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EFFECTS OF INTRA-DUODENAL INFUSIONS OF FAT ON THE FOOD INTAKE OF SHEEP

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SUMMARY

The intra-duodenal infusion of 100 to 150 ml of peanut oil over 17 hours depressed food intake in seven sheep and also caused a reduction in stomach movements and led to diarrhoea. The reduced food intake preceded the other effects. Fifty millilitres of peanut oil infused into the duodenum over 17 hours did not have any of these effects.

More rapid infusions of smaller amounts of peanut oil, olive oil, soya bean oil, a hydrolysate of peanut oil and of oleic acid (11.5 or 23 ml over 30 minutes) led to a reduction in the movements of both the reticulum and rumen. "B sequences" of rumen contractions were less affected than were "A sequences". A depression of food intake was also observed on some occasions with the more rapid infusions. The hydrolysate of peanut oil and oleic acid both had more profound effects than did peanut oil or olive oil.

Intra-duodenal infusions of 100 ml heavy liquid paraffin B.P. over 17 hours failed to depress the food intake, reduce the motility of the reticulum or rumen or to produce diarrhoea. More rapid infusions of paraffin appeared to increase the frequency of reticulum and rumen movements.

The significance of these observations in relation to food intake regulation is discussed.

INTRODUCTION

Ogilvie *et al.* (1961) reported that the composition of fat depots in the sheep could be altered by the intra-duodenal administration of triglyceride. Normally in adult ruminants little of the triglyceride of the diet escapes hydrolysis and reaches the small intestine unchanged (Garton, 1965), although more may do so with high fat diets. In the course of further experiments aimed at a more extensive investigation of the influence on fat depot composition of infusions of fat into the duodenum (undertaken in collaboration with R. A. Barton of Massey University, and F. B. Shorland of Fats Research Division, D.S.I.R.), the opportunity was taken to study the effects of such infusions on food intake and also on movements of the reticulum and rumen.

In animals with a simpler stomach, it has been reported that the presence of fat in the duodenum leads to a reduction or complete cessation of gastric acid and pepsin secretion and a diminution of gastric motility: these effects have been attributed to the actions of the hormone enterogastrone released from the duodenum (*cf. e.g.*, Babkin, 1950; Gregory, 1962). The action of fatty acids is more profound than is that of triglyceride. A recent report of a comparison of the actions of triolein and oleic acid was provided by Long and Brooks (1965) who have also surveyed the literature on this point. Menguy (1960) concluded that the inhibition by fat of gastric secretion and motility depended on the presence of both bile salts and lipase in the intestinal lumen. He considered that the inhibition was related "to the presence of a stable fatty emulsion within the lumen of the intestine".

Hill (1965) has described a similar reduction in acid secretion by the abomasum and an "inhibition of abomasal and forestomach motility" of sheep during the presence of fat in the duodenum. Bathgate and Hill (unpublished, cited by Hill, 1965) found a reduction in the flow of digesta from the abomasum of sheep on a diet containing 10% palm oil: no such effect was observed when the diet contained 5% palm oil. Severe diarrhoea and loss of appetite have been reported by Phillips (1965) after small amounts of linoleic and oleic acid were infused into the duodenum of sheep.

Reid (1957) studied the effects on cows of the administration into the rumen or the omasum of five mineral oils (ranging from heavy liquid paraffin B.P. to a very light paraffin high in isoparaffins). He found a depression of food intake only with the light paraffins. The actions of these were greater when they were administered into the omasum and when they were emulsified. Both procedures hastened the onset of the effect and, in addition, intensified and prolonged it.

The present observations are of a preliminary nature. They are on the effects on food intake, stomach movements, or both, when peanut oil, olive oil, soya bean oil, a hydrolysate of peanut oil, oleic acid or heavy liquid paraffin B.P. were infused into the duodenum of sheep at differing rates and in different total amounts.

METHODS

Nine ewes, 12 to 18 months of age, 24.5 to 33.5 kg bodyweight, were the experimental subjects. In all, perspex cannulae were placed in the duodenum about 10 cm below the pylorus; both sub-abdominal (Phillipson, 1952) and rib-bed (McDonald, 1953) location of the cannulae were employed.

