein. Adjustment for protein metabolism gives the nonprotein RQ, depression of which indicates more definitively an increase in the proportionate rate of fat oxidation.

It is not feasible to assess protein metabolism in neonatal animals during short-term experiments, and therefore nonprotein RQ was not determined in the present or previous experiments with piglets (17, 18). An increase in the proportionate rate of protein catabolism theoretically could have depressed RQ in cold-stressed piglets, but it is improbable that this alone would have accounted for the observed results. Assuming protein's RQ is 0.83 and a substrate mixture consisting only of protein and carbohydrate, at RQ = 0.90, protein would account for 59% of the substrate while at RQ = 0.85 it would account for 88%. These values are unreasonably high: data on fasting nitrogen balance (5), impaired gluconeogenic capability (11), and high plasma glucocorticoid levels (21) indicate that utilization of endogenous protein for heat production is not appreciable in neonatal piglets. Fasted piglets held either at 31° (warm, but below thermoneutrality) or at 12° (cold) relied on endogenous protein for less than 5% of their substrate, although the proportionate rate of protein catabolism was slightly higher in the colder environment

(5). Exogenous protein is probably not used appreciably for heat production by neonatal piglets either, especially by 12-hr-olds in the present study. An inhibitor in sow colostrum (22) impairs protein digestion (23); before gut closure, ingested proteins are absorbed intact (24).

Instead it is probable that an increase in the proportionate rate of fat oxidation depressed RQ in piglets during cold stress. In a previous study (9), sympathetic impairment by reserpine was more deleterious to cold-resistive ability of piglets at 30 hr than at 6 hr of age, implicating sympathetic function in thermoregulatory development during the first 2 postnatal days. Since there is no significant change in heat-conserving mechanisms in piglets at this time (3), it was suggested (9) that sympathetic function is involved in the development of the regulation of heat production (2). Both injected norepinephrine and cold exposure resulted in higher plasma FFA levels in piglets after the first postnatal day (9), suggesting a less well-developed adipokinetic response to norepinephrine in younger piglets. Therefore, since plasma FFA level is an important determinant of fatty acid oxidation rate in the liver (25) and skeletal muscles (26), it is likely that the cold-induced RQ depression observed in the present study was caused by sympathetic mobilization, release, and subsequent oxidation of endogenous lipid reserves. However, the adipokinetic response to cold apparently occurred already at 12 hr postnatum in the present study, and therefore the absence of increased plasma FFA levels in younger piglets after norepinephrine or cold in the previous experiment (9) may have owed also to rapid catabolism of released FFA at this age. Yet at 5° in the present study 84-hr-old piglets did have lower RQ than did 12-hr-olds (0.85 vs. 0.90), which supports the concept (9) of an age-dependent increase in the proportionate rate of fat catabolism during cold stress. Even if RQ were the same in the cold as at thermoneutrality, the absolute fat-catabolic rate would be higher in the cold because the proportionate fat-catabolic rate remained the same while metabolic rate increased.

The fat content of sow milk approximately doubles during the first 3 days postpartum (27, 28), and there is a concomitant increase in plasma FFA levels in suckled piglets (9, 11, 29). The lower RQ in older piglets observed previously (17) and in the present study were therefore expected.

The conclusions here are that neonatal piglets increase the proportionate fat-catabolic rate upon acute cold exposure as early as 12 hr postnatum and that there is an age-dependent increase in the proportionate fat-catabolic rate in piglets. The former conclusion is in disagreement with the suggestion (7) that piglets cannot increase the rate of lipid oxidation in response to cold until they are about 1 wk old, but the present conclusions agree with the concept (9) that the postnatal improvement in thermostability in piglets is due in part to a postnatal increase in the proportionate fat-catabolic rate during metabolic response to cold stress. The effect may be either an additive one, *i.e.*, metabolic rate is higher in older piglets simply because of supplemental fat catabolism, or a case of lipid catabolism partially supplanting carbohydrate metabolism, which could conceivably be beneficial to total metabolic response. The neonatal piglet responds to cold by mobilizing carbohydrate (8), but glucose apparently cannot be utilized efficiently at this time (8, 11), possibly because insulin insufficiency—due either to incipient hypothermia (30) or catecholamines (31, 32)—impairs carbohydrate utilization during cold stress. Thus, during the first postnatal day or so, when the piglet relies more on carbohydrate as substrate (4, 5), heat-productive capacity would be limited. A higher lipid-catabolic rate during cold stress in older piglets could provide emergency heat production (33) to prevent hypothermia and/or to supplant carbohydrate catabolism during cold stress (31).

Summary. Respiratory exchange was measured in piglets aged either 12 or 84 hr, first at thermoneutrality (35°) and then in the cold (5°). Mean RQ for 12-hr-old piglets were 0.95 at 35° and 0.90 at 5°; for 84-hr-olds, 0.90 at 35° and 0.85 at 5°. Significant effects of environmental temperature ($p <$

.01) and age ($p<.05$) were found. There was no significant interaction between temperature and age; piglets of both ages had depressed RQ in the cold and older piglets had lower RQ at both environmental temperatures. These results were interpreted to mean that the proportionate fat-catabolic rate was higher during cold stress than at thermoneutrality and that it was higher in both environments at 3 days of age than at 12 hr.

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Received Dec. 15, 1969. P.S.E.B.M., 1970, Vol. 134.