glycogen need not necessarily be imputed to the conversion of fat to carbohydrate.

The low R.Q. may be ascribed chiefly to the incomplete combustion of fat. Both *in vivo*[6] and *in vitro*[7] it has been demonstrated that the liver is a source of acetone substances, products of incomplete combustion of fat. The complete combustion of fat yields a R.Q. of 0.7. However, the combustion to the 4-carbon stage would give a R.Q. below 0.7, since the acetone substances themselves possess R.Q.'s above that value. According to Knoops' classical theory of β-oxidation, the R.Q. of palmitic acid with the production of diacetic acid would be 0.63. However, with Jowett and Quastel's conception[8] of multiple alternate oxidation the R.Q. may fall to any level.

Another factor which must be taken into consideration for the production of low hepatic R.Q.'s is that of the function of the liver to produce urea, for the carbon utilized in this process would not be eliminated in respiration. This phenomenon may, therefore, lower the R.Q. Whatever the exact processes involved in the production of this low R.Q. may be, there is a striking correlation between the average values of the R.Q.'s of the liver of fat-fed (0.58), fasted (0.59-0.60), and depancreatized animals (0.59),

Summary. Thirty-seven observations of the R.Q. of the liver of cats depancreatized 48-72 hr. revealed an average R.Q. of 0.59.

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Gastric Vagi in the Dog. Erroneous Assumption of Uninterrupted Vagal Innervation in the Pavlov Pouch.*

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The fundamental difference in concept between the Pavlov pouch and the Heidenhain pouch is that the vagal innervation of the former is intact. Fig. 1, reproduced from Khigine[1] and Pavlov,[2, 3]

6 Goldfarb, W., and Himwich, H. E., *J. Biol. Chem.*, 1933, **101**, 441.

7 Jowett, M., and Quastel, J. H., *Biochem. J.*, 1935, **29**, 2181.

8 Jowett, M., and Quastel, J. H., *Biochem. J.*, 1935, **29**, 2159.

* Supported in part by a grant from The Friedsam Foundation.

1 Khigine, P. P., *Arch. des Sciences Biol.*, 1894, **3**, 461.

2 Pavlov, I. P., *Ergeb. d. Physiol.*, 1902, **1**, part 1, 246.

3 Pavlov, I. P., *The Work of the Digestive Glands*, 2nd ed., London, 1910.

indicates the anatomical concept upon which they based their operative procedure. According to this diagram, after the anterior vagus trunk leaves the anterior gastric plexus, it descends the anterior surface of the stomach along the lesser curvature to the pylorus. The main posterior vagus trunk, however, after leaving the posterior gastric plexus, descends the corresponding stomach surface along the greater curvature to approximately the beginning of the pars pylorica. The incision which separates the pouch from the main stomach passes between these two main trunks and their arborizations. Consequently, the posterior trunk passes intact through the sero-muscular isthmus which joins the pouch to the stomach proper, insuring the integrity of the vagus supply to the pouch.

With only minor modifications in technique, the method of Khigine and Pavlov has been utilized by practically all physiologists who found use in their work for a "vagus-intact" pouch. These investigators, as well as other writers on the subject, state without reservation that in the Pavlov pouch the integrity of the nervous connections is preserved, and most of them employ as illustration the Pavlov diagram shown herewith, (Cannon,[4] Lönnquist,[5] Bickel and Katsch,[6] Thomsen,[7] Carlson,[8] Smidt,[9] Loeper,[10] Bayliss,[11] Boldyreff,[12] Lim, Ivy, and McCarthy,[13] Wright,[14] Babkin,[15] Starling,[16] Howell,[17] Bodansky,[18] MacLeod,[19] and Mathews.[20])

This classic description of the course of the posterior gastric

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4 Cannon, W. B., *Am. J. Med. Sci.*, 1906, **131**, n.s., 563.

5 Lönnquist, B., *Skan. Arch. f. Physiol.*, 1906, **18**, 194.

6 Bickel, A., and Katsch, G., *Chirurgische Technik zur Normalen und Pathologischen Physiologie des Verdauungs Apparates*, Berlin, 1912.

