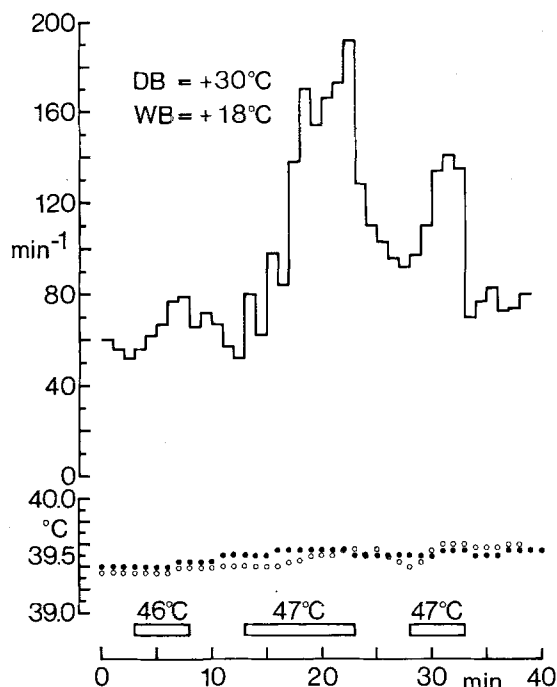


was calculated from the flow rate and the difference between inlet and outlet temperature, amounted to 0.005 watt/kg for 1°C difference between rectal temperature and perfusion temperature. At the most intense levels of stimulation, this could increase mean body temperature at a rate of 0.008°C/min. The experiments were performed in the conscious animals 3 to 6 days after surgery.

The Figure shows an experiment in dog 1 at an air temperature of + 30°C. 3 periods of spinal cord warming were performed by perfusing the thermode with water of



Selective warming of the peripherally denervated spinal cord in a conscious dog and its effect on respiratory rate (above). Filled circles: Rectal temperature. Open circles: Temperature in the vertebral canal at the level of the lowest intact segment. Bars and numbers: Stimulation periods and temperature of the water used to perfuse the thermodes.

46–47°C. In all warming periods, clear increases of respiratory rate up to a peak value of 195 min⁻¹ were found. Since rectal temperature and peridural space temperature at the level of the lowest intact segment (Th 10) changed insignificantly⁴, this panting response was elicited by signals originating in the peripherally denervated part of the spinal cord. The rapid rate of respiration was accompanied by all the characteristic signs of panting which occur in the intact animal when it is exposed to an external or internal heat load: i.e. increased salivation, opened mouth and protrusion of the tongue. However, in contrast to the typical pattern of response to spinal cord warming in intact dogs⁴, the highest levels of respiratory rate were found towards the ends of the stimulation periods. This may have been caused by the paralysis of the lower part of the body, which generally rendered panting difficult and seemed to oppose the thermal drive, when higher respiratory rates were expected.

The Table comprises the results of 14 periods of warming the denervated part of the spinal cord in the 3 animals. In 2 of the 3 animals, the respiratory rate during the control periods was higher than the normal resting values in conscious dogs⁵. This was due to the elevated air temperature, which was chosen to facilitate responses. However, in all cases respiratory rate increased during spinal warming and declined after spinal warming had been finished. This effect was least pronounced in animal 2, in which the spinal roots were cut intradurally.

In conclusion, the experiments have shown that the lumbar and sacral spinal cord, after being deprived of all inputs via dorsal or possibly ventral⁶ roots, can still generate temperature signals and convey them to supraspinal centers to produce panting. These findings extend earlier results about the generation of thermoregulatory cold defence responses in dogs⁷ and pigeons⁸ with dorsal roots cut.

⁴ C. JESSEN, *Pflügers Arch. ges. Physiol.* 297, 53 (1967).

⁵ O. HALLWACHS, *Pflügers Arch. ges. Physiol.* 271, 748 (1960).

⁶ R. E. COGGESHALL, J. D. COULTER and W. D. WILLIS JR., *Brain Res.* 57, 229 (1973).

⁷ K.-A. MEURER, C. JESSEN and M. IRIKI, *Pflügers Arch. ges. Physiol.* 293, 236 (1967).

⁸ R. NECKER and W. RAUTENBERG, *Pflügers Arch. ges. Physiol.* 360, 287 (1975).

