Factors affecting the voluntary intake of food by cows

4.* The behaviour and reticular motility of cows receiving diets of hay, oat straw and oat straw with urea

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The relationship between the voluntary intake of roughage by cattle and the rate of disappearance of digesta from the reticulo-rumen was considered earlier (Campling, Freer & Balch, 1961, 1962). It was shown that the voluntary intake, by cows, of hay, oat straw or oat straw with urea was directly related to the rate at which digesta disappeared from the reticulo-rumen by digestion and absorption and by the onward passage of food residues. These findings have led us to investigate some of the factors that affect the passage of food residues from the reticulo-rumen, which include (*a*) the mean time of retention of food particles in the reticulo-rumen, and (*b*) the rate of flow of digesta from the reticulo-rumen to the omasum. Rate of passage, as measured by the mean retention time, and the rate of flow were defined by Balch (1961). The interrelationship of these two factors and the extent to which one can vary independently of the other have not previously been explored.

It was shown earlier (Campling *et al.* 1961, 1962) that the voluntary intakes of hay, oat straw and oat straw with urea were inversely related to the mean times of retention of food residues in the reticulo-rumen, even when the times of retention were measured at equal levels of intake. It seemed likely that factors affecting the rate at which food particles were reduced to a size suitable for transfer to the omasum would largely determine their mean time of retention in the reticulo-rumen. The rate of digestion of food is clearly an important factor, but the extent and efficiency of mastication of food during the acts of eating and rumination may also be concerned.

When a ruminant is established on any diet, the mean daily flow of organic matter from the reticulo-rumen to the omasum must equal the daily intake of food organic matter less the amount that disappears daily by absorption from the reticulo-rumen and by eructation of rumen gases. From the observations of Wester (1926), Schalk & Amadon (1928), Balch, Kelly & Heim (1951) and Stevens, Sellers & Spurrell (1960) it appears possible that the rate of flow of digesta from the reticulum to the omasum is related to the frequency of contraction of the reticulum and to the amount of digesta transferred to the omasum during each primary contraction of the reticulo-rumen. There was little previous evidence to suggest how these two factors vary in order to effect changes in the flow of digesta from the reticulo-rumen with different diets. Moreover, apart from the work of Balch (1952, 1958), there is little information on the

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frequency of reticular contraction in cattle receiving different diets, and none which applies to single roughages given alone at different levels of intake.

As part of the investigations previously reported (Campling *et al.* 1961, 1962) the frequency of the biphasic contraction of the reticulum and the time spent eating and ruminating were recorded throughout the 24 h, when the cows were offered (1) hay, (2) oat straw, and (3) oat straw with urea. Cows were offered these diets *ad lib.* and at controlled levels of intake. The results are here considered in relation to the mean retention time of food residues in the reticulo-rumen and the mean rate at which organic matter was transferred to the omasum. Supplementary observations were made on the effect of altering the time during which cows had access to a roughage on their behaviour (that is to say on the time spent eating, ruminating, resting, standing and lying) and on their voluntary intake of the roughage.

EXPERIMENTAL

Observations were made on a total of seven adult, non-lactating, non-pregnant Friesian and Shorthorn cows in six experiments.

Plan of experiments

Expt 1. The behaviour and the frequency of reticular contraction of four cows were compared when they were offered oat straw or hay (1) *ad lib.*, (2) restricted to 10 lb daily and (3) restricted to a quantity calculated to produce the same daily output of faecal dry matter from both foods. A change-over design was used.

Expt 2. The same observations were compared in three cows when oat straw was offered daily *ad lib.* (1) with no urea, (2) with 150 g urea and 500 g sucrose and (3) with 150 g urea. A Latin square design was used.

Expt 3. The same observations were compared in two cows when 10 lb of oat straw were offered daily (1) with no urea, (2) with 150 g urea and 500 g sucrose. A change-over design was used. Subsequently, the behaviour and the reticular motility of each cow was recorded when oat straw was offered *ad lib.* with 150 g urea and 500 g sucrose daily.

Expt 4. The same observations were compared in three cows when oat straw was offered daily (1) *ad lib.* without urea, (2) in the same quantities as those consumed in (1) with 150 g urea and (3) *ad lib.* with 150 g urea. A Latin square design was used.

Expt 5. The behaviour and the voluntary intake of hay were compared in four cows when hay was offered *ad lib.* once daily (1) for $4\frac{1}{2}$ h/day and (2) for 24 h/day. A change-over design was used.

Expt 6. One cow was used to investigate the effect of altering the length of time during the day for which it had access to roughage on its behaviour, on its reticular motility and on its voluntary intake of the roughage. The treatments were: (1) hay, continuous access, (2) hay for $4\frac{1}{2}$ h/day, (3) hay for 2 h/day, (4) oat straw, continuous access, (5) oat straw for $4\frac{1}{2}$ h/day, (6) oat straw for 2 h/day, (7) oat straw + 150 g urea/day, continuous access, (8) oat straw + 150 g urea/day for $4\frac{1}{2}$ h/day.

Other aspects of Expts 1–4 have been reported by Campling *et al.* (1961, 1962).

Management of cows

Each cow had a permanent rumen fistula which was closed by means of the cannula and bung described by Balch & Johnson (1948). The cows were housed in one shed on individual standings separated by concrete walls 4 ft in height, and had sufficient room to lie down.

Foods

Two batches of oat straw and two batches of hay were used: straw A in Expts 1–3, straw B in Expts 4 and 6, hay A in Expts 1 and 5 and hay B in Expt 6. The chemical composition of each roughage is shown in Table 1. Each cow received daily 40 g of a proprietary mineral mixture (Churn 105, British Glues and Chemicals Ltd), together with a weekly supplement of a vitamin A and D concentrate (Drivite, Boots Pure Drug Co. Ltd).