7 Thomsen, E., *Studier over Neurogen og Cellulaer Achyli*, Copenhagen, 1921.

8 Carlson, A. J., *Phys. Rev.*, 1923, **3**, 1.

9 Smidt, H., *Arch. f. Klin. Chir.*, 1923, **125**, 26.

10 Loeper, M., *Histoire de la Secretion Gastrique*, Paris, 1924.

11 Bayliss, Sir W. M., *Principles of General Physiology*, 4th ed., London, 1924.

12 Boldyreff, W. N., *Ergeb. Physiol.*, 1925, **24**, 399.

13 Lim, R. K. S., Ivy, A. C., and McCarthy, J. E., *Quart. J. Exp. Physiol.*, 1925, **15**, 13.

14 Wright, S., *Applied Physiology*, 2nd ed., London, 1928.

15 Babkin, B. P., *Die Aüssere Sekretion der Verdauungsdrüsen*, 2nd ed., Berlin, 1928.

16 Starling, E. H., *Principles of Human Physiology*, 5th ed., Phil., 1930.

17 Howell, W. H., *A Textbook of Physiology*, 11th ed., Phil., 1930.

18 Bodansky, M., *Introduction to Physiological Chemistry*, 3rd ed., New York, 1934.

19 Macleod, J. J. R., *Physiology and Biochemistry in Modern Medicine*, 7th ed., St. Louis, 1935.

20 Mathews, A. P., *Principles of Biochemistry*, New York, 1925.

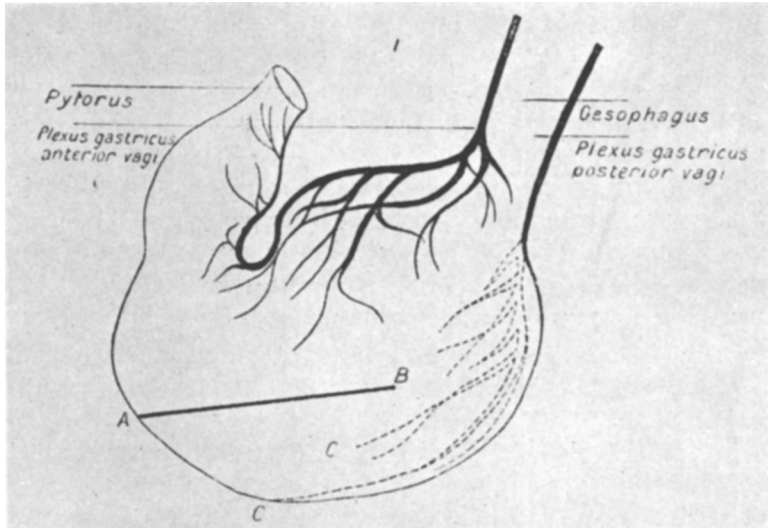

FIG. 2.—*A-B.* Line of incision. *C.* Flap for forming stomach pouch of Pavlov.

FIG. 1.
Gastric Vagi and Incision for Pavlov Pouch. Reproduced from Pavlov (1910).

vagus in dogs differs radically from that found in the human. Therefore it was decided as a preliminary to further work to study by actual dissection the course of the vagi in the dog in relation to pouch formation. We were unable to confirm the description given by Pavlov, observing, on the contrary, that in all essentials, the distribution was the same as in the human. Although we subsequently found that this observation had been reported several times previously in the surgical and anatomical literature (see discussion), apparently it had been overlooked or ignored by practically all physiological investigators. Since the recognition of this fact may prove vital to further quantitative investigation of the response of fundus pouches to vagal stimulation, a summary of our anatomical findings and their possible bearing on the behavior of Pavlov pouches is warranted.

Dissections were performed upon 20 dogs, all mongrels. Four of them were Pavlov pouch dogs; the remainder normal, unoperated animals. The Perman[21] method of clearance was used as an adjunct to dissection in the fresh state, but was found to offer little added clarity to nerve identification. The nerve distribution in all animals examined was the same.

[21] Perman, E., *Acta Chir. Scand.*, 1935, **77**, Suppl. 38.