Fermentative Digestion of Food in the Colobus Monkey, *Colobus polykomos*

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Summary. Fermentation of leafy food occurs in the enlarged saccus gastricus of the colobus monkey with the formation of volatile fatty acid, as in the rumen of ruminant animals. About half of the digestible organic matter and cellulose of the diet is digested in this way.

Although herbivorous mammals do not secrete cellulolytic enzymes, they are able to digest cellulose in their food by subjecting it to microbial fermentation. The microbes are accommodated either in an enlarged compartment of the stomach, as in ruminant animals, or in an enlarged caecum and colon, as in horses. While there are many herbivores that employ gastric fermentation, among the primates only the colobus, langur and proboscis monkeys, the Colobinae, appear to have adopted this mode of digestion^{3,4}. This subfamily lead an arboreal life, feeding mainly on leaves, fruit and seeds. The first part of the stomach, the saccus gastricus, is greatly

enlarged⁵ and it is here that food is fermented yielding gases and volatile fatty acids similar to those produced

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² We wish to thank the Inter-University Council, the Nuffield Foundation and the Wellcome Trust for financial support. Mr P. J. S. DEWEY kindly made the determinations of cellulose and lignin.

³ R. J. MOIR, *Handbook of Physiology* (Ed. C. F. CODE; American Physiological Society: Washington, D.C. 1968), sect. 6, p. 2673.

⁴ T. BAUCHOP, *A. Rev. Microbiol.* 25, 429 (1971).

⁵ W. C. D. HILL, *Proc. zool. Soc. Lond.* 122, 127 (1952).

Table I. Weights of animals and of their digestive tracts and salivary glands

	<i>Colobus</i> A	<i>Colobus</i> B
Body weight (kg)	6.2	3.4
Gut weights (g)		
Stomach	197	114
Small intestine	69	68
Large intestine	66	35
Salivary gland weights (g)		
Both parotids	8.0	7.6
Both submaxillaries	4.6	2.7
Both sublinguals	1.6	1.0

in the rumen of sheep and cattle⁶⁻⁸. The contents of the saccus then pass to the second part of the stomach, the tubus gastricus, where they are acidified.

While it is clear that this fermentation in the saccus is qualitatively similar to that seen in the rumen, it is not known how important it is quantitatively. It was, therefore, decided to study the disappearance of food from the various compartments of the gut of slaughtered colobus monkeys by use of the lignin ratio technique.

Two young male colobus monkeys were provided for study. They were housed separately in small cages. We wished to feed them on a single species of plant to avoid there being any uncertainty concerning the food eaten. The only plant available locally that these monkeys would eat in any quantity was *Commelinum benghalense*, an exotic succulent plant, which was offered fresh each day. Even so, the monkeys, who were not accustomed to confinement, ate only about 400 g fresh weight daily and were in a rather emaciated condition when slaughtered after receiving this diet for 3 weeks.

Each monkey in turn was anaesthetised by an i.p. injection of pentobarbitone sodium. The abdominal cavity was opened and clamps were placed at the junction between the saccus and the tubus, at the pylorus and at the ileo-caecal junction. The gastro-intestinal tract was then excised and the monkey was killed. The contents of each compartment of the gut were rapidly removed, weighed and mixed. A sample was taken within 5 min of excision for determination of pH; this was then acidified and frozen for subsequent analysis of volatile fatty acids (VFA) by Markham distillation, and of total nitrogen by a Kjeldahl procedure. The remainder of the contents

was dried at 105°C for dry matter determination. One portion of the dry sample was ashed at 500°C for 16 h to measure organic matter by loss of weight, and another was analyzed for cellulose⁹ and acid-detergent lignin¹⁰.

Some anatomical measurements are given in Table I. Table II shows the composition of the food and of the digesta. Large amounts of epithelium had been shed into the contents of the small intestine and so this sample was excluded from further consideration. The contents of the large intestine were divided into a fluid portion (caecum plus first 20 cm of colon) and a pasty portion (remainder of colon and rectum). A 24-hour faeces collection was available from *Colobus* B. It can be seen that a fairly high concentration of VFA was found in both the saccus gastricus and the caecum-colon. The pH remained near neutrality. Higher concentrations of VFA were found in the saccus of 2 colobus monkeys shot in the wild by OHWAKI et al.⁸. The interval between death and preparation of samples for VFA determination in the wild monkeys, 35 and 41 min, was greater than the 10 min that elapsed in our monkeys. This may partly explain the greater acidity of the stomach contents of the former, though their rich diet of fruit and seeds will no doubt have led to a more rapid fermentation than that of our rather inappetent leaf-eating monkeys.