Table 1. *Chemical composition of the foods*

Food	Dry matter (%)	Crude protein	Ether extract	Crude fibre	Nitrogen-free extract	Ash
		As percentage of food dry matter				
Hay A	83·0	8·7	1·8	31·1	52·1	6·3
Hay B	84·1	11·9	2·5	34·0	44·2	7·4
Straw A	84·6	2·9	2·2	40·6	48·9	5·4
Straw B	81·0	3·3	1·4	41·2	44·1	10·0

Supplementary urea, with or without sucrose, in Expts 2–4 and 6 was dissolved in 20 lb of tap water and given as a continuous infusion into the reticulo-rumen, to avoid affecting the taste of the straw. Cows on control treatments received a daily infusion of 20 lb of tap water.

Feeding

Each diet was offered once daily at 10.00 h and, with *ad lib.* feeding in Expts 1–4, uneaten food was removed and weighed after 4½–5 h, by which time the cows had ceased eating. Each cow received each diet for 18 days before recordings were made.

Recording apparatus

The technique used for recording the contractions of the reticulum was similar to that described by Balch *et al.* (1951). In each cow a small balloon (2 in. × 1½ in. when inflated) mounted on a perforated brass tube was retained in the reticulum by a brass weight of about 1 kg. The lightly inflated balloon was connected by pressure tubing, through the rumen fistula, to a tambour placed vertically in an Evershed and Vignoles recorder. In all experiments except Expt 1 a similar balloon was placed under a side strap on a leather head-stall to record jaw movements. Each tambour operated a pen which provided a continuous record of pressure changes at 0·5 in./min. Records of pressure changes in the reticulum and of jaw movements were made simultaneously. With each diet, recording began immediately before a meal and continued for 72 h.

The records were analysed, as described by Balch (1952), to determine the time each

cow spent eating, ruminating, resting, standing and lying. Resting was a residual activity during which the cows were neither ruminating nor eating. The contractions of the reticulum were counted during each period of unchanged activity and the frequency of contraction with each activity was calculated. For this purpose each double or triple contraction of the reticulum was counted as one contraction.

RESULTS

To demonstrate the extent of differences between cows the results of Expt 1 are presented as mean values for the individual cows, but most of the other results are reported as mean values for each treatment with the appropriate standard error. The cows in Expt 1 were chosen because they differed widely in their individual voluntary intake of roughages.

Experiment 1

As the voluntary intake of straw was about 10 lb daily, recordings with this roughage were made, in effect, at only one level of intake. The mean voluntary intake of hay at the time of recording was 22·0 lb/day and recordings were also made when it was restricted to 15 and 10 lb/day. For each activity, the mean values for behaviour and reticular motility for a period of 24 h with each diet were calculated and are shown in Table 2.

Table 2. *Expt* 1. *Mean time spent daily* (*min*) *in eating, ruminating and resting by individual cows receiving diets of hay and straw, and the number and frequency*/100*min* (*f*) *of reticular contractions during each activity*

		Mean daily food intake	Total contractions		Eating			Ruminating			Resting		
						Contractions			Contractions			Contractions	
Cow	Food	(lb)	No.	*f*	Time (min)	No.	*f*	Time (min)	No.	*f*	Time (min)	No.	*f*
E	Straw	10·6*	1728	120	241	361	150	508	463	91	691	904	131
	Hay	24·2*	1656	115	254	375	148	718	687	96	468	594	127
		15·0	1464	102	98	148	151	383	404	105	959	912	95
		10·0	1231	85	65	94	145	190	218	115	1185	919	78
F	Straw	9·8*	1557	108	201	283	141	501	388	77	738	886	120
	Hay	24·7*	1782	124	267	397	149	632	660	104	541	725	134
		15·0	1674	116	122	184	151	444	466	105	874	1024	117
		10·0	1586	110	102	151	148	350	364	104	988	1071	108
G	Straw	9·7*	1536	107	198	259	131	425	395	93	817	882	108
	Hay	21·0*	1750	122	201	318	158	533	599	112	706	833	118
		15·0	1657	115	134	222	166	463	508	110	843	927	110
		10·0	1357	94	90	128	142	240	251	105	1110	978	88
H	Straw	8·6*	1693	117	219	311	142	538	542	101	683	840	123
	Hay	18·1*	1717	119	237	330	139	720	802	111	483	585	121
		15·0	1696	118	197	250	127	607	767	126	636	679	107
		10·0	1628	113	80	115	144	413	520	126	947	993	105
Mean	Straw	9·7*	1629	113	215	304	141	493	448	91	732	877	119
	Hay	22·0*	1726	120	240	355	148	650	686	106	550	685	125
		15·0	1623	113	138	201	146	474	536	113	828	886	107
		10·0	1451	101	84	122	145	298	338	113	1058	991	94

* Food offered *ad lib.*

Eating. Cows offered hay *ad lib.* spent, on average, 240 min/day eating, or 10·9 min/lb food. When the intake of hay was restricted to 15 lb and 10 lb/day the mean time spent eating fell to 9·2 and 8·4 min/lb respectively. Cows offered straw *ad lib.* ate on average for 215 min/day, or 22·2 min/lb food. Cow H, which had the lowest voluntary intake, ate both roughages at a slower rate than the other three cows. Differences between these three cows, however, were small and were not related to the amount they would voluntarily consume.

As previous workers (Schalk & Amadon, 1928; Balch, 1952; Reid & Cornwall, 1959) have observed, the frequency of reticular contraction during the act of eating was higher than that found during any other activity. The mean value for the hay diets was 146 contractions/100 min and was little affected by the level of intake. The mean value for the straw diets was 141 contractions/100 min, but the difference between the two roughages was not consistent. Differences between cows were also relatively small and inconsistent.

