

## Factors affecting the voluntary intake of food by sheep

### 2. The role of distension and tactile input from compartments of the stomach

BY W. L. GROVUM

*Department of Biomedical Sciences, Ontario Veterinary College,  
University of Guelph, Guelph, Ontario, N1G 2W2, Canada*

(Received 20 June 1978 – Accepted 19 December 1978)

1. Sheep equipped with rumen and abomasal cannulas were given *ad lib.* access to ground and pelleted lucerne (*Medicago sativa*) hay except for periods of up to 6 h immediately before experimental sessions in which food intake was measured while various stomach compartments were either distended or subjected to tactile stimulation from a probe.
2. Inserting a probe, consisting of two collapsed balloons tied onto the end of a polyethylene tube, into the reticulum depressed intake by 24% after 30 min of feeding ( $P < 0.025$ ). Compensatory feeding was observed during the 30 min period immediately following removal of the probes. There were no effects of having a probe in the abomasum.
3. Distension of the reticulum with 0–800 ml water in a balloon depressed intake by 0.2 g/ml after 30 min of feeding ( $P < 0.05$ ). Removing the balloons from the animals allowed them to make up the deficit in intake completely within 30 min. Distending the rumen by 800 ml had no effect on intake ( $P > 0.05$ ). Distending the abomasum with up to 1000 ml water in a balloon depressed intake by 0.11 g/ml after 30 min of feeding with compensatory feeding being significant ( $P < 0.05$ ) but incomplete.
4. Combinations of reticular distension up to 800 ml and of abomasal distension up to 1200 ml did not have additive depressing effects on intake.

The intake of roughage diets by ruminants is thought to be limited by distension of the rumen, since distending it with water in balloons reduced the *ad lib.* intake of hay by cows (Campling & Balch, 1961). Grovum & Phillips (1978) concluded that distension of one or more of the compartments of the sheep stomach may have limited the intake of chopped lucerne (*Medicago sativa*) hay since distension of the intestines did not appear to be an important signal of satiety. In the series of experiments now reported an attempt was made to identify the importance of distension and tactile input from the reticulum, rumen and abomasum as signals of satiety. Distension of the reticulum reduced the intake of food more than did distension of the abomasum. Tactile inputs to the reticulum but not the abomasum reduced intakes. The rumen was the least likely origin of satiety signals from the physical stimuli applied.

#### EXPERIMENTAL

##### *Sheep and surgery*

Cross-bred Suffolk wethers were used in all of the experiments. Sheep nos. 1–5 were 2 years of age and weighed  $82 \pm 2$  kg whereas sheep nos. 6–13 were lambs of  $31 \pm 1.5$  kg body-weight with a functional rumen. The animals were treated for internal parasites with subcutaneous injections of a broad-spectrum anthelmintic (Tramisol; Cyanamid). External parasites when evident were killed with a dusting powder containing Malathion. The animals were fitted with abomasal and rumen cannulas in a single operation and were allowed to recover for 14 d before the experiments commenced.

*Housing, feeding and diets*

The sheep were held in metabolism cages in a room which was always illuminated. Ground and pelleted lucerne hay (g/kg: 950 dry-matter, 144 protein (nitrogen  $\times$  6.25), 81 ash, 400 acid-detergent fibre, 27 fat) was available *ad lib.* except during periods of deprivation immediately before the experimental sessions. Water was continuously available.

*Procedures*

On a typical day of an experiment this schedule of feeding was followed except that the length of the deprivation period was not always constant:

Fresh food and water were made available	08.00–09.00 hours
Sheep were deprived of food but not water (deprivation period was 335 min in this instance)	09.00–14.35 hours
Treatments imposed (reticulum distended):	
Before feeding	14.25–14.35 hours
During feeding	14.35–15.09 hours
Food intakes were recorded	
0–10 min	14.35–14.45 hours
10–20 min	14.47–14.57 hours
20–30 min	14.59–15.09 hours
Treatments were withdrawn (balloons removed)	15.09–15.20 hours
Compensatory food intakes were measured	
30–40 min	15.20–15.30 hours
40–50 min	15.32–15.42 hours

The treatments were imposed according to a  $5 \times 5$  Orthogonal Latin Square Design in all Expts except Expts nos. 2 and 4.