In addition to the duodenal cannulae, four animals had partial exteriorizations prepared of the reticulum (Titchen, 1958b) and of the rumen (Reid and Titchen, 1959; Reid, 1963), and one animal had a rumen fistula (Jarrett, 1948). The animals were housed indoors in individual stands, in which they were restrained by a sling and either head-stocks or a collar and chain. Simple separators (designed by A. L. Bryant) placed under the wire floors of the stands allowed the collection of urine and faeces. The animals were accustomed to the stands, the experimental diet and the experimental procedures for several weeks before the influence of infusions into the duodenum was examined.

Intra-duodenal infusions were made with the aid of a Palmer (London) constant-speed slow infusion apparatus. The materials which were infused (all of them undiluted) were peanut oil (3 samples), olive oil, soya bean oil, a hydrolysate of peanut oil, oleic acid (May & Baker) and heavy liquid paraffin B.P. (White Oil 890, donated by Mobil Oil New Zealand Ltd.). The vegetable oils were all refined products sold for human consumption. Two rates of infusion were used — slow infusions in which 50, 100 or 150 ml were administered over 17 hours, and faster infusions, in which 11.5 or 23 ml were administered over 30 minutes.

The feed was chaffed meadow hay which contained a high proportion of red clover (*Trifolium pratense* L.). Samples for dry matter (D.M.) determinations were taken from each sack of chaff used and dried for 24 hours at 91°C in an oven with an air-circulating fan. The D.M. content was found to be 84 to 87%. Daily, each animal was offered a weighed quantity of feed, the greater part of which was given at 10 a.m., the remainder between noon and 3 p.m., according to the rate of eating. From time to time, the feed in the bin was turned by hand and any spillage returned. At 9.30 a.m. on the following day the feed was removed, and the refusals and spillage then dried for 24 hours in the oven and weighed to allow calculation of the D.M. intake.

Water was available for 23 hours of the day. A standard volume (usually 4,000 ml) of fresh water was provided each morning at 10 a.m. and the amount consumed found by measuring the volume left at 9.00 a.m. the following day. Care was taken to keep the animals' water buckets clean.

Urine was measured by volume, faeces by weight at 9.00 a.m. each day. After being weighed, the faeces were mixed and samples taken for D.M. determinations. When diarrhoea occurred, normal and abnormal faeces were separated wherever possible, weighed, and separate D.M. determinations made.

Kymographic records of the activity of the reticulum and rumen were obtained with the method described briefly by Reid and Titchen (1959). Records of jaw movements were obtained with a balloon-transducer system and an electronic recorder (Reid *et al.*, 1960) or with a balloon-tambour system, kymographically.

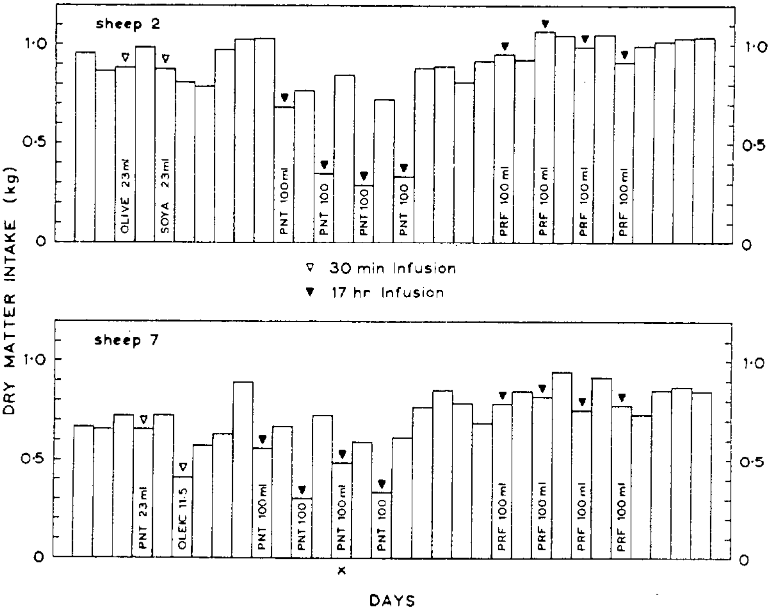

Fig. 1

The effects of intra-duodenal infusions of oils and oleic acid on the daily dry matter intakes of two sheep fed chaffed ryegrass/red clover hay. Infusions of 23 ml of olive, soya bean (SOYA) or peanut (PNT) oil over 30 minutes, starting 90 minutes after the food was offered, had little effect on the day's intake, whereas 11.5 ml of oleic acid (OLEIC) administered under the same conditions reduced the intake on the day of the infusion and, possibly, on the day following also. Infusions of 100 ml of peanut oil over 17 hours starting 30 minutes after the food was offered, reduced the intake on the day of the infusion, but infusions of 100 ml of heavy liquid paraffin, B.P. (PRF), given under the same conditions had little effect on intake. On one day (marked with cross), the infusion of peanut oil into sheep 7 was delayed until 3 hours after the food was offered: the effect on intake appeared to be less than when the infusion started 30 minutes after feeding.

