# Studies on digestion and absorption in the intestines of growing pigs

## 6. Measurements of the flow of amino acids

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1. Digesta were collected from seventeen pigs initially of 30 kg live weight fitted with single re-entrant cannulas in either the duodenum, jejunum or ileum. A further twenty-four pigs were used in a conventional digestibility trial.

2. The pigs received three types of diet containing: barley, fine wheat offal, white fish meal, minerals and vitamins (diet BWF); starch, sucrose, maize oil, cellulose, minerals and vitamins and either groundnut (diet SSG) or casein (diet SSC).

3. Amino acids were measured in samples representative of the digesta flow in 24 h periods and in the faeces collected in 5 d periods.

4. For each diet the total flow in 24 h periods in the duodenum for aspartic acid, threonine, serine and glycine exceeded or equalled intake, while the amounts of the other amino acids were usually rather less than intake.

5. For each diet in the jejunum, the amounts of glycine and cystine exceeded intake in 24 h periods, while methionine, arginine and tyrosine were the most rapidly absorbed amino acids anterior to the cannula site. On average 0·22, 0·25 and 0·31 of the dietary amino acids were absorbed anterior to the cannula site for diets BWF, SSG and SSC, respectively.

6. For each diet in the ileum, the least apparently absorbed dietary amino acids were glycine and cystine. On average 0·81, 0·83 and 0·95 of the dietary amino acids were absorbed anterior to the cannula site for diets BWF, SSG and SSC, respectively.

7. There was net disappearance of most amino acids in the large intestine, but some net accumulation occurred in this region.

8. The results are discussed in relation to the amino acid composition of endogenous secretions (particularly glycine in bile), protease and peptidase specificity, free amino acid absorption and the role of the microflora in the large intestine.

For many years the progress of digestion and absorption of dietary proteins in simple-stomached animals has been studied in the rat and dog. Recently, similar studies have also been made in pigs equipped with re-entrant intestinal cannulas, usually placed in the proximal duodenum or the terminal ileum in order to estimate the total weight of protein, or amino acids, absorbed in the small intestine for example, Zebrowska & Buraczewska (1972*b*), Ivan & Farrell (1976). These studies have usually been made with very small numbers of animals, and have rarely used barley-based diets of the kind used in the United Kingdom and western Europe in practical pig production.

The object of this study was to measure the flow of amino acids at four intestinal sites from three diets of contrasting amino acid composition in order (*a*) to assess the extent of addition of endogenous amino acids to the digesta in the duodenum, (*b*) to investigate whether the pattern of digestion and absorption of proteins differed in the jejunum, (*c*) to determine what changes occurred in the amino acid composition of the digesta as it passed through the large intestine, and (*d*) to consider the value of ileal amino acid absorption information as indicators of availability. The results presented here are part of a long-term study on the digestive processes in growing pigs: results have already been published on the flow of digesta and its pH (Braude *et al.* 1976), the flow of dry matter, ash and water (Low *et al.* 1978), the flow of various minerals (Partridge, 1978), and the flow of nitrogen (Low, 1979).

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Table 1. *Composition of experimental diets (g/kg diet)*

| Ingredients | Diets BWF and $BWF_t$* | Ingredients | Diet SSG¶ | Diet SSC |
|---|---|---|---|---|
| Barley meal | 713·5 | Maize starch | 277·0 | 612·7 |
| Fine wheat offal | 200·0 | Sucrose | 276·9 | 100·0 |
| White fish meal | 70·0 | Maize oil | 30·0 | 30·0 |
| NaCl | 2·7 | Solka Floc‡ | 20·0 | 30·0 |
| $CaHPO_4.2H_2O$ | 5·6 | Groundnut meal | 350·0 | — |
| $CaCO_3$ | 6·2 | Casein | — | 184·0 |
| Vitamin mix no. 1† | 2·0 | Trace mineral mix§ | 10·0 | 10·0 |
| $CuSO_4.5H_2O$ | 1·0 | $CaHPO_4.2H_2O$ | 17·9 | 20·6 |
| | | $CaCO_3$ | 4·6 | 4·6 |
| | | Vitamin mix no. 2‖ | 2·0 | 2·0 |
| | | Choline HCl | 1·1 | 1·1 |
| | | NaCl | 5·0 | 5·0 |
| | | L-lysine HCl | 2·5 | — |
| | | DL-methionine | 3·0 | — |
| Amino acid | | Amino acid | | |
| Aspartic acid | 10·1 | Aspartic acid | 15·8 | 12·1 |
| Threonine | 5·2 | Threonine | 3·8 | 7·3 |
| Serine | 6·3 | Serine | 6·9 | 9·9 |
| Glutamic acid | 26·8 | Glutamic acid | 26·2 | 37·8 |
| Proline | 11·7 | Proline | 6·1 | 18·8 |
| Glycine | 8·4 | Glycine | 8·3 | 3·1 |
| Alanine | 7·2 | Alanine | 5·4 | 5·1 |
| Cystine | 2·3 | Cystine | 2·1 | 0·9 |
| Valine | 6·6 | Valine | 5·6 | 9·9 |
| Methionine | 2·6 | Methionine | 4·6 | 4·4 |
| Isoleucine | 4·9 | Isoleucine | 4·6 | 7·7 |
| Leucine | 9·9 | Leucine | 8·7 | 14·9 |
| Tyrosine | 4·1 | Tyrosine | 5·4 | 9·4 |
| Phenylalanine | 6·1 | Phenylalanine | 7·0 | 8·5 |
| Histidine | 3·4 | Histidine | 3·2 | 4·8 |
| Lysine | 6·8 | Lysine | 7·2 | 13·3 |
| Arginine | 8·3 | Arginine | 15·4 | 6·1 |

