A study of the late effect of division of the pulmonary branches of the vagus nerve on the gaseous metabolism, gas exchange, and respiratory mechanism in dogs / by Walter M. Boothby, Boston, and V.N. Shamoff, Petrograd from the surgical service and respiration laboratory of the Peter Bent Brigham Hospital, Boston, Mass.

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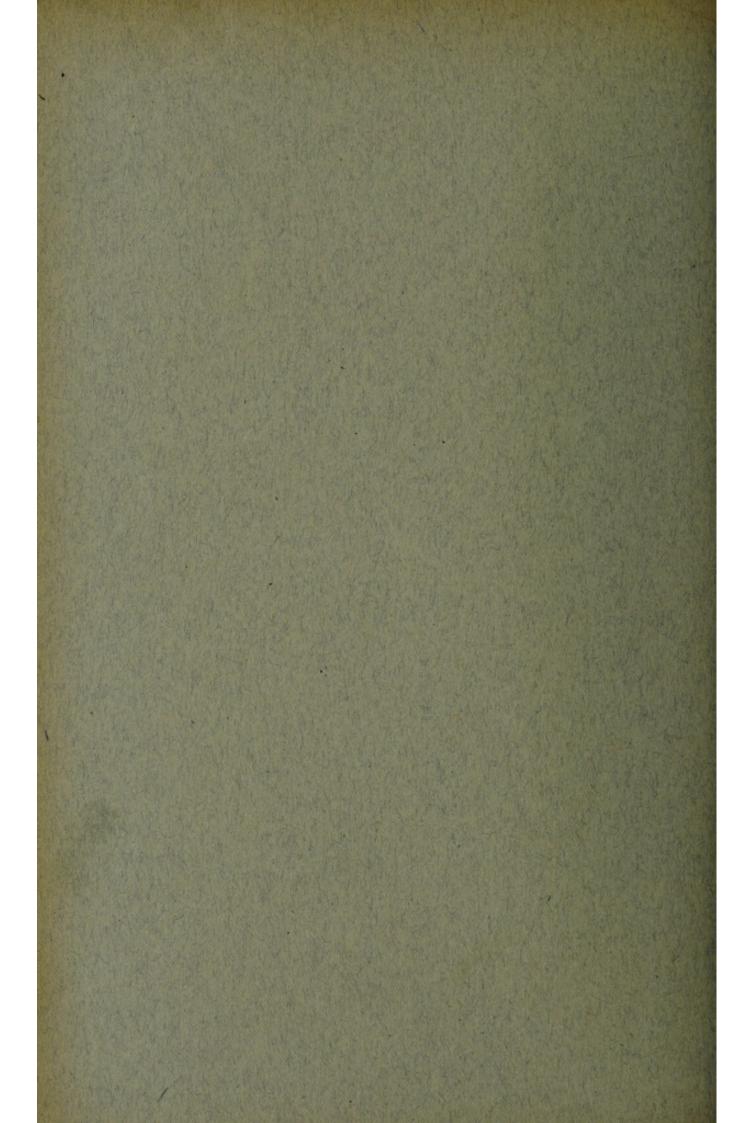


