

that govern GLP-1 secretion are poorly known. To investigate the secretory activity of the GLP-1 producing cells, a model of isolated vascularly perfused rat colon was developed. In this preparation, polarized endocrine cells are submitted to well-defined luminal and blood-borne stimuli.

Loops of proximal colon were separated from adjacent tissues and perfused via the superior mesenteric artery with a Krebs–Heinseleit buffer containing 25% erythrocytes, 3% bovine albumin, amino acids and glucose. After a 20-min control basal period, stimuli were applied for 30 min. GLP-1 was measured in the portal effluent with antiserum 199D that cross-reacts 100% with GLP-1 (7–36 amide), 84% with GLP-1 (1–36 amide) and less than 0.1% with other peptides of the glucagon family. Luminal infusion of glucose (5%) induced GLP-1 release (plateau at  $45 \pm 10$  fmol/2 min from a basal value of  $16 \pm 2$  fmol/2 min,  $p < 0.05$ ) while starch (0.5%), oleic acid (100 mM), amino acids (29.6 g/l) and short-chain fatty acids (acetate, propionate, butyrate: 5, 20, 100 mM) did not modify basal secretion. Pectin (0.1–2%) produced GLP-1 secretion (maximal value at 200% above basal with 0.5% pectin). Cellulose or gum arabic did not release GLP-1. Hyodeoxycholate, the major bile acid in the colon (2–20 mM), induced a significant GLP-1 release (secretion rate 35–46 fmol/2min,  $p < 0.05$ ) while cholate or deoxycholate did not. Arterial infusion of the neuropeptide bombesin ( $10^{-7}$  M) produced a biphasic GLP-1 secretion (transient rise at 290% of basal followed by a sustained response:

400% of basal). Calcitonin gene-related peptide ( $5 \times 10^{-8}$  M), isoproterenol ( $\beta$ -adrenergic agonist,  $10^{-6}$  M) and bethanechol (cholinergic agonist,  $10^{-4}$  M) induced a sharp GLP-1 release. The effects of 3 hormones released by the proximal gut on the secretion of GLP-1 were then tested. The glucose-dependent insulinotropic polypeptide: GIP (0.25, 0.5, 1 nM) provoked a dose-dependent GLP-1 response (integrated release: RI of  $71 \pm 48$  fmol/30 min at the physiological concentration of 0.25 nM, NS: maximal effect at the supraphysiological concentration of 1 nM, RI:  $410 \pm 71$  fmol/30 min,  $P < 0.001$ ). CCK (100 pM) and secretin (50 pM) had no effect on GLP-1 release. Finally, the combined perfusion of GIP (0.25 or 1 nM, arterial) and butyrate (5 or 20 mM, luminal) produced a GLP-1 secretion that was 4–6 fold higher than the sum of individual responses.

In conclusion, GLP-1 release is induced by luminal factors, neurotransmitters and an intestinal hormone (GIP). The synergistic effect between butyrate and GIP suggest that GLP-1 secretion is the result of complex relationships between factors operating at the luminal and basal sides of L cells in the colon.

#### IV. Energy expenditure

##### Determination of energy cost of standing in preruminant calves from continuous measurements in respiration chambers.

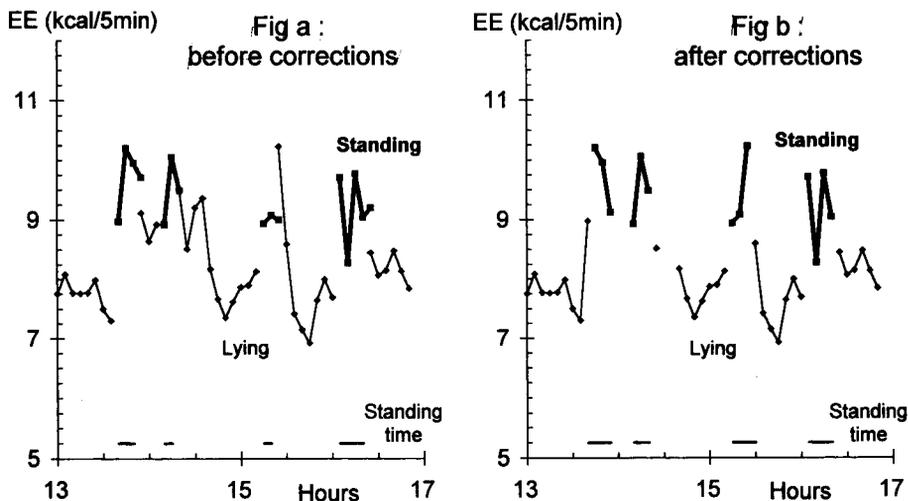


Fig 1. Variation in EE with time: a before correction; b after correction (Y Anglaret, I Ortigues).

