

THE PREDOMINANT INFLUENCE OF THE LEFT VAGUS  
NERVE UPON CONDUCTION BETWEEN THE  
AURICLES AND VENTRICLES IN THE DOG.\*

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PLATE 74.

It has been shown by one of us (1) that the normal production of impulses in the region of the sino-auricular node is inhibited by stimulation of the right vagus nerve to a greater extent than by stimulation of the left. Earlier observations, which are fully discussed in that paper, had indeed indicated that such might prove to be the case; but a clear demonstration of the preponderating influence of the right vagus upon the sino-auricular node, in which structure the normal impulses are almost certainly generated, had not been published.

In the same paper, as in the discussed observations of previous workers, it was stated that the left vagus had an influence upon the tissues uniting auricle and ventricle which was not obtained on stimulating the right vagus nerve, stimulation of the left vagus nerve producing high grades of heart-block. A comparison of the right and left vagi in this respect has not been possible in previous experiments, for the reason that the right vagus slows the auricle to a greater extent than does the left. It seemed possible to us that the profound effect of left vagal stimulation upon conduction over the A-V junction, and the absence of such effect or the observation of a lesser effect upon stimulation of the right vagus upon the same region of the heart, may have been due to the usual difference in the retardation of auricular rate. For we know that auriculoventricular heart-block is favored by high auricular rate (2 and 3). We

\*Dr. Lewis's expenses have been defrayed by grants from the Graham Research Fund and the Royal Society. The observations were undertaken in London. Received for publication, September 25, 1913.

therefore determined to examine the influence of right and left vagal stimulation upon A-V conduction while the auricular rate was maintained artificially at a constant level.

#### METHOD.

Dogs<sup>1</sup> were employed exclusively and were anesthetized with morphia, paraldehyde, and ether. Records of the heart beat were taken electrocardiographically, lead II being utilized. The cut vagi have been stimulated by means of a faradic current, the primary circuit of the inductorium being excited at a constant voltage, the secondary coil being placed at fixed points, and the leads from secondary coil to right and left nerves, running through a simple mercurial commutator, having equal resistances. The right and left vagus nerves have been stimulated alternately, usually the right nerve first, but from time to time the left. Sufficient time for complete recovery elapsed between successive stimulations. On occasion we reversed the positions of the stimulating electrodes, but our results remained the same.

The auricles were controlled by rhythmic induction shocks, at or a little above threshold value, applied through a window in the chest wall to the right auricular appendix or to the area surrounding the sino-auricular node; we chose this area for stimulation so as to ensure auricular complexes of identifiable form.

#### RESULTS.

The detailed results of seven experiments are given in the following tables. Each experiment includes a number of observations. The effects of right and left vagal stimulation are expressed in the end columns: P-R + signifies a prolongation of conduction interval; 2:1, 3:1, 4:1, etc., expresses the ratio of auricular and ventricular rates and the degree of heart-block; 2:1<sup>3</sup> indicates the occurrence of three 2:1 cycles; A. F. indicates the onset of auricular fibrillation sometimes seen upon stimulation; "slight slowing" refers to slowing of the whole heart without alteration of sequence. Each experiment is summarized at the end of the corresponding section of the table. The first column tells whether the auricles were artificially maintained at a constant rate of action ("As stim."), or

<sup>1</sup> The operative procedures were undertaken by Lewis.

whether the observation consisted of simple vagal stimulation ("control"). The rate of the auricles, under one or the other condition, is given in the second column. The remaining columns refer to the length of stimulation and the position of the secondary coil.

We may briefly sum up our results in a second table (table II). In five out of seven experiments, simple stimulation of the right and left vagus ("controls") yielded the customary effects and characteristic differences of effect. The right vagal stimulation yielded profound slowing of the whole heart,<sup>2</sup> or stoppage of the auricle with escape of the ventricles; the left vagal stimulation a moderate degree of auricular retardation with the development of partial heart-block. In two experiments (dogs DU and DW) right and left stimulations yielded, in the control observations, simple slowing of the whole heart, in one case the effect of the left nerve being the greater, in the other case the effects being equal on the two sides and being accompanied by an equal increase of the conduction interval.

