Site and Rate of Active Transport of L-Lysine in the Intestine of the Fowl 1,2

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ABSTRACT A study was made to determine whether the avian small intestine was capable of actively transporting L-lysine from the mucosal to the serosal surface against a concentration gradient; and if it was, whether the rate of transport varied along the length of the intestine. The rate of active transport of L-lysine across the intestinal wall of the fowl was determined at 6 levels of the small intestine; the upper and lower halves of the duodenum, of the jejunum and of the ileum. Transport rates were calculated both as the amount of lysine transported per unit weight of dried intestine and per length of live intestine. These data indicated no active transport of lysine by the duodenum but active transport by the jejunum and ileum. Based on weight, the jejunal and ileal levels transported 7.0 μmoles of lysine/g of dried intestine per hour. Based on length, the rate of active transport progressively decreased significantly from the upper jejunal to lower ileal regions of the small intestine. It was concluded that rates of L-lysine transported across the intestinal wall based on unit length represented true physiological differences between the various intestinal segments studied.

Kratzer (1) concluded that all amino acids were absorbed by simple diffusion. He measured the rate of absorption of 15 amino acids (including L-lysine) from the intestinal tract of White Leghorn chicks using the Cori method. In this procedure a measured volume of solution was introduced into the crop of an unanesthetized chicken, and at the end of the experimental period the animal was killed, and the unabsorbed gastrointestinal tract contents were analyzed.

Hagihira et al. (2), using everted sacs of intestine and an initial 1 mM amino acid concentration in the mucosal and serosal fluids, successfully demonstrated that L-lysine is actively transported across the intestinal wall of the hamster against a concentration gradient. According to Wilson (3), Hagihira showed that the rate of active L-lysine transport is approximately the same in the upper, mid, and lower small intestine of the hamster. Larsen et al. (4) obtained similar results using everted sacs of rat small intestine.

Since the Kratzer study, Paine and Newman (5), and Lin and Wilson (6) have found evidence that the L-isomers of methionine and histidine, and the L-isomer of tyrosine, respectively, are transported across the intestinal wall of the chick by a selective process.

Imondi and Bird (7) investigated the site of nitrogen absorption in the fowl and found that the percentage of dietary nitrogen which disappeared from each intestine level progressively decreased from the upper jejunum to the lower ileum.

The present investigation was undertaken to gain a more thorough understanding of the physiological absorption in the avian intestine. The specific aims of the investigation were to determine whether the avian intestine was capable of actively transporting L-lysine from the mucosal to the serosal surface against a concentration gradient; and if it was, at what rate the lysine was transported across the various levels of the intestine (upper and lower halves of the duodenum, of the jejunum, and of the ileum).

EXPERIMENTAL PROCEDURE AND MATERIALS

The procedure and the radiometric techniques used have been presented in

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detail in a previous paper (8). A modification of the Wilson and Wiseman (9) in vitro everted sac technique was used.

The mucosal and serosal fluid contained an initial 1 mM lysine concentration and an initial 1.78 mM glucose concentration (8). The salts and glucose used to prepare the mucosal and serosal fluid were A.C.S. certified.

Chromatograms of the L-lysine hydrochloride and radiograms of the L-lysine

\(^{14}\)C hydrochloride (hereafter lysine) (specific activity: 130 μCi/mnmole) indicated both compounds to be pure. Chromatograms and radiograms of the postincubation serosal fluids from all 6 levels of intestine studied showed that lysine was the only ninhydrin-sensitive and radioactive compound present. It was assumed, therefore, that the results of all radioactivity analyses were direct measurements of the amount of lysine present. All chromatograms and radiograms were developed on Whatman no. 1 chromatographic paper with n-butanol:acetic acid:water (4:1:5) solvent mixture, and sprayed with ninhydrin. A chromatogram scanner was used to locate the lysine-\(^{14}\)C following chromatography.

The intestinal segments were obtained from young adult White Leghorn cockerels maintained with the modified 1965 New England College Conference broiler starting diet.

The statistical analysis for all data was performed according to Snedecor’s approximate method of analysis of variance for block design with disproportionate subclass numbers (10).