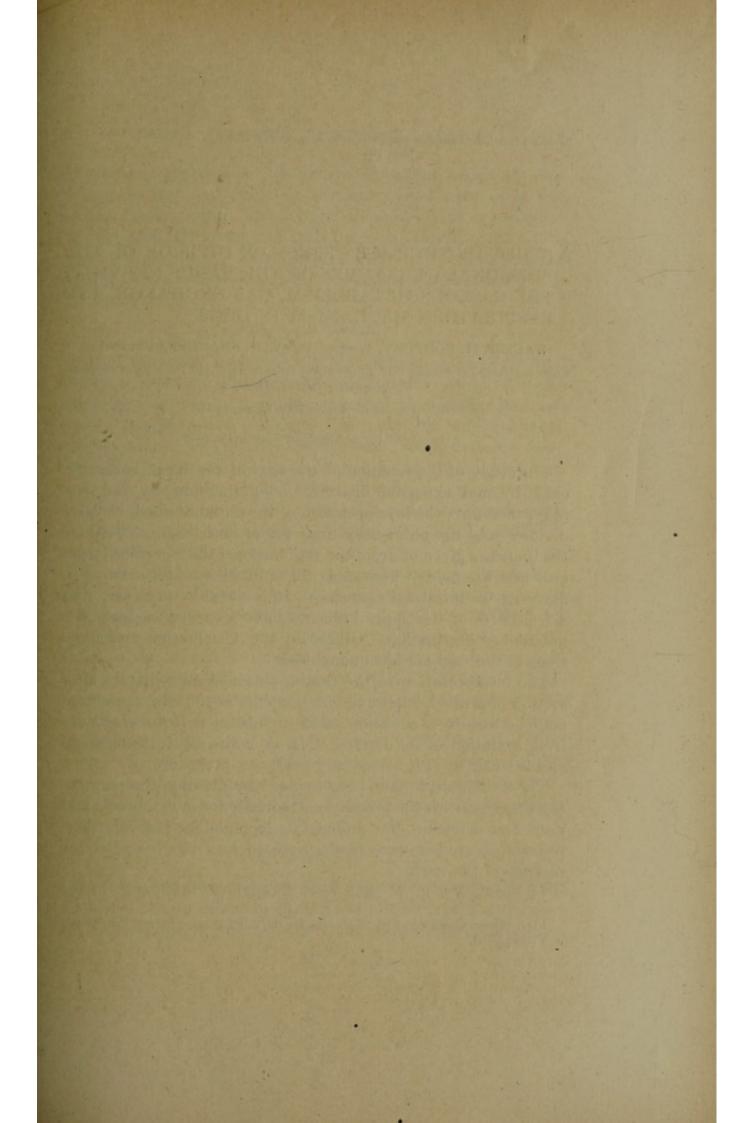
BY

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A STUDY OF THE LATE EFFECT OF DIVISION OF THE PULMONARY BRANCHES OF THE VAGUS NERVE ON THE GASEOUS METABOLISM, GAS EXCHANGE, AND RESPIRATORY MECHANISM IN DOGS

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CLINIC OF PROFESSOR CUSHING

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The study of the function of the vagi in the lungs is complicated by their extensive distribution to other organs. To simplify, therefore, the interpretation of the data obtained, we have divided only the pulmonary branches of both vagi. These are the branches given off from the vagi between the recurrent laryngeal and the point where each vagus divides into its two primary gastro-intestinal branches. It is possible, however, that a few fibres of the upper branches have a cardiac instead of a pulmonary destination. Otherwise the distribution and functions of the vagi are left unimpaired.

The interpretation of the results obtained immediately after section of a nerve is always questionable, as the effect produced may be due to a cessation of its influence, or to overactivity from irritation of its divided ends, or indirectly to the general and local effect of the necessary operative procedure.

These difficulties have been avoided by dividing the pulmonary branches with the precautions requisite for intrathoracic surgery and allowing the animals to completely recover. The respiratory studies were made three to four months after the division of the vagi.

For convenience we shall refer throughout this paper to the

¹ Dr. Shamoff was recalled to Russia for military service before this article was completed.

animals thus prepared as vagotomized dogs, but we wish to emphasize the fact that only the pulmonary, and possibly a few cardiac, branches were divided and that the other branches of the vagi were left intact and their functions therefore were presumably unimpaired. In consequence our data cannot be compared with the results obtained immediately after section of the vagi in the neck.

EFFECT ON HEALTH

Out of the series of eleven dogs operated on we had four permanent recoveries. The cause of death in the unsuccessful experiments was usually a diffuse bronchial pneumonia; less frequently a supperative pleurisy. The pulmonic infection was, however, more frequent after operation on the vagus nerve than after other intrathoracic operations, a series of which were being carried on at the same time. The post-operative recovery was in every way similar to that of animals which had undergone other intrathoracic operations and none of the deaths could be traced to the division of the vagi.

The four animals that recovered quickly became strong and active. Their diet was liberal and consisted of cooked lean meat and bread, and for exercise they were allowed the freedom of an outdoor pen. Our animals were the only dogs living permanently in the animal house during the spring and summer out of a shifting population of about twenty dogs. The vagotomized dogs became strong, active and playful, but they showed no tendency to gain in weight, remaining, in fact, abnormally thin. Furthermore, they were all quite severely affected with the mange. We do not know whether this lean and mangy condition was in any way dependent on an obscure derangement of the metabolic processes caused by the interference with the vagus supply of the lungs.