TABLE I.

Dog DS. August 5, 1913.

Experiment.	Rate of heart.	Vagus.	Length of stimulus in seconds.	Secondary coil at	Right.	Left.
1. Control..	105.0	Left	6.2	23	As stopped; 1 Vs escaped	P-R ++, 4:1.
2. Control..	99.0	Right	5.2	23		
3. As stim..	194.0	Left	5.0	23	15:1, 2:1 <sup>2</sup> , P-R ++	19:1, P-R ++.
4. As stim..	194.0	Right	5.0	23		
5. As stim..	192.0	Left	4.6	25	No effect	P-R +, 1:1.
6. As stim..	192.0	Right	5.4	25		
7. As stim..	143.1	Left	5.2	25	P-R ++, 2:1 <sup>4</sup>	P-R ++, 4:1 <sup>2</sup> , 2:1 <sup>2</sup> .
8. As stim..	137.0	Right	6.0	20		
9. As stim..	138.4	Right	5.3	25	P-R ++, 2:1 <sup>3</sup> , A.F.	P-R ++, 1:1.
10. As stim..	138.4	Left	5.7	25		

*Summary.*—The control stimulations showed the usual differences between stimulation of the right and left nerves. With the auricular rate maintained, the left gave a higher grade of block than the right on two occasions, the same grade on one, and a lesser grade on one occasion.

<sup>2</sup> With or without slight prolongation of the conduction interval.

*Dog DT. August 11, 1913.*

Experiment.	Rate of heart.	Vagus.	Length of stimulus in seconds.	Secondary coil at	Right.	Left.
1. As stim...	No time marker	Right	5.0	20	3:I, 4:I <sup>2</sup> , 3:I, 2:I	4:I, 2:I <sup>2</sup> , 4:I, 2:I <sup>2</sup> .
		Left	5.0	20		
2. As stim...	No time marker	Right	5.0	20	3:I, 2:I, 3:I <sup>2</sup> , 2:I	2:I, 3:I, 1:I, 2:I.
		Left	5.0	20		
3. As stim...	210.0	Left	4.8	20	3:I, 4:I, 13:I (2RVs), 2:I	3:I, 5:I, 4:I, 2:I <sup>2</sup> .
	210.0	Right	5.5	20		
4. Control...	180.0	Left	4.5	20	3P'+3RVs	2:I <sup>2</sup> .
	175.6	Right	5.2	20		
5. As stim...	210.0	Left	5.3	22	P-R+	P-R slightly+.
	195.6	Right	5.2	22		
6. As stim...	219.0	Left	4.8	20(?)	P-R+, 2:I <sup>2</sup> , 1:I, 2:I <sup>2</sup>	P-R+, 2:I.
	217.0	Right	5.2	20(?)		
7. As stim...	212.2	Right	4.9	21	5:I, 4:I <sup>2</sup> , 3:I, 2:I	P-R+, 3:I, 2:I, 3:I, 2:I <sup>2</sup> .
	216.6	Left	5.6	21		

*Summary.*—Control stimulations gave usual differences in reaction to right and left vagal stimulations. With the auricular rate maintained, right vagal stimulation gave greater degrees of heart-block than the left on all six occasions.

*Dog DU. August 14, 1913.*

Experiment.	Rate of heart.	Vagus.	Length of stimulus in seconds.	Secondary coil at	Right.	Left.
1. Control...	184.2	Left	5.5	21	Slowing only	Slowing only.
	182.0	Right	4.6	21		
2. As stim...	228.3	Left	4.6	21	3:I <sup>2</sup> , 4:I, 3:I, 10:I, A.F.	3:I, 6:I, 8:I, 1:I, 1(regular):I.
	232.0	Right	6.4	21		
3. Control...	201.0	Right	5.5	22	Slight slowing only	Moderate slowing only.
	196.5	Left	4.9	22		
4. As stim...	225.6	Right	5.2	21½	2:I <sup>2</sup> , 1:I <sup>2</sup> , 2:I, 5:I, 3:I	20:I, A.F.
	228.6	Left	5.1	21½		
5. Control...	192.0	Right	5.3	21½	Moderate slowing only	More slowing than R; no block.
	188.4	Left	6.2	21½		

*Summary.*—The control stimulations gave an unusual effect. Simple slowing was obtained with stimulation of both nerves, the effect being greater on the left side. The auricular rate being maintained, no difference was found in the degree of block produced by stimulating the two nerves.

