I. LIVER REGENERATION FOLLOWING CHLOROFORM INJURY AS INFLUENCED BY THE FEEDING OF CASEIN OR GELATIN *

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This paper continues the investigation of liver cell repair as influenced by diet factors. Other papers¹ show the influence of meat, fat and carbohydrate feeding on the reconstruction of liver cells. It has been pointed out that a uniform central liver necrosis involving half or more of the liver cells can be readily produced by chloroform anesthesia or chloroform injection following a standard fasting period. Under favorable diet conditions this liver necrosis may be completely repaired by the formation of new liver cells in a period of from seven to ten days. The solution or autolysis and removal of the dead liver cells precedes the construction of new liver cells. The construction of this great mass of liver cells is a truly remarkable reaction which is worthy of much study. This speed of growth or reproduction far exceeds the new growth seen in the most malignant neoplasms or even growing embryonic tissues. It seemed highly desirable to study this new formation of specialized cells to determine the factors which may control, favor or hamper the cell reconstruction.

It is very significant that abundant carbohydrate feeding (cane sugar) is quite favorable to rapid liver cell repair and complete cell repair may be attained without the intake of any nitrogenous material. This shows very careful conservation of nitrogenous fractions in the body and proves that sugar may at times act directly by conservation of protein split products in its protein sparing action.

Glycogen is so intimately concerned in the life cycle of the liver cell that possibly sugar feeding has greater influence for the rapid development of liver cells than of other body cells. Fat apparently is not concerned in this liver cell repair and in the diet under such conditions seems to be inert, although furnishing energy requirements.

The repair and construction of red blood cells have been studied in this laboratory² and stand in marked contrast to the liver cell construction. Carbohydrate has a minimal influence on the red cell con-

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1. Davis, N. C.; Hall, C. C., and Whipple, G. H.: *Arch. Int. Med.* **23**:689 (June) 1919. Davis, N. C., and Whipple, G. H.: *ibid.* **23**:711 (June) 1919.

2. Whipple, G. H.; Hooper, C. W., and Robscheit, F. S.: *Am. J. Physiol.* **53**:167, 1920.

struction as contrasted with meat proteins, for example. This indicates wide individual variation in the repair or reconstruction complex of various body cells.

We hope to study the influence of several simple proteins and protein split products upon this standard repair of liver cells. At this time we wish to report in detail the experiments dealing with two common proteins, one of which (casein) is a complete protein and the other (gelatin) an incomplete protein.

Casein may be considered a representative of the "complete proteins" (Abderhalden, Fischer, and others). The amino-acid glyocoll, which is absent, is known to be synthesized in animal metabolism when needed. The content of cystine is relatively low. Gelatin³ is quite high in glyocoll, but lacks the important amino-acids tyrosin, tryptophan and cystin, and is, therefore, an "incomplete protein." Both casein and gelatin are readily obtained commercially in a comparatively pure condition.

It is interesting to compare the assistance given by such different substances in the rapid repair of body tissue. Obviously our short feeding experiments of seven to ten days are not comparable with the long continued growth and general maintenance experiments.

METHOD

The routine of our regeneration experiments has been described elsewhere.¹ In brief: The animal is starved for a short period; a liver injury is obtained either by chloroform anesthesia or by subcutaneous injection of chloroform; feeding is begun the day after administration of the drug; a biopsy specimen for microscopic examination is removed from the liver on the second day (this shows the initial injury, with practically no repair); feeding is continued for any desired period following operation, usually about seven days; a liver specimen is then secured either by another operation or by sacrifice of the animal (this shows the amount of regeneration which has taken place in the liver parenchyma). An animal may frequently be used for two or more experiments.

Dogs seldom eat pure gelatin or pure casein from their food pans in any considerable amounts. It has been found satisfactory, though somewhat laborous, to make a thin casein mush in warm water and feed it to the animals by spoon. Gelatin is always given in warm solution by stomach tube. A suitable amount of salt is given with both substances. The animals will often retain their food better if the desired ration is given in divided doses throughout the day.

3. Fischer, E.; Levene, P. A., and Aders, R. H.: *Ztschr. f. physiol. Chem.* **35**:70, 1902. Levene, P. A., and Beatty, W. A.: *Ibid.* **49**:252, 1906.