METABOLISM

The basal respiratory metabolism was determined by means of a Benedict respiration apparatus and all the experimental details were carried out in the manner and with all the precautions recommended by Benedict.² During the experimental investigation all the animals were living under identical conditions. Before experimentation food was withheld for at least fourteen hours. To record any movements made by the animal during an experiment a pneumograph was passed across the hind quarters. In the last column of Table III we have paraphrased this record.

In order to obtain a graphic curve of the respirations, use was made of an air tight mask over the dog's head, instead of using the calorimeter box described by Benedict. As the application of such a mask must be absolutely air tight, we give in detail the technic finally adopted by us. A Tissot mask³ fitting snugly over the dog's snout was held in place by straps passing behind the ears. Very thin rubber tissue was placed over the eyes, and about a quarter inch layer of vaseline was spread over the mask, head and neck of the dog. Over this was pulled a long bag made of rubber dental dam which reached to the base of the neck. The whole was firmly bound down by the even application of bandages. The vaseline, pressed down into the hair, made an air tight connection capable of withstanding an air pressure of fifteen centimeters of water.

During the first application of the mask, the dogs were somewhat frightened. Therefore, on the first day we merely connected them to the respiration apparatus without carrying through an actual experiment. After becoming accustomed to the mask and apparatus, it was surprising how quietly the dogs would lie on the padded table for hours at a time without restraint.

To check the results obtained from the Benedict apparatus we determined the respiratory exchange on two of the vagus dogs by the method of collecting, measuring, and analyzing the expired air. The accuracy of the method is essentially a question of the efficiency of the respiratory valves. For this reason,

² Benedict: Ein Universalrespirationsapparat. Deutsch. Arch. f. Klin. Med. 1912, evii, 155-200.

³ Tissot: Nouvelle method de mesure et d'inscription du debit et des mouvements respiratoires de l'homme et des animaux. Journ. d. Phys. et Path. Gen., 1904, vi, 688-700.

in addition to the Tissot valves on the mask, we also placed on the inspiratory side a large especially constructed valve, similar to the Douglas valve made by Siebe, Gorman & Co. The technic was essentially that described by Douglas⁴ for the determination of the total respiratory exchange in man, excepting that a 30 L. calibrated spirometer was used instead of a bag and meter.

It will be noted that the spirometer experiments show a slightly lower oxygen consumption and carbon dioxide elimination as well as a slightly lower respiratory quotient than do the experiments with the Benedict apparatus. As the experimental pe-

TABLE I Summary of respiratory exchange experiments

	CARBON	DIOXIDE	oxy				
SUBJECT	Per min.	Per kilo per min.	Per min.	Per kilo per min.	RESP. QUO.		
	cc.	cc.	ec.	cc.			
Normal Dog			111111111111111111111111111111111111111		10000		
No. 1	33	5.9	44	7.8	0.75		
Vagus Dogs			70000		No. of the last of		
No. 18	93	7.0	123	9.3	0.75		
No. 15	89	6.9	119	9.2	0.75		
No. 23	99	6.0	134	8.1	0.74		
No. 11	94	6.6	114	8.0	0.82		

riod extended over four and sometimes five hours, during which time the dog was lying at rest without food or drink, and as the spirometer experiments were the last performed, it is probable that the metabolism was slightly lower than it had been earlier in the day.

In Table III, at the end of the paper, are given the essential data and the calculated results of our experiments on the metabolism of the vagotomized dogs, together with the results obtained on a perfectly normal animal, living under the same conditions, and with the experiments conducted in an identical manner. The data is summarized in Table I in which are given the aver-

⁴ Douglas: A method for determining the total respiratory exchange in man. Jour. Physiol., 1911, xlii, Proc. Physiol. Soc., Mar. 18.

ages of the experiments for each dog. Figure I shows a part of a typical curve obtained in a metabolism experiment on one of the vagotomized dogs (dog No. 15).

From these experiments it is evident that the gaseous metabolism is in no demonstrable way affected by the division of the pulmonary branches of the vagi.

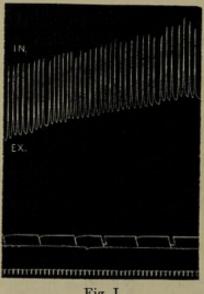


Fig. I.



Fig. II.

Fig. I. Subject, Dog No. 15. Weight, 12.9 kg. No food for fourteen hours. Section of a curve obtained in one of the metabolism experiments on above dog. Upper curve is written by the spirometer on the Benedict respiration apparatus. The second curve is from the work adder, from which the total ventilation is calculated. Third curve is made by a tambour attached to a pneumograph, passing over the dog's hind quarters. This curve shows whether or not the animal was quiet during the experiment. Lower curve is the time in 5 seconds.