Dog DV. August 15, 1913.

Experiment.	Rate of heart.	Vagus.	Length of stimulus in seconds.	Secondary coil at	Right.	Left.
1. Control...	112.5	Right	Signal not photographed	25 1/2	Slowing only	6:1 (Vs stopped).
	114.6	Left		25 1/2		
2. As stim...		Right	Signal not photographed	23	No effect	2:1 <sup>2</sup> , 6:1, 5:1, 2:1 <sup>2</sup> alternation.
		Left		23		
3. As stim...	164.0	Right	5.1	22	3:1, 2:1 <sup>5</sup> , P-R+	15:1, 2:1 <sup>2</sup> , P-R+.
	165.0	Left	5.3	22		
4. As stim.	189.0	Right	Only 3.6 stim. photographed	22	2:1 <sup>6</sup> , P-R+ alternation	16:1, 2:1 <sup>2</sup> , P-R+.
	192.0	Left		5.2		
5. As stim... Control...	186.0	Right	5.9	22	P-R+, 2:1 <sup>2</sup>	P-R+, 2:1 <sup>4</sup> .
	163.05	Left	6.1	22		
6. Control...	171.6	Right	5.1	21	Slowing with P-R+	P-R+, 2:1 <sup>4</sup> .
	167.4	Left	5.1	21		
7. As stim...	192.0	Right	5.6	21	Disordered rhythm, 2:1 <sup>2</sup> , 4:1, 5:1, 2:1	P-R+, 8:1, 4:1 <sup>2</sup> , 2:1 <sup>2</sup> .
	194.0	Left	5.3	21		

Summary.—The control stimulations gave the usual effects. The auricular rate being maintained, left vagal stimulation produced a greater degree of heart-block than the right on all four occasions.

Dog DW. August 18, 1913.

Experiment.	Rate of heart.	Vagus.	Length of stimulus in seconds.	Secondary coil at	Right.	Left.
1. Control...	156.0	Right	5.7	22	Slowing with P-R slightly +	Slowing with P-R slightly +.
	154.5	Left	5.5	22		
2. As stim...	192.0	Right	5.6	22	P-R slightly +, 5:1, 4:1, 6:1, 2:1, 4:1 <sup>3</sup> , 2:1	P-R++, 5:1, 12:1, A.F.
	186.0	Left	5.6	22		
3. As stim...	188.4	Right	6.1	22	6:1, 12:1, 2:1	8:1, 12:1, A.F.
	184.5	Left	6.2	22		

Experiment.	Rate of heart.	Vagus.	Length of stimulus in seconds.	Secondary coil at	Right.	Left.																			
4. As stim...	186.0	Right	6.2	22½	P-R +, 2:I <sup>2</sup> , 1:I <sup>2</sup> , 2:I <sup>3</sup>	P-R ++, 2:I <sup>4</sup> , 4:I, 2:I.																			
	186.0	Left	5.6	22½			5. Control...	156.3	Right	5.6	22½	Slowing with P-R slightly +	Slowing with P-R slightly +.	159.0	Left	6.3	22½	6. As stim...	180.0	Right	5.3	22½	P-R +, 2:I <sup>2</sup> , 1:I, 2:I <sup>2</sup>	P-R ++, 2:I <sup>6</sup> .	180.0
5. Control...	156.3	Right	5.6	22½	Slowing with P-R slightly +	Slowing with P-R slightly +.																			
	159.0	Left	6.3	22½			6. As stim...	180.0	Right	5.3	22½	P-R +, 2:I <sup>2</sup> , 1:I, 2:I <sup>2</sup>	P-R ++, 2:I <sup>6</sup> .	180.0	Left	5.8	22½								
6. As stim...	180.0	Right	5.3	22½	P-R +, 2:I <sup>2</sup> , 1:I, 2:I <sup>2</sup>	P-R ++, 2:I <sup>6</sup> .																			
	180.0	Left	5.8	22½																					

*Summary.*—The control effects were unusual in type, simple slowing of equal amounts being obtained from the right and left vagi. The auricular rate being maintained, left vagal stimulation produced a greater degree of heart-block than the right on all four occasions.