* Diet BWF after milling through a 1 mm mesh; this diet was given to pigs with ileal re-entrant cannulas and to some pigs in the digestibility trial.

† Supplied (/kg diet): 0·75 mg retinol, 7·50 μg cholecalciferol, 3·25 mg riboflavin, 30·00 μg cyanocobalamin, 15·75 mg nicotinic acid, 13·00 mg pantothenic acid, 3·25 mg pyridoxine, 200·00 mg choline chloride, 2·00 mg DL-α-tocopheryl acetate.

‡ Brown & Co., Berlin, New Hampshire, USA.

§ Supplied (/kg diet): 4·47 g $K_2CO_3$, 1·73 mg $MgCO_3.H_2O$, 0·33 g $FeSO_4.7H_2O$, 60 mg $MnSO_4.H_2O$, 0·10 g $ZnCO_3$, 8·00 mg NaF, 17·50 mg $CuSO_4.5H_2O$, 6·00 mg $CoCl_2$.

‖ Supplied (/kg diet): as vitamin mix no. 1 (omitting choline chloride) and in addition 2·00 mg thiamin, 50·00 μg biotin, 0·50 mg pteroylmonoglutamic acid, 20·00 mg *p*-aminobenzoic acid, 194·00 mg *myo*-inositol, 30·00 mg ascorbic acid, 2·00 mg menaphthone.

¶ 64% of the methionine and 35% of the lysine in diet SSG are supplied in crystalline form as DL-methionine and L-lysine hydrochloride.

## EXPERIMENTAL METHODS

*Animals.* Castrated male pigs from the Large White herd of the National Institute for Research in Dairying were used. Seventeen pigs were fitted with single re-entrant cannulas (Ash, 1962) as follows: (*a*) duodenum, approximately 0·15 m from the pylorus and distal to the bile and pancreatic ducts (six pigs); (*b*) jejunum, 2·0–2·5 m from the pylorus (i.e. 13–17% of the distance along the small intestine) (five pigs); or (*c*) the ileum, 0·3 m from the ileo-caecal junction (i.e. over 98% of the distance along the small intestine) (six pigs). The initial live weight of the pigs was approximately 30 kg.

A further twenty-four pigs of initial live weight 17–19 kg and without cannulas were used for a conventional digestibility trial.

*Housing, cannula design, surgery, sample collection.* As described by Braude *et al.* (1976).

*Diets.* Details of the composition, including that of amino acids, is given in Table 1. The values are the averages for the various batches of diets used during the study which lasted for 5 years. Although the N contents of the diets were similar, the amino acid compositions differed markedly. The dry diet was mixed with water (1:2·5, w/v) and given to pigs twice daily at 09.00 hours and 15.00 hours. The animals were weighed weekly and fed on a scale based on their live weight (Barber *et al.* 1972). On this scale pigs of 20 kg live weight received 1·05 kg air-dry diet/d; the amount increased linearly to 2.40 kg at 60 kg live weight. Each of the diets was offered to pigs with re-entrant cannulas (for 10–12 d/diet). The pigs without cannulas received a single diet throughout the trial. Diet SSG contained added crystalline lysine and methionine. No free amino acids were added to the other diets.