Fig. II. Subject, Dog. No. 11. Five days after division of the pulmonary branches of the right vagus (the left had been divided about two weeks previously). Tracing written by a tambour around the chest and is not quantitative. Dog panting. Time in seconds.

RESPIRATORY RHYTHM

Lewandowsky⁵ and other observers have noted a marked prolongation of the inspiratory phase after vagotomy. To our surprise no trace of this phenomenon occurred in any of our vagotomized animals.

⁵ Lewandowsky: Nagels Hdbk. d. Phys., i, 38.

Dog No. 11 on withdrawal of the intratracheal tube for insufflation anaesthesia, after the second operation, showed on the table a deep Cheyne-Stokes type of respiration with great rhythmical exertion of all the respiratory muscles, and the expiratory phase was much prolonged. At the time we considered the phenomenon as possibly of vagal origin. The animal recovered from the operation rapidly, and five days later we obtained the tracings reproduced in Figures II and III. Figure II is the respiratory curve made by a tambour fastened around the chest.

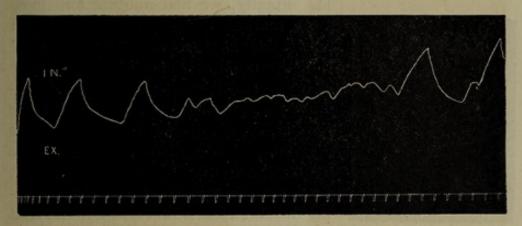


Fig. III. Subject, Dog. No. 11. Curve obtained a few hours after that of Fig. II. Quantitative respiration curve from the Benedict apparatus and shows the irregularity of the respiratory rhythm, resembling the Cheyne-Stokes type. Time in seconds.

Figure III is a spirometer tracing obtained by connecting the animal with the Benedict apparatus, as described above. This breathing shows typical Cheyne-Stokes characters. In every way it resembles the artificial Cheyne-Stokes respiration shown by Haldane and Douglas⁶ to be produced in normal persons by breathing through a long tube. It is evident that the changes in the gases of the alveolar air, blood, and ventilation centre, which cause rhythmic breathing, would be produced equally as well by a partial pneumothorax as by breathing through a tube.

In Figure IV is given an example of the respiratory curve obtained from this same animal four months later. Neither in

⁶ Haldane and Douglas: The experimental production of Cheyne-Stokes breathing in normal persons. Int. Phys.-Kongr. Wien., 1910, viii.

this or any of the other tracings is there any evidence of the persistence of the rhythmic Cheyne-Stokes type of respiration. The only possible abnormality is the occasional slight prolongation of the pause at the end of expiration. It is therefore probable that the pneumothorax had by this time entirely disappeared.

Several dogs subsequently operated on showed no signs of this phenomenon, even when branches of both vagi were divided at one stage. Consequently we decided that the division of the vagus was not the cause of the abnormal respiration of dog No.

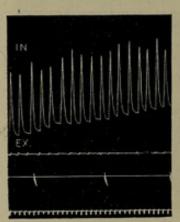


Fig. IV. Subject, Dog No.11. About fourmonths after obtaining the curves in Figures II and III. It shows possibly a slight and irregular prolongation of the pause at the end of expiration. Time in 5 seconds.

11. Finally, we had another and even more marked example of this type of respiration as follows: On removal of the intratracheal tube the dog became evanotic and it was necessary to reintroduce the tube to maintain life. respiratory exertions of the animal were extreme and it appeared as though the diaphragm and intercostal muscles might not be working synchronously. On opening the abdomen, however, we found that the diaphragm and chest muscles were contracting in perfect unison and to an obviously great extent. As the air-way was free, we were at a loss to explain the phenomenon until it was suggested that a pneumothorax existed; on investigation the lungs were found two-thirds collapsed.

We therefore believe our technic for avoiding pneumothorax in dog No. 11 was faulty and that the Cheyne-Stokes respiration, existing for about a month after the operation, was due to difficult aëration of the lungs from the existence of a partial pneumothorax, and was consequently independent of the vagus operation. The prolongation of the expiratory phase in Figure IV, four months after the operation, is so slight that it cannot be classed as really abnormal.