*Dog DX. August 21, 1913.*

Experiment.	Rate of heart.	Vagus.	Length of stimulus in seconds.	Secondary coil at	Right.	Left.																																																				
1. Control...	134.6	Right	5.12	23	Slowing only	3:I, 2:I <sup>2</sup> , P-R +.																																																				
	135.0	Left	5.14	23			2. As stim...	203.4	Right	5.00	23	P-R, 2:I <sup>5</sup>	P-R ++, 17:I, 2:I.	201.0	Left	4.92	23	3. As stim... (Figures 3 and 4)	195.0	Right	4.88	23	P-R +, 2:I <sup>2</sup>	P-R ++, 18:I.	204.0	Left	5.12	23	4. Control... (Figures 1 and 2)	159.6	Right	5.36	23	Slowing only	3:I, 2:I <sup>3</sup> , P-R +.	156.9	Left	5.29	23	5. As stim... (Figures 5 and 6)	193.5	Right	5.40	23½	P-R slightly +, 1:I	P-R ++, 5:I, 3:I, 3:I <sup>2</sup> .	188.1	Left	4.89	23½	6. Control...	152.1	Right	5.16	23½	Slowing only	P-R +, 3:I, 2:I <sup>3</sup> .	152.1
2. As stim...	203.4	Right	5.00	23	P-R, 2:I <sup>5</sup>	P-R ++, 17:I, 2:I.																																																				
	201.0	Left	4.92	23			3. As stim... (Figures 3 and 4)	195.0	Right	4.88	23	P-R +, 2:I <sup>2</sup>	P-R ++, 18:I.	204.0	Left	5.12	23	4. Control... (Figures 1 and 2)	159.6	Right	5.36	23	Slowing only	3:I, 2:I <sup>3</sup> , P-R +.	156.9	Left	5.29	23	5. As stim... (Figures 5 and 6)	193.5	Right	5.40	23½	P-R slightly +, 1:I	P-R ++, 5:I, 3:I, 3:I <sup>2</sup> .	188.1	Left	4.89	23½	6. Control...	152.1	Right	5.16	23½	Slowing only	P-R +, 3:I, 2:I <sup>3</sup> .	152.1	Left	5.14	23½								
3. As stim... (Figures 3 and 4)	195.0	Right	4.88	23	P-R +, 2:I <sup>2</sup>	P-R ++, 18:I.																																																				
	204.0	Left	5.12	23			4. Control... (Figures 1 and 2)	159.6	Right	5.36	23	Slowing only	3:I, 2:I <sup>3</sup> , P-R +.	156.9	Left	5.29	23	5. As stim... (Figures 5 and 6)	193.5	Right	5.40	23½	P-R slightly +, 1:I	P-R ++, 5:I, 3:I, 3:I <sup>2</sup> .	188.1	Left	4.89	23½	6. Control...	152.1	Right	5.16	23½	Slowing only	P-R +, 3:I, 2:I <sup>3</sup> .	152.1	Left	5.14	23½																			
4. Control... (Figures 1 and 2)	159.6	Right	5.36	23	Slowing only	3:I, 2:I <sup>3</sup> , P-R +.																																																				
	156.9	Left	5.29	23			5. As stim... (Figures 5 and 6)	193.5	Right	5.40	23½	P-R slightly +, 1:I	P-R ++, 5:I, 3:I, 3:I <sup>2</sup> .	188.1	Left	4.89	23½	6. Control...	152.1	Right	5.16	23½	Slowing only	P-R +, 3:I, 2:I <sup>3</sup> .	152.1	Left	5.14	23½																														
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	188.1	Left	4.89	23½			6. Control...	152.1	Right	5.16	23½	Slowing only	P-R +, 3:I, 2:I <sup>3</sup> .	152.1	Left	5.14	23½																																									
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	152.1	Left	5.14	23½																																																						

*Summary.*—The control stimulation gave the usual differences on the two sides. With the auricular rate maintained, left vagal stimulation gave greater degrees of heart-block on all three occasions.