*Sample preparation and analysis.* During 24 h collections 5% of the digesta collected from pigs with duodenal or jejunal cannulas was removed every hour (every 6 h from pigs with ileal cannulas) and accumulated in a bottle stored at 1°. As soon as possible after the end of each 24 h collection the accumulated digesta were sampled, freeze-dried, ground and stored at −20° until analysis. Faeces were accumulated over 5 d periods and were then mixed, sampled and treated as digesta thereafter. Samples of diets, freeze-dried digesta and faeces were hydrolysed with constant-boiling hydrochloric acid in round-bottomed flasks under reflux condensers for 24 h at 110°. The hydrolysates were analysed according to the method of Moore & Stein (1954). Cystine and methionine were analysed separately by the method of Moore (1963).

N was measured by the Kjeldahl method.

*Presentation of results and statistical analysis.* The amounts of each amino acid were expressed as weight collected in 24 h:weight in diet eaten in 24 h (output:intake).

The average output:intake values for each 24 h collection period for each pig on a diet were subjected to analysis of variance. The average values for the four faeces collection periods from each of the pigs without cannulas were similarly treated.

The standard error of the difference between the means was not the same for each pair of cannula sites or for each pair of diets because different numbers of pigs completed collections for the various site and diet combinations. The least and greatest values for standard error of difference are given. The statistical methods used in these studies were described in more detail by Braude *et al.* (1976).

To aid interpretation of the results Table 4 shows the weights of amino acids eaten and outputs in 24 h for a 40 kg pig receiving 1·70 kg air-dry diet/24 h. The average weight of the cannulated pigs and those used in the digestibility trial was 40 kg.

## RESULTS

The mean 24 h output:intake values for the amino acids in digesta in the duodenum, jejunum and ileum are shown in Table 2, and for those in the faeces in Table 3. For completeness, results are included for diet SSG although collections were completed in only two pigs on this diet in the duodenum and two in the ileum, because of intermittent scouring and palatability problems: consequently, results for this diet in the duodenum and ileum should be viewed with caution.

*Between-site differences for a given diet.* For each diet there was a progressive reduction in the mean output:intake values as the small intestine was traversed for all amino acids except cystine, for which values in the jejunum were higher than in the duodenum. There

Table 2. *Mean 24 h output: diet intake values in digesta from pigs with intestinal re-entrant cannulas at one of three sites*

(No. of pigs completing collections in parentheses)

| Diet* ... | BWF | | | SSG | | | SSC | | | SE of difference between diet means | | SE of difference between site means | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site ... | Duodenum (6) | Jejunum (5) | Ileum‡ (5) | Duodenum (2) | Jejunum (5) | Ileum (2) | Duodenum (6) | Jejunum (4) | Ileum (6) | Lowest value | Highest value | Lowest value | Highest value |
| Aspartic acid | 1·13a | 0·77b | 0·28c | 1·00a | 0·75a | 0·15b | 1·09a | 0·82b | 0·06c | 0·039 | 0·223 | 0·099 | 0·172 |
| Threonine | 1·08a | 0·81b | 0·28c | 1·07a | 0·96a | 0·37b | 0·99a | 0·78a | 0·09b | 0·042 | 0·219 | 0·094 | 0·162 |
| Serine | 1·05a | 0·79b | 0·23c | 1·03a | 0·75b | 0·21c | 1·07a | 0·68b | 0·09c | 0·029 | 0·207 | 0·084 | 0·146 |
| Glutamic acid | 0·89a | 0·70b | 0·14c | 0·97a | 0·76a | 0·15b | 0·95a | 0·70b | 0·04c | 0·022 | 0·109 | 0·068 | 0·118 |
| Proline | 0·90a | 0·85a | 0·14b | 1·28a | 1·10b | 0·37c | 1·03a | 0·62b | 0·03c | 0·057 | 0·123 | 0·121 | 0·210 |
| Glycine | 1·39a | 1·13a | 0·28b | 1·36a | 1·18a | 0·33b | 1·91a | 1·31b | 0·21c | 0·046 | 0·289 | 0·125 | 0·217 |
| Alanine | 1·09a | 0·70b | 0·23c | 1·17a | 1·01a | 0·24b | 1·26a | 0·64b | 0·09c | 0·033 | 0·182 | 0·086 | 0·149 |
| Cystine† | 0·93a | 1·39b | 0·33c | 1·20a | 1·49a | 0·34b | 1·39a | 1·52b | 0·29c | 0·026 | 0·350 | 0·115 | 0·190 |
| Valine | 0·88a | 0·69a | 0·18b | 1·13a | 0·80b | 0·12c | 0·88a | 0·75a | 0·05b | 0·026 | 0·068 | 0·085 | 0·146 |
| Methionine† | 0·63a | 0·61a | 0·17b | 0·85a | 0·60b | 0·07c | 0·79a | 0·62b | 0·04c | 0·032 | 0·154 | 0·060 | 0·095 |
| Isoleucine | 0·80a | 0·70a | 0·19b | 1·07a | 0·80b | 0·17c | 0·93a | 0·77a | 0·06b | 0·022 | 0·106 | 0·075 | 0·131 |
| Leucine | 0·86a | 0·65b | 0·16c | 0·87a | 0·79a | 0·17b | 0·95a | 0·64b | 0·04c | 0·020 | 0·083 | 0·057 | 0·099 |
| Tyrosine | 0·90a | 0·58b | 0·16c | 0·76a | 0·62a | 0·09b | 1·01a | 0·54b | 0·03c | 0·019 | 0·122 | 0·089 | 0·155 |
| Phenylalanine | 0·92a | 0·65b | 0·17c | 0·86a | 0·72a | 0·07b | 1·02a | 0·67b | 0·03c | 0·018 | 0·108 | 0·067 | 0·116 |
| Histidine | 0·80a | 0·61b | 0·19c | 0·90a | 0·80a | 0·19b | 0·83a | 0·72b | 0·04c | 0·025 | 0·159 | 0·081 | 0·140 |
| Lysine | 1·00a | 0·70b | 0·22c | 0·90a | 0·72a | 0·16b | 1·04a | 0·57b | 0·03c | 0·022 | 0·134 | 0·101 | 0·175 |
| Arginine | 0·95a | 0·58b | 0·11c | 0·89a | 0·40b | 0·07c | 1·03a | 0·54b | 0·04c | 0·018 | 0·268 | 0·130 | 0·224 |
| (Nitrogen) | 0·98 | 0·88 | 0·25 | 1·00 | 0·97 | 0·22 | 0·98 | 0·73 | 0·09 | | | | |