According to our experiments, the respiratory rhythm is not

affected by division of the pulmonary branches of the vagi. Our evidence is, therefore, against Meltzer's hypothesis, which is an elaboration of that of Hering and Breuer, that the respiratory rhythm is normally controlled by stimuli created by the alternate expansion and collapse of the lungs and which pass to the respiratory centre over two separate sets of nerves fibres in the vagus trunk. It is to be noted, however, that our experiments are not concerned with the question whether the vagi contain fibres that, on electrical stimulation, will incite or inhibit respiration, but only with the part which they are supposed to play in the normal regulation of respiration.

RESPONSE TO AN INCREASE OF CARBON DIOXIDE AND TO A DECREASE OF OXYGEN IN THE INSPIRED AIR

In the preceding section we have shown that division of the pulmonary branches of the vagi did not demonstrably affect respiration when breathing normal air. To gain still further evidence in regard to the possible functions of the vagi over the respiratory process, we arranged the following experiments.

The soda lime absorber was removed from the Benedict respiration apparatus and a large air container inserted to increase the total volume of air in the apparatus. In consequence, the carbon dioxide in the inspired air gradually increased; the oxygen at the same time decreased somewhat, though not sufficiently to be a material factor in the experiment.

The character of the response to the gradual increase of the carbon dioxide is shown in Figure V, together with the analyses of the inspired air samples obtained at the points indicated.

These experiments confirm the findings of Haldane and Lorrain Smith⁹ that the stimulation of the vagus nerve endings by carbonic acid has nothing to do with hyperpnoea.

⁷ Meltzer: The self-regulation of respiration. N. Y. Med. Jour., 1890, li, Jan. 18; lii, Nov. 22.

^{*} Hering and Breuer: Die Selbsteuerung der Athmung durch den Nervus Vagus. Sitzgsber. d. Wiener Acad., Math.-natur., 1868, lvii, 672; lviii, 909.

⁹ Haldane and Lorrain Smith: The physiological effects of air vitiated by respiration. Jour. Path. and Bact., 1892, i, 168-186.

The effect of oxygen want was tested by introducing air instead of oxygen into the Benedict apparatus to maintain a constant air volume, and at the same time to lower gradually the oxygen percentage (the carbon dioxide being absorbed as usual). Under these conditions the respirations increased quite markedly in rate but only slightly in depth, as shown by Figure VI. A more pronounced effect is shown in Figure VII, where the oxygen was low throughout the experiment. The effect of



Fig. V. Subject, Dog No. 18. Upper curve is the spirometer tracing showing reaction to the gradual increase of CO_2 in the inspired air. The middle curve is made by the work adder and shows the total ventilation. Lower curve is the time in 5 seconds. Samples of the inspired air were taken at the points indicated. (1) CO_2 , 0.51 per cent; O_2 , 18.00 per cent; (2) CO_2 , 2.73 per cent; (3) CO_2 , 4.80 per cent; (4) CO_2 , 6.03 per cent; O_2 , 10.68 per cent. At point A the tap on the apparatus was turned to allow the CO_2 to accumulate; at B the tap was turned so that the CO_2 was absorbed. The change in the level of the tracing before A is due to adding O_2 . The change upwards at B is due to the absorption of CO_2 ; and the change downwards to a rapid addition of O_2 . These changes in the level of the curve have no significance as far as the subject is concerned.

oxygen want, as shown in these two figures, is unlike that obtained from the rise in the alveolar carbon dioxide pressure, as shown by Figure V, where the depth of the respiration is more markedly increased than the rate.

The curves here shown of the effect of carbon dioxide increase and oxygen want are in every way similar to those obtained by Haldane and others for the effect of such conditions in man; they are similar to the curves obtained by us on a normal dog.

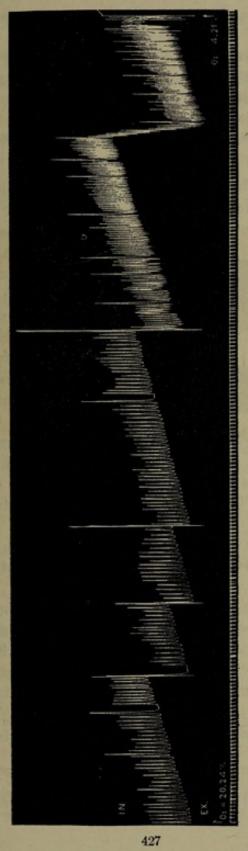


Fig. VI. Subject, Dog No. 18. Shows reaction to a gradual decrease in the O2 in the inspired air from 20.24 per cent at the beginning to 4.21 per cent at the end. Time in 5 seconds.