EXPERIMENTAL OBSERVATIONS

In the accompanying table are summarized the results of feeding experiments with casein and gelatin. Protocols follow.

LIVER REPAIR INFLUENCED BY FEEDING OF CASEIN AND GELATIN

Experiment	Liver Injury	Feeding, Days	Average Daily Amount Food, Gm.	Liver Repair	Remarks
Casein					
No. 1 Dog 20-41	55-60% necrosis; trace of fat	8	100	20% unrepaired; no fat	Some vomiting on 2d day; developed distemper; killed
No. 2 Dog 20-66	60-65% necrosis; slight trace of fat	9	120	15% unrepaired	Vomiting on 2d day; bright and active
No. 4 Dog 20-111	50-55% necrosis; fat moderate	7	100	20-25% unregenerated; fat heavy around central veins	Vomiting on 3d day; wound broke down; killed
No. 5 Dog 21-18	30-35% necrosis; trace of fat	9	100	Regeneration prac- tically complete	No vomiting; maintained weight
No. 8 Dog 21-26	45-50% necrosis; fat heavy to lobule periph- eries	9	60	10-15% unregener- ated; fat mod- erate	No vomiting; died under anesthesia at final opera- tion; necropsy negative
Gelatin					
No. 3 Dog 20-66	60-65% necrosis; slight trace of fat	9	68	15% unrepaired; slightest possible trace of fat	Vomiting on 4th day; bright and active
No. 6 Dog 21-18	60-65% necrosis; fat heavy to lobule periph- eries	9	100	Regeneration prac- tically complete; heavy trace of fat in central cells	Vomiting on 3d day; weak toward end of experiment
No. 7 Dog 21-26	60-65% necrosis; fat heavy to lobule periph- eries	9	60	10% unregenerated; fat moderate	Vomiting on 8th day; bright and active
No. 9 Dog 20-77	20-30% necrosis; severe injury up to 40%; slight scat- tering of fat	9	50	Regeneration prac- tically complete; slightest possible trace of fat	Vomiting on 2d day; in good con- dition throughout
No. 10 Dog 20-108	60% necrosis	9	65	10-15% unre- generated	No vomiting; died under anesthesia at 2d operation; kidney sections show slight ne- phritis

EXPERIMENT 2.—Casein Feeding. Dog 20-66. White mongrel male.

Jan. 8, 1920. Weight, 21.12 pounds. Just recovered from distemper; in good condition. Isolated for starvation after daily feeding.

January 9, 10 and 11. No food.

January 12. Weight, 19.5 pounds. Active. Chloroform anesthesia, 1 hour (5:10 to 6:10 p. m.).

January 13. Weight, 19.5 pounds. Active. Left 125 gm. casein, and salt, and a little beef extract (all moistened) in cage.

January 14. Weight, 19 pounds. Active. Ate about 75 gm. casein left in cage. Piece of liver removed at 2:30 p. m. Vomited later. Left a little casein in cage—no forced feeding.

January 15. Weight, 18.5 pounds. Bright and active. 120 gm. casein by spoon feeding.

January 16. Weight, 19 pounds. Bright and active. 125 gm. casein by spoon feeding.

January 17. Weight, 18.7 pounds. Bright and active. 125 gm. casein by spoon feeding.

January 18. Weight, 18.7 pounds. Bright and active. 125 gm. casein by spoon feeding.

January 19. Weight, 18.4 pounds. Bright and active. 125 gm. casein by spoon feeding.

January 21. Piece of liver removed at 2:30 p. m.

January 28. Wounds almost well. In excellent condition.

Sections: First operation, from 60 to 65 per cent. necrosis. Slight trace of fat.

Sections: Second operation. 15 per cent. unrepaid.

EXPERIMENT 5.—*Casein Feeding.* Dog 21-18. Young brindle mongrel, male.

Sept. 14, 1920. Weight, 25.5 pounds. In good condition. Old keratitis and staphyloma of right eye suggest previous distemper infection. Isolated after daily feeding; fasting begun.

September 15, 16 and 17. No food.

September 19. Weight, 23.8 pounds. Chloroform anesthesia for forty-five minutes (3 to 3:45 p. m.). Gave 10 mg. sodium cyanid in 100 c.c. physiologic sodium chlorid solution intravenously during thirty-five minutes of anesthesia.