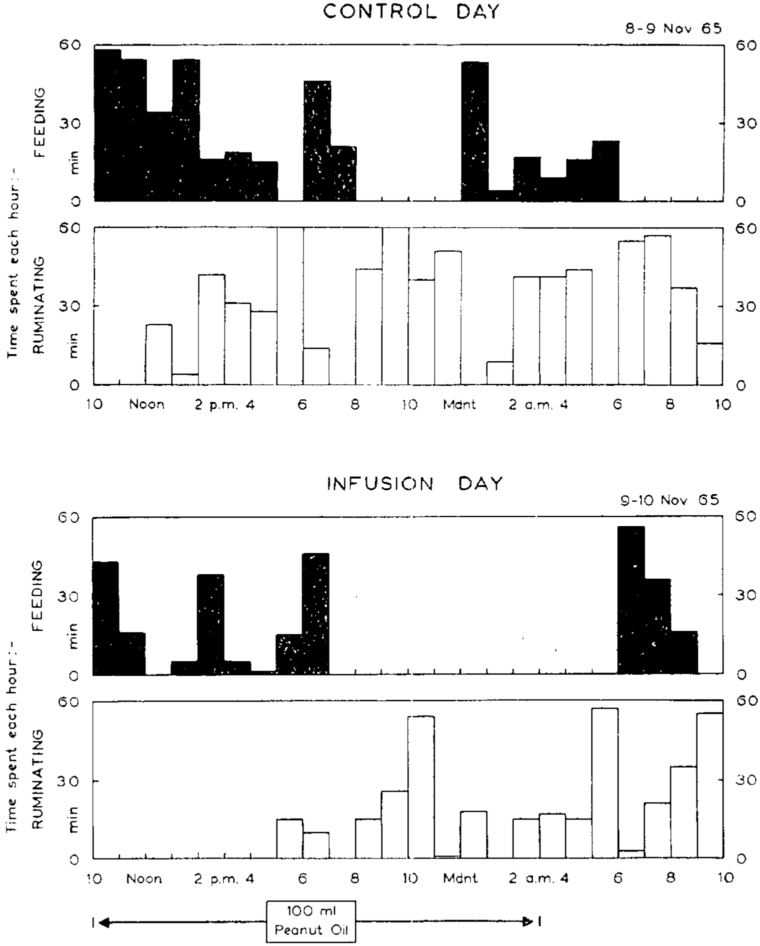

Fig. 2

The pattern of feeding and rumination in a sheep on two successive days, above, a control (non-infusion) day and below, a day on which 100 ml of peanut oil was infused into the duodenum over 17 hours, starting at the time the food was offered in the morning. The infusion day was the ninth of a series in which the oil was given on every alternate day. On the control day, the dry matter intake was 947.5 g, the total time spent eating was 459 minutes, and the total time spent ruminating was 696 minutes: the corresponding figures for the infusion day were 378.0 g, 275 minutes, and 358 minutes. The information was extracted from records of jaw movements, made with the balloon/electronic pressure-transducer system and a Sanborn heated stylus pen recorder.

RESULTS

Seven animals received continuous slow infusions into the duodenum of peanut oil, of either 100 or 150 ml over 17 hours, equivalent to a dose rate of 0.18 to 0.49 ml/kg B.W./hr. The infusions, which were given no more frequently than on alternate days, were started at the time the fresh feed was offered in the morning (10 a.m.) or 30 minutes thereafter. All of these sheep showed a marked reduction in their food intake on the day of the infusion (see Fig. 1).

Both direct observation and jaw recordings showed that the normal patterns of feeding and rumination exhibited by the sheep were altered (Fig. 2). The initial period of feeding was abbreviated, sometimes to one-half of that observed in control animals or in infused animals on "control", *i.e.*, non-infusion, days. This reduced period of feeding was usually succeeded by a period of rumination, but thereafter there was only desultory eating with short periods of rumination and long periods of inactivity. Intensive feeding commonly resumed 3 to 4 hours after the infusion ended.