*Expt. 1. Reticular distension*

Sheep (nos. 1–5) were deprived of food but not water for 335 min to make them hungry. Before feeding, a fairly rigid probe, consisting of two concentric balloons tied onto the end of a polyethylene tube (6 mm i.d., 9 mm o.d.), was directed through the rumen cannula into the reticulum. The balloons were then either not distended (control) or distended with 200, 400, 600 or 800 ml warm water. The trays of food for the individual animals were weighed before feeding commenced and after three successive periods of feeding each lasting 10 min. The balloons were then removed from the sheep. To ascertain if the animals would compensate for any deficits in intake due to the treatments just imposed, the sheep were fed again and intakes were determined for another 20 min.

Distension levels of up to 800 ml were used because the volume of pelleted food that the animals normally consumed after a deprivation period of 335 min was approximately 670 ml. This was exclusive of saliva and other fluids entering the stomach during a meal. Thus if the reticulum was signalling satiety by sensing distension it would have to respond to a volume change of approximately 800 ml or less.

The presence of the balloon in the reticulum was verified by recording biphasic and triphasic pressure waves from the reticulum in association with the normal mixing and regurgitation of contents respectively. The sheep usually began to ruminate immediately after the probe was placed in the reticulum.

*Expt 2. Distension of the rumen*

A procedure similar to that described in Expt 1 was used except that the deprivation period was 339 min, the probe was inserted into the rumen and a simple cross-over design was used. Food intakes when just the probe was in place were compared with those when the

balloon was distended with 800 ml water. The experiment was replicated twice with sheep nos. 1–5 and the means of the observations were analysed with Student's paired *t* test.

#### *Expt 3. Abomasal distension*

Sheep nos. 1–5 were deprived of food but not water for 356 min and the procedure described previously was followed. Before feeding, a probe consisting of two finger-shaped balloons tied concentrically onto the end of a polyvinyl tube (3 mm i.d., 5 mm o.d.) was inserted into the abomasum via the abomasal cannula. The balloons were either not distended (control) or they were inflated with 250, 500, 750 or 1000 ml warm water. Food intakes were measured while these treatments were imposed and after they were removed.

The effects of different levels of abomasal distension on motility of the reticulo-reticulum were studied in preliminary experiments to establish the limits of the treatments. Distending the abomasum with 250 ml water in a balloon had only a slight and transient inhibitory effect on motility of the reticulo-rumen. However 1000 ml distension markedly decreased amplitude of contractions and markedly increased the interval between them. Some adaptation was noticed but the motility trace never returned to normal while the abomasum was distended with 1 l water.

#### *Expt 4. Tactile inputs from the reticulum and the abomasum*

The control animals in Expts nos. 1 and 3 had probes of negligible volume in their stomachs which were not inflated with water. This was a reasonable control against which to test the effect of distension on intake but it was not known whether the presence of the probes *per se* in the stomach suppressed intake. Thus in this experiment the food intakes of sheep were compared when no probes were inserted (control) and when probes as described for Expts 1 and 3 were inserted into the reticulum or the abomasum respectively.

*Part A.* Five sheep (nos. 1–5) were deprived of food but not water for 356 min. Just before feeding the animals were either not fitted with a probe (days 1 and 8), fitted with a reticular probe (days 6 and 9) or fitted with an abomasal probe (days 5 and 7). The sheep were fed and their intakes during three successive 10-min feeding sessions were recorded. Intakes were recorded for three more sessions of feeding after the probes were removed from the reticulum or the abomasum to ascertain if compensatory feeding would occur.

*Part B.* The effect on intake of inserting a fairly rigid probe into the reticulum was tested, as described previously, in another eight sheep (nos. 6–13) to supplement the results obtained in part A. These sheep were considerably lighter than those used in part A, but this seemed of little consequence since the probes were of negligible volume. The probes were used only as a means of imparting tactile stimulation to the reticulum and the reticulo-ruminal fold. A simple cross-over design was used and the experiment was replicated twice. The deprivation period was 309 min. Student's paired *t* test was used to compare the mean intakes of thirteen sheep with and without reticular probes.