Most of the VFA produced in the rumen of sheep and cattle is absorbed directly and little flows to the abomasum and intestine. The VFA produced in the saccus of the colobus monkey was also largely absorbed from the stomach, though it is not possible from our results to determine whether the saccus or the tubus was the most important site of absorption. The contents of the tubus were sufficiently acid (pH 2.2 and 2.4) to arrest further fermentation. The high concentration of VFA in the caecum-colon indicates that fermentation was proceeding actively in this organ as well, though the relatively small dry weight of contents suggests that digestion in this compartment is of subsidiary importance.

In sheep and cattle normal ruminal fermentation is prevented if the rumen contents become too acid. It is therefore important that a fraction of the volatile fatty acids produced are neutralized to provide a well buffered

⁶ H.-J. KUHN, *Folia primatol.* 2, 193 (1964).

⁷ T. BAUCHOP and R. W. MARTUCCI, *Science* 161, 698 (1968).

⁸ K. OHWAKI, R. E. HUNGATE, L. LOTTER, R. R. HOFFMAN and G. MALOY, *Appl. Microbiol.* 27, 713 (1974).

⁹ K. NEHRING, *Arch. Tierernähr.* 19, 453 (1969).

¹⁰ H. K. GOERING and P. VAN SOEST, *Agricultural Handbook* (U.S. Department of Agriculture, 1970), No. 379.

Table II. The composition of the food and the contents of the digestive tract

	Wet weight (g)	Dry matter (DM) (g/100 g wet weight)	Lignin (g/100 g DM)	Cellulose (g/100 g DM)	Total N (g/100 g DM)	Volatile fatty acids (mM/l)	pH
<i>Commelinum benghalense</i>	—	9	9	15	3.7	—	—
<i>Colobus</i> A							
Saccus gastricus	426	5	10	14	3.1	65	6.5
Tubus gastricus	36	4	11	—	4.0	4	2.4
Caecum + proximal colon	100	10	11	11	2.4	80	7.2
Distal colon + rectum	78	20	15	15	2.6	—	—
<i>Colobus</i> B							
Saccus gastricus	130	9	14	11	4.0	53	7.0
Tubus gastricus	47	11	17	13	3.1	3	2.2
Caecum + proximal colon	34	21	15	—	2.7	47	7.2
Distal colon + rectum	22	31	12	—	3.1	—	—
Faeces	105	28	18	12	2.4	—	—

Table III. Progressive disappearance of food constituents during passage through the digestive tract.

	Dry matter	Organic matter	Cellulose	Total N
<i>Commelinum benghalense</i>	100	100	100	100
<i>Colobus A</i>				
Saccus gastricus	90	86	82	76
Tubus gastricus	85	72	—	90
Caecum + proximal colon	80	66	56	52
Distal colon + rectum	60	55	60	41
<i>Colobus B</i>				
Saccus gastricus	62	59	46	67
Tubus gastricus	54	51	46	45
Caecum + proximal colon	62	51	—	45
Distal colon + rectum	74	64	—	62
Faeces	48	40	39	31

The concentration relative to lignin in the gut contents is given as a percentage of that in the food.

medium at about pH 6. The Ruminantia do this mainly by secreting large volumes of alkaline saliva¹¹. The contents of both saccus and caecum-colon of our colobus monkeys were quite well buffered, 10 ml of supernatant fluid from the saccus requiring 0.7 ml N-H₂SO₄ to reduce the pH below a value of 3, and an equal volume from the caecum-colon requiring 1.5 ml N-H₂SO₄. It is not clear

how the colobus maintains the buffered nature of the contents of its saccus. This compartment, like the camel's rumen¹², has a glandular epithelium which may secrete an alkaline fluid, but the colobus also has well-developed salivary glands (Table I) though nothing is known of the volume or composition of the saliva secreted.