The intra-duodenal infusion of 50 ml of peanut oil over 17 hours (0.10 to 0.11 ml/kg B.W./hr) was without effect on the feed intake of the two sheep in which it was tested. Both of these sheep exhibited a marked depression of appetite when 100 ml of peanut oil was infused into the duodenum over 17 hours.

Four of the six animals infused with 100 or 150 ml over 17 hours showed a marked change of demeanour which was first apparent 3 to 4 hours after the start of the infusion and continued until after the infusion had ended. In its most exaggerated form this change was evident as the animals lying in their slings with head held low and back arched so that the thoraco-lumbar regions were highest. The animals which did not show this change in posture became quieter than was usual and reacted less to the presence of strangers and other disturbances. One of the animals which did show the marked change in posture intermittently stood and then slumped back into its sling. The episodes of standing sometimes occurred at the same rate as did the reticulum contractions and "A sequences" (Reid, 1963) of rumen contractions. However, no obvious relationship between any one part of the "A sequence" of reticulum and rumen contraction and the standing was disclosed.

Diarrhoea occurred in all the animals infused at 100 or 150 ml over 17 hours; it was not apparent less than 16 hours after the start of an infusion and did not continue for more than 16 hours after the infusion ceased. The recovery from diarrhoea was marked by a transition from foul-smelling, fluid material, lighter than normal, to semi-solid, faecal masses still light in colour, to aggregates of soft pellets still lighter than normal in colour, until, eventually, dark pellets of faeces were passed. The appearance of the diarrhoea never preceded the reduction in food intake; and further, after the infusion had ended, intensive feeding recommenced at a time when the diarrhoea was most marked. The D.M. content of the frankly liquid faeces and that of the pellets of faecal material are contrasted in Fig. 3. Diarrhoea did not develop in those animals which received only 50 ml of peanut oil over 17 hours.

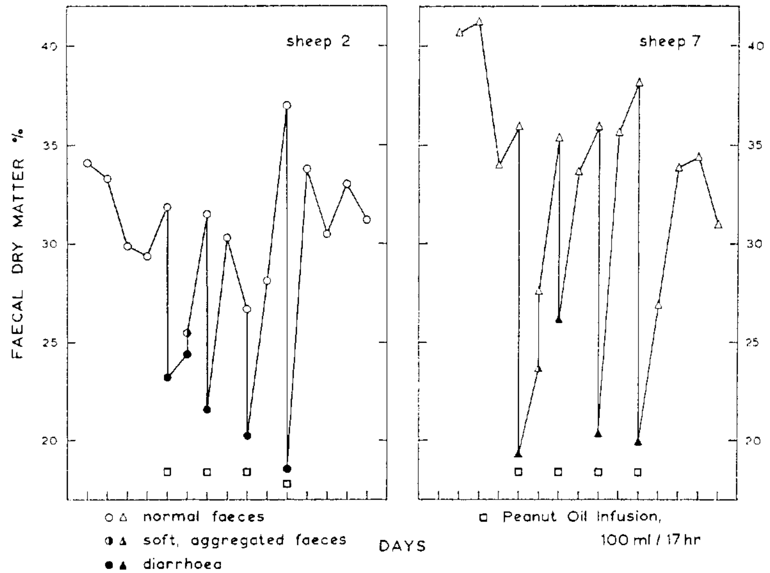

Fig. 3

Effects of intra-duodenal infusions of 100 ml of peanut oil over 17 hours on the dry matter content (D.M. %) of the faeces of two sheep fed chaffed ryegrass/red clover hay. On each infusion day, normal pelletted faeces were voided for 16 hours or more after the start of infusion and before diarrhoea occurred. There are thus two points plotted for each infusion day, one representing the normal faeces, the other, the abnormal faeces. Abnormal faeces continued to be voided for a time on the day following an infusion, but, except on the first such day, the proportion of abnormal faeces was small. Data from the same experiments shown in Fig. 1.

With successive infusions of peanut oil, differences in the reactions of animals were observed. All of the sheep which received infusions into the duodenum at a rate of 100 ml over 17 hours on alternate days showed a more marked depression of food intake on the second day of the infusion than they did on the first. On later days of infusion, some animals showed lesser effects, others more marked effects. Irregular responses to successive infusions were observed after four or five had been undertaken. If a respite from infusions was given, the pattern of responses described above was repeated when the infusions were resumed.