The following between-diet differences were significant ($P < 0·05$): Duodenum: cystine, methionine BWF < SSG, SSC; isoleucine, proline SSG > BWF; glycine SSC > BWF, SSG; valine SSG > BWF, SSC; phenylalanine SSC > SSG; jejunum: leucine, proline, alanine SSG > BWF, SSC; isoleucine SSG, SSC > BWF; ileum: threonine, serine, glutamic acid, alanine, valine, methionine, isoleucine, leucine, histidine, lysine BWF, SSG > SSC; aspartic acid, tyrosine, phenylalanine BWF > SSC; proline SSG > SSC.

a, b, c values with different subscripts indicate significant ($P < 0·05$) between-site differences for a given amino acid and diet.

* For details, see Table 1.

† Methionine and cystine were estimated on samples from three, three and two pigs for diets BWF, SSG and SSC respectively, in the jejunum.

‡ Diet $BWF_t$, see Table 1.

Table 3. *Mean 24 h amino acid output:diet intake values in faeces of pigs without cannulas and* SE *of difference of ileal digesta-faeces comparisons*

(No. of pigs completing collections in parentheses)

| | Diet* | | | | SE of difference of two diets means in faeces† | SE of difference of ileal digesta-faeces comparisons‡ | |
|---|---|---|---|---|---|---|---|
| | BWF (6) | $BWF_t$ (6) | SSG (6) | SSC (6) | | Lowest value | Highest value |
| Aspartic acid | 0·32 | 0·26 | 0·18 | 0·04 | 0·020 | 0·028 | 0·039 |
| Threonine | 0·30 | 0·25 | 0·34 | 0·03 | 0·021 | 0·029 | 0·040 |
| Serine | 0·22 | 0·19 | 0·18 | 0·02 | 0·013 | 0·021 | 0·029 |
| Glutamic acid | 0·15 | 0·13 | 0·14 | 0·02 | 0·013 | 0·016 | 0·023 |
| Proline | 0·16 | 0·11 | 0·27 | 0·02 | 0·017 | 0·036 | 0·051 |
| Glycine | 0·20 | 0·17 | 0·26 | 0·09 | 0·018 | 0·027 | 0·038 |
| Alanine | 0·30 | 0·25 | 0·35 | 0·07 | 0·023 | 0·027 | 0·038 |
| Cystine | 0·16 | 0·18 | 0·14 | 0·07 | 0·028 | 0·050 | 0·070 |
| Valine | 0·26 | 0·22 | 0·29 | 0·02 | 0·018 | 0·022 | 0·031 |
| Methionine | 0·19 | 0·23 | 0·11 | 0·03 | 0·036 | 0·034 | 0·048 |
| Isoleucine | 0·25 | 0·20 | 0·27 | 0·02 | 0·016 | 0·020 | 0·029 |
| Leucine | 0·23 | 0·20 | 0·24 | 0·02 | 0·019 | 0·022 | 0·030 |
| Tyrosine | 0·23 | 0·20 | 0·17 | 0·03 | 0·015 | 0·018 | 0·026 |
| Phenylalanine | 0·22 | 0·19 | 0·21 | 0·02 | 0·018 | 0·019 | 0·027 |
| Histidine | 0·18 | 0·13 | 0·20 | 0·03 | 0·025 | 0·028 | 0·039 |
| Lysine | 0·28 | 0·24 | 0·30 | 0·03 | 0·026 | 0·028 | 0·040 |
| Arginine | 0·17 | 0·14 | 0·19 | 0·03 | 0·032 | 0·028 | 0·039 |
| (Nitrogen | 0·26 | 0·21 | 0·24 | 0·03) | | | |