September 18. Weight, 23.3 pounds. A little dull. Gave 100 gm. casein and salt by spoon feeding.

September 20. Weight, 23.5 pounds. A little dull. Gave 100 gm. casein and salt as before. Piece of liver removed at 3 p. m. Liver looks injured in gross.

September 21. Weight, 23.25 pounds. Dull. Nose shows slight discharge. 100 gm. casein.

September 22. Weight, 23.4 pounds. Dull. Nose shows slight discharge. 100 gm. casein.

September 23. Weight, 23.4 pounds. Wound infected, but not broken down. 100 gm. casein.

September 24. Weight, 23.7 pounds. Nose condition clearing up. 100 gm. casein.

September 25. Weight, 23.7 pounds. No nasal discharge. Thin purulent oozing from wound. 100 gm. casein.

September 26. Weight, 23.8 pounds. Constipation probably accounts for some of gain in weight. 100 gm. casein.

September 27. Weight, 23.7 pounds. Wound superficially open. 100 gm. casein. Operation at 2:30 p. m. Small piece of liver removed.

Sections: First operation, from 30 to 35 per cent. necrosis; trace of fat.

Sections: Second operation, almost complete regeneration; less than 10 per cent. not filled out. Slightest possible trace of fat.

EXPERIMENT 6.—*Gelatin Feeding.* Dog 21-18. Young brindle mongrel, male.

Oct. 19, 1920. Weight, 30.7 pounds. Former operative sites in good condition. Isolated after daily feeding; fasting begun.

October 20, 21 and 22. No food.

October 23. Weight, 27.5 pounds. Active and in good condition. Chloroform anesthesia for forty-five minutes (3:40 to 4:25 p. m.). 100 c.c. physiologic sodium chlorid solution intravenously during anesthesia.

October 24. Weight, 27 pounds. Active. 100 gm. gelatin and salt in 300 c.c. water by stomach tube.

October 25. Weight, 25.5 pounds. Active. No vomiting. 100 gm. gelatin given in divided doses. Piece of liver removed at 2:30 p. m.

October 26. Weight, 25.5 pounds. Bright and active. 100 gm. gelatin in divided doses (partly vomited).

October 27. Weight, 25.4 pounds. Active. 100 gm. gelatin as before. No vomiting.

October 28. Weight, 25 pounds. Rather quiet. 100 gm. gelatin as before. No vomiting.

October 29. Weight, 25.1 pounds. Quiet and somewhat weak. 100 gm. gelatin as before. No vomiting.

October 30. Weight, 25.25 pounds. Rather weak. Removed stitches yesterday evening and wound has opened because of infection. 100 gm. gelatin in divided doses. No vomiting.

October 31. Weight, 24.75 pounds. Seems bright, but not active. 100 gm. gelatin at one feeding. No vomiting.

November 1. Weight, 24.5 pounds. Inactive. 100 gm. gelatin at one feeding. No vomiting. Piece of liver removed at 3:30 p. m.

Sections: Third operation, from 60 to 65 per cent. necrosis; fat heavy to lobule peripheries.

Sections: Fourth operation, almost complete filling in of lobules (less than 10 per cent. unregenerated); lobule centers show heavy trace of fat.

EXPERIMENT 7.—*Gelatin Feeding*. Dog 21-26. Young, long-haired mongrel, female.

Oct. 5, 1920. Weight, 18.8 pounds. In good condition: active. Isolated after daily feeding; fasting begun.

October 6, 7 and 8. No food.

October 9. Weight, 16.9 pounds (7.7 kilos). Active. Chloroform anesthesia for forty-five minutes (3:35 to 4:20 p. m.). During forty minutes of this time 260 c.c. of 1 per cent. sodium carbonate in hypertonic saline solution (1.4 per cent.) were given intravenously (approximately 34 c.c. per kilo).

October 10. Weight, 16.25 pounds. Bright and active. Gave 60 gm. gelatin and salt in 200 c.c. water by stomach tube.

October 11. Weight, 16.5 pounds. Active. No vomiting yesterday. 60 gm. gelatin. Piece of liver removed at 4 p. m. Liver looks fatty.

October 12. Weight, 16.4 pounds. Quiet. 60 gm. gelatin by stomach tube (lost a little).

October 13. Weight, 15.75 pounds. More active today. 60 gm. gelatin. No vomiting.