The esophageal vagi followed a simple, constant pattern. Each nerve, after supplying branches to the various thoracic viscera, divided into a ventral and a dorsal branch. Corresponding branches anastomosed, forming ventral and dorsal trunks. The union of the ventral branches occurred just distal to the base of the heart; of the dorsal, about three-quarters of an inch above the diaphragm. Small branches were supplied to the esophagus by these trunks, but plexus formation was not observed. Both trunks entered the abdomen through the esophageal hiatus in the diaphragm and passed between the 2 layers of lesser omentum.

On the stomach, the branching and course of both ventral and dorsal trunks were found to be almost exactly symmetrical (Figs. 2, 3). Slightly above the cardia, each gave one or 2 twigs to the lower esophagus, the under surface of the diaphragm, and to the cardia. Immediately below, several fair-sized branches, or one larger one which promptly divided into 2 or 3, were given off to supply the fundus and the proximal part of the body of the

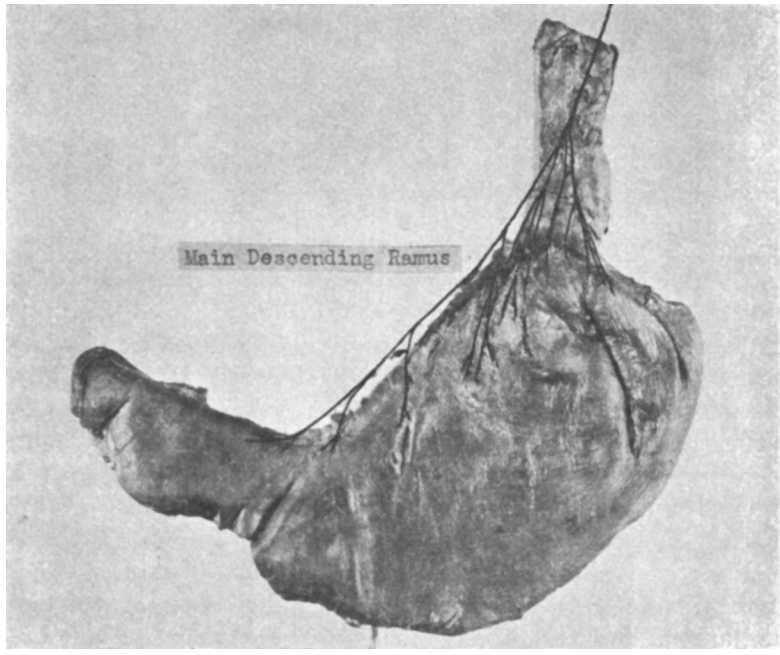

FIG. 2.

Photograph of anterior surface of dog's stomach, showing anterior vagal trunk (stained with India ink) running along lesser curvature. (Site of initiation of branching elevated, and angulation of branches increased by upward traction on nerve.)

stomach. At the same level, a large branch passed from the ventral trunk to the porta hepatis, and from the dorsal to the coeliac plexus. *Both* main trunks then descended within the omental bursa parallel to the lesser curvature of the stomach to about one inch from the pylorus. (McCrea's observation, that the gastric portion of the dorsal trunk reached the stomach, not through the omental bursa, but through the gastro-pancreatic fold, could not be verified.) Each trunk gave rise in its passage toward the pylorus to 3 to 5 more branches which passed transversely toward the greater curvature between the corresponding stomach surface and its serosal covering, to disappear in the musculature about one-third of the distance across the stomach surface. All gastric branches ran in a direction approximately at right angles to the long axis of the stomach. *No branch, great or small, was seen to traverse the stomach wall along the greater curvature.*

Neither an anterior nor a posterior gastric plexus was observed, although an occasional fine intercommunicating twig connected the fundal branches. Rarely, the main anterior and posterior descend-