It is possible, therefore, to conclude that the vagus nerve does not contain fibres which transmit impulses arising from variations in the composition of the alveolar air.

INFLUENCE OF THE VAGUS ON THE SECRETORY POWER OF THE LUNGS

Maar¹⁰ has described experiments which, he believed, showed evidence of the influence of the vagus nerve on the gas secretion of the lungs. Krogh¹¹ later pointed out that the results obtained

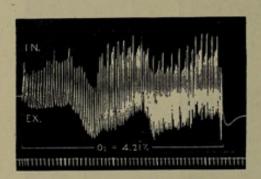


Fig. VII. Subject, Dog No. 18. This curve obtained about twenty minutes after the curve in Fig. VI. It shows the reaction on being suddenly made to breathe air containing only 4.21 per cent of O₂. Time in 5 seconds.

by Maar could be explained by a vasomotor, instead of a direct secretory influence.

The metabolic experiments already cited indicate that there is no impairment of the gas exchange function of the lungs. However, as Haldane and Douglas¹² only claim a secretory action in a condition of oxygen want, we arranged a few experiments to test the effect on the oxygen intake under conditions of oxygen want.

The Benedict apparatus was

arranged with an extra container to enlarge the total volume of air in the apparatus, and air (carbon dioxide free), was used instead of oxygen to maintain a constant volume. In other respects the metabolic experiments were conducted as those described previously. The analyses of the inspired air at the beginning and at the end of the experiments, together with the metabolic data, are given in Table II.

¹⁰ Maar: Exp. Untersuchungen uber den Einfluss des Nervus Vagus und des Nervus Sympathicus auf den Gaswechsel der Lungen. Skand. Arch. f. Physiol., 1902, xiii, 269-336.

¹¹ Krogh: On the mechanism of the gas exchange in the lungs of the tortoise. Skand. Arch. f. Physiol., 1909, xxiii, 200-216.

¹² Haldane and Douglas: The causes of the absorption of oxygen by the lungs. Jour. Phys., 1912, xliv, 4, 305-354.

From these experiments it is evident that in spite of the low oxygen tension in the inspired air (about 30 mm.), the animals absorbed as much oxygen per minute as when breathing pure air. In fact, they showed in several instances a distinctly greater intake. This is due to the fact that the very low oxygen tension, necessarily existing in the blood, caused the animals to be somewhat restless. In the region of the belly it was easily seen that the blood was quite cyanotic.

TABLE II

Respiratory exchange under conditions of oxygen want

			NO.	PREVIO	OUS MEAL	DI	BON OX- OE	oxy	GEN	To the	-	GEN
DATE	POG	DOG	EXPER.	Time	Character	Per min.	Per min. Per kilo per min.		Per kilo per min.	RESP. QUO.	Start	End
		kilos				cc.	cc.	cc.	cc.		per cent	per cent
Aug. 24	No. 18	13.2	1	8/23; 12 n.	Meat diet largely	100	7.6	120	9.1	0.84	20.24	4.21
Oct. 7	No. 11	14.2	1	Annual Control of the	Meat diet largely	104	7.3	114	8.0	0.91	24.71	11.14
Oct. 7	No. 11		2	The state of the s	Meat diet largely		160				1	
Oct. 7	No. 11		3	3.30 p.m.	Meat diet largely						20.03	
Oct. 7	No. 11		4	3.30 p.m.	Meat diet largely	1	100				12.51	
The same					De Survius	110	7.7	113	8.0	0.97	1	

These experiments throw no direct evidence on the question of gas secretion as opposed to the theory of simple diffusion. They do, however, indicate that the process of gas exchange is not interfered with by the cessation of its vagus nerve supply. It is fair to presume that if the lungs were a true secretory organ for oxygen, interference with the nerve supply would result in a greater impairment of the function than if the gas passed through the organ according to the physical laws of diffusion.

Therefore, as the passage of oxygen through the lungs, even at a low tension, is apparently not interfered with by the division of the vagi, the evidence offered is against the assumption of a secretory function of the lungs, or at least, it indicates that if such a function does exist the vagi do not govern the secretory action.