October 14. Weight, 15.5 pounds. Rather quiet. 60 gm. gelatin in divided doses. No vomiting.

October 15. Weight, 15.4 pounds. Quite active. 30 gm. gelatin in morning, 60 gm. in evening.

October 17. Weight, 14.5 pounds. Active. 75 gm. gelatin. Wound open a little.

October 18. Weight, 14.6 pounds. Bright and active. 75 gm. gelatin (Vomited some last night.) Piece of liver removed at 2:30 p.m. Encountered a little peritoneal fluid, slightly cloudy.

Sections: First operation: 45 to 50 per cent. necrosis; fat heavy to lobule peripheries.

Sections: Second operation: about 10 per cent. unregenerated; fat moderate.

EXPERIMENT 8.—*Casein Feeding*. Dog 21-26. Young, long-haired mongrel, female.

November 16, 1920. Weight, 18.9 pounds. In good condition. Dog had a touch of distemper since last used, but has recovered. Isolated after daily feeding; fasting begun.

November 17, 18 and 19. No food.

November 20. Weight, 16.6 pounds (7.55 kilos). In good condition, active. Chloroform anesthesia for forty-five minutes (2:05 to 2:50 p. m.). During forty minutes of this period 260 c.c. hypertonic saline solution (1.4 per cent.) was given intravenously (34 + c.c. per kilo).

November 21. Weight, 16 pounds. Bright and active. 60 gm. casein and salt by spoon feeding.

November 22. Weight, 16.5 pounds. Bright and active. 60 gm. casein and salt by spoon feeding. Some casein was vomited yesterday. Piece of liver removed at 12 noon; fatty and friable.

November 23. Weight, 16.25 pounds. Somewhat weak. There appears to have been some oozing from wound. 60 gm. casein in divided doses.

November 24. Weight, 16 pounds. Bright and active. 60 gm. casein in divided doses.

November 25. Weight, 16 pounds. Bright and active. 60 gm. casein at one feeding.

November 26. Weight, 16.1 pounds. Bright and active. 60 gm. casein at one feeding.

November 27. Weight, 15.9 pounds. Bright and active. 60 gm. casein at one feeding.

November 28. Weight, 15.6 pounds. Bright and active. 60 gm. casein at one feeding. Wound healing nicely.

November 29. Weight, 15.4 pounds. Bright and active. 60 gm. casein at one feeding. Operation in afternoon; dog died under anesthesia. Necropsy essentially negative.

Sections: Third operation: from 45 to 50 per cent. necrosis; fat heavy to lobule peripheries.

Sections: Necropsy: from 10 to 15 per cent. unregenerated; fat moderate.

EXPERIMENT 9.—*Gelatin Feeding.* Dog 20-77. Young female terrier.

Feb. 21, 1920. Weight, 11.5 pounds. Active and in good condition. Isolated after daily feeding; fasting begun.

February 22, 23, 24 and 25. No food.

February 25. Weight, 10 pounds. Active. Chloroform anesthesia one hour and ten minutes (3:20 to 4:30 p. m.).

February 26. Weight, 9.5 pounds. Active. 50 gm. gelatin in 200 c.c. water by stomach tube.

February 27. Weight, 9.5 pounds. Active. 50 gm. gelatin in 200 c.c. water by stomach tube. Food partly vomited. Piece of liver removed at 10:30 a. m.

February 28. Weight, 9.5 pounds. Active. 50 gm. gelatin by stomach tube.

February 29. Weight, 9.1 pounds. Active. 50 gm. gelatin by stomach tube.

March 2. Weight, 8.75 pounds. Active. 50 gm. gelatin by stomach tube.

March 2. Weight, 8.6 pounds. Active. 50 gm. gelatin by stomach tube.

March 3. Weight, 8.4 pounds. Active. 50 gm. gelatin by stomach tube.

Operation wound opening slightly.

March 4. Weight, 8.2 pounds. Rather quiet. 50 gm. gelatin by stomach tube.

March 5. Weight, 8.2 pounds. Rather quiet. 50 gm. gelatin by stomach tube. 3:30 p. m., removed piece of liver.

Sections: Second operation: from 25 to 30 per cent. necrosis, injured up to 40 per cent, with scattering of fat.

Sections: Third operation; slightest possible trace of fat; repair almost complete.