#### *Expt 5. Reticular and abomasal distension*

Food intakes of sheep were depressed in Expts nos. 1 and 3 by distending the reticulum or the abomasum. This experiment was done to ascertain if combinations of reticular and abomasal distension would have additive or synergistic effects in depressing intakes. Five sheep (nos. 1–5) were used in four separate trials (A, B, C, D), each of which was conducted according to a 5 × 5 Latin square design. Generally the sheep were deprived of food to induce hunger as described previously (see p. 426) and just before the time of feeding the treatments described in Table 1 were imposed. Food intakes during three intervals of 10 min were recorded. The probes were then removed from the animals and food was presented for

Table 1. *Expt 5. Summary of treatments imposed on hungry sheep to ascertain if reticular and abomasal distension had additive effects in depressing their intakes of pelleted lucerne (Medicago sativa) hay*

Trial	Deprivation period (min)	Treatment no.	Distension (ml water in probe)	
			Reticulum	Abomasum
A	345	1	0	0 (probe in place)
		2	0	300
		3	0	600
		4	0	900
		5	0	1200
			(no probe in place)	
B	363	1	0 (probe in place)	0
		2	200	0
		3	200	400
		4	200	800
		5	200	1200
			(probe in place)	
C	352	1	0 (probe in place)	0
		2	400	0
		3	400	400
		4	400	800
		5	400	1200
			(probe in place)	
D	356	1	0 (probe in place)	0
		2	800	0
		3	800	400
		4	800	800
		5	800	1200
			(probe in place)	

another three periods totalling 30 min in duration: (note that in trial A reticular probes were not inserted into the animals).

## RESULTS

### *Expt 1. Reticular distension*

There was a significant inverse relationship between reticular distension and food intake by hungry sheep after 10, 20 and 30 min of feeding (Table 2). In one sense the threshold for effect appeared to be between 400 and 600 ml distension, since the intakes for 600 ml but not 400 ml distension were significantly smaller than those when no distension was applied. However, since intakes decreased in a stepwise manner with increasing extent of distension and since only the linear regression effect was significant, it could be argued that even 200 ml distension was sensed by the sheep and resulted in a reduction in intake. After the probes were removed from the sheep, their intakes of food were positively associated with the previous extent of reticular distension. The regression coefficient of +0.206 g food/ml distension (Table 2) indicated that after 20 min of compensatory feeding the sheep had almost completely made up their deficits in intake occurring during the first 30 min of the experiment (-0.211 g/ml distension). The total intakes for the 50 min of feeding during the experiment were similar for all treatments.

### *Expt 2. Rumen distension*

Distending the rumen with 800 ml water in balloons had no significant effect on intake. The intakes with and without distension were 217 and 231 g after the first 10 min of feeding, 362 and 360 g after 20 min and 392 and 417 g after 30 min. Intakes in the 20 min following removal of the probes from the rumen were 136 g in the treatment group and 105 g in the control group. These values were not significantly different.

Table 2. Expt 1. Effect of distending the reticulum on food intake by sheep after food but not water was withheld for 335 min (n 5)

Period after deprivation (min)	Analyses of variance of 5 × 5 Latin square					Regression analyses		
	Distension (ml)					Slope (g/ml)	F	r
	0	200	400	600	800			
			Mean food intakes (g)					
0-10	223 <sup>a</sup>	191 <sup>a</sup>	163 <sup>ab</sup>	104 <sup>b</sup>	116 <sup>b</sup>	-0.151 ± 0.026	****	-0.55
10-20	81	87	45	53	68	-0.031 ± 0.024	NS	-0.19
0-20	305 <sup>a</sup>	278 <sup>ab</sup>	208 <sup>ab</sup>	157 <sup>b</sup>	183 <sup>ab</sup>	-0.182 ± 0.046	****	-0.48
20-30	67	50	12	20	52	-0.030 ± 0.019	NS	-0.25
0-30	371 <sup>a</sup>	329 <sup>ab</sup>	220 <sup>ab</sup>	177 <sup>b</sup>	236 <sup>ab</sup>	-0.211 ± 0.059	****	-0.48
				Compensatory feeding with source of distension removed				
30-40	102 <sup>bc</sup>	89 <sup>c</sup>	147 <sup>ab</sup>	178 <sup>a</sup>	166 <sup>a</sup>	+0.109 ± 0.024	****	+0.60
40-50	31	54	107	126	92	+0.010 ± 0.032	****	+0.52
30-50	133 <sup>b</sup>	143 <sup>b</sup>	254 <sup>ab</sup>	303 <sup>a</sup>	259 <sup>ab</sup>	+0.206 ± 0.047	****	+0.63
				Total intakes for the experiment				
0-50	504	471	474	480	494	-0.006 ± 0.051	NS	-0.01

a, b, c Mean values with different superscripts differed significantly by a sequential variant of the Q method. NS, not significant.

\* P < 0.05, \*\* P < 0.025, \*\*\* P < 0.01, \*\*\*\* P < 0.005.