Dog DY. August 21, 1913.

Experiment.	Rate of heart.	Vagus.	Length of stimulus in seconds.	Secondary coil at	Right.	Left.																																																																																	
7. Control.	230.4	Right	5.6	23	Slowing with P-R slightly +	P-R ++, 3:I, 2:I <sup>4</sup> .																																																																																	
	227.6	Left	4.72	23			8. As stim..		Right	5.2	23	P-R +, 4:I, 6:I, 4:I <sup>2</sup> , 2:I <sup>2</sup>		9. Control.	211.4	Right	5.2	22 ½	Slowing with P-R +	P-R ++, 2:I <sup>3</sup> .	210.0	Left	5.16	22 ½	10. As stim..	210.0	Right	5.32	22 ½	P-R +, 3:I, 2:I, 6:I, 3:I	P-R +, 4:I, 8:I, 4:I, 2:I.	210.0	Left	5.14	22 ½	11. Control.	198.0	Right	5.44	22 ½	Slowing with P-R slightly +	P-R +, 3:I, 2:I <sup>4</sup> .	198.0	Left	5.56	22 ½	12. As stim..	210.0	Right	5.4	22 ½	P-R +, finally A.F.	P-R +, 12:I, 4:I, 2:I <sup>2</sup> .	212.0	Left	5.2	22 ½	13. Control.	188.1	Right	4.98	22 ½	Slowing with P-R +	P-R +, 3:I, 4:I, 2:I <sup>3</sup> .	185.1	Left	5.4	22 ½	14. As stim..	240.0	Right	5.92	22 ½	P-R +, 3:I, 6:I, 8:I, 3:I, 2:I	P-R +, 18:I (+I LVs), 3:I, 2:I.	243.6	Left	5.0	22 ½	15. Control.		Right	4.72	22 ½	Slowing with P-R +	P-R +, 9:I, 2:I.	173.8
8. As stim..		Right	5.2	23	P-R +, 4:I, 6:I, 4:I <sup>2</sup> , 2:I <sup>2</sup>																																																																																		
9. Control.	211.4	Right	5.2	22 ½	Slowing with P-R +	P-R ++, 2:I <sup>3</sup> .																																																																																	
	210.0	Left	5.16	22 ½			10. As stim..	210.0	Right	5.32	22 ½	P-R +, 3:I, 2:I, 6:I, 3:I	P-R +, 4:I, 8:I, 4:I, 2:I.	210.0	Left	5.14	22 ½	11. Control.	198.0	Right	5.44	22 ½	Slowing with P-R slightly +	P-R +, 3:I, 2:I <sup>4</sup> .	198.0	Left	5.56	22 ½	12. As stim..	210.0	Right	5.4	22 ½	P-R +, finally A.F.	P-R +, 12:I, 4:I, 2:I <sup>2</sup> .	212.0	Left	5.2	22 ½	13. Control.	188.1	Right	4.98	22 ½	Slowing with P-R +	P-R +, 3:I, 4:I, 2:I <sup>3</sup> .	185.1	Left	5.4	22 ½	14. As stim..	240.0	Right	5.92	22 ½	P-R +, 3:I, 6:I, 8:I, 3:I, 2:I	P-R +, 18:I (+I LVs), 3:I, 2:I.	243.6	Left	5.0	22 ½	15. Control.		Right	4.72	22 ½	Slowing with P-R +	P-R +, 9:I, 2:I.	173.8	Left	4.88	22 ½															
10. As stim..	210.0	Right	5.32	22 ½	P-R +, 3:I, 2:I, 6:I, 3:I	P-R +, 4:I, 8:I, 4:I, 2:I.																																																																																	
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Summary.—The control stimulations gave the usual differences on the two sides. With the auricular rate maintained, stimulation of the left vagus gave greater degrees of heart-block than the right on all three occasions.