SUMMARY

All the branches of both right and left vagi between the recurrent laryngeal and the two primary gastro-intestinal branches were divided. Three to four months after recovery from the operation the effect of such a division of the vagi on the respiratory function of the lungs was tested in several ways and compared with similar experiments carried out on a dog with intact vagi.

The following evidence was obtained.

- 1. The metabolism of the vagotomized dogs as evidenced by the oxygen consumption and the carbon dioxide elimination per minute, as well as the respiratory quotient, was in no way abnormal or demonstrably affected.
- 2. The respiratory rhythm in three out of the four dogs showed no abnormality whatever. One animal showed a very slightly prolonged wait at the end of expiration before beginning inspiration, together with a slight irregularity in respiration. This same dog immediately after operation exhibited a Cheyne-Stokes type of respiration, probably due to a post-operative partial pneumothorax.
- 3. The response of the respiratory mechanism to an increase of carbon dioxide and decrease of oxygen in the inspired air was in no way different from the normal response so well known in man or from that found in a normal animal.
- 4. The passage of oxygen, even at a low tension, through the lungs, whether by diffusion or by secretion, was not demonstrably affected by division of the pulmonary branches of the vagi.

CONCLUSION

The pulmonary branches of the vagus nerves do not appear to transmit impulses that control functions in any way essential to life. More specifically they do not appear to possess any demonstrable power over the normal regulation of the gaseous metabolism, the pulmonary ventilation, or the gas exchange in the lungs. TABLE III