† SE =  $\sqrt{\frac{\text{Error mean square}}{5}}$

Table 3. *Expt 3. Effect of distending the abomasum on food intake by sheep after food but not water was withheld for 356 min (n 5)*

Period after deprivation (min)	Analyses of variance of 5 × 5 Latin square					Regression analyses				
	Distension (ml)					Slope (g/ml)	F	r	F	r
	0	250	500	750	1000					
		Mean food intakes (g)								
0-10	203	155	227	186	145	-0.034 ± 0.033	NS	-0.20	NS	-0.20
10-20	121a	81ab	86ab	61b	57b	-0.060 ± 0.016	*	-0.59	****	-0.59
0-20	324	236	313	247	201	-0.094 ± 0.045	NS	-0.39	NS	-0.39
20-30	42	20	25	29	13	-0.020 ± 0.012	NS	-0.28	NS	-0.28
0-30	366	256	338	276	214	-0.114 ± 0.046	NS	-0.45	*	-0.45
		Compensatory feeding with source of distension removed								
30-40	56	95	78	81	103	+0.031 ± 0.012	*	+0.38	**	+0.38
40-50	34	39	36	33	50	+0.010 ± 0.011	NS	+0.14	NS	+0.14
30-50	90	134	114	114	152	+0.042 ± 0.021	NS	+0.36	NS	+0.36
		Total intakes for the experiment								
0-50	456	391	452	390	366	-0.072 ± 0.032	NS	-0.39	**	-0.39

a, b, c Mean values with different superscripts differed significantly by a sequential variant of the Q method.

NS, not significant.

\*  $P < 0.05$ , \*\*  $P < 0.025$ , \*\*\*  $P < 0.01$ , \*\*\*\*  $P < 0.005$ .

† SE calculated from the equation given in Table 2.

Table 4. *Expt 4. Effect of tactile stimulation of the reticulum and the abomasum on food intake by sheep after food but not water was withheld for 356 min (n 5)*

Period after deprivation (min)	Mean food intake (g)			F		
	Normal (no probes) (1)	Reticular probe (2)	Abomasal probe (3)	1 v. 2	2 v. 3	1 v. 3
				1 v. 2	1 and 3	1 v. 3
0-10	246	244	282	NS	NS	NS
0-20	390	312	428	***	****	NS
0-30	448	360	492	**	***	NS
Compensatory feeding with probes removed						
30-40	57	88	44	NS	NS	NS
30-50	84	150	68	NS	*	NS
30-60	104	162	74	NS	NS	NS
Total intakes for the experiment						
0-60	552	522	566	NS	NS	NS

NS, not significant.

\*  $P < 0.05$ , \*\*  $P < 0.025$ , \*\*\*  $P < 0.01$ , \*\*\*\*  $P < 0.005$ .*Expt 3. Abomasal distension*

There was a tendency for food intake to decrease as the extent of abomasal distension increased (Table 3). The effect was significant as a linear regression component of the analysis of variance of intakes during 30 min of feeding. Over the period, each 1 ml distension suppressed intake by 0.11 g. There was a large amount of variability in the results since intakes were depressed by up to 42% after 30 min of feeding, but these effects were still not statistically significant in the analysis of variance. When the balloons were removed from the sheep, significant amounts of compensatory feeding were observed with intakes increasing in accordance with increasing severity of the previous treatments (Table 3).

*Expt 4. Tactile inputs from the reticulum and the abomasum*

*Part A.* Similar quantities of food were eaten by normal sheep and by those fitted with abomasal probes (Table 4). However, intakes were depressed by 25% relative to normal consumption after 20 and 30 min of feeding ( $P < 0.01$ ) when a probe was placed in the reticulum (Table 4). When the reticular probes were removed, compensatory feeding occurred over 20 min which was statistically significant ( $P < 0.05$ ).

*Part B.* Food intakes with and without reticular probes in thirteen sheep were 181 and 213 g after 10 min of feeding, 62 and 101 g between 10 and 20 min, 242 and 314 g after 20 min, 29 and 43 g between 20 and 30 min (NS) and 271 and 357 g after 30 min respectively. These differences were all significant ( $P < 0.025$ ) unless otherwise indicated. Food intakes were significantly greater ( $P < 0.005$ ) when the probes were removed from the sheep than when nothing was done to them, with intakes being 73 and 37 g after 10 min of compensatory feeding, 47 and 22 g between 10 and 20 min, 120 and 59 g after 20 min, 16 and 17 g between 20 and 30 min (NS) and 137 and 76 g after 30 min respectively.

