The Nature of the Fatty Acids of Rats Growing Walker Carcinoma 256*†

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The bodies of rats bearing Walker carcinoma 256 become depleted of fat, while the lipids of the blood plasma increase markedly (10). In the present experiments the nature of the fatty acids of tumor, of host rats, and of pair-fed control rats without tumors was studied in order to interpret the changes in lipid metabolism occasioned by tumor growth.

MATERIALS AND METHODS

Diets.—Male Wistar rats were placed on a semi-synthetic diet at weaning, and the food consumption of each was measured. A week later each rat was paired with one of equal body weight and food consumption. At this time one rat of each pair was designated as the experimental rat which would receive a tumor transplant; the other rat, his pair-fed control, consumed the amount of diet eaten by the experimental rat. Six days after pairing, the experimental rat alone received a subcutaneous transplant of Walker carcinoma 256. Two different diets were used: Diet 262 (16) contained 21.3 per cent Crisco by weight; the other, Diet 290C (19), contained 49.4 per cent elaidin by weight. The elaidin was substituted for all the carbohydrate of the diet in order to minimize the synthesis of fatty acids from carbohydrate and thereby force elaidic acid into the tissues. A test rat that ate the elaidin diet ad libitum for 2 months prior to the experiment had an entirely normal growth curve; no abnormalities were revealed at autopsy.

Preparation of tissues for analysis.—Rats to be sacrificed were anesthetized with diethyl ether. Blood for analysis was obtained from the hearts of the animals on Crisco; the animals on elaidin were not bled but were allowed to asphyxiate. The gastrointestinal tract of each rat was removed, slit open, washed out, and ground with the carcass. Liver and tumor (including any large metastases) were removed, weighed, and minced. Carcass, liver, and tumor, respectively, were frozen and dried in the frozen state (lyophilized). The dry material was weighed, ground, and mixed; duplicate portions of each tissue approximating 1 gm. were accurately weighed.

Extraction of lipids.—Each weighed portion of dry carcass, liver, or tumor, wrapped in porous filter paper, was suspended beneath the drip of a reflux condenser connected by a ground glass joint with a flask on a hot plate. Each sample was hot-extracted for 5 and 3 hours, respectively, with fresh portions of a 3:1 mixture of 95 per cent ethyl alcohol and diethyl ether, then for two periods of 3 hours with a 1:1 mixture of chloroform and methyl alcohol.

ANALYSES

1. Total lipid.—Analysis for total lipid of the blood plasma was carried out by a method previously described (2, 10). The extracts from each sample of dry tissue were combined and the solvent removed under partial vacuum at a temperature not exceeding 50° C. The residue was extracted with a 0.1 mixture of purified petroleum ether and redistilled chloroform and the extract washed with 50 per cent ethyl alcohol. The solution of lipids was transferred to a weighed flask, the solvent removed under nitrogen, and the flask and contents dried to constant weight.

2. Saponification of lipid.—To the weighed sample of total lipid dissolved in 3:1 ethyl alcohol-dimethyl ether was added approximately 5 drops of saturated aqueous sodium hydroxide per 0.1 gram of lipid. The flask was covered with a watch glass and the contents heated on the hot plate to sticky
dryness. The residue was transferred to a 50-ml.
centrifuge tube by means of 50 ml of 50 per cent ethyl alcohol
and the volume brought to 20 ml. The solution was
thoroughly extracted with two separate portions of 6:1 petroleum ether-chloroform solution
and the extracts of steroids discarded. The alcohol
solution was then acidified to Congo Red with 0.6 N
hydrochloric acid and the fatty acids extracted
with at least two portions of purified petroleum ether.
The extracts were combined in a volumetric flask,
the solution made to volume, and aliquots containing about 3 mg. of fatty acids taken for
determination of amount (1) and iodine number (23).

3. Separation of solid and liquid fatty acids.—The
removal of alcohol-insoluble material consisting of
unsaponifiable phospholipid and the separation
of solid and liquid fatty acids were carried out
as described by Sinclair (18, 19). Iodine numbers
were determined on each fatty acid fraction
(23). The sum of each solid and corresponding
liquid acid fraction equalled from 90.2 to 106.8 per
cent (median = 99.9 per cent) of the known
amount of purified, mixed fatty acid taken for the
separation.

