Observation on the Oscillatory Frequency and the Pulse Rate of the Salamander under the Influence of Low Barometric Pressure[1)]

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Introduction

In a series of experiments in which the influence of low atmospheric pressure on the physiology of animals was investigated the writers have been struck with the fact that the cold blooded animals, amphibians, insects etc. show great resistance against low barometric pressure. The chief reason which might account for this is, of course, the low metabolism of the animal which expends only a small amount of oxygen for living as compared with the higher animal. However, it is more than surprising that *Hynobius**, a kind of salamander native to Hokkaido can endure a pressure as low as 250 mm. Hg for longer than 2 days without fatal effect, losing only 0.3–0.4 grams of body weight.

Hereafter it is proposed to undertake some precise investigation of the acclimatization of this animal to low atmospheric pressure in the hope that much light may be thrown upon the general problem of physiology under low pressure. In the following pages the changes of frequency of the respiratory movements and that of the pulse of *Hynobius* at various stages of low atmospheric pressure will be described.

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* *Hynobius retardatus* DUNN, one and the same species of Urodelan Amphibia abounds in Hokkaido.

Method of Experiment

The apparatus (Fig. 1) employed for the experiment consists of a manometer (A) and a low pressure chamber of 1375 c.c. volume (B) in which the animal is placed during the experiment. A Geade's rotary vacuum pump (D) was used to draw out the air from the low pressure chamber. It has proved to be advantageous to regulate the pressure by means of a small chamber inserted between B and the vacuum pump and equipped with leading in and drawing out capillaries shown as C in the figure. These parts of the apparatus were connected with rubber tubes, the junctions being firmly tied up with copper wire and packed with the Ramsay-grease to make air-tight.

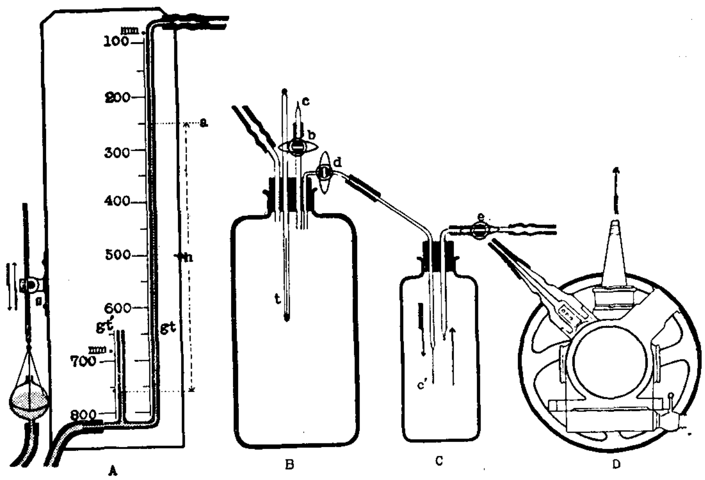

Fig. 1.

Before the experiment the animal was first anaesthetized in water containing 0.5% chloretone and then operated so as to make the heart visible externally. Particular care was taken to remove a part of the abdorminal skin close to the heart and not to touch the mesenterial membrane which bounds the thoracic cavity. The animal appeared not seriously harmed by the operation and behaved just as normal 2 days after the treatment at the time when the experiment was made. The lowest pressure in the experiment was 150 mm. Hg in all cases. The observation on the oscillation movement and the pulse rate of the animal in the low pressure chamber was made from outside.

Observation on the frequency of the pulmonary respiration and that of the oscillatory movement

It is known that the respiration of the land-living amphibians is effected by means of two different movements. The one is the oscillatory movement in which the animal constantly moves the skin of the lower jaw up and down to exchange the air in the buccal cavity for fresh through the nostril. The close distribution of the blood capillaries in the buccal or pharyngeal region is assumed to be provided for the respiration. The other one is the pulmonary respiration induced by the movement of the thoracic respiratory muscles, emptying the lung at first and at once filling it again with the mouth open. At the ordinary room temperature the former occurs about 140 times per minute on the average, while the latter appears generally to occur 5 to 6 times per minute. However, it was observed naturally under various conditions that both the oscillatory and the pulmonary respiration do not occur absolutely in regular frequency all the time. They are variable to some extent as such and subject to an individual variation.