In all the experiments, while the auricular rate was maintained at a constant level throughout an observation, profound changes in conduction were obtained, but the effects were unequal on the two sides. In all but one experiment the left vagus was the more potent in producing heart-block. In the single experiment (DT) in which the right nerve seemed more potent than the left in this respect, the difference in effect was relatively small. It is of interest to note

that in the control stimulations of this experiment, conduction effects were noted only upon stimulation of the left nerve. This experiment suffices to emphasize the impossibility of comparing the actual conduction defects produced by simple stimulation of the two nerves, and the necessity of maintaining a constant auricular rate.

TABLE II.

No. of dog.	Date.	Controls.	Effect on conduction present.		Greater effect on conduction.
			Right.	Left.	
DS	Aug. 5, 1913	Usual effects with characteristic difference	+	+	Left.
DT	Aug. 11, 1913	Usual effects with characteristic difference	+	+	Right.
DV	Aug. 15, 1913	Usual effects with characteristic difference	+	+	Left.
DX	Aug. 21, 1913	Usual effects with characteristic difference	+	+	Left.
DY	Aug. 21, 1913	Usual effects with characteristic difference	+	+	Left.
DU	Aug. 14, 1913	Simple slowing on both sides, the left being more effective	+	+	Left.
DW	Aug. 18, 1913	Simple and equal slowing on the two sides	+	+	Left.

Briefly, our results clearly indicate that both right and left vagal stimulation hinders the passage of impulses from auricle to ventricle, and show that the difference in action is quantitative rather than qualitative. The left nerve has more control over the junctional tissues than the right. Now we have seen that so far as impulse formation in the auricle is concerned, the opposite is the case, the right nerve being the more potent; yet here again the difference is quantitative rather than qualitative. We may sum up our knowledge of the vagi in the dog in the statement that while both nerves usually affect impulse formation and impulse conduction, the right nerve chiefly controls the former and the left nerve the latter.

These facts are of more interest in the light of recent physio-



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EXPLANATION OF PLATE 74.

The figures are all taken from dog DX, August 21, 1913. They are from lead II. The interval between each pair of ordinates equals 0.04 of a second. The uppermost line is a signal showing the duration of the stimulus applied to the vagus nerve.

FIG. 1. Stimulation of right vagus nerve. Control.

FIG. 2. Stimulation of left vagus nerve. Control.

FIG. 3. Stimulation of right vagus nerve. The auricles received 195 induction shocks per minute.

FIG. 4. Stimulation of left vagus nerve. The auricles received 204 induction shocks per minute.

FIG. 5. Stimulation of right vagus nerve. The auricles received 193.5 stimuli per minute.

FIG. 6. Stimulation of left vagus nerve. The auricles received 188.1 stimuli per minute.

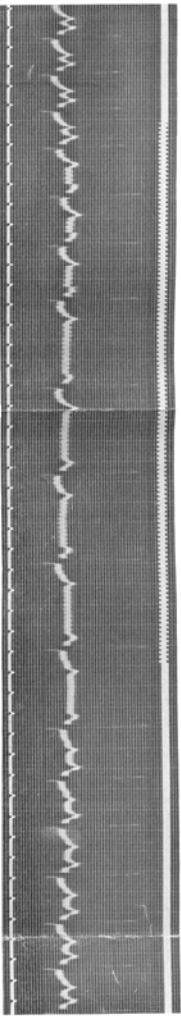


FIG. 1.

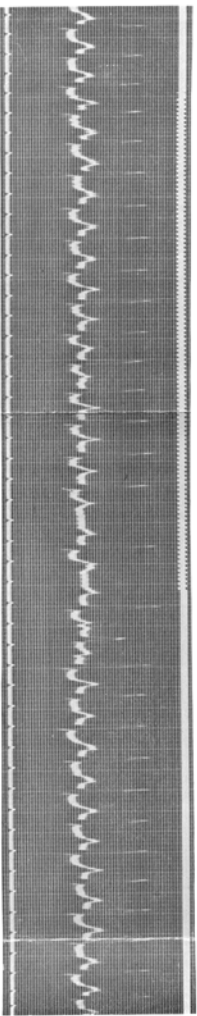


FIG. 2.