RESULTS

1. Lysine transport based on weight of dried intestinal sac. The milligrams of lysine actively transported per gram of dried sac by the upper and lower levels of the duodenum after 40, 60, and 80 minutes of incubation are shown in Table 1. Since there were no appreciable differences in the amount of lysine transported across the duodenal wall for the three incubation periods, and since the amounts transported were very close to zero, it was concluded that the duodenum did not actively transport lysine. The finding that glucose was actively transported by both levels of the duodenum under like conditions demonstrated the integrity of the duodenal active transport system.

The upper and lower levels of both the jejunum and the ileum did transport lysine against a concentration gradient (Table 2). There were no significant dif-

TABLE 1

Milligrams \(^{1}\) of L-lysine actively transported across the upper and lower levels of the duodenal wall of the avian intestine after 40, 60 and 80 minutes of incubation at 37°

<table>
<thead>
<tr>
<th>Incubation time</th>
<th>Upper duodenum</th>
<th>Lower duodenum</th>
</tr>
</thead>
<tbody>
<tr>
<td>min</td>
<td>mg/g</td>
<td>mg/g</td>
</tr>
<tr>
<td>40</td>
<td>-0.104</td>
<td>-0.049</td>
</tr>
<tr>
<td>60</td>
<td>-0.164</td>
<td>-0.073</td>
</tr>
<tr>
<td>80</td>
<td>-0.113</td>
<td>-0.073</td>
</tr>
</tbody>
</table>

\(^{1}\) Each value is the average of 2 observations and is expressed per gram of dried sac or per 8 cm of intestine.

TABLE 2

Milligrams \(^{1}\) of L-lysine per gram of dried sac actively transported across the upper and lower levels of the jejunal and the ileal walls of the avian intestine after 40, 60 and 80 minutes of incubation at 37°

<table>
<thead>
<tr>
<th>Incubation time</th>
<th>Jejunum</th>
<th>Ileum</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Upper level</td>
<td>Lower level</td>
</tr>
<tr>
<td>min</td>
<td>0.407 ± 0.107 (^{3}) (4) (^{2})</td>
<td>0.576 ± 0.117</td>
</tr>
<tr>
<td>40</td>
<td>0.866 ± 0.199 (5)</td>
<td>0.750 ± 0.176 (10)</td>
</tr>
<tr>
<td>60</td>
<td>1.722 ± 0.200 (6)</td>
<td>1.330 ± 0.265 (7)</td>
</tr>
</tbody>
</table>

\(^{1}\) There were no significant differences among these 4 levels with respect to their abilities to actively transport lysine.

\(^{2}\) Means ± SE of mean.

\(^{3}\) Numbers in parentheses are number of observations.
ferences among these 4 levels with respect to their abilities to transport lysine. The rate of transport across these levels for 40, 60, and 80 minutes of incubation was linear (P < 0.01) and there was no significant interaction between intestinal level and incubation time. Consequently, one straight regression line calculated from the data in table 2 represents the average rate of active lysine transport across these four intestinal levels (fig. 1). The average rate of active lysine transport under the conditions of these studies, was calculated to be 1.028 mg or 7.03 μmoles/g of dried sac per hour. Also presented in figure 1 is the mean amount of lysine transported by each level during each of the three incubation intervals.

2. Lysine transport based on length of live intestinal sac. The milligrams of lysine activity transported by an 8-cm length of live intestine from each of the 6 levels of the small intestine during the three incubation periods are tabulated in tables 1 and 3. These data indicate that the upper and lower levels of the duodenum (table 1) did not transport lysine, whereas the other 4 levels did (table 3). There were no significant differences among the lower four intestinal levels with respect to their ability to actively transport lysine. Their rate of transport with time was linear (P < 0.01).

There was a significant interaction (P < 0.05) between intestinal level and incubation time. This variation in rate of transport with time is shown in figure 2.

**TABLE 3**

<table>
<thead>
<tr>
<th>Incubation time</th>
<th>Jejunum</th>
<th>Ileum</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Upper level</td>
<td>Lower level</td>
</tr>
<tr>
<td>40 min</td>
<td>0.130 ± 0.043 (6)</td>
<td>0.176 ± 0.051 (9)</td>
</tr>
<tr>
<td>60 min</td>
<td>0.294 ± 0.077 (7)</td>
<td>0.297 ± 0.067 (10)</td>
</tr>
<tr>
<td>80 min</td>
<td>0.842 ± 0.308 (5)</td>
<td>0.634 ± 0.190 (7)</td>
</tr>
</tbody>
</table>

1 There were no significant differences among these 4 levels of intestine with respect to their abilities to actively transport lysine although there was a significant time x level interaction (P < 0.05).