The following differences between ileal digesta (Table 2) and faeces were significant ($P < 0·05$): diet $BWF_t$:glycine, cystine, leucine, histidine; diet SSG:alanine, cystine, valine, isoleucine, leucine, tyrosine, phenylalanine, lysine, arginine; diet SSC:serine, glycine, cystine.

Significant ($P < 0·05$) differences between amino acids in faeces were: all amino acids BWF, SSG > SSC; proline BWF > $BWF_t$; glycine SSG > BWF; aspartic acid BWF, $BWF_t$ > SSG.

* For details, see Table 1.

† Based on the interaction between litters and diets (15 df).

‡ Comparison of the mean values for digesta collections for pigs cannulated at the ileal site with the mean value for faecal collections for six pigs without cannulas, SE of difference based on a pool of the variation between-pigs-within diets for the ileal digesta (10 df) and the variation between-litters-within-diets for faeces (20 df).

were major differences between amino acids in the rates of absorption anterior to the jejunal cannula site for each of the diets. The differences between amino acids in their rates of digestion and absorption between the jejunal and ileal cannula sites were generally more limited than in the proximal small intestine.

Comparison of the mean output:intake values for ileal digesta and faeces showed some evidence of an increase in the amounts of alanine, valine, methionine, isoleucine, leucine, tyrosine, phenylalanine, lysine and arginine for diets $BWF_t$ and SSG during transit through the large intestine, but no corresponding evidence for diet SSC. Increases in the amounts of some amino acids and decreases in the amounts of others as a result of transit through the large intestine were probably the result of microbial activity in this region. Although approximately 50% of certain amino acids entering the large intestine from diet SSC disappeared during transit through this organ, the actual weights of amino acid that disappeared were small.

The statistical significance of between-site differences in output : intake values for each amino acid are shown in Tables 2 and 3.

*Between-diet differences at a given site.* In the duodenum the output:intake values for

Table 4. *Daily intakes of amino acids in the diet and amounts in digesta and faeces collected during 24 h periods (g) calculated for a pig of 40 kg live weight given 1·7 kg air-dry diet and 4·25 l water/24 h*