It is noteworthy that GOTO (1934) showed very clearly in this salamander that the volume of gas exchanged through the skin amounts to more than half of the total including the buccal and pulmonary respiration. Therefore, the pulmonary respiration of the salamander seems not essential to the animal as compared with the other higher animals.

Experiment 1. In the experiment in which a male animal of 7.9 grams body weight was used, the frequency of the oscillatory movement was observed, first at succeeding stages of decreasing atmospheric pressure down to 150 mm. Hg and then at increasing pressures up to normal. In addition the frequency of the pulmonary respiration was observed at the various stages of the pressure but at irregular intervals. The time required for lowering the pressure to the minimum was 80 minutes. The animal remained at the minimum for 10 minutes. Then the air was gradually added to restore the original pressure within the course of 28 $^1/_3$ minutes. The results obtained are shown in the following table (Table 1).

Table 1

Pressure change (mm. Hg)	Required time (min. sec.)
761	0.00
650	3.55
550	8.30
500	11.28
450	15.00
400	19.20
350	24.46
300	31.25
270	37.14
250	41.37
230	46.46
200	56.05
180	64.20
160	74.05
150	80.00
Remained for 10 min.	
150	90.00
200	92.09
300	96.10
400	100.11
500	104.23
550	106.40
600	108.21
650	109.57
700	112.04
730	114.04
761	118.20

Oscillatory number per ½ min.	Pulmonary number per min.	Pressure (mm.) at the measurement
74	5	761
80	—	700
75	—	680
73	—	650
74	—	600
68	—	580
64	—	530
75	—	500
58	—	480
—	9	450
48	—	430
52	—	410
69	—	400
79	—	380
77	—	350
50	—	320
65	—	300
47	—	290
60	—	270
31	—	250
—	11	240
27	—	230
20	—	210
25	—	200
—	12	195
26	—	180
45	—	160
36	—	150

Oscillatory number per ½ min.	Pulmonary number per min.	Pressure (mm.) at the measurement
—	11	after 1 min.
38	—	,, 3 ,,
64	—	,, 4 ,,
64	—	,, 5 ,,
—	10	,, 6 ,,
36	—	,, 8 ,,
41	—	,, 10 ,,
56	—	210
47	—	260
41	—	310
—	12	325
37	—	360
69	—	400
27	—	450
29	—	500
36	—	550
68	—	600
32	—	650
39	—	700
—	8	730
69	—	761
—	6	after 1 min.
65	—	,, 3 ,,
64	—	,, 5 ,,
60	—	,, 7 ,,
—	6	,, 8 ,,
64	—	,, 10 ,,

Temperature, 20.3—20.6°C

A glance at the table shows that the oscillatory frequency decreases gradually keeping pace with the decrease of the atmospheric pressure while the number of the pulmonary respiration increases towards the minimum pressure. At the normal barometric pressure the number of the lung respiration is 5. The former decreases to 96 at 430 mm. Hg while the latter increases to 9 at 450 mm. Hg. At the lowest pressure the oscillation becomes almost one half of the initial number, showing 72 per minute. On the contrary, the frequency of the pulmonary respiration doubles, giving 11 movements per minute. During 10 minutes stay under the influence of

150 mm. Hg, the oscillation shows some irregular frequency becoming sometimes 128 and sometimes 72 in number per minute. But in general it becomes less active in this depressed condition.