Rumination. The cows ruminated, on average, for 650 min/day or 29·5 min/lb food when offered hay *ad lib.* The amount of rumination per lb of food was almost the same at all levels of hay intake: 29·8 min/lb with 10 lb hay and 31·6 min/lb with 15 lb hay. When straw was offered *ad lib.* the time spent ruminating was 493 min daily or 50·8 min/lb food. The only consistent difference between animals was that cow H ruminated for 40·5 min/lb hay and for 62·6 min/lb straw, compared with the three other cows, whose mean values were 27·2 and 47·6 respectively. Cow H was 14 years old; recordings made when she was 9 years old show that she ate 18 lb of a similar hay in 11 min/lb and ruminated for 26 min/lb hay.

When the cows received hay the mean frequency of reticular contraction was 111 contractions/100 min and was not affected by the amount of hay eaten. The frequency of contraction was consistently lower with a diet of straw, with a mean value of 91 contractions/100 min, corresponding to an increase in the mean interval between regurgitations from 55 sec with hay to 65 sec with straw. Again, the only consistent individual differences were shown by cow H whose mean frequency of reticular contraction was 120/100 min with hay and 101/100 min with straw. The frequency of reticular contraction was usually lower when the cows were lying down than when they were standing, but the mean difference was only 7 contractions/100 min.

Resting. As the mean intake of hay increased from 10·0 to 22·0 lb/day, the daily time during which the cows were neither eating nor ruminating fell from 17·63 to 9·17 h, and the mean frequency of reticular contraction increased from 94 to 125 contractions/100 min. The mean frequency of contraction was always lower when the cows were lying down than when they were standing and this difference increased from 11 to 21 contractions/100 min as the mean intake of hay was reduced from 22·0 to 10·0 lb/day.

In cows receiving about 10 lb straw, the mean frequency of reticular contraction was 119/100 min, considerably higher than was found with the same amount of hay.

Mean frequency of reticular contraction. As the mean intake of hay increased from 10·0 to 22·0 lb, the mean daily frequency of contraction rose from 101 to 120/100 min owing to the increase in the time spent eating and in the frequency of contraction while

the animals were resting. The slower rate at which the straw was eaten resulted in a mean daily frequency of contraction of 113/100 min, similar to that recorded with 15 lb hay.

Experiments 2–4

The mean duration of each activity and the respective frequency of reticular contraction with each diet are shown in Table 3. The mean times spent eating and ruminating/lb of straw are shown in Table 4.

Table 3. *Mean time spent daily (min) in eating, ruminating and resting by cows receiving diets of straw, with or without urea or urea and sucrose, and the number and frequency/100 min (f) of reticular contractions during each activity*

Expt no.	Food	Mean daily straw intake (lb)	Total contractions		Eating			Ruminating			Resting		
						Contractions			Contractions			Contractions	
			No.	*f*	Time (min)	No.	*f*	Time (min)	No.	*f*	Time (min)	No.	*f*
2	Straw	11·8*	1700	118	217	306	141	523	563	108	700	832	119
(three	Straw+urea	16·3*	1653	115	244	345	141	447	502	112	749	806	108
cows)	Straw+urea and sucrose	16·2*	1630	113	237	329	139	487	527	108	716	774	108
3	Straw	10·0	1733	120	171	254	149	441	456	103	828	1023	124
(two	Straw+urea and sucrose	10·0	1446	100	87	124	143	284	313	110	1069	1009	94
cows)	Straw+urea and sucrose	18·3*	1655	115	217	314	145	492	536	109	731	805	110
4	Straw	12·4*	1689	117	231	320	139	423	437	103	786	932	119
(three	Straw+urea	12·7	1552	108	138	195	141	327	354	108	975	1003	103
cows)	Straw+urea	17·6*	1700	118	260	360	138	435	477	110	745	863	116

* Straw offered *ad lib.*

Table 4. *Mean time (min/lb food) spent in eating and ruminating by cows receiving diets of oat straw with or without urea and sucrose, and mean number/day of periods of rumination*

Expt no.	Food	Mean daily straw intake (lb)	Time spent eating	Time spent ruminating	No. of periods of rumination
2	Straw	11·8*	18·4	44·3	12
(three cows)	Straw+urea	16·3*	15·0	27·4	12
	Straw+urea and sucrose	16·2*	14·6	30·1	13
	S.E. of difference		1·31	3·24	
3	Straw	10·0	17·1	44·1	13
(two cows)	Straw+urea and sucrose	10·0	8·7	28·4	13
	Straw+urea and sucrose	18·3*	11·9	26·9	15
4	Straw	12·4*	18·6	34·1	11
(three cows)	Straw+urea	12·7	10·9	25·7	12
	Straw+urea	17·6*	14·8	24·7	11
	S.E. of difference		1·21	3·68	

* Straw offered *ad lib.*

Eating. The cows in Expt 2 which were offered oat straw *ad lib.* ate on average for 24 min longer when urea or urea with sucrose was infused into the rumen. The mean time spent in eating 1 lb of straw decreased, however, from 18·4 to 14·8 min when

these infusions were given. Similar differences were obtained in Expts 3 and 4 when straw was offered *ad lib.* In Expts 3 and 4 the time spent eating decreased still further, to 8·7 and 10·9 min/lb respectively, when the intake of straw was restricted during the infusion of urea, with or without sucrose. Despite these differences in the mean rate of eating, the mean frequency of reticular contraction during eating was not affected by any of the treatments.

Rumination. When oat straw was offered *ad lib.*, the cows ruminated for 423–523 min/day. The administration of urea or urea and sucrose had relatively little effect on the total time spent ruminating but was accompanied by a decrease in the time spent ruminating/lb straw in all three experiments.