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The energy cost of standing (ECS) is non-negligible and variable. It can account for up to 25% of whole animal energy expenditure (EE) and should thus be taken into account. This paper reports a simple method of calculating ECS using continuous indirect calorimetry measurements in respiration chambers. EE and posture (standing/lying obtained by an on/off contactor) were measured in 4 preruminant calves at discrete intervals once every 5 min over 2 d. Calculation of EE includes a correction for dead space.

A frequent and non-reproducible lack of concomitance between posture and EE changes is observed in the results as well as a large variability in EE (fig 1a). This makes ECS difficult to measure. Thus, it appeared necessary to confirm or modify the attribution of EE data to the 'quietly lying' or 'standing' postures. Some 'lying' data were eliminated as non-representative of 'quietly lying' if they were superior to the upper limit of the unilateral confidence interval ( $p < 0.005$ ) calculated for each 'lying' period. In addition, the attribution of the first EE data of each 'standing' period and the first 2 following 'lying' EE data were reconsidered. Data superior to the 'lying EE + 1/2 average increment of EE due to standing' (as initially observed) were attributed to the standing posture. All these corrections accounted for the low measurement frequency used and a variable activity in each posture. Corrections improved the synchronization between EE and posture changes, and the discrimination of the 'standing' periods (fig 1). They increased the time spent standing from  $326 \pm 31$  (SE) to  $383 \pm 34$  min/d. This rise remained below measurement errors (5 min on average per standing period). For each standing period ECS was then calculated by difference between average 'standing' EE and the 'quietly lying' EE baseline surrounding this period. Daily intra-animal variability in ECS ranged from 16 to 33% (CV), and ECS was independent of the duration of the standing periods. Daily average ECS was  $7.46 \pm 0.55$  cal/kg LW/min over the 8 daily kinetics, *ie* 23.8% above the lying EE. This value was much lower and less variable than that measured by regression between total daily EE and total daily time spent standing ( $35.5 \pm 14.4$  cal/kg LW/min,  $n = 8$ ). On the other hand, it was close to that obtained by

Nienaber *et al* [(1987) Energetics of activity using indirect calorimetry. In: *Energy Metabolism of Farm Animal* (PW Moe, HF Tyrell, PJ Reynolds, eds), Rowman and Littlefield, Totowa NJ, USA, 164-167] in newborn calves and sheep using a complex calculation method.

A simple and reliable determination of ECS is thus made possible for each standing period, on a small number of animals, and interpretation of daily changes in EE can thereby be improved.

### **Estimation of the energy balance in concurrently pregnant and lactating rabbit does during their second pregnancy.**

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Rabbit does can be mated shortly after parturition and sustain concurrent pregnancy and lactation. This intensive reproduction rhythm is used in husbandry. However, the energy requirements of concurrently pregnant and lactating does are poorly known. The aim of this experiment was to compare the energy balance of pregnant does (P group,  $n = 72$ ) and pregnant and lactating does (PL,  $n = 79$ ), in breeding conditions. All females were mated within 12 h after the first parturition (day 0). The does had similar live weights at mating ( $3\ 491 \pm 28$  g) in both groups, and were fed a commercial diet (17.5% CP, 9.74 MJ DE/kg) *ad libitum*. They were slaughtered on day 28 of the second pregnancy to study body characteristics and foetal weight. Energy requirements for maintenance ( $420$  kJ/kg<sup>0.75</sup> for P does and  $468$  kJ/kg<sup>0.75</sup> for PL does), milk production ( $155$  g/d;  $8.29$  kJ/g; efficiency of utilization = 0.63), and uterus + foetus growth ( $2.43$  J and  $1.76$  MJ in P and PL groups; efficiency of utilization = 0.27) were calculated according to Parigi-Bini *et al* [(1991) Utilization and partition of digestible energy in primiparous rabbit does in different physiological states. 12th Symp Energy Metabolism Farm Anim Zurich, 17 Sept].

Does in the P group gained weight during the first (548 g) and the second (236 g) half of pregnancy, whereas PL does gained weight during the first half of pregnancy (525 g) but lost weight during the second half of gestation ( $-191$  g). At slaughter, the weights of carcass ( $-17.5\%$ ), skin ( $-20\%$ ), and adipose tissue ( $-71\%$ ) were lower in the PL group than in the P group ( $P < 0.01$ ). The weights of pregnant ute-