The pulmonary respiration at the lowest pressure keeps a constant frequency of 10 in number per minute. At the ascending series of pressure the frequency of both the oscillatory and the pulmonary movements approaches gradually to the original state until at last it gains 138 and 6 per minute respectively at the normal pressure. Approximately the same frequency may be seen at the corresponding stage of pressure in the increasing series as in the decreasing. Strictly speaking, however, there exists too great an irregularity in the oscillatory movement to allow any sort of general conclusion. At

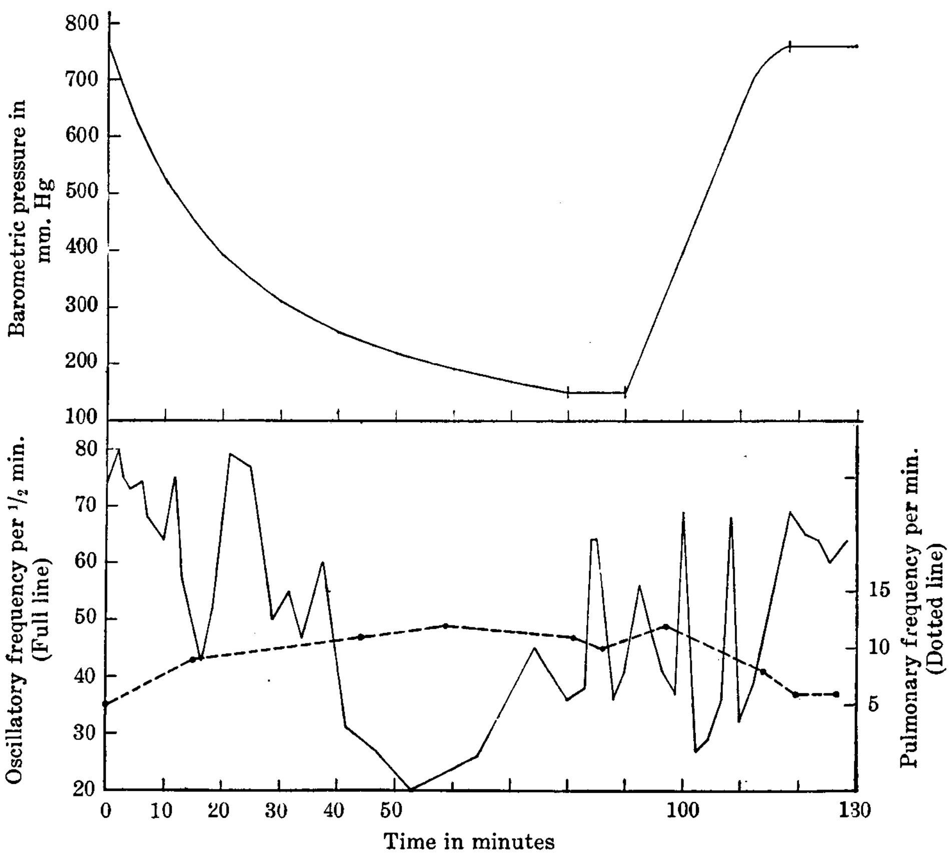

Fig. 2.

present one must be content with the mere fact that the movement becomes less active at the lower pressure in contrast to the irritated movement of the pulmonary respiration. The above data are expressed diagrammatically as foregoing (Fig. 2).

Experiment 2. The same tendency of the oscillatory movement in relation to the low pressure as in experiment 1 is shown in another experiment in which, a female of 7.3 grams body weight was used, as indicated in the following table and graph (Table 2 and Fig. 3). In this case a rapid rise of the pressure from the lowest was made instead of gradual increase.

Table 2

Pressure change (mm. Hg)	Required time (min. sec.)
754	0.00
700	1.46
600	5.55
500	11.27
450	15.01
400	19.20
350	24.48
300	31.50
275	36.16
250	41.40
225	48.27
200	56.15
185	62.05
165	71.27
150	80.00
Remained for 10 min.	
150 ↓ 754	90.00 ↓ 90.00

Temperature, 21.2—21.4°C

Oscillatory number per $^1/_2$ min.	Pressure (mm.) at the measurement
57	754
59	685
61	640
56	595
39	535
58	495
51	440
33	395
45	345
46	300
34	270
20	250
8	220
31	200
41	185
41	165
34	150
20 after 3 min. 25 ,, 5 ,, 19 ,, 7 ,, 15 ,, 9 ,,	150 mm.
41 after 0 min. 59 ,, 3 ,, 46 ,, 5 ,, 39 ,, 7 ,, 40 ,, 9 ,, 42 ,, 14 ,,	754 mm.