In one animal, the effects of the infusion of 100 ml of peanut oil over 17 hours into the duodenum were compared with the effects when the same amount of oil was infused in the same manner into the rumen. In contrast to the marked effects of intra-duodenal administration, intra-ruminal infusion of peanut oil at this dose rate appeared to have little effect on food intake (Fig. 4) and did not cause diarrhoea.

More rapid intra-duodenal infusions of peanut oil, a hydrolysate of it, soya bean oil, olive oil or oleic acid all had effects on stomach movements which differed in

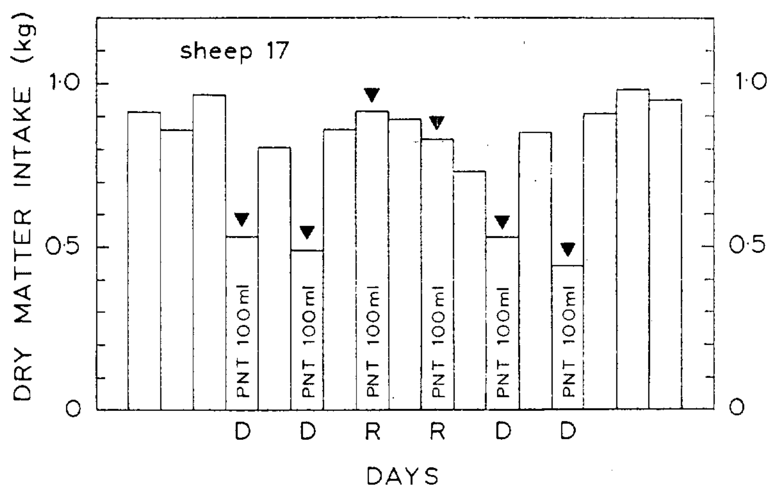

Fig. 4

A comparison of the effects on daily dry matter intake, of intra-duodenal (D) and intra-ruminal (R) infusions of 100 ml of peanut oil (PNT) over 17 hours, starting 30 minutes after food was offered. In contrast to the intra-duodenal infusions, the intra-ruminal infusions had little effect on intake.