*Expt 5. Reticular and abomasal distension*

There was an inverse relationship between reticular distension and food intake when the abomasum was not distended. This can be seen in Fig. 1 by comparing intakes when only the probe was in the reticulum with those when the probe was distended with various

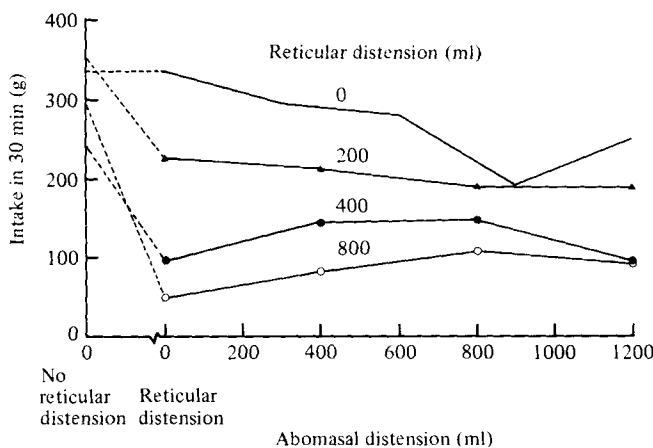


Fig. 1. Expt 5. Effect of combinations of reticular and abomasal distension on the intake of food by hungry sheep. When no reticular distension was applied (— — —), probes were in the reticulum except when the effect of abomasal distension *per se* (line for 0 ml) was tested.

amounts of water. When the reticulum was distended with 800 ml water in the probe, 47 g food/30 min was consumed. Superimposing various extents of abomasal distension on 800 ml reticular distension did not significantly alter intake ( $P > 0.05$ ) although there was a tendency for it to increase with increasing distension of the abomasum. In contrast with this response was the effect of abomasal distension in the absence of reticular distension (Fig. 1), where intake decreased in proportion to abomasal distension. This decrease in intake, however, was not significant even though 1200 ml distension reduced intake by 34%. These results indicated clearly that the depressing effects of either reticular or abomasal distension on the intake of food by sheep were not additive when combinations of both types of distension were applied simultaneously.

#### DISCUSSION

The intake of food by hungry sheep was depressed consistently by distending the reticulum with up to 800 ml water in a balloon attached to the end of a polyethylene tube (Expt nos. 1 and 3). If the receptors mediating the response were in the reticulo-ruminal fold one would expect distension of either the reticulum or the cranial sac to have similar effects on intake. With this qualification in mind the response was attributed to reticular distension. This did not produce any signs of discomfort nor did it inhibit water consumption by thirsty sheep (Grofum, 1978). The response was thus specific for food. Additional evidence indicating that the sheep were not adversely affected by the treatment is that immediately after the probes were removed, the sheep made up most if not all of their previous deficits in intake. The reticulum contracts twice during each mixing cycle and presumably empties most of its contents into the cranial sac and other parts of the rumen, but this does not detract from the argument that reticular distension may inhibit intake since the reticulum is immediately refilled by back-flow from the cranial sac and the rumen and is quiescent for most of the mixing cycle (Reid & Cornwall, 1959). To ascertain if reticular distension limits meal size of various diets, measurements must be made of the amount of contents that are held in the quiescent reticulum during the course of a meal. Two points making this at least a possibility are that (a) food of high specific gravity has been shown by Schalk & Amadon (1928) to drop mainly into the reticulum and cranial sac of cattle during a meal and (b) the density of tension receptors in the smooth muscle was found by Iggo (1955)



and Leek (1969) to be much greater in the reticulum and the cranial sac than in the rumen. It is thus feasible that reticular distension may limit meal size even when concentrate diets are offered because of their relatively high specific gravity. This line of reasoning is contrary to the neat division of satiety signals between physical factors for most roughage diets of low to medium quality and chemical or physiological factors for foods of high digestibility (Conrad *et al.* 1964; Montgomery & Baumgardt, 1965; Dinius & Baumgardt, 1970). The idea that physical factors may be partially responsible for limiting intake of a concentrate diet is also suggested from the experiments of Ørskov (1978) in which urea supplementation of whole barley increased its intake in sheep by up to 41%. The response was presumably due to an increase in fermentation rate and hence a decrease in volume of contents in the reticulo-rumen rather than to an improvement in the protein status of the animal (Egan, 1965*a*) since in another experiment the outflow of protein from the rumen was not influenced by the supplementation (Ørskov *et al.* 1971).