*Means ± se of mean.

*Numbers in parentheses are number of observations.

**DISCUSSION**

1. Lysine transport based on weight of dried intestinal sac. The results of the lysine transport study based on a unit of weight of dried tissue (table 1 and fig. 1) indicate there is a high degree of similarity between the avian and mammalian classes.

![Fig. 1 Average rate per gram of dried sac of L-lysine across the upper and lower half of the jejunum and ileal walls of the avian intestine; each point represents a mean of 4 to 10 determinations.](https://academic.oup.com/jn/article-abstract/93/2/198/4775905)
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In the present investigation no significant differences were found in the ability of the upper and lower levels of the avian jejunal and ileal intestine walls to actively transport lysine. According to Wilson (3), Hagihira showed that the upper, mid, and lower levels of the hamster small intestine actively transport lysine at the same rate against a concentration gradient. Larsen et al. (4) observed similar activity by the rat small intestine.

There was no lysine transport in the avian duodenum (table 1) in the present investigation. It is not clear whether Hagihira et al. (2) and Larsen et al. (4) made studies of this region.

The rate of active lysine transport across the upper and lower portions of the avian jejunal and ileal intestine walls in the present investigation was calculated to be 7.0 μmoles/g of dried sac per hour. This value is in close agreement with Hagihira's value, 7.7 μmoles/g of sac per hour in the hamster.

2. Lysine transported based on length of live intestinal sac. The data tabulated in table 3 and plotted in figure 2 indicate that the rate of lysine transport across the intestinal wall per unit length of intestine decreased progressively from the upper jejunum to the lower ileum. Although these results may appear to contradict the results based on tissue weight, they do not.

The dry weight of 8-cm lengths of live intestine is shown in table 4. Although a unit length of the upper level of the jejunum transported almost twice as much lysine as a unit length of the lower level of the ileum at the end of 80 minutes of incubation (table 3), the rate of transport based on tissue weight is similar for the 2 levels, because the upper jejunum has approximately twice the weight of the lower ileum per unit length.

Both Verzar and McDougall (11) using the pigeon, and Imondi and Bird (12), using the chick, demonstrated a progressive decrease in the length of the villi from the duodenum through the ileum. Consequently, there must be a corresponding decrease in the mucosal absorptive area per unit length of intestine. These findings probably explain the observed decrease in the rate of transport from the upper jejunum to lower ileum when the rates are based on intestinal length. It is not known why the differences in transport rate were not manifested at 40 and 60 minutes of incubation. Possibly individual variation among the birds overshadowed any existing rate differences.

From the transport rates based on intestinal length, the observations of Verzar and McDougall (11), and those of Imondi and Bird (12), it is concluded that the rate of lysine absorption and the

### TABLE 4

<table>
<thead>
<tr>
<th>Intestinal level</th>
<th>Dry wt g/8 cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper jejunum</td>
<td>0.4395</td>
</tr>
<tr>
<td>Lower jejunum</td>
<td>0.4309</td>
</tr>
<tr>
<td>Upper ileum</td>
<td>0.3049</td>
</tr>
<tr>
<td>Lower ileum</td>
<td>0.2592</td>
</tr>
</tbody>
</table>
area of mucosal absorptive surface of the avian small intestine levels below the duodenum are closely correlated. Thus, the progressive decrease in the rate of lysine transport per unit length from the upper jejunum to the lower ileum noted in this study is probably a reflection of the corresponding decrease in mucosal absorptive surface. Consequently, the transport rates based on intestinal length appear to be more nearly a true representation of the physiological differences among the various levels of the avian intestine to actively absorb lysine than the values based on intestinal weight.

The results reported by Imondi and Bird (7) add further support to this conclusion. They showed, by means of an in vivo nonabsorbable marker technique, that the percentage of dietary nitrogen which disappeared per intestinal level decreased progressively from the upper jejunum to the lower ileum. Since their results were presented as absolute values instead of being based on intestinal weight or intestinal length, they are true values within the limitations of their experimental procedure.

LITERATURE CITED