| Diet*... | BWF | | | | | | SSG | | | | | SSC | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site... | Diet | Duo-denum | Jejunum | Ileum† | Faeces | | Diet | Duo-denum | Jejunum | Ileum | Faeces | Diet | Duo-denum | Jejunum | Ileum | Faeces |
| Aspartic acid | 17·2 | 19·4 | 13·2 | 4·8 | 5·5 | 4·5† | 26·8 | 26·8 | 20·1 | 4·0 | 4·8 | 20·6 | 22·5 | 16·9 | 1·2 | 0·8 |
| Threonine | 8·9 | 9·6 | 7·2 | 2·5 | 2·6 | 2·2 | 6·5 | 7·0 | 6·2 | 2·4 | 2·2 | 12·4 | 12·3 | 9·7 | 1·1 | 0·4 |
| Serine | 10·7 | 11·2 | 8·5 | 2·5 | 2·4 | 2·0 | 11·8 | 12·2 | 8·8 | 2·5 | 2·1 | 16·8 | 18·0 | 11·4 | 1·5 | 0·3 |
| Glutamic acid | 45·6 | 40·6 | 31·9 | 6·4 | 6·8 | 5·9 | 44·5 | 43·2 | 33·8 | 6·7 | 6·2 | 64·3 | 61·0 | 45·0 | 2·6 | 1·3 |
| Proline | 19·9 | 17·9 | 16·9 | 2·8 | 3·2 | 2·2 | 10·4 | 13·3 | 11·4 | 3·8 | 2·8 | 32·0 | 33·0 | 19·8 | 1·0 | 0·6 |
| Glycine | 14·2 | 19·7 | 16·0 | 4·0 | 2·8 | 2·4 | 14·1 | 19·2 | 16·6 | 4·7 | 3·7 | 5·2 | 9·9 | 6·8 | 1·1 | 0·5 |
| Alanine | 12·2 | 13·3 | 8·5 | 2·8 | 3·7 | 3·0 | 9·2 | 10·8 | 9·3 | 2·2 | 3·2 | 8·7 | 11·0 | 5·6 | 0·8 | 0·6 |
| Cystine | 3·9 | 3·6 | 5·4 | 1·3 | 0·6 | 0·7 | 3·5 | 4·2 | 5·2 | 1·2 | 0·5 | 1·6 | 2·2 | 2·4 | 0·5 | 0·1 |
| Valine | 11·2 | 9·9 | 7·7 | 2·0 | 2·9 | 2·5 | 9·6 | 10·8 | 7·7 | 1·2 | 2·8 | 16·9 | 14·9 | 12·7 | 0·8 | 0·5 |
| Methionine | 4·5 | 2·8 | 2·7 | 0·8 | 0·9 | 1·0 | 7·9 | 6·7 | 4·7 | 0·6 | 0·9 | 7·4 | 5·8 | 4·6 | 0·3 | 0·1 |
| Isoleucine | 8·4 | 6·7 | 5·9 | 1·6 | 2·1 | 1·7 | 7·9 | 8·5 | 6·3 | 1·3 | 2·1 | 13·1 | 12·2 | 10·1 | 0·8 | 0·4 |
| Leucine | 16·9 | 14·5 | 11·0 | 2·7 | 3·9 | 3·4 | 14·8 | 12·9 | 11·7 | 2·5 | 3·6 | 25·4 | 24·1 | 16·3 | 1·0 | 0·5 |
| Tyrosine | 7·0 | 6·3 | 4·1 | 1·1 | 1·6 | 1·4 | 9·2 | 7·0 | 5·7 | 0·8 | 1·6 | 15·9 | 16·1 | 8·6 | 0·5 | 0·3 |
| Phenylalanine | 10·3 | 9·5 | 6·7 | 1·8 | 2·3 | 2·0 | 11·9 | 10·2 | 8·6 | 0·8 | 2·5 | 14·4 | 14·7 | 9·6 | 0·4 | 0·4 |
| Histidine | 5·7 | 4·6 | 3·5 | 1·1 | 1·0 | 0·7 | 5·5 | 5·0 | 4·4 | 1·0 | 1·1 | 8·1 | 6·7 | 5·8 | 0·3 | 0·2 |
| Lysine | 11·6 | 11·6 | 8·1 | 2·6 | 3·2 | 2·8 | 12·3 | 11·1 | 8·9 | 2·0 | 3·7 | 22·6 | 23·5 | 12·9 | 0·7 | 0·7 |
| Arginine | 14·1 | 13·4 | 8·2 | 1·6 | 2·4 | 2·0 | 26·2 | 23·3 | 10·5 | 1·8 | 5·0 | 10·4 | 10·7 | 5·6 | 0·4 | 0·3 |

* For details, see Table 1. † Diet $BWF_t$, see Table 1.

Table 5. *Proportion of diet, digesta or faeces nitrogen present in the form of amino acids for growing pigs*

| | Diet* | | | |
|---|---|---|---|---|
| Diet | BWF | $BWF_f$ | SSG | SSC |
| | 0·75 | 0·75 | 0·80 | 0·90 |
| Duodenum | 0·75 | — | 0·79 | 0·94 |
| Jejunum | 0·63 | — | 0·60 | 0·84 |
| Ileum | — | 0·57 | 0·59 | 0·53 |
| Faeces | 0·62 | 0·64 | 0·71 | 0·87 |

* For details, see Table 1.

each diet were similar, but in the jejunum these values became more variable; in the ileum the values for diets $BWF_f$ and SSG were similar and much higher than the values for diet SSC. The values for the faeces were again higher for diets $BWF_f$ and SSG than for diet SSC. Values for the finely-milled diet $BWF_f$ were lower than for its normally-milled counterpart diet BWF.

It is notable that even though substantial proportions of the lysine and methionine in diet SSG were in free crystalline form, these amino acids were not absorbed at a greater rate between the duodenum and jejunum than for diets BWF and SSC, in which the amino acids were supplied in protein form.

The significance of between-diet differences at a given site is shown in Tables 2 and 3.

In all instances, the interpretation of output:intake values should be made with care since the intakes of amino acids by weight varied between the diets; these differences can be seen in Table 4.