Distension of the rumen has been implicated as the main factor limiting the intake of roughage diets by ruminants (Crampton *et al.* 1960; Blaxter *et al.* 1961; Balch & Campling, 1962; Montgomery & Baumgardt, 1965; Ulyatt *et al.* 1967; Baile & Forbes, 1974). The results of Expts nos. 1 and 2 indicated that the reticulum could detect distension similar in magnitude to the volume of the meal but that the rumen could not. It might be argued that this could be expected, based on the relatively small size of the reticulum. However the fact remains that if the size of a meal is limited by physical factors, then some organ(s) must have the receptors to detect small increments in volume(s) of contents and thus generate the signals which ultimately terminate ingestive behaviour. The lack of effect of rumen distension is also not surprising considering that the grinding and pelleting of roughage diets usually decreases the volume of contents in the reticulo-rumen. Each 1 ml water added to the reticulum depressed intake by 0.2 g in a 30 min feeding period, which admittedly is not much but still exceeds considerably the depression of daily intakes of 0.05 g/ml when the rumens of cattle fed hay for 3–4 h per day were distended with up to 45 kg water in bladders (Campling & Balch, 1961). This comparison must however be viewed with caution because of differences in species, forms of the diets and duration of the treatment and the deprivation periods in the two experiments. If the bladders and 45 kg water were added to the rumen of the cows before feeding, this would have increased the amount of contents in the reticulo-rumen from 75 to 120 kg, the total weight being slightly in excess of the 114 kg found normally in the cows after feeding ceased (Campling *et al.* 1961). It thus seems reasonable to ask why the cattle ate anything immediately after the bladders were inflated with water if distension of the rumen signalled satiety. Why was the average size of the daily meal lasting 3–4 hours only depressed by 25% when the rumen was already distended by 45 l with the bladders? Although it is possible that distension of the rumen eventually signalled satiety in these cows, there is at least a possibility that food accumulating in the reticulum and the cranial sac could have depressed intake in this experiment, assuming that reticular distension has the same effect on food intake in cattle and in sheep. There is a large increase in the volume of contents in the rumen when cattle are given access to food for 6 h periods each day (Baile & Forbes, 1974) but this is not proof that distension of the rumen limited intake. The satiety signals may have been generated by the reticulum, the cranial sac or the abomasum if the contents of these structures increased in proportion to that in the rumen. This information is not presently available in the literature. Similarly the fact that additions of digesta (Campling & Balch, 1961) or food (Weston, 1966) to the rumen depressed oral intake cannot be used to indicate that rumen distension limited intake. The fact that rumen volumes in cows and sheep fed *ad lib.* were less on a diet of straw than they were with hay (Campling *et al.* 1961; Egan, 1970, 1971) is difficult to explain if a certain critical extent of rumen distension was entirely responsible for producing satiety. Egan (1970) suggested

that the critical distension value might be different for different diets, and Egan (1965*b*) indicated that it might be positively associated with nitrogen status. Season or day length also appeared to alter the satiating influences of distension when deer were given diets of heather and *Agrostis-Festuca* spp. (Milne *et al.* 1978). The greater intakes of roughage by sheep during the summer than during the winter (Gordon, 1964) may be associated with the fact that gut fill at slaughter was greater when sheep were exposed to 16 h daylight/d than with 8 h/d (Brown *et al.* 1978). These experiments along with the positive associations that exist between rumen digesta content and voluntary intake in overfat, pregnant and lactating cattle (Campling, 1970; Forbes, 1977*a*) indicate again that no one level of fill is associated with satiety. A multitude of factors impinging on contents in the reticulo-rumen influence the rate of production of small food particles which can escape through the reticulo-omasal orifice and thus alter rumen volume and intake, but receptors somewhere ultimately need to be stimulated to produce satiety. The conditions under which rumen distension controls intake and how it does this certainly need to be better defined. In summary the grounds for concluding that rumen distension controls intakes of roughage diets seem at present to be inadequate as, in addition to the above-mentioned inconsistencies, there is work for (Campling & Balch, 1961; Davies, 1962) and against this concept (Carr & Jacobson, 1967; Baile *et al.* 1969; present study).