EXPERIMENTS AND RESULTS

Rats on Crisco diet.—Table 1 shows the total lipid
and fatty acid content, the solid and liquid fatty
acids expressed as percentage of total fatty acids,
and the iodine number of each fatty acid fraction
for carcass and tumor and for pair-fed control rats
(see Table 3 for mean values). The carcass of each
tumor-bearing rat contained less fatty acid than
the pair-fed control; the decrease was more pronounced in rats with tumors comprising over 8 per
cent of the body weight. Accompanying the decrease
in carcass fatty acids was an increase in total lipid of the blood for each tumor-bearing rat as
compared to his pair-fed control. In considering
the data of Table 1, attention will be focused on the
seven rats with tumors comprising 8 per cent
or more of the total body weight, since they

TABLE 1

THE FATTY ACID CONTENT OF TUMOR-BEARING (E) AND OF PAIR-FED (C) RATS ON CRISCO DIET

<table>
<thead>
<tr>
<th></th>
<th>Blood plasma</th>
<th>Carcass</th>
<th>Solid acids</th>
<th>Liquid acids</th>
<th>Tumor</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total lip</td>
<td>Diff. R-C</td>
<td>Total lip</td>
<td>Per cent</td>
<td>F.A.</td>
</tr>
<tr>
<td></td>
<td>mg. per cent</td>
<td></td>
<td>mg. per cent</td>
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</tr>
<tr>
<td>E</td>
<td>7 306 + 68  32.5 85.0 48.6 51.3 54.3 107.1 0.5</td>
<td>no analyses</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>283 48.4 54.4 48.8 62.6 51.0 114.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E</td>
<td>10 355 + 143  41.2 53.7 44.2 56.6 56.7 106.4 1.0</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>C</td>
<td>250 46.6 55.3 47.2 56.6 54.3 108.2</td>
<td></td>
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</tr>
<tr>
<td>E</td>
<td>15 600 + 319  21.6 15.1 46.2 54.6 57.0 111.1 12.8 16.6 9.8 45.9 44.4 63.3 121.7</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>C</td>
<td>231 59.8 58.5 47.0 56.7 54.3 108.2</td>
<td></td>
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</tr>
<tr>
<td>E</td>
<td>17 1,600 + 266  17.0 11.9 48.3 49.1 55.5 118.7 25.1 15.8 7.6 34.6 26.7 68.2 138.0</td>
<td></td>
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<tr>
<td>C</td>
<td>258 41.7 54.7 42.4 45.9 58.8 107.3</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>E</td>
<td>19 290 - 51  31.4 26.0 55.6 63.9 46.7 112.4 8.3 14.2 7.3 30.5 26.0 66.9 135.5</td>
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<tr>
<td>E</td>
<td>22 435 + 220  20.8 16.7 48.7 60.5 51.1 112.6 18.6 15.0 7.0 35.7 24.6 67.4 129.0</td>
<td></td>
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<tr>
<td>C</td>
<td>213 53.4 46.5 49.1 51.2 52.5 106.4</td>
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<tr>
<td>E</td>
<td>28 470 + 129  29.2 23.6 48.5 54.9 57.6 40.6 108.2 16.4 15.9 8.7 35.1 28.9 64.6 133.9</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>C</td>
<td>241 34.7 30.1 40.8 47.9 60.6 106.6</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>E</td>
<td>28 300 + 42  7.7 3.6 52.5 68.7 68.1 145.4 36.6 15.3 6.7 33.1 27.1 68.4 126.6</td>
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<tr>
<td>C</td>
<td>238 39.7 27.2 35.8 42.7 58.9 107.1</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>E</td>
<td>30 550 + 270  8.0 3.6 56.3 67.2 68.8 158.0 23.8 15.7 5.7 27.1 26.0 68.7 156.0</td>
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<tr>
<td>C</td>
<td>280 47.3 40.9 41.6 49.0 58.7 105.7</td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

* B.V. = Body weight of rat plus tumor.
† No dry weight obtained.
F.A. = fatty acids.

showed more pronounced effects of the tumor on the
host.

The fatty acid composition of the tumor differed
qualitatively and quantitatively from that of both
the host and control rat. Except in the two rats
with large, older tumors where carcass fatty acids
were low, the fatty acids made up a much smaller
percentage of the dry residue of the tumor than of
the carcass. The percentage of solid acids in the
host and control rat. Except in the two rats
with large, older tumors where carcass fatty acids
were low, the fatty acids made up a much smaller
percentage of the dry residue of the tumor than of
the carcass. The percentage of solid acids in the
tumor was significantly lower with a lower iodine
number, while the percentage of liquid acids was
correspondingly higher and the iodine number
higher than in the carcass of the tumor-bearing rat.

The fatty acid composition of the host rat was
qualitatively similar to that of the control rat,
except for the iodine numbers of the liquid fatty acids which were significantly higher in rats with tumors. The percentage and iodine numbers of the solid fatty acids tended to be higher in rats with tumors, with the exception of the last two rats with larger older tumors where the situation was reversed.

The livers of tumor-bearing and control rats on the Crisco diet showed no significant differences in content of total lipid or in fatty acid composition. However, the water content of the liver, expressed as the percentage of either wet tissue or fat-free wet tissue, was significantly higher in rats with tumors than in control rats, as observed for acids higher with higher iodine numbers than in the controls.