The frequency of reticular contraction during rumination was consistently higher during urea administration than when straw was offered alone, but the difference was always small.

Resting. When straw was offered *ad lib.* in Expt 2, the administration of urea, with or without sucrose, was accompanied by a decrease in the mean frequency of reticular contraction from 119 to 108 contractions/100 min. A similar decrease was observed in Expts 3 and 4 and was most marked when the intake of straw was restricted, in the presence of urea, to the amount voluntarily consumed in its absence.

Mean frequency of reticular contraction. In these three experiments the mean frequency of reticular contraction when straw was offered *ad lib.* in the absence of urea (117–120 contractions/100 min) was slightly higher than it was during urea administration (113–118 contractions/100 min). When the intake of straw was restricted during urea administration the mean frequency of contraction fell to 100–108 contractions/100 min, as a result of the shorter time spent eating and the reduced motility during rest.

Table 5. *Expt* 5. *Mean daily intake of food, and time spent in eating and ruminating by four cows with access to hay, offered* ad lib., *for either* 24 *h or* $4\frac{1}{2}$ *h each day*

		Time spent		Time spent/lb food		
Access (h)	Hay intake (lb)	Eating (min)	Ruminating (min)	Eating (min)	Ruminating (min)	Eating + ruminating (min)
24	26·0	392	618	15·1	23·8	38·9
$4\frac{1}{2}$	20·5	258	546	12·6	26·6	39·2

Experiment 5

The mean results for each treatment are shown in Table 5. When the cows had continuous access to hay they ate, on average, 26·0 lb daily, and when access was restricted to $4\frac{1}{2}$ h/day the daily intake fell by 21 % to 20·5 lb. The restriction in the time of access was also accompanied by a decrease in the mean time spent eating, from 15·1 to 12·6 min/lb, and an increase, from 23·8 to 26·6 min/lb, in the mean time spent ruminating. The total time spent eating and ruminating, per lb food, was almost the same with both treatments.

Experiment 6

The voluntary intake of roughage and reticular motility in one cow with each diet and her behaviour are shown in Table 6.

Voluntary intake of food. When the time of access to the food was restricted from 24 to 4½ h/day, the mean voluntary daily intake of hay fell by 14%, of oat straw by 19% and of oat straw in the presence of urea by 11%. The further restriction of access to 2 h/day had, proportionately, a greater effect, and the mean daily intake of hay was 39% less and of oat straw 38% less than the amounts eaten when the cow had continuous access to these foods.

Table 6. *Expt* 6. *Mean daily intake of food, time spent in eating, ruminating and resting, number and frequency/*100 *min* (*f*) *of reticular contractions during each activity, and time spent in eating and ruminating per lb of food by a cow receiving diets of hay, oat straw or oat straw with urea, offered* ad lib. *once daily for different periods of time*

			Eating			Ruminating			Resting			Time spent/lb food		
				Contractions			Contractions			Contractions				Eating +
Food	Access (h)	Food intake (lb)	Time (min)	No.	*f*	Time (min)	No.	*f*	Time (min)	No.	*f*	Eating (min)	Rumi-nating (min)	rumi-nating (min)
Hay	24	29·6	405	651	161	565	593	105	470	658	140	13·7	19·1	32·8
	4½	25·3	261	446	171	534	587	110	645	1025	159	10·3	21·1	31·4
	2	17·9	122	183	150	434	526	121	884	1230	139	6·8	24·2	31·0
Straw	24	13·8	343	560	163	474	455	96	623	942	151	24·9	34·3	59·2
	4½*	11·2	251			392			797			22·4	35·0	57·4
	2	8·5	121	197	163	358	351	98	961	1511	157	14·2	42·1	56·3
Straw with urea	24	20·4	348	542	156	496	518	104	596	844	142	17·1	24·3	41·4
	4½	18·2	264	437	166	456	502	110	720	1011	140	14·5	25·1	39·6

* Reticular motility was not recorded.

Rate of eating. The cow ate its food more rapidly when access to it was restricted to 4½ h daily and more rapidly still when access to it was limited to 2 h. The times spent in eating per lb hay were 13·7 and 6·8 min respectively for continuous access and for 2 h access; for oat straw the corresponding times were 24·9 and 14·2 min/lb.

Time spent ruminating. When access to a food was restricted, the decrease in the time spent eating was accompanied by an increase in the time spent ruminating, so that with each food the total time spent eating and ruminating was about the same whatever the period of access. The mean time this one cow spent eating and ruminating was 57·6 min/lb with straw, 41·1 min/lb with straw in the presence of urea, and 31·7 min/lb with hay.

DISCUSSION

Rate of eating. Under the conditions of these experiments, three factors appear to have controlled the mean rate at which the roughages were eaten: (1) the rate at which the roughage was broken down in the reticulo-rumen, (2) the daily time of access to the roughage, and (3) the amount of roughage offered.

When hay and straw were offered *ad lib.* in Expt 1, hay was eaten approximately twice as fast as straw. It was shown in Expt 6 that this difference did not result from the particular feeding régime adopted in Expt 1 and was evident whatever the length of time of access to these roughages. Nor was this difference due largely to differences in the palatability, as defined by Campling *et al.* (1962), of hay and straw, since it was shown in Expts 2–4 that the rate at which straw was eaten was markedly increased by the intraruminal infusion of a solution of urea. The main effect of the urea was to increase the rate of disappearance of digesta from the reticulo-rumen (Campling *et al.* 1962) and it seems probable from our results that the rates at which these roughages, of similar physical form, were eaten may have depended largely on the rate at which each roughage was broken down in the reticulo-rumen and on the contribution which mastication, during eating and ruminating, made to this breakdown.