Food intakes were depressed by placing a probe of negligible volume in the reticulum (Expt no. 4), so the control intakes in Expts nos. 1 and 5 were probably lower than they would have been in normal sheep. This would account as well for the rather large amount of compensatory feeding noticed in the control animals in these experiments once the probes were removed from the reticulum. Since the probes made the sheep ruminate immediately after they were inserted into the reticulum, it is likely that they generated substantial afferent activity from epithelial receptors (mechanoreceptors) known to exist in that organ (Ash & Kay, 1957; Harding & Leek, 1972; Leek, 1973). Thus it could be that the factors that make sheep ruminate can also induce satiety via the afferent activity from these epithelial receptors. Perhaps ruminants eat less of poorer-quality roughage diets which require a lot of rumination simply because of the increased activity of these epithelial receptors. If this is true then rumen volume may be irrelevant as a satiety signal.

Abomasal distension was less effective than reticular distension in suppressing intake ( $-0.11$  v.  $-0.21$  g/ml respectively). The lack of any additive effects of abomasal and reticular distension in Expt no. 5 was not expected and was difficult to explain. Abomasal distension of up to 1 l was substantial, considering that the mass of abomasal contents found on slaughtering six sheep given chopped lucerne hay *ad lib.* was  $729 + 66$  g (Grofum & Phillips, unpublished observations) and that the 1 l distension markedly depressed motility of the reticulo-rumen. Hodgson (1971) reported that grinding and pelleting a diet of dried grass markedly increased the amount of abomasal contents in calves compared to when the same food was given in a chopped form (722 v. 222 g). The grinding and pelleting decreased the mass of rumen contents from 10.6 to 3.7 kg. Therefore if abomasal distension signals satiety it is more likely to occur with roughage diets that are ground and pelleted than when they are given as hay or in the chopped form. This has been suggested before by Campling *et al.* (1963). Since there is no information available on the changes in volume of abomasal contents during a meal, the significance of abomasal distension in limiting meal size of solid food is not known. However Boyne *et al.* (1956) found that ewes given a mixed diet consisting largely of ground maize, hay and decorticated groundnut meal had approximately 650 g contents in the abomasum before a meal of 1624 g food and approximately 1450 g contents at 2 h after the meal was finished. During feeding, ground hay left the reticulo-rumen of sheep and cattle much faster than long hay (Campling *et al.* 1963, Van Niekerk *et al.* 1973). This response, along with an increased rate of gastric secretion

during feeding (McLeay & Titchen, 1975) would tend to increase the amount of digesta present in the abomasum during a meal. Whether or not this would be sufficient to trigger satiety is not known. Abomasal distension may be a factor limiting fluid intake in calves and lambs, as Pettyjohn *et al.* (1963) found that nutrient intakes decreased when milk substitutes contained less than 100 g dry-matter/kg and Towbin (1949) found that drinking in dogs was inhibited by distending the stomach with air in a balloon.

The concept that the intake of poor- to medium-quality roughage diets is controlled by distension of the rumen should be re-evaluated. Attention should be given in these experiments to the role of tactile stimulation of the reticulo-rumen, and of distension of the reticulum and the abomasum as factors limiting consumption of food by ruminants. The references cited in this discussion included work on cattle, sheep and deer without distinguishing between them because there is limited information on this subject. There is presently no reason to suspect that the mechanisms controlling intake are different in these species, but caution is still in order when such generalizations are made. The effects of distension and tactile stimulation of various stomach compartments on intake could well be different for different diets, but as yet this is not known. The present data are limited to ground and pelleted hay, and again caution is needed in applying the results to other diets. The mechanisms whereby nutritional status of the animal (Egan, 1965*a*; 1970), endocrine factors during pregnancy and lactation (Forbes, 1977*b*) and changes in day length (Milne *et al.* 1978) alter the satiating influence of distension should be investigated, as this may uncover a way of increasing intake and hence the production of protein when ruminants are given poor- to medium-quality roughages.

The technical assistance of Karen Gordon and funding from the National Research Council of Canada and the Ontario Ministry of Agriculture and Food are gratefully acknowledged.