The average value of 16.7 per cent of the fat-free dry residue for total lipid of the livers of tumor-bearing rats was significantly less than 19.4 per cent for the controls. The water content of the livers of the experimental rats was not elevated. This terminal decrease in total lipid parallels the premortal decrease in nitrogenous substances of the liver found by Sherman et al. (15).

A summary of the mean values for the fatty acid data of Tables 1 and 2 is presented in Table 3. The statistical analysis (5) of the data is indicated. It will be noted from this table that in the Crisco

**TABLE 2**

The Fatty Acid Content of Tumor-Bearing (E) and of Pair-fed (C) Rats on Elaidin Diet

<table>
<thead>
<tr>
<th>Days after</th>
<th>Total lipid per</th>
<th>E</th>
<th>C</th>
<th>E</th>
<th>C</th>
<th>E</th>
<th>C</th>
<th>E</th>
<th>C</th>
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<th>C</th>
<th>E</th>
<th>C</th>
<th>E</th>
<th>C</th>
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<tr>
<td>Transplant</td>
<td>per cent dry,</td>
<td>22</td>
<td>82</td>
<td>11.5</td>
<td>9.1</td>
<td>50.9</td>
<td>58.3</td>
<td>86.8</td>
<td>43.0</td>
<td>195.5</td>
<td>59.4</td>
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<td>51.9</td>
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<td>47.3</td>
<td>154.2</td>
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<td>Elaidic per</td>
<td>F.A.</td>
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<td>82</td>
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<td>11.5</td>
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<td>46.4</td>
<td>155.7</td>
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* B.W.—Body weight of rat plus tumor.

Walker tumor 256 by McEwen and Haven (13) and confirmed by others (7, 15).

**Rates on elaidin diet.**—Table 2 shows the total lipid and fatty acid content, the solid, liquid, and elaidic acid expressed as the percentage of total fatty acids, and the iodine number of the solid and liquid fractions for carcass and tumor and for control rats. With the exception of the rat sacrificed 28 days after transplantation of tumor, the carcass of the tumor-bearing rat contained much less fatty acid than that of the control rat.

Unlike the rats on the Crisco diet (Table 1), the fatty acid composition of the tumor showed no significant qualitative difference from that of the carcass of the host rat, except in the percentage of liquid acids which was higher in tumor than rat (Table 3). On the other hand, the carcasses of the rats with tumors differed markedly in fatty acid composition from those of the controls. The percentage of solid acids was significantly lower with lower iodine numbers and the percentage liquid

**DISCUSSION**

The progressive growth of Walker carcinoma 256 in rats has previously been shown to cause an increase in total lipid of the blood plasma (3, 10), consisting essentially of an increase in the fatty acid fraction. Likewise, the total lipid content of the host rat was found to decrease significantly (10, 14) during growth of the tumor. That this decrease was primarily in the fatty acid fraction of the total lipid is evident from the results of the present experiments. In spite of the higher fat content of the diet, tumor rats on elaidin suffered a greater depletion of the carcass fatty acids than did rats on Crisco, an effect doubtless due to the
larger tumors. On a diet containing only 8 per cent Crisco, the marked loss of lipid from the carcass of rats during progressive growth of this tumor, as compared to pair-fed rats ingesting exactly the same amount of diet, has been attributed to an increase in the caloric requirement of the host (14).

Although the amount of total (unseparated) fatty acid of tumors was essentially the same on both diets, the greater content of solid, unsaturated acids (elaidic acid) when elaidin was fed replaces oleic acid, as Sinclair believed (19), then fatty acids in the tumors caused a decrease in the degree of unsaturation of the latter. If elaidic acid replaces oleic acid, as Sinclair believed (19), then the iodine number of the liquid fraction is also inversely related to the total amount of fatty acids left in the rat. When roughly two-thirds of the fatty acids were gone (compared to the control), the iodine number rose sharply.

A similar relationship was established by Hodge et al. (11) for the fasting mouse; the iodine number of the total lipid of the carcass increased slowly until about three-quarters of the utilizable lipid was burned, after which interval the iodine number increased rapidly.

Complete metabolism (burning) of the saturated and only slightly unsaturated acids would spare the highly unsaturated acids for their structural function of incorporation into phospholipids (17). In the host rat, whose fat stores were completely exhausted because of the presence of a large tumor, the fatty acids probably consisted almost entirely of phospholipid fatty acids, which might account for their similarity to the fatty acids of tumor, a tissue rich in phospholipid. Smedley-MacLean (20, 21) ascribed the disappearance of highly unsaturated acids from the skin of rats bearing Walker 256 to their utilization in the formation of tumor tissue. Our data support this theory, since in tumor, regardless of diet, the liquid acids predominated in amount over the solid acids, a situation which might conceivably create a demand for liquid acids on the part of the growing tumor.