From the results of Expt 6 it may be concluded that the time for which the cows had access to the roughages had a relatively small effect on the rate of eating until access was restricted to less than $4\frac{1}{2}$ h/day. Although the rate of eating increased markedly when access was restricted to 2 h, the increase was insufficient to prevent a reduction in food intake and the effect of time of access on the rate of eating was to some extent confounded by the effect of the reduction in the intake of food.

When, in Expts 1 and 4, the intake of hay and of straw with urea was restricted the foods were eaten at a faster rate than when they were offered *ad lib.* With the restricted diets, the amount of digesta in the reticulo-rumen immediately before a meal was considerably less than when the roughages were offered *ad lib.* (Campling *et al.* 1961, 1962), which is possibly the reason for the faster rate of eating. Throughout these experiments, only the mean rates of eating were measured, but Balch (1958) and Reid & Cornwall (1959) have reported a decline in the rate of eating during certain meals, which may also be associated with changes in the amount of digesta in the reticulo-rumen.

Rumination. In these experiments the mean time spent ruminating per lb food appeared to depend mainly on (1) characteristics of the roughage, which appeared to affect the rate at which it was broken down in the reticulo-rumen and (2) the rate at which the roughage was eaten.

It has been shown that the regurgitation reflex can be initiated by tactile stimulation of the walls of the reticulum (Schalk & Amadon, 1928; Balch, 1952; Ash & Kay, 1957). It would be expected that straw would provide a greater amount of tactile stimulation per lb food than straw with urea, which was digested in the reticulo-rumen to a greater extent (Campling *et al.* 1962), and similarly that both these diets would provide more stimulation, per lb, than hay.

In Expts 5 and 6 it was shown that the increased rate of eating observed when the time of access to each roughage was restricted was associated with an increase in the time spent ruminating per lb food. It is possible that when access was restricted the food was chewed less during eating and provided a greater amount of stimulation to rumination while in the reticulo-rumen. The effect of this complementary relationship between the time spent eating and the time spent ruminating was that the total time spent eating and ruminating per lb of each roughage consumed was almost constant,

as shown in Tables 5 and 6. This observation may mean that a fixed amount of chewing per lb roughage, whether in eating or rumination, may be necessary to reduce the food particles to a size suitable for onward passage from the reticulo-rumen.

It appeared from the results of Expts 1, 3 and 4 that the time spent ruminating per lb roughage was not appreciably affected by the amount eaten. This result is in contrast to the observation by Hancock (1954) that the time spent ruminating per lb dried grass rose with decreasing intake. Although the time spent eating was not stated in that report, it is possible that at levels of intake lower than those used by us the food was eaten at a greatly increased rate, with a compensating increase in the time spent ruminating. Gordon (1958) found no relationship between the quantity of hay ingested by sheep and the amount of rumination. This may be a species difference, but it is not possible to compare the results with those presented here, since the level of hay intake in Gordon's experiment was confounded with the amount of concentrates eaten.

Table 7. *Expt* 1. *Mean daily number of periods of rumination, and mean duration of each period for individual cows receiving each diet*

	Hay							
	Ad lib.		15 lb/day		10 lb/day		Straw *ad lib.*	
Cow	No.	Duration (min)	No.	Duration (min)	No.	Duration (min)	No.	Duration (min)
E	16	44·0	16	23·5	10	19·0	16	31·2
F	14	46·1	14	31·0	15	23·8	12	40·7
G	18	29·1	20	22·8	18	13·6	21	20·2
H	14	50·3	15	39·7	12	35·9	16	33·6
Mean	16	42·4	16	29·3	14	23·1	16	31·4

In our experiments, the direct relationship between the amount of food eaten and the time spent ruminating was due to alterations in the length of each period of rumination rather than to changes in either the number of periods or their distribution throughout the interval between meals. This observation is in agreement with those of Kick, Gerlaugh, Schalk & Silver (1937) on the time spent ruminating by steers offered equal amounts of lucerne hay in the long, chopped, or ground form. As shown in Table 7, when hay was offered *ad lib.* in Expt 1 there were, on average, sixteen periods of rumination daily with a mean duration of 42·4 min/period. As the intake of hay was reduced the mean duration of the periods fell, but not until the intake was restricted to 10 lb was the mean number of periods reduced, and then in only two of the cows. A similar pattern was observed in Expts 3 and 4, although the number of periods characteristic of an individual cow then varied from 9 to 20/day. Fig. 1 shows, for each of the three levels of hay intake in Expt 1, the mean proportion of the total daily ruminating time which occurred in each 30 min period of the day. It is clear that the distribution of rumination throughout the period between meals was similar at all levels of intake and was fairly uniform apart from a decline during the 5 h before feeding. These results show that, in a cow established on a diet, the total daily time

spent ruminating is regulated through the adjustment of the length of the periods of rumination, which are relatively constant in number and distribution. The time cows spent ruminating per lb roughage was inversely related to the digestibility of the roughage. It is therefore possible that the total time spent ruminating was proportional to the amount of tactile stimulation provided by the diet.