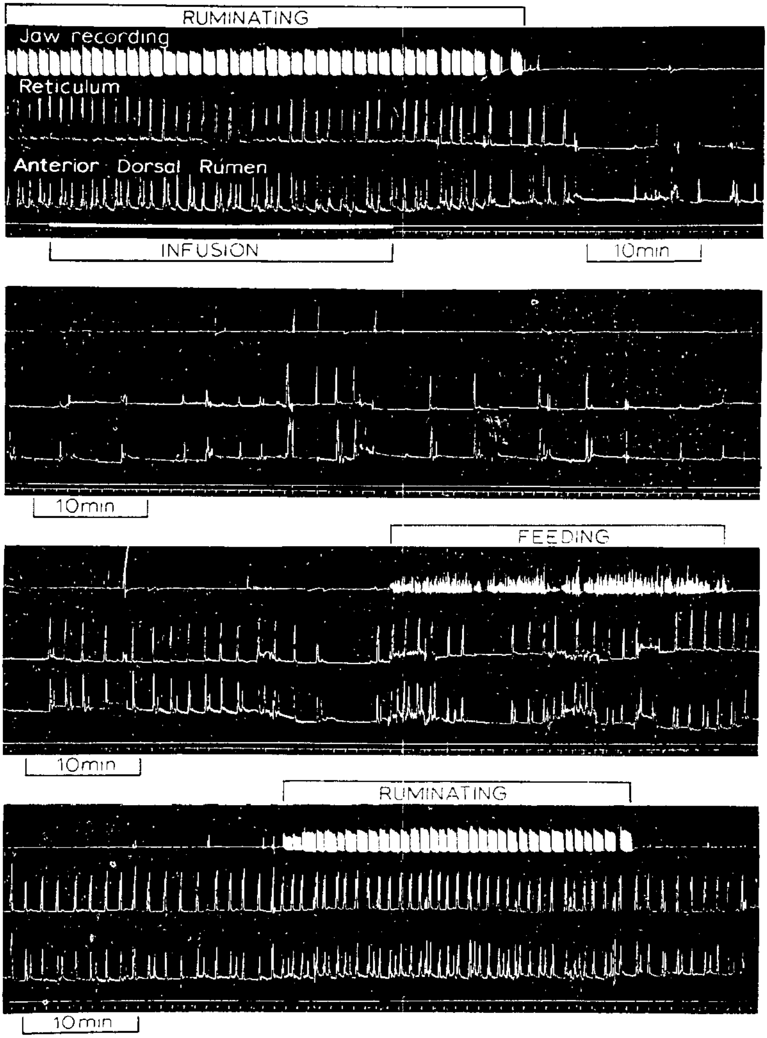

Fig. 5

The effects on reticulum and dorsal rumen contractions of an infusion of 23 ml of peanut oil over 30 minutes, starting 90 minutes after the food was offered. Kymographic records of (from above down): jaw movements; the contractions of a partial exteriorization of the reticulum; the contractions of an exteriorization of the anterior dorsal rumen; infusion signal; 1-minute time signal. The tracing has been divided into four sections and set out one below another in order. A reduction in gastric motility was evident

Continued opposite page

intensity according to the substance infused. The sensitivity of different animals varied. Figure 5 illustrates the reduction of stomach movements recorded in a sheep which received an intra-duodenal infusion of 23 ml of peanut oil over 30 minutes, a dose of 1.64 ml/kg B.W./hr. This infusion commenced 90 minutes after fresh food had been provided. A reduction in the frequency of reticulum and associated rumen contractions (the "A sequence") was first apparent 37 minutes after the infusion started and persisted for the next 150 minutes. During the periods in which no "A sequences" were present, "B sequences" continued to occur and eructation was, as normally, associated with these.

Intra-duodenal infusions of 100 ml of heavy liquid paraffin B.P. over 17 hours, starting 30 minutes after the food was offered, were given to two sheep, the dose rate being 0.20 to 0.23 ml/kg B.W./hr. In contrast to the effects of infusion of the same amount of peanut oil in the same manner, the paraffin infusions did not appear to reduce the daily food intake, did not cause diarrhoea, and did not reduce reticulum or rumen movements. The effects on food intake were not clear-cut: there may have been an increase in intake on the day of, or the day following, an infusion. The food intakes of the two sheep when they received infusions of heavy liquid paraffin and of peanut oil may be compared in Fig. 1. The D.M. content of the faeces collected on control and on paraffin infusion days are shown in Fig. 6, which should be compared with Fig. 3.

Infusions of 11.5 to 23 ml of heavy liquid paraffin over a period of 30 minutes (0.80 to 1.84 ml/kg B.W./hr) had no inhibitory effects on stomach movements: if anything, there was an increase in the frequency of "A sequences" with these faster infusions.

Figure 5 continued

37 minutes after the start of the infusion, followed 8 minutes later by a long period in which contractions were infrequent. During this period, "A sequences" (reticulum and associated rumen contractions) were inhibited to a greater extent than were "B sequences" (independent rumen contractions), which continued to occur at fairly regular intervals. Alternating periods of regular gastric motility and inhibition preceded the return to apparently normal motility some 190 minutes after the infusion was started.

The reticulum exteriorization was located close to the lateral root of the rumeno-reticular fold and a small artefact associated with each dorsal rumen contraction is visible in the recording from this exteriorization. The irregularies in the baseline of the recordings from both exteriorizations were due to the animal standing and then lying back in its sling.

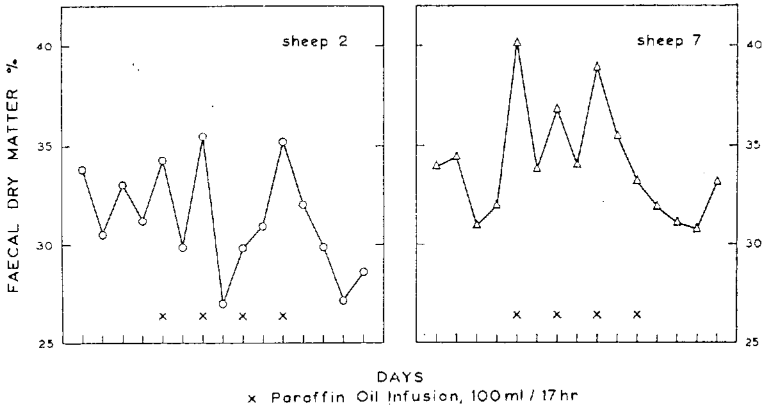

Fig. 6

The effects of intra-duodenal infusions of 100 ml of heavy liquid paraffin B.P. over 17 hours, on the dry matter content (D.M. %) of the faeces of two sheep. This treatment did not cause diarrhoea: on most infusion days, the faecal D.M. % was actually increased. Data from the same experiments shown in Fig. 1.