The following experiments were undertaken with the idea of supplementing a sugar diet with casein. The protein was digested with pancreatic extract so that it became soluble. Since the digest was very nauseating, an attempt was made in one experiment to give it by the intraperitoneal route. In addition to the animals in Experiments 12 and 13, another dog was given sugar and casein digest by stomach tube. This dog died on the sixth day after chloroforming with very toxic symptoms and autopsy showed less than one-half of the liver injury repaired.

It is clear that this casein digest amino-acid mixture was much more toxic to a dog poisoned by chloroform than to a normal animal. The significance of this observation is not apparent but further investigation of this point should be made.

EXPERIMENT 11.—*Casein Digest Intraperitoneally. Control. Dog 20-78.* Long-haired mongrel, male.

Feb. 4, 1920. Given 5 gm. casein digest dissolved in 35 c.c. physiologic sodium chlorid solution, intraperitoneally. No reaction.

February 5 and 6. Dog clinically as usual.

February 7. 10 gm. casein digest intraperitoneally. No reaction.

Feb. 8 and 9. As well as usual.

February 10. Sacrificed. Necropsy negative.

EXPERIMENT 12.—*Sugar Feeding; Casein Digest Intraperitoneally. Dog 20-64.* Large, black spaniel, female.

Feb. 7, 1920. Weight, 33.75 pounds. In excellent condition. Isolated after daily feeding; fasting begun.

February 8, 9 and 10. No food.

February 11. Weight, 29.6 pounds. Active. Chloroform anesthesia for one hour and five minutes (3:30 to 4:35 p. m.).

February 12. Weight, 29.2 pounds. Bright and active. 100 gm. cane sugar and kaolin by stomach tube.

February 13. Weight, 28.6 pounds. Somewhat dull and weak. Food as yesterday. Piece of liver removed at 3:45 p. m.; gross appearance of severe injury. (Sections show from 50 to 55 per cent. necrosis.)

February 14. Weight, 29 pounds. Dog is quite sick. Pulse rapid and weak; temperature subnormal. No jaundice or hemorrhages; 100 gm. cane sugar by stomach tube; 5 gm. protein digest intraperitoneally in 25 c.c. water. All intraperitoneal injections given under light ether anesthesia.

February 15. Weight, 29.3 pounds. Weak, but not so sick as yesterday. Sclera jaundiced. 100 gm. sugar by stomach tube; 5 gm. protein digest in 20 c.c. fluid intraperitoneally.

February 16. Weight, 28.3 pounds. Still weak. 100 gm. sugar by stomach tube; 10 gm. protein digest in 45 c.c. fluid intraperitoneally.

Feb. 17. Weight, 28 pounds. Sugar as before; 10 gm. protein digest in 30 c.c. fluid intraperitoneally.

February 18. Weight, 27.6 pounds. 150 gm. sugar by stomach tube; 15 gm. protein digest in 45 c.c. water intraperitoneally.

February 19. Weight, 27.25 pounds. Sugar and protein digest as yesterday. Weak.

February 20. Weight, 25.1 pounds. Sugar and protein digest as yesterday. Vomited a little. Very weak. Great quantities of thin, reddish-brown diarrhea. Died about noon.

Necropsy Report.—All tissues intensely jaundiced. Some hemorrhage into abdominal wall, especially around operative site and points of injection. Peritoneal cavity contains some fluid, perhaps largely from injection in morning; fluid looks blood tinged. Peritoneal surfaces and mesentery are engorged and purplish; there are occasional fibrin deposits; a loop of intestine is adhered to anterior wall on left side. Fat overlying pericardium appears hemorrhagic. Heart negative. Blood is massively clotted.

Lungs are mottled light and dark (mostly posterior), but there seem to be no hemorrhages or consolidation.

Liver, in addition to jaundice, is extremely mottled, suggesting great lack of repair. There are a number of small antemortem clots throughout the parenchyma.

Spleen shows extensive hemorrhages.

Kidneys: dark; cortices somewhat swollen and cloudy, suggesting parenchymatous degeneration.

Mucosa of gastro-intestinal tract and bladder negative.

Microscopic Report.—Lungs: hemorrhagic exudate; congestion. Spleen and lymph nodes: hemorrhages and necrosis. Liver: from 10 to 15 per cent. not repaired. Kidneys: cloudy swelling.