Reticular motility. Although there were differences between the cows, the mean frequency of reticular contraction during eating was relatively constant with the different diets used in these experiments and was not affected by the amount of food eaten or by the mean rate of eating. The number of reticular contractions during eating depended entirely, therefore, on the daily time spent eating. The frequency of

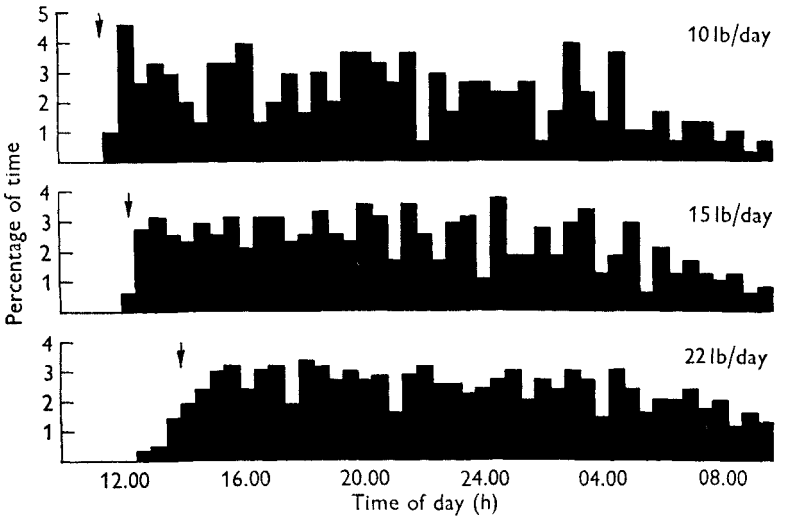

Fig. 1. Expt 1. Mean percentage of the total time spent ruminating daily by four cows which occurred in each 30 min period of the day, at each of three levels of intake of hay; the arrows show the mean times at which eating ceased.

reticular contraction was also relatively constant with the different diets during rumination, but there was a consistent, though slight, tendency for the mean frequency to increase as the digestibility of the roughage increased.

There was a direct relationship between the intake of roughage and the mean frequency of reticular contraction while the cows were resting. It is possible that this relationship resulted from stimulation of the alimentary tract by the food residues passing through it and it may therefore be of greater significance that there was an equally close relationship between reticular motility during rest and the daily time spent ruminating. From the results of Expt 1 shown in Fig. 2, it was calculated that there was a mean increase of 9 reticular contractions/100 min during rest for each increase of 100 min in the mean daily time spent ruminating. In Expts 3 and 4 the corresponding value for oat straw with urea was 10 contractions/100 min. However, the results of Expt 6 suggest that this relationship was altered when the time of access to a roughage was sufficiently restricted to cause an appreciable rise in the rate of eating.

As shown in Fig. 3, from the results of Expt 1, the mean frequency of reticular contraction during rest fell during the night (18.00 h–06.00 h), particularly at the lower levels of hay intake. During this 12 h period 64–76 % of the total resting time was spent lying down, whereas during the day 70–81 % of the resting time was spent

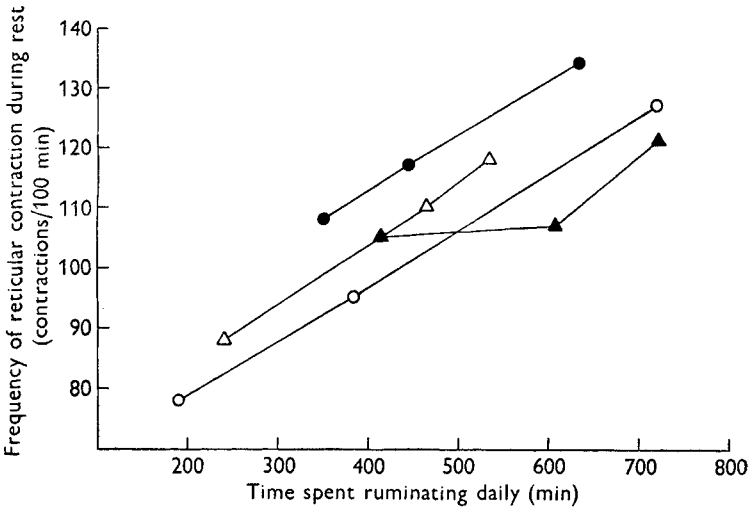

Fig. 2. Expt. 1. Relationship between the mean time spent daily in ruminating, and frequency of reticular contraction during rest, for each of four cows receiving hay at three levels of intake. ○—○, cow E; ●—●, cow F; △—△, cow G; ▲—▲, cow H.

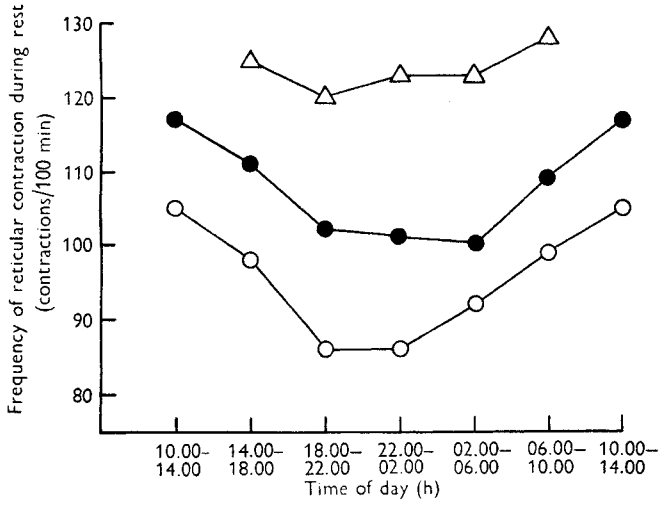

Fig. 3. Expt 1. Mean frequency of reticular contraction during rest in successive 4 h periods of the day at three levels of intake of hay by four cows. ○—○, 10 lb/cow daily; ●—●, 15 lb/cow daily; △—△, 22 lb/cow daily.

standing. Table 8 shows that the diurnal pattern in the mean frequency of reticular contraction during rest was due mainly to these changes in the ratio of time standing to time lying and only slightly, but increasingly with falling intake, to diurnal variation

in reticular motility while either standing or lying. In contrast, the increase in reticular motility during rest, which was associated with an increase in intake, was due to an increase in the frequency of contraction both while standing and lying, and not to any decrease in the proportion of the time spent lying, which in fact increased from 45 to 57% of the total resting time.