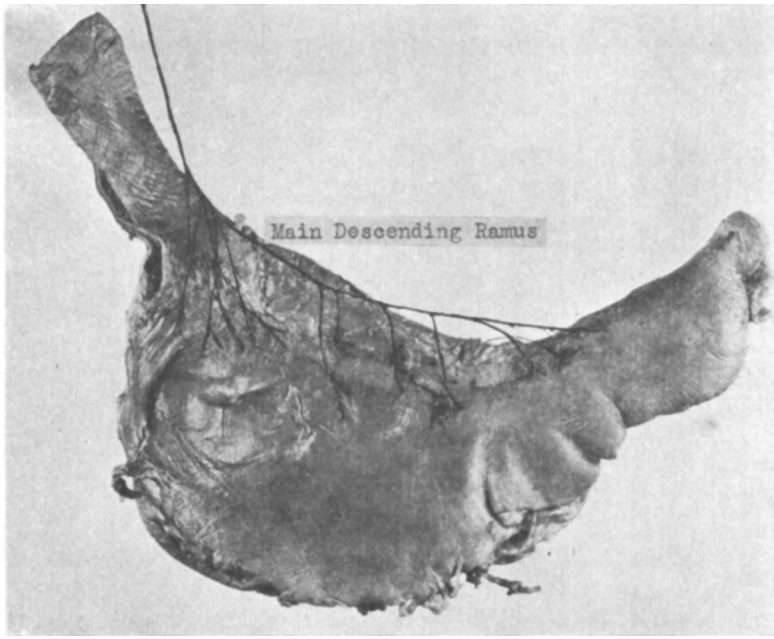

FIG. 3.

Photograph of posterior surface of dog's stomach, showing posterior vagal trunk (stained with India ink) running along lesser curvature. (Site of initiation of branching elevated, and angulation of branches increased by upward traction on nerve.)

ing rami were connected proximally by a small twig. No significant difference in size between the anterior and posterior trunks was observed, nor in the number of their branches, nor in the distance from the pylorus to which they could be followed. The pylorus was innervated by nerves of both sympathetic and vagal origin descending from the porta hepatis. At times, the hepatic branch of the anterior vagal trunk could be followed from its origin, through the hepatic portal, down to the pylorus. At other times its identity was lost in the maze of sympathetic fibers present in the region of the portal fissure.

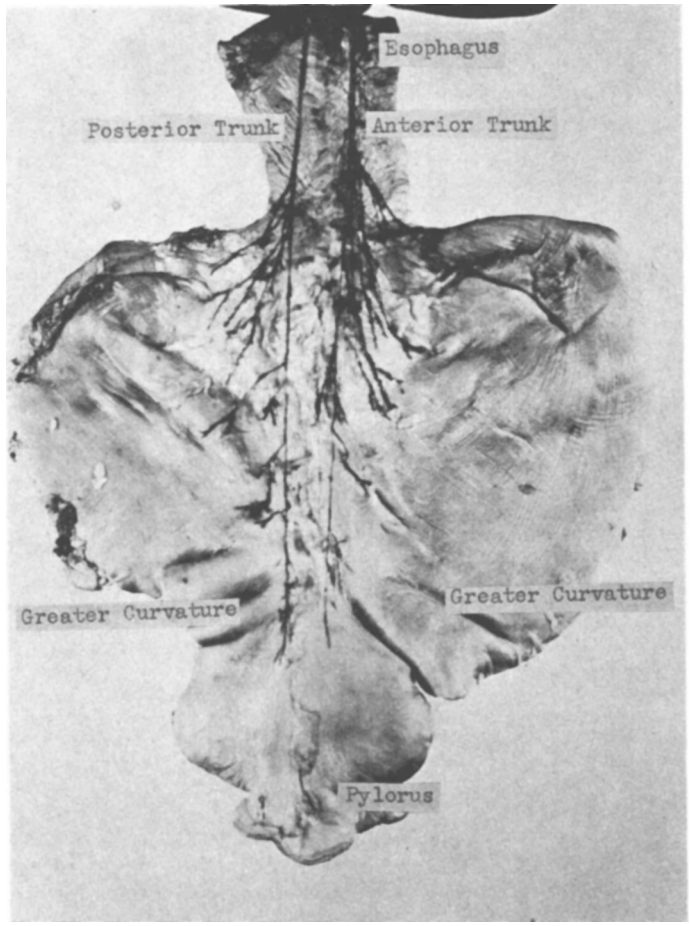

FIG. 4.
Photograph of dog's stomach, incised along greater curvature. Note symmetry of vagal trunks in their course along lesser curvature.