Table 5 shows that the proportion of N in amino acid form was lower in the jejunum than in the duodenum; a further reduction occurred between the jejunum and the ileum followed by an increase in the large intestine.

## DISCUSSION

*Duodenum.* In the duodenum the amounts of some amino acids flowing in 24 h exceeded the diet intake in the same period, while the amounts of others were less than intake; in the former instance endogenous secretion appeared to have exceeded any absorption which may have occurred anterior to the cannula site, while in the latter instance absorption appeared to have exceeded endogenous secretion. The digesta in the duodenum contained the secretions of the salivary glands, oesophagus, stomach, biliary system, pancreas and duodenum, mixed with the diet. While these secretions cannot be separated from the dietary components of the digesta, the known composition of some of the secretions aids interpretation of the results of this study.

There is no satisfactory information on the amounts of amino acids secreted by the salivary glands, the oesophagus or the stomach of growing pigs. The predominance of glycine in the duodenal digesta is probably associated with the fact that it is a major constituent of hyocholic acid which is the main bile salt in pigs. From Table 4 it can be calculated that 5·5, 5·1 and 4·7 g glycine were added to the digesta in 24 h for diets BWF, SSG and SSC respectively: these values compare well with estimates of 5–7 g glycine/24 h in the bile secreted by 35 kg pigs receiving the same diets (I.E. Sambrook, personal communication). The high levels of aspartic acid, serine, threonine and alanine in duodenal digesta may be due to the fact that porcine pancreatic juice is rich in these amino acids (Corring & Jung, 1972). Threonine and proline have been shown to form 50 and 25% respectively of

porcine intestinal mucus (Degand *et al.* 1972), and these amino acids are also found in relatively high concentration in water-soluble gastric mucus (Snary & Allen, 1971). The amounts of glycine found in the present study were also similar to those found by Zebrowska & Buraczewska (1972*a*) in the duodenal digesta of pigs given a protein-free diet. The relatively high levels of threonine, serine and proline may also be due to their abundance in the juice secreted by the wall of the small intestine (Horszczaruk *et al.* 1974).

In spite of these endogenous additions of some amino acids and the apparent absorption of others, the duodenal digesta composition for each diet was generally similar to that of the diets; this similarity of duodenal digesta composition to diet composition has also been noted by Tkachev & Pakhno (1970) and Zebrowska (1973*a*) in similar studies.

Direct comparisons between the results obtained here and published values are difficult to make because of differences in diet composition or intake; the latter point is illustrated by the study of Ivan & Farrell (1976) in which a diet very similar to diet SSC was fed once per d at two-thirds of the level used here. These authors found a substantially different amino acid composition in the duodenal digesta, perhaps because endogenous secretions (which appear to be secreted at a relatively constant level irrespective of protein intake) formed a greater proportion of the amino acids.

The method of collecting digesta samples also has a bearing on N (and therefore, amino acid) flow in the duodenum: when digesta were collected manually there was approximately 15% more N flow in the duodenum in 24 h than when it was collected from the same pigs by a semi-automated method (Low & Zebrowska, 1977). This may explain why Zebrowska & Buraczewska (1972*a*), who gave a diet similar to diet SSC, collected 10–15% more amino acids in 24 h than were collected in this study.

*Jejunum.* The range of output:intake values at this site for different amino acids was large for each of the diets. This may be associated with (*a*) the physical and chemical nature of the dietary proteins and associated compounds, (b) different rates of absorption of different amino acids, (*c*) different rates of enzymic hydrolysis of different sections of protein chains, (*d*) microbial transformation of amino acids or (*e*) interactions between nutrients. Very little is known about the effect of the physical and chemical nature of the proteins in the diets used in this study on digestion. The role of the microflora in the small intestine on amino acid composition remains unknown.

The pattern of amino acid disappearance in this region of the gut for diet SSC showed few similarities with the pattern of absorption of amino acids from enzymically-hydrolysed casein infused into a small intestinal loop (Zebrowska & Buraczewska, 1972*b*), except for rapid absorption of arginine and tyrosine and for slow absorption of threonine. A very different pattern was obtained by Lazarov & Ivanov (1973) when an equimolar amino acid solution was infused into Thiry-Vella loops in growing pigs. These studies suggest that the results presented here do not appear to be related simply to the rates of absorption of free amino acids.

An interesting feature of the results for diet SSG was that much more arginine was apparently absorbed anterior to the jejunal cannula than for the other diets even though the amount of lysine apparently absorbed was less than for the other diets (and 28% of the lysine in this diet was in free form). Arginine and lysine appear to share a common transport system and arginine has been shown to compete more successfully than lysine for absorption in other species, and also in a small-scale study in pigs (Buraczewski *et al.* 1970).