Intra-duodenal infusions of the hydrolysate of peanut oil and of oleic acid had more profound effects than any other infusions undertaken. The immediate effects appeared sooner and persisted longer. A continuing depression of the intake of food was observed, particularly with the larger doses, on the day after the infusion was given (see Fig. 1).

DISCUSSION

In the experiments reported here, the infusion of 100 ml of peanut oil into the duodenum over 17 hours, starting at or about the time food was offered, invariably resulted in a reduction of food intake on that day. The effect on feeding was evident 1.5 to 3 hours after the start of the infusion and continued throughout the remainder of the infusion period, and for 3 hours or more ofter the infusion ended. There are a number of physiological mechanisms which might be involved in bringing about this diminution of food intake. They include direct or indirect effects arising from the presence of the oil, or its breakdown products, in the gut, and after absorption, in the body.

The reduction of gastric secretion and motility when oil is introduced into the intestine of rats is thought to depend on the presence of the appropriate conditions for emulsification and presumably on micelle formation (Menguy, 1960). Similarly, the depression of food intake in ruminants with intra-duodenal infusions of oils appears to depend on their being emulsified. This is indicated from the present experiments in which heavy liquid paraffin B.P. did not reduce food intake or inhibit stomach movements, and also from previous experiments in which it was found that the effects of light paraffins were enhanced by emulsification (Reid, 1957). Liquid paraffin is not normally absorbed in anything but very small amounts; more absorption of it has been demonstrated when it is introduced into the intestine after being formed, outside the body, into an emulsion with particle size of less than 0.5 μ (Frazer *et al.*, 1945).

Menguy (1960) has discussed the possibility that some of the inhibitory effects of fats might be due to osmotic stimulation. In man, gastric emptying time may be prolonged by the entry into the duodenum of markedly hypertonic material (Hunt *et al.*, 1951). It may be postulated that such an effect is reflex and brought about by stimulation of osmoreceptors in the duodenum. Bathgate and Hill (cited by Hill, 1965) found that the passage of digesta from the abomasum was delayed when sheep were fed a diet containing 10% palm oil.

In contrast to possible reflex effects on gastric emptying, the inhibitory action of fat on gastric secretion is attributed to the actions of the hormone enterogastrone. Janowicz and Grossman (1951) concluded that enterogastrone did not affect the quantity of food taken by dogs. No experimental evidence is available on the effects of enterogastrone preparations in sheep.

Enterogastrone might, in ruminants, exert an indirect effect on food intake by virtue of the reduction of gastric secretion. Acid, in the strength in which it is secreted by oxyntic cells, introduced into the isolated abomasum of decerebrate sheep serves as a strong stimulus to contractions of the reticulum (Titchen, 1958b). Iggo (1957) found, in studies on single afferent fibres of the vagus nerve, evidence for acid receptors in the cat's stomach. It might be argued that the diminution of gastric secretion following the introduction of fat into the duodenum results in the withdrawal of a strong afferent stimulus to reflex contractions of the reticulum and rumen. A relation between flow through the reticulo-omasal orifice and the motility of the reticulum, rumen, reticulo-omasal orifice and omasum has been recognized (Stevens *et al.*, 1960). Reduction in the motility of the reticulum and rumen could result in a diminished rate of passage of digesta from these regions into the abomasum. If this occurred, a reduction in food intake would be expected. Balch and Campling (1962) and Blaxter (1962) have emphasized the possible relationship between flow of ingesta from the reticulo-rumen and food intake.

Another explanation on the same lines which may be offered is that the inhibition of food intake is an indirect result of the delay in abomasal emptying and due to abomasal distension. It has been established that abomasal distension inhibits reticulum and rumen contractions in conscious sheep (Phillipson, 1939), and in anaesthetized (Dussardier, 1955) or decerebrate preparations (Titchen, 1958a, 1960). Both in animals with a simpler stomach and in ruminants a factor considered of importance in achieving satiation is gastric distension (Anand, 1961; Stevenson, 1964; Balch and Campling, 1962; Blaxter, 1964). The relative importance of distension respectively of the reticulum, rumen, omasum and abomasum in terms of satiety mechanisms has not been investigated as yet.