The depressed condition of the oscillatory movement at the low barometric pressure steadily recovered at the normal pressure in spite of the sudden rise of the pressure within a short period.

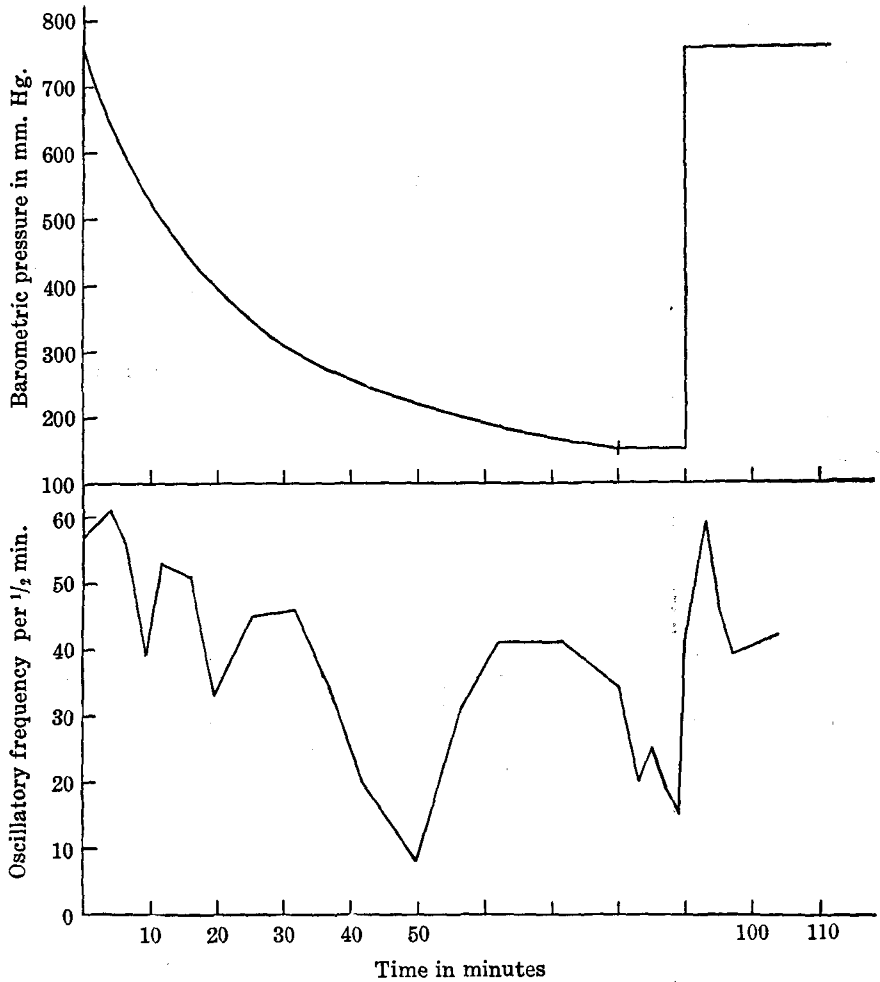

Fig. 3.

Effet of low pressure on the pulse rate

The frequency of the pulse in the salamander varies from 44 to 48 in number per minute at the normal atmospheric pressure at a temperature of about 20°C. Four series of experiments were carried out in which the pulse number was counted at different degrees of pressure.

Experiment 3. A male of 6.2 grams body weight was used. Seventy-nine minutes in this case were taken to reach the minimum pressure from the normal and 36 minutes to restore the original state. The results obtained are arranged in the following table (Table 3).