The mobilization of fat occurred early in the growth of the tumor (Table 1) while the food intake was normal and before the carbohydrate and protein stores of the animal were exhausted. Both our experiments and those of Smedley-MacLean indicate that fat may be mobilized for the purpose of providing a plentiful supply of the essential unsaturated fatty acids for building tumor tissue. Since the experiments of Hodge (11) and Longenecker (12) show that fat is mobilized nonselectively, the demands of the growing tumor for unsaturated acids for formation of phospholipids and for the esterification of cholesterol (8) might

<table>
<thead>
<tr>
<th>TABLE 3</th>
</tr>
</thead>
</table>

The mean values and significance of the difference between the means for the fatty acid composition of tumor, of tumor rat and of control rat

Summary of Data from Tables 1 and 2

|          | Tumor | Control
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<thead>
<tr>
<th></th>
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<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>P value*</td>
</tr>
<tr>
<td>Tumor</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B.W. (av. 90.2)</td>
<td>33.9</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Solid F.A. per cent</td>
<td>66.8</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Liquid F.A. per cent</td>
<td>77.0</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>I.N. solid F.A.</td>
<td>59.1</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>I.N. liquid F.A.</td>
<td>188.5</td>
<td>N.S.</td>
</tr>
</tbody>
</table>

|          |       |          |       |          |
| Elaidin |       |          |       |          |
| B.W. (av. 97.9) | 28.6 | N.S. | 34.6 | <0.01 | 49.1 |
| Elaidic acid per cent | 46.7 | N.S. | 52.8 | <0.01 | 62.0 |
| Liquid F.A. per cent | 51.2 | <0.01 | 45.4 | <0.01 | 80.3 |
| I.N. solid F.A. | 54.6 | N.S. | 59.1 | <0.01 | 71.3 |
| I.N. liquid F.A. | 138.5 | N.S. | 151.5 | <0.01 | 106.9 |

* Significance of the difference between the means of tumor and of carcass of tumor-bearing rats.
† Significance of the difference between the means of tumor-bearing and control rats.
‡ Only data from pairs of rats with tumors over 6 per cent of total body weight are summarized here.
§ Not significant.

Summary: In the Crisco series the tumor rat differs from the tumor and control rat. In the elaidin series the tumor rat is similar to the carcass of tumor-bearing rats. The entrance of elaidic acid into the phospholipid fraction of this tumor has been shown previously (9). The increase in solid, unsaturated fatty acids in the tumors caused a decrease in the degree of unsaturation of the latter. If elaidic acid replaces oleic acid, as Sinclair believed (19), then the iodine number of the liquid acids should have increased. The reason for the lack of increase in the degree of unsaturation of the liquid acids is not known, but the possibility exists that only so much unsaturation per se is necessary for tumor tissue and growth. If some is available in the solid fatty acid fraction, then the liquid acids, although reduced in amount, need not be more unsaturated.
create an excess of saturated fats to be burned. An excess of nonprotein foods is known to stimulate tissues to increase oxygen consumption, the effect of which would be to force a higher caloric requirement on the host. The marked lipemia also indicates a slow removal of fat from the blood, a condition which would be aggravated by impaired activity of lipase and esterase as established for the tissues of rats bearing tumors other than Walker 256 (4, 6, 22).

SUMMARY

1. Rats bearing Walker carcinoma 256 and rats without tumors that ate the same amount and kind of diet containing either Crisco or elaidin were compared with respect to: (a) total lipid content of blood plasma and carcass and (b) amount and degree of unsaturation of solid and liquid fatty acids.

2. The total lipid content of the blood plasma was higher, while that of the carcass was lower in rats with tumor. The rise in blood lipids occurred early in tumor growth.

3. In rats with small tumors, the nature of the fatty acids of the carcass differed markedly from that of the tumors and was closely similar to that of the controls.

4. In rats with large tumors, the fatty acids of the carcass were closely similar qualitatively to those of the tumor and significantly different from those of the pair-fed controls.

5. The degree of unsaturation of the liquid fatty acids was greater in carcasses of tumor-bearing rats than in controls.

6. In the carcass of the tumor-bearing rat the degree of unsaturation of the liquid fatty acids was inversely related to the fatty acid content of the rat.

7. In brief, the effect of the growing tumor on the host seems to be (a) to cause a lipemia, (b) to decrease the fatty acid content of the host, (c) to cause the ratio of solid to liquid fatty acids to become like that in tumor, and (d) to increase the degree of unsaturation of the liquid acids of the host.

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The Nature of the Fatty Acids of Rats Growing Walker Carcinoma 256

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