There is now little support for the oldest of the theories concerned in the regulation of the ingestion of food, namely a relation between stomach contractions and appetite. The present experiments make it difficult to accept any such relationship in the sheep. Although the resumption of feeding in the sheep, from which the tracing shown as Fig. 5 was obtained, occurred during a series of contractions of the reticulum and rumen, in other animals feeding was observed in the absence of any such contractions. A relationship between food intake and stomach contractions may not be associated with the presence or absence of reticulum and rumen contractions but with some other activity — for example, motility of the reticulo-omasal orifice, the abomasum or of the pylorus.

Changes in blood composition following the absorption of the oils or their metabolites may have contributed to the effects on food intake. One of the several chemostatic hypotheses proposed for the regulation of the intake of food by animals with a simpler stomach is a lipostatic mechanism (see Anand, 1961; Stevenson, 1964). Briefly, this depends on the notion that blood-borne metabolites derived from endogenous fat metabolism exert an action on centres in the central nervous system concerned in satiety or hunger. In the present experiments, one effect of the infusion of fat was the change in demeanour of the animals. It appeared that the introduction of the fatty material into the duodenum led to a change in excitability — presumably affecting the central nervous system. Bell (1958) reported changes in the electro-encephalogram with the intravenous infusion of short-chain, steam-volatile fatty acids: no such changes have been reported in sheep with the administration of longer chain fatty acids. A decrease in food intake was shown by Ullyatt (1964) when concentrations of short-chain fatty acids in the rumen were increased, and he discussed the possible relationship between blood levels of these acids and intake regulation. No studies on blood composition were made in the present experiments.

It is suggested that the observations reported here provide a further indication of factors concerned in the regulation of food intake. They emphasize the recognized complexity of the mechanisms and the impossibility of accepting any single factor as a sole determinant in the regulation of food intake; rather it appears to be a closely co-ordinated affair depending on afferent impulses from the gut arising from at least distension, tactile, osmotic and chemical stimulation and on both direct and indirect responses of the central nervous system to concentrations of substances in the blood.

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DISCUSSION

PROFESSOR I. E. COOP: *The suggestion is made from the infusion experiments that the presence of fat in the duodenum and small intestine is a factor which can limit voluntary intake. In at least one of the experiments, it appeared that the effect was much reduced if lesser amounts were infused into the duodenum. How do the amounts of trigylceride expected to pass through the duodenum of a grazing animal compare with the amounts infused in these studies?*

C. S. W. REID: The amounts of trigylceride entering the duodenum of the grazing animal appear to be small: the great proportion of dietary trigylceride is hydrolysed to free fatty acids in the rumen. In these preliminary experiments, no chemical analyses of duodenal contents have so far been carried out, and we therefore do not know how much we are exaggerating the normal mechanisms when the oils are infused. However, when considering this question, the following points should be borne in mind:

(1) The rate of infusion is slow — 100 ml/17 hr corresponds to a rate of 5.9 ml/hr, or approximately 0.1 ml/min. The effects on feeding was evident 1.5 to 3 hours after the start of the peanut oil infusions, when only some 9 to 18 ml had been administered.

(2) Because of the probable effects of intra-duodenal infusions of triglycerides on abomasal emptying, no simple calculation of concentrations in the duodenum based on the infusion rates and the published figures for rates of flow of the duodenal contents can be made.

(3) Most of the trigylceride infused into the duodenum will be hydrolysed into free fatty acids and glycerol. We have found free fatty acids to be more potent than the parent triglycerides.

(4) Substances other than lipids will release enterogastrone. These include protein degradation products and polysaccharides, which are also present in the duodenal contents.

A. W. F. DAVEY: *Would the speakers please comment on why the ruminal infusions of peanut oil did not reduce intake.*

DR REID: Dilution in the stomach contents, particularly after hydrolysis, is presumably an important factor. Such dilution, and any metabolic loss in the stomach, would result in lower duodenal concentrations of oil and fatty acids than when the same amount of oil is infused directly into the duodenum. Larger doses of oil given intra-ruminally might be expected to have an effect on intake, as would be suggested by the observations of Bathgate and Hill [see introduction to paper].