The results of this study suggest that the known specificity of the pancreatic proteases and peptidases are important determinants of essential amino acid absorption. If enzyme supply is assumed to be non-limiting, then from knowledge of enzyme specificity one can predict that phenylalanine, arginine, lysine and tyrosine would be released most rapidly into short peptide or free amino acid form ready for absorption followed later by leucine,

methionine, valine, isoleucine, threonine and histidine. This pattern is similar to that observed in this study.

*Ileum.* The results presented here for diet SSC are similar to those reported by Zebrowska & Buraczewska (1972*a*) and Ivan Farrell (1976) for similar diets. There is no information in the literature for comparison with diets BWF and SSG.

A notable feature of the results is that the output:intake values for glycine, for each diet, were higher than for most other amino acids. It is interesting to note from Table 4 that only a small proportion of the amounts of endogenous glycine in the duodenum disappeared during transit through the large intestine. If the endogenous glycine was mainly present in bile salt form then it is reasonable to assume that most of the bile salts were absorbed in the small intestine rather than in the large intestine. This has been found to be the situation for man (Danielsson, 1963).

The high levels of cystine found in the ileal digesta are comparable with the information from Ivan & Bowland (1976) and Zebrowska & Buraczewski (1977). It seems possible that some cystine-containing peptides were resistant to digestion or that competition for absorption occurred: studies with a protein-free diet (Holmes *et al.* 1974) suggest that the amounts of endogenous cystine in the ileum are small, so the cystine which resisted digestion and absorption may have been of dietary origin. The study by Holmes *et al.* (1974) showed that high levels of threonine were present after feeding pigs on protein-free diets and this observation corresponds with the high levels of threonine found in this study.

*The large intestine.* During transit through the large intestine changes were seen in the amino acid composition of digesta: there was net disappearance of some amino acids and net accumulation of others. Present evidence suggests that the absorption of intact amino acids by the large intestine in growing pigs occurs either at a very low level or not at all (Zebrowska, 1973*b*; Olszewski, 1975). The accumulation of amino acids in the lumen of the large intestine as a result of mucosal cell shedding doubtless occurs but has not been accurately measured.

A major influence on the composition of amino acids in the digesta after transit through the large intestine is microbial activity, and this is the probable explanation for the finding that more of the N in the faeces was in amino acid form than in ileal digesta, particularly for diet SSC (Table 5). Michel (1966) showed that the bacterial flora of the large intestine can deaminate all amino acids, and Zebrowska (1973*b*) showed that the N from amino acids infused into the terminal ileum was almost completely absorbed and then rapidly excreted, suggesting that the amino acids were metabolized before absorption to compounds of no nutritional value. Mason *et al.* (1976) estimated that at least half the amino acids in pig faeces were contained in bacteria. The amino acid composition of the faeces collected in the present study from diet BWF was very similar to the composition of the faecal bacteria collected by Mason *et al.* (1976) from pigs given a similar diet. This suggests that the amino acid composition of faeces from diet BWF reflects the composition of bacteria rather than undigested diet residues, and this may have been the situation for the other diets also.

It is of interest to note that the amounts of faecal amino acids from diet SSC (in which the dietary protein was virtually completely digested and absorbed) were similar to the amounts quoted in the literature for pigs fed on protein-free diets (e.g. Dammers, 1964): this suggests that obligatory N and amino acid losses as a result of feeding diets containing normal levels of protein are comparable with those after feeding pigs on a protein-free diet. This observation does not validate the classical method of measuring the true digestibility of amino acids in view of the importance of the large intestinal microflora in metabolizing undigested dietary amino acids.

Because of the role of the large intestinal microflora, Payne *et al.* (1968) suggested that amino acid absorption measurements can be made with greater validity in

the digesta from the terminal ileum than from faeces. Although the ileal digesta and faeces amino acid compositions in the present study were often similar, the values in the ileum are likely to be of greater nutritional meaning. Ultimately, it would be useful to be able to relate the absorption of dietary amino acids, measured at the terminal ileum, to other aspects of N metabolism (e.g. N balance): in this connection it is of interest to note that the pigs used to estimate the amino acid content of faeces were also used for N balance measurements: 40 kg pigs given diet SSC received 33% more amino acids in the diet than those given diet BWF but absorbed 56% more amino acids (on a weight basis, using ileal values uncorrected for endogenous amino acids) and retained 56% more N. It would be of interest to see whether such a relationship holds for other diets.

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