EXPERIMENT 13.—*Sugar and Casein Digest Feeding. Dog 20-76.* Black mongrel, female.

April 28, 1920. Weight, 14.75 pounds. In good condition (three previous experiments). Isolated after daily feeding; fasting begun.

April 29 and 30. No food.

May 1. Weight, 13.25 pounds (6.023 kilos). Dog in good condition. Gave 1.27 c.c. chloroform (0.21 c.c. per kilo) plus twice its volume liquid petrolatum subcutaneously.

May 2. Weight, 13.1 pounds. Bright and active. Gave by stomach tube 50 gm. cane sugar, 15 gm. protein digest and a little kaolin.

May 3.—Weight, 12.9 pounds. Vomited some yesterday. Food as yesterday except 5 gm. less amino-acids. Vomited some about one and a half hours after feeding. Operation at 2:30 p. m. Cut out one of preceding operative scars; no difficulties. Piece of liver removed.

May 4. Weight, 12.6 pounds. Active. Fed 100 gm. cane sugar and 15 gm. protein digest in divided doses, by stomach tube.

May 5. Weight, 12.3 pounds. Active. Food as yesterday. Some vomiting in morning.

May 6. Weight, 12.1 pounds. Active. Food as yesterday. Some vomited in morning. Put dog in metabolism cage; to receive less water.

May 7. Weight, 12 pounds. Quiet. Food as yesterday. Not vomited.

May 8. Weight, 11.4 pounds. Quiet. Food as yesterday. Partly vomited.

May 9. Weight, 11 pounds. Quiet. Gave 50 mg. cane sugar and 15 gm. protein digest. Largely vomited.

May 10. Dog is quite weak. Operation at 11 a. m.

The value of the experiment is much decreased because of vomiting. On some days there was little or no vomiting, and when it did occur it was often late; however, probably one third or one half of food was lost. Feces were passed on three occasions during experiment, small amounts of soft, brown material.

Operation on Second Day: 45 to 50 per cent. necrosis; fat moderate.

Operation on Ninth Day: about 15 per cent. unregenerated; trace of fat.

Note: Casein digest yields only 28 mg. amino-nitrogen per gram, indicating that approximately 17.5 per cent. of mixture consists of amino-acids.

DISCUSSION

A comparison of the liver regeneration on diets of casein and gelatin shows that in this series the results have been about the same,—the superiority, if any, resting with gelatin. This means that the liver cells were not repaired entirely by amino acids coming from the gelatin, but that the latter must necessarily have been supplemented by “building stones” from endogenous katabolic waste material perhaps in part from the necrotic liver cells.

Regeneration with these isolated proteins has been equal to that with meat diets, better than that on starvation or with fat diet, and less complete than that with mixed table scraps, bread and milk, or even a pure carbohydrate diet.¹ One might infer that in the rapid regeneration of liver cell protein the conservation of metabolic end products plays a larger part than the furnishing of new protein material. Evidently, under certain conditions, energy requirements have precedence over reparative processes to the extent that incoming protein material may be stripped by de-aminization, to a point where synthesis of cell protoplasm is hampered.

Owing to the tendency to vomiting, it has usually been necessary to give less of gelatin than of casein per day. Loss of weight has been less marked in the case of casein feeding.

In experiment 7, carbonate solution was given intravenously during chloroform anesthesia, while in Experiment 8 on the same dog only saline solution was injected, yet the injuries were identical. Whether or not chloroform causes an acidosis, and this in turn is relieved by alkaline therapy, has no bearing on our work—carbonate solution intravenously certainly is not able to prevent in any measure the liver injury caused by chloroform.

SUMMARY

Gelatin, although an "incomplete protein," seems to be equally as efficacious as casein in the regeneration of liver parenchyma destroyed by chloroform.

After a 50 to 60 per cent. necrosis, a feeding period of nine days with either substance will restore the liver to within 10 or 15 per cent. of normal. This liver cell regeneration is comparable to that obtained with a meat diet, approaches that given by a high carbohydrate diet, is definitely less than with a full mixed diet, but greater than with a fat diet or with fasting.

The liver repair on gelatin feeding emphasizes again the important fact that the body is able to conserve certain amino acids or split products from its endogenous wastage products and recast these groups into the complex liver cell.