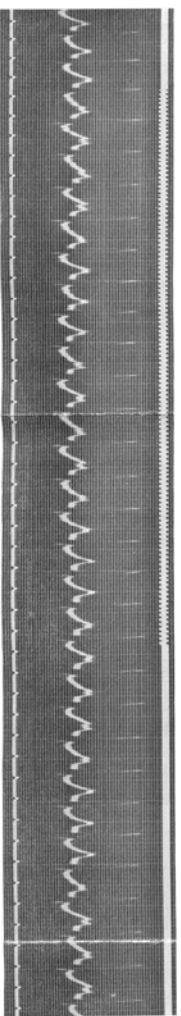


FIG. 3.

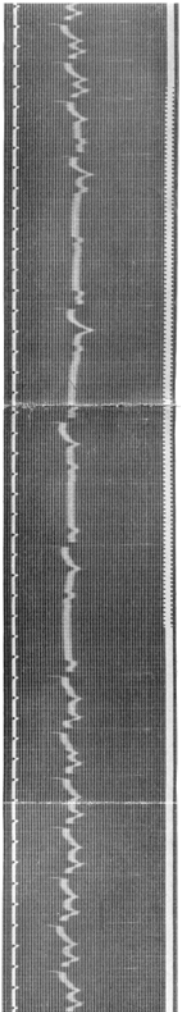


FIG. 4.

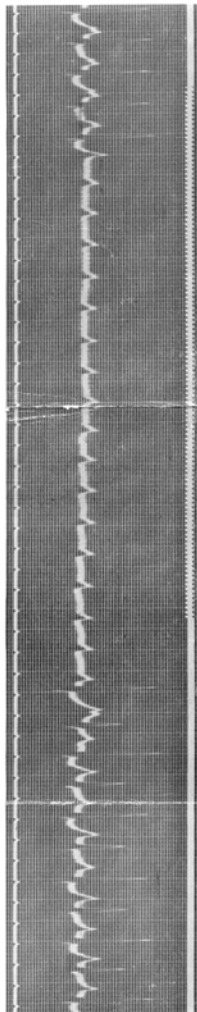


FIG. 5.

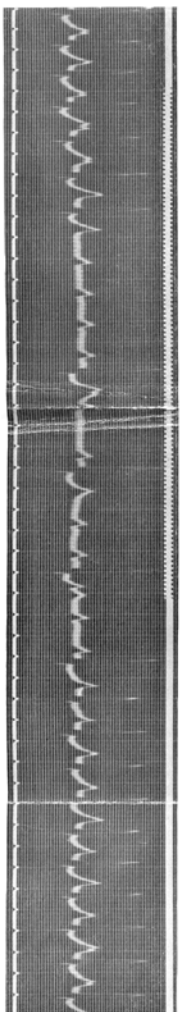


FIG. 6.

(Cohen and Lewis: Influence of Left Vagus Nerve)

logical and morphological observations. We are taught, on the one hand, that the sino-auricular node is the site of normal impulse formation; and, on the other, that the auriculoventricular node and the tissue which joins it to the auricle is the upper end of the conduction system. These structures, situated at the mouths of the superior vena cava and at the coronary orifice (the representatives of the right and left ducts of Cuvier), have been regarded by Mackenzie (4) as homologous structures, or, at all events, portions of them. He calls the upper node or pacemaker the right-sided, the lower node or commencement of the conduction system the left-sided remnant of a ring of special tissue which, in the lower vertebrate heart, surrounds the sino-auricular orifice. Our observations lend support to this view, for we find, that in the dog the right and left vagus nerves have in certain degree a selective action, each acting most potently upon that remnant which it is suggested is homolateral with it.

In conclusion, we would draw attention to the general bearing of these and similar observations upon the view that rhythmicity and conductivity are separate functions of the same heart muscle. The strict separation of these functions as a mental concept is essentially Engelmann's (5) and is dependent upon his experimental observation that vagal impulses, awakened reflexly, may show an effect upon one and not upon the other. It seems to us more probable, in the light of modern studies, that these selective effects are rather the result of changes in the direction taken by the efferent impulses, and that the efferent limb of the arc may be now the right, now the left inhibitory nerve. The action of the nerve impulse then is upon tissues happening to be specially endowed with certain attributes, a selective action of anatomical rather than of physiological significance.

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