#### REFERENCES

- Ash, R. W. & Kay, R. N. B. (1957). *J. Physiol., Lond.* **139**, 23*P*.  
 Baile, C. A. & Forbes, J. M. (1974). *Physiol. Rev.* **54**, 160.  
 Baile, C. A., Mayer, J. & McLaughlin, C. (1969). *Am. J. Physiol.* **217**, 397.  
 Balch, C. C. & Campling, R. C. (1962). *Nutr. Abstr. Rev.* **32**, 669.  
 Blaxter, K. L., Wainman, F. W. & Wilson, R. S. (1961). *Anim. Prod.* **3**, 51.  
 Boyne, A. W., Campbell, R. M., Davidson, J. & Cuthbertson, D. P. (1956). *Br. J. Nutr.* **10**, 325.  
 Brown, W. B., Jones, R. & Forbes, J. M. (1978). *Proc. Nutr. Soc.* **37**, A 99.  
 Campling, R. C. (1970). In *Physiology of Digestion and Metabolism in the Ruminant*, p. 228 [A. T. Phillipson, editor]. Newcastle upon Tyne: Oriel Press Ltd.  
 Campling, R. C. & Balch, C. C. (1961). *Br. J. Nutr.* **15**, 523.  
 Campling, R. C., Freer, M. & Balch, C. C. (1961). *Br. J. Nutr.* **15**, 531.  
 Campling, R. C., Freer, M. & Balch, C. C. (1963). *Br. J. Nutr.* **17**, 263.  
 Carr, S. B. & Jacobson, D. R. (1967). *J. Dairy Sci.* **50**, 1814.  
 Conrad, H. R., Pratt, A. D. & Hibbs, J. W. (1964). *J. Dairy Sci.* **47**, 54.  
 Crampton, E. W., Donefer, E. & Lloyd, L. E. (1960). *J. Anim. Sci.* **19**, 538.  
 Davies, H. L. (1962). *Proc. Aust. Soc. Anim. Prod.* **4**, 167.  
 Dinius, D. A. & Baumgardt, B. R. (1970). *J. Dairy Sci.* **53**, 311.  
 Egan, A. R. (1965*a*). *Aust. J. agric. Res.* **16**, 451.  
 Egan, A. R. (1965*b*). *Aust. J. agric. Res.* **16**, 463.  
 Egan, A. R. (1970). *Aust. J. agric. Res.* **21**, 735.  
 Egan, A. R. (1971). *Aust. J. agric. Res.* **23**, 347.  
 Forbes, J. M. (1977*a*). *Anim. Prod.* **24**, 203.  
 Forbes, J. M. (1977*b*). *Anim. Prod.* **24**, 91.  
 Gordon, J. G. (1964). *Nature* **204**, 798.  
 Grovum, W. L. (1978). *Experientia* **34**, 202.  
 Grovum, W. L. & Phillips, G. D. (1978). *Br. J. Nutr.* **40**, 323.  
 Harding, R. & Leek, B. F. (1972). *J. Physiol., Lond.* **223**, 32*P*.  
 Hodgson, J. (1971). *Anim. Prod.* **13**, 449.

- Iggo, A. (1955). *J. Physiol., Lond.* **128**, 593.  
Leek, B. F. (1969). *J. Physiol., Lond.* **202**, 585.  
Leek, B. F. (1973). *J. Physiol., Lond.* **227**, 22P.  
McLeay, L. M. & Titchen, D. A. (1975). *J. Physiol., Lond.* **248**, 595.  
Milne, J. A., MacRae, J. C., Spence, A. M. & Wilson, S. (1978). *Br. J. Nutr.* **40**, 347.  
Montgomery, M. J. & Baumgardt, B. R. (1965). *J. Dairy Sci.* **48**, 569.  
Ørskov, E. R. (1978). Proceedings, *University of Guelph Nutrition Conference for Feed Manufacturers*, 14th ed. Toronto: Departments of Nutrition and Animal and Poultry Science, University of Guelph.  
Ørskov, E. R., Fraser, C. & McDonald, I. (1971). *Br. J. Nutr.* **25**, 243.  
Pettyjohn, J. D., Everett, J. P. & Mochrie, R. D. (1963). *J. Dairy Sci.* **46**, 710.  
Reid, C. S. W. & Cornwall, J. B. (1959). *Proc. N.Z. Soc. Anim. Prod.* **19**, 23.  
Schalk, A. F. & Amadon, R. S. (1928). *Bull. N. Dak. agric. Exp. Stn* no. 216.  
Towbin, E. J. (1949). *Am. J. Physiol.* **159**, 533.  
Ulyatt, M. J., Blaxter, K. L. & McDonald, I. (1967). *Anim. Prod.* **9**, 463.  
Van Niekerk, A. I., Greenhalgh, J. F. D. & Reid, G. W. (1973). *Br. J. Nutr.* **30**, 95.  
Weston, R. H. (1966). *Aust. J. agric. Res.* **17**, 939.