By assuming that lignin is wholly indigestible, the apparent digestibility of the dietary constituents shown in Table II may be estimated. The amount of each component remaining undigested in successive compartments of the gut is given by its concentration per g lignin in the digesta divided by its concentration per g lignin in the food. Table III gives the values obtained, expressed as percentages of the amounts eaten. About 40–50% of dry matter, organic matter and cellulose had disappeared by the time the distal colon was reached, and some further loss appeared to take place before the faeces were voided in *Colobus B*. Both the saccus and the large intestine seemed to be important sites of digestion. Total nitrogen showed a rather greater apparent digestibility.

The absence of cellulolytic activity in colobus stomach contents reported by KUHN⁶ and by OHWAKI et al.⁸ was probably due to the diets of fruit and seeds being eaten by their animals. Foods rich in starch and sugar are associated with suppression of cellulolysis in cattle and sheep. Our observations indicate that microbial fermentation of food, including extensive cellulolysis, can occur in the colobus monkey receiving a leafy diet.

¹¹ R. N. B. KAY, *Wild Rev. Nutr. Diet.* 6, 292 (1966).
¹² R. H. ECKERLIN and C. E. STEVENS, *Cornell Vet.* 63, 436 (1973).

Increased Plasma Creatine Kinase Activity in Rabbits: Effect of Systematically Repeated Blood Sampling¹

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Summary. Various physical, chemical and biological factors are involved in an increased plasma creatine kinase activity. Repeated blood sampling induced in all rabbits studied a reaction of similar pattern but of different intensity, expressed by a maximum of plasma CPK activity. The physiological origins of this variation of CPK activity seems to be, as seen in control animals, the consequence of emotional stress due to handling and possibly an additional stress due to the venepunctures.

Increased plasma or serum creatine kinase activity (E.C.: 2-7-3-2; CPK) is generally used in pathology to detect cardiac (myocardial infarction) or muscular anomalies (dystrophy or hypertrophy)²; it would also enable the determination of the degree of stress susceptibility which partially conditions certain pathological forms of muscular hypertrophy in pigs³⁻⁶.

Interpretation of a significant increase in this enzymatic activity may be complicated by many factors, such as ingestion of alcohol, strenuous exercise^{7,8}, hypothyroidism⁹⁻¹¹, cerebrovascular disease, burns, adaptation to cold¹², i.m. injections¹³, or, as in man, emotional stress^{2,14}.

During experiments on several breeds of rabbits, we observed, as have many scientists, a considerable variability in the results; this led us to examine the importance of another factor which could affect the plasma CPK activity, that is systematically repeated blood sampling.

Material and methods. In a preliminary study on both anesthetized and non-anesthetized rabbits, we verified

¹ Supported by Grant No. 73.7.1654 of the Délégation générale à la Recherche scientifique et technique.
² W. GARCIA, *J. Anim. med. Assoc.* 228, 1395 (1974).
³ W. M. ALLEN and D. S. P. PATTERSON, *Proc. 2nd Int. Symp. Condition Meat Quality Pigs*, Zeist, 1971 (Pudoc, Wageningen), p. 90.
⁴ M. V. V. REDDY, L. L. KASTENSCHMIDT, R. G. CASSENS and E. J. BRISKEY, *Life Sci.* 10, 1381 (1971).
⁵ M. C. BERMAN, P. J. CONRADIE and J. E. KENCH, *Agroanimalia* 4, 93 (1972).
⁶ P. B. ADDIS, D. A. NELSON, R. T.-I. MA. and J. R. BURROUGHS, *J. Anim. Sci.* 38, 279 (1974).
⁷ F. Q. NUTTALL and B. JONES, *J. Lab. clin. Med.* 71, 847 (1968).
⁸ K. J. MARTIN and G. NICHOLS, *Aerosp. Med.* 45, 67 (1974).
⁹ J. ITELSON, J. RUBINSTEIN, L. GAIST and R. MENACHE, *Rev. fr. Etud. clin. biol.* 13, 905 (1968).
¹⁰ F. A. GRAIG and G. ROSS, *Metabolism* 12, 57 (1963).
¹¹ W. M. MCCONAHEY, *Annls intern. Med.* 71, 1022 (1969).
¹² J. H. PETAJAN, M. T. VOGWILL and M. B. MURRAY, *J. appl. Physiol.* 27, 528 (1969).
¹³ H. Y. MELTZER, S. MROZAK and M. BOYER, *Am. J. med. Sci.* 259 42 (1970).
¹⁴ G. OWEN and R. J. KERRY, *Br. med. J.* 4, 75 (1974).