Mean time of retention of food residues in the reticulo-rumen. Results presented earlier (Campling *et al.* 1961, 1962) showed that the voluntary intake of hay, oat straw or oat straw with urea was inversely related to the mean retention time of food residues in the reticulo-rumen, even when the retention time was measured at equal levels of intake. The results in Table 9 show that there was a direct relationship within each experiment between the total time spent eating and ruminating per lb of each roughage and the mean retention time in the reticulo-rumen of residues from that roughage.

Table 8. *Expt* 1. *Mean time (min) spent in standing resting and lying resting by four cows given hay, and mean frequency/*100 *min* (*f*) *of reticular contraction during the day* (06.00–18.00 *h*) *and the night* (18.00–06.00 *h*)

	06.00–18.00 h						18.00–06.00 h					
	Standing		Lying		Total		Standing		Lying		Total	
Intake (lb)	Time (min)	*f*	Time (min)	*f*	Time (min)	*f*	Time (min)	*f*	Time (min)	*f*	Time (min)	*f*
10	406	104	94	81	500	104	171	102	377	82	548	88
15	290	116	90	96	380	111	157	110	283	96	440	101
22*	166	129	72	122	238	127	75	132	240	119	315	122

* Hay offered *ad lib.*

Table 9. *Mean retention time of food residues in the reticulo-rumen and mean time spent in eating and ruminating/lb food by cows on diets of hay, oat straw and oat straw with urea at different levels of intake*

Expt no.	Food	Mean daily food intake (lb)	Mean time spent eating and ruminating (min/lb)	Mean retention time of residues in the reticulo-rumen (h)
1	Straw	9·7*	73	73
(four cows)	Hay	10·0	38	61
	Hay	15·0	41	52
	Hay	22·0*	40	50
3	Straw	10·0	61	98
(two cows)	Straw + urea and sucrose	10·0	37	63
4	Straw	12·4*	53	81
(three cows)	Straw + urea	12·7	37	62
	Straw + urea	17·6*	40	56

* Food offered *ad lib.*

An inverse relationship was also found in Expt 1 between the voluntary intake of hay by individual cows and the mean retention time of residues when measured at equal levels of intake. The results presented here suggest that, with the exception of

cow H, differences in the mean retention time were not related to individual differences in the time spent eating and ruminating per lb food, although there may have been important differences in the efficiency of chewing. Neither were these individual retention times related to differences in the frequency of reticular contraction, but it is possible that differences in the amplitude of peristaltic contraction in the hind gut could be important.

Mean rate of flow of digesta out of the reticulo-rumen. Movement of digesta from the reticulo-rumen to the omasum can occur only when the orifice is open and a pressure difference exists between the two organs. Stevens *et al.* (1960) measured the pressure gradient across the orifice and the flow velocity in the omasal canal and showed that in each primary cycle of contraction flow towards the abomasum occurred at the height of the second reticular contraction and during relaxation of the omasal canal after its primary contraction. They suggested that the greatest volume of flow occurred at the latter time. Either flow towards the abomasum or back flow followed the secondary contraction of the omasal canal. As the flow to the omasum, therefore, seems to be greater during the primary contraction than flow in either direction during the secondary contraction, which in any event is less frequent than the primary contraction, it appears probable that the frequency with which digesta pass to the omasum is related to the frequency of primary contraction of the reticulo-rumen. The amount of organic matter transferred during each primary contraction will depend, however, on the size of the pressure gradient across the orifice and on the consistency of digesta lying near the omasal orifice. Stevens *et al.* (1960) have suggested that the amplitude of the contraction of the omasal canal is controlled, in part at least, by the degree of abomasal distention. Pressure in the reticulo-rumen will depend on the force exerted on the contents by the activity of the musculature of the walls and pillars of the organ.

The mean weight of organic matter passing through the reticulo-omasal orifice per primary contraction and relaxation has been calculated for each diet by subtracting from the intake of organic matter the amount estimated to have been digested in the reticulo-rumen (Campling *et al.* 1961, 1962). These values are shown in Table 10 and it is apparent, as shown in Fig. 4, that there was a linear relationship between the amount of food eaten and the mean amount of organic matter transferred per primary contraction, regardless of the type of food. For each increase of 1 kg in the weight of organic matter consumed by the cow there was a mean increase of 0·27 g in the amount of organic matter transferred to the omasum per primary contraction. The amount transferred depended on the weight of roughage consumed and not on the nature of the roughage. With straw offered *ad lib.*, however, the amount of organic matter transferred per contraction was 2·0 g whereas with hay offered *ad lib.* it was 3·6 g.

The mean daily rate of flow of organic matter with each food was also directly related to the mean frequency of reticular contraction. It was so mainly because more time was spent in eating a larger quantity of food and contractions were more frequent during eating. However, a change in the mean rate of flow per contraction was of much greater importance than a change in the mean frequency of contraction in effecting a change in the mean daily rate of flow of organic matter. For example, in Expt 1, the mean frequency of reticular contraction increased by only 19% when the

daily intake of hay rose from 10 to 22 lb, whereas the corresponding increase in the amount of organic matter transferred to the omasum per contraction was 80%. Similarly, the higher mean rate of flow of digesta from the reticulo-rumen of cows offered hay *ad lib.* than from those offered straw *ad lib.* was due almost entirely to a change in the amount of organic matter transferred per primary contraction.