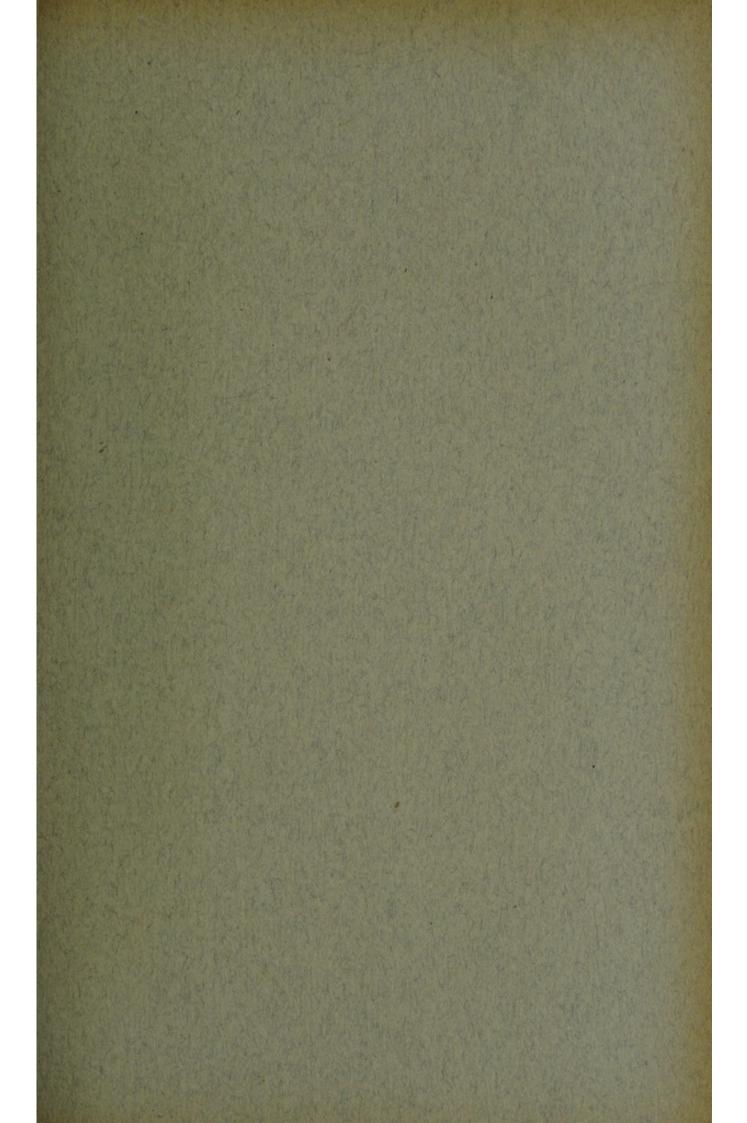
Respiratory exchange

-		ACTIVITY OF DOG			Very quiet.	Very quiet	Shivered during entire experiment		Very quiet Occasional movements Occasional movements			
	KOE	on?	Hesp. C		0.70	0.76	0.82	0.75	0.75	0.75		
	ЕХСИА	per kilo se nim. o		8	7.3	7.1	8.9	7.8	8.9 9.7 9.4	9.3		
	TORY	Ox	per min.	ė	41	40	20	4	117	123		
-	RESPIRATORY EXCHANGE	per min. Doxide		per kilo gion		8	5.2	5.4	7.3	5.9	6.7	7.0 123
		Oğ	per min.	99	29	30	41	33	888	93		
	SPIROMETER EXPERIMENT	Hesb. Quo.							0.73	87 123 0.71		
	SPIROMETER EXPERIMENT	·u	CO ₂ Der mi Der mi	8					87 119 89 122 80 116 93 134	123		
	SP	n.	ber mi	8					88 88 88	87		
	PREVIOUS MEAL	aracter			Meat diet largely	Meat diet largely	Meat diet largely		Meat diet largely Meat diet largely Meat diet largely			
	PREVI				9/7; 11 a.m.	9/7; 11 a.m.	9/8; 3.30 p.m.		8/23; 12 n. 8/23; 12 n. 8/23; 12 n.			
	ON.				1 6	00	4		- 64 60			
	D D G H		kilos	5.6	5.6	5.6		13.2				
	w pod			Normal	No. 1	No. 1	No. 1		Vagus Dogs No. 18 No. 18 No. 18			
-	DATE				Sept. 8		Sept.		Aug. 24 Aug. 24 Aug. 24			

TABLE III-Continued.

	ACTIVITY OF DOG			Whining during last three minutes of experiment	Restless	Very quiet	Absolutely quiet	Restless Moved once		Very restless	Quiet	Occasionally restless	Very quiet	Very quiet	Moved once slightly Absolutely quiet		continuo	Shivering part of experi-	ment Quiet	Shivering and somewhat	Tognicas	
NGE	·on;	P. qsoH		92.0	0.70	0.77	0.77	0.76	0.75	0.73	0.71	0.73	08.0	0.75	0.74	0.74	68.0	0.81	08.0	0.77		0.82
RESPIRATORY EXCHANGE	Oxygen	per kilo per min.	.00	8.6	7.6	8.7	8.1	9.8	9.2	10.4	8.2	8.2	7.6	7.8	7.5	8.1	9.6	7.5	7.2	7.6		8.0
TORY	0	per min.	8	126	125	112	105	127	119	173	136	136	126	129	125	134	137	107	102	108		114
RESPIRA	Carbon	per min.	89.	7.4	6.7	9.9	6.2	6.8	6.9	7.5	5.8	0.9	6.0	5.8	5.6	0.9	8.6	6.1	5.8	5.8		9.9
	ರೆದೆ	per min.	8	96	87	38	8	8 8	89	125	96	66	100	8	8 28	66	122	87	82	88	1	8
SPIROMETER	100	P. qsoH		0.67	0.76				0.72	1												
PER	.n	per mi	8	93	88	74101			97	1						1			114			
SP	.0	CO ₂ per mi per mi	g	62	74				102	1												
PREVIOUS MEAL		Character		Meat diet largely	Meat diet largely	Meat diet largely	diet	Meat diet largely Meat diet largely		Meat diet largely	Meat diet largely	Meat diet largely	Meat diet largely	Meat diet largely	Meat diet largely Meat diet largely		Meat diet largely	Meat diet largely	Meat diet largely		The state of the s	The state of the s
PREVIO		Time		8/26; 4 p.m.	8/26; 4 p.m.	4		8/26; 4 p.m. 8/26; 4 p.m.	120	9/1: 3.30 p.m.	3.30	3.30	3.30	9/2; 3.30 p.m.	9/2; 3.30 p.m. 9/2; 3.30 p.m.	- The state of the	9/10; 3.30 p.m.	9/10; 3.30 p.m.	9/10; 3.30 p.m.	9/10; 3.30 p.m.	The state of the s	
.01	LN3D	пизаха	1	-	63	3	4	0 9	1	1-	2				9 2		-	53		4		
1	WEIGHT	Dod	Ai'os	12.9	12.9	12.9	12.9	12.9	1	16.6	16.6	16.6	16.6	16.6	16.6			14.2	14.2	14.2		
-	900			No. 15	No. 15		No. 15	No. 15 No. 15		No. 23				No. 23	No. 23 No. 23			No. 11	No. 11	No. 11		
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