In addition to various minor differences, the description of Khigine and of Pavlov of the gastric distribution of the vagus nerve differs from the above in one vital respect; namely, they believed that the posterior vagal trunk coursed along the *greater curvature* of the stomach, rather than along the *lesser curvature,* symmetrically with the ventral trunk (Fig. 4). Nowhere in their work did they indicate that they had carried out actual dissection to demonstrate the course of the vagi. Instead, Khigine[22] in his original thesis, refers to Ellenberger and Baum,[23] whose description and illustration he utilized. What other literature on the gastric vagi in dogs we were able to find was entirely in accord in essential points with our observations (Latarjet,[24] Stahnke,[25] McCrea,[26] Bradley,[27] Perman[21]).

On the basis of our observations, it follows that the posterior vagal trunk does not pass uninjured through the isthmus of a pouch prepared by the Pavlov technique. On the contrary, both main trunks remain entirely outside the pouch, and roughly 75% or more of the branches from these trunks are transected by the incisions recommended by Pavlov—incisions roughly parallel to the long axis of the stomach, and hence approximately at right angles to the direction of vagal branching. Four of our dissections were done on dogs which had previously been provided with Pavlov pouches by the usual technique. In these there were found only one or 2 fine fibers crossing the stomach in the direction of the isthmus of the pouch. Not only did these branches not traverse the length of the pouch, but grossly, were not even seen to reach its isthmus. Examination of the other stomachs revealed that had Pavlov pouches been made in them, the identical condition would have resulted. Perman recognized the fact that the Pavlov technique involved the sacrifice of the bulk of the vagal supply to the pouch. Nevertheless, he accepted the pouch secretion as not being essentially different from that in other parts of the stomach, believing the sparse nerve communications on the proximal part of the pouch sufficient for this purpose. While it is possible that the few fibers which run toward the pouch isthmus might be able to supply the entire pouch through

22 Khigine, P. P., Inaugural Dissertation, St. Petersburg, 1894. (Communication from Dr. B. P. Babkin).

23 Ellenberger, W., and Baum, H., *Systematische und Topographische Anatomie des Hundes,* Berlin, 1891.

24 Latarjet, M., *Lyon Medical,* 1921, **130**, 166.

25 Stahnke, E., *Arch. f. Klin. Chir.,* 1924, **182**, 1.

26 McCrea, E. D., *J. Anat.,* 1924-25, **59**, 18.

27 Bradley, O. C., *Topographical Anatomy of the Dog,* 3rd ed., New York, 1935.

microscopic lateral branches or through the myenteric plexuses, it is no less likely that their physiological action would be limited to what anatomically seems to be their natural sphere of influence, the fundus of the pouch. In the latter case, one would be dealing with an incompletely innervated pouch, and it might be expected that the response of such a pouch to vagal stimuli would be equally incomplete.

Data available in the literature were insufficient to indicate whether or not Pavlov pouches did respond completely to vagal stimuli despite the anatomical considerations elucidated above. In order to determine whether there exists a physiological parallel to the observed anatomical deficiency, a technique is required for the quantitative determination of degree of vagal response. As far as we could determine, the criteria in use for pouch differentiation have only been employed qualitatively, nor do they seem to have been sufficiently refined or elaborated to permit their application to quantitative use even if so desired. The concept of "varying degree of vagal response" does not appear to have been generally appreciated, one of only 2 designations (vagal or non-vagal, Pavlov or Heidenhain) having been applied to pouches according to their response. Although in light of our anatomical findings, intermediary values of pouch response might well be expected, with the criteria as used one could not distinguish a *partial* vagal response from a *complete* one.

The authors are at present preparing pouches according to a new technique by which the vagus will be anatomically undisturbed. They propose to compare the secretory responses of this type of pouch with those of typical Pavlov and Heidenhain pouches. In this manner it is hoped that the exact status of the Pavlov pouch will be arrived at, and that standards for determining the exact functional capacity of a pouch may be formulated.