Table 10. *Estimated mean weight of organic matter transferred per contraction of the reticulum from the reticulo-rumen to the omasum*

Expt no.	Food	Mean daily intake of organic matter (kg)	Weight of organic matter leaving reticulo-rumen/day (kg)	Total number of reticular contractions/day	Weight of organic matter leaving reticulo-rumen/contraction (g)
1 (four cows)	Straw	4·16*	3·21	1629	2·0
	Hay	4·25	2·85	1451	2·0
	Hay	6·38	4·27	1623	2·6
	Hay	9·35*	6·26	1726	3·6
3 (two cows)	Straw	4·29	3·13	1733	1·8
	Straw+urea and sucrose	4·29	3·05	1446	2·1
4 (three cows)	Straw	5·06*	4·00	1689	2·4
	Straw+urea	5·19	3·58	1552	2·3
	Straw+urea	7·19*	5·03	1700	2·9

* Food offered *ad lib.*

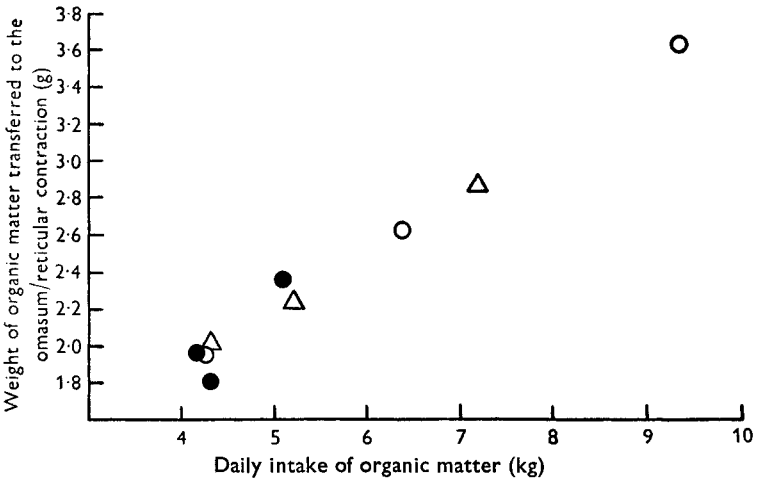

Fig. 4. Expts 1, 3 and 4. Relationship between the mean daily intake of organic matter and the amount of organic matter transferred from the reticulo-rumen to the omasum during each cycle of reticulo-ruminal movement on diets of hay, oat straw and oat straw with urea. For details of cows receiving each diet see Table 10. ○, hay; ●, oat straw; △, oat straw with urea.

When hay or straw was offered *ad lib.* once daily, the amounts of these roughages voluntarily consumed by the cows were so regulated, in relation to the respective rates of disappearance of digesta from the reticulo-rumen, that a relatively constant amount of digesta remained in the reticulo-rumen immediately before the next meal. Our

results show that with increasing amounts of each roughage there was a proportional increase in the time spent chewing, during eating and rumination. The increased amount of chewing must have produced an increased number of particles suitable for transfer to the omasum. The linearity of the relationship in Fig. 4 shows that up to the limit of the voluntary intake of each roughage this increased transfer was readily accomplished by an increase in the amount of organic matter transferred to the omasum when related to each primary contraction. Therefore it seems unlikely that, when the roughages were offered *ad lib.*, intake was limited by the amount of organic matter which could be transferred per contraction. This reasoning leads to the conclusion that, in these experiments, the major factor limiting the retention time of organic matter in, and the mean rate of flow of organic matter from, the reticulo-rumen, and hence the voluntary intake of hay and oat straw, was the time required for particles of food residues to be reduced to a size suitable for transfer to the omasum. This time was influenced both by the rate of microbial breakdown of the digesta and by chewing.

SUMMARY

1. The behaviour and reticular motility of a total of seven dry fistulated cows was recorded in six experiments with diets of hay, oat straw or oat straw with urea administered by intraruminal infusion. These roughages were offered *ad lib.* and in controlled quantities and the effect of altering the daily time of access to roughages offered *ad lib.* was also investigated. In each cow a small air-filled balloon in the reticulum was connected to a tambour operating a pen to give continuous recordings for 72 h with each treatment. In five of the experiments simultaneous recordings were made from a balloon strapped against the jaw.

2. When hay was offered *ad lib.* once daily for $4\frac{1}{2}$ h, the mean times spent eating and ruminating were 10·9 and 29·5 min/lb respectively compared with times of 22·2 and 50·8 min/lb respectively for straw offered *ad lib.* In another experiment the intraruminal administration of urea with a diet of straw offered *ad lib.* caused a decrease in the mean time spent eating and ruminating from 18·6 and 34·1 min/lb respectively to 14·8 and 24·7 min/lb respectively. The restriction of the daily time of access to food offered *ad lib.* from 24 to 2 h did not affect these differences between the diets but the rate of eating each food increased and there was a complementary increase in the time spent ruminating per lb food. Therefore for each roughage the total time spent eating and ruminating per lb food was relatively constant, and it is suggested that this characteristic value for each roughage was associated with the rate of disappearance of organic matter from the reticulo-rumen.

3. The mean frequencies of the biphasic contractions of the reticulum during eating and rumination, were relatively constant with all diets and at all levels of intake although the frequency was much higher during eating than during rumination. The mean frequency of contraction during rest with a diet of hay or of oat straw with urea increased by 9–10 contractions/100 min for each increase of 100 min in the total daily time spent ruminating. The mean daily frequency of reticular contraction for each food was directly related to the quantity of food allowed. This relationship was due

mainly to the time spent in eating but also to an associated effect on the frequency of contraction during rest.

4. There was a direct linear relationship between the amount of food eaten, regardless of the type of food, and the amount of organic matter transferred to the omasum per primary contraction. Changes in the frequency of primary contractions were of much less importance in effecting a change in the mean rate of flow of organic matter. It seemed unlikely that, when these roughages were offered *ad lib.*, intake was limited by the amount of organic matter which could be transferred to the omasum per contraction. It is suggested that the limit to the amount of each of these roughages eaten is the result rather of the time required for the breakdown of food particles by chewing and digestion to a size at which they can be transferred through the reticulo-omasal orifice.

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