Table 3

Pressure change (mm. Hg)	Required time (min. sec.)
756	0.00
650	3.42
550	8.24
500	11.20
450	14.50
400	19.08
350	24.31
300	31.28
260	38.55
250	41.15
230	46.10
200	55.35
180	63.18
160	72.55
150	79.00
Remained for 10 min.	
150	89.00
200	90.58
300	95.04
400	99.10
500	103.25
550	105.45
600	108.19
650	111.07
700	114.50
730	118.05
756	125.00

Pulse number per min.	Pressure (mm.) at the measurement
48	756
50	690
50	620
50	590
51	560
51	540
55	510
52	480
52	460
51	440
52	420
53	390
53	370
54	350
53	320
52	300
54	280
53	250
54	230
53	220
53	200
57	190
54	180
58	170
54	160
55	150

Pulse number per min.	Pressure (mm.) at the measurement
59 after 3 min.	150 mm.
58 ,, 5 ,,	150 mm.
59 ,, 8 ,,	150 mm.
62 ,, 10 ,,	150 mm.
59	190
60	210
59	240
59	260
59	290
58	320
58	340
57	360
58	390
56	410
54	460
55	500
55	560
54	620
53	660
51	690
50	710
49	730
48	750
48	756
48 after 3 min.	756 mm.
48 ,, 5 ,,	756 mm.
47 ,, 8 ,,	756 mm.
46 ,, 10 ,,	756 mm.

Temperature, 19.3–19.6°C

Generally speaking the pulse number increases gradually as the pressure of the surrounding air decreases. At 756 mm. Hg which was the normal pressure at the time of observation it shows 48 and then at 390 mm. Hg it becomes 53 per minute. At the lowest pressure the pulse frequency increases to 55 per minute. After 10 minutes at

150 mm. Hg the frequency attains 62, but the irritated condition of the heart recovered by degrees with the rise of the pressure. Almost the same pulse number in the ascending series was counted as at the corresponding pressure of the descending series and at last the initial number at the normal pressure is attained. The state of decreasing of the pressure in relation to time, and the number of the pulse at the corresponding stage are shown graphically as follows (Fig. 4).

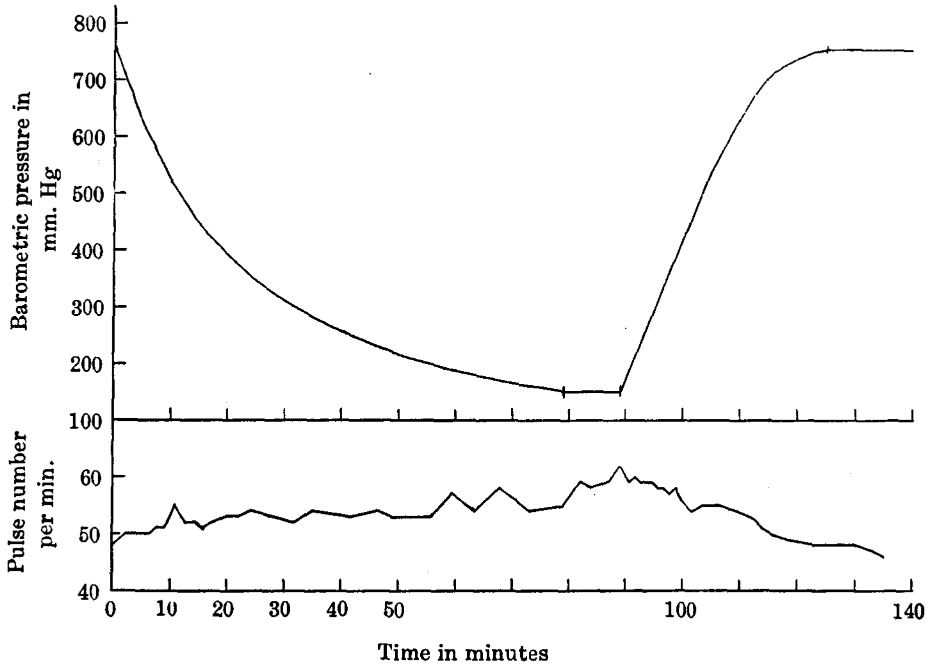

Fig. 4.

Experiment 4. In experiment 4 also a male of 6.8 grams body weight was used. It took 80 minutes to make the pressure as low as 150 mm. Hg starting from normal atmospheric pressure and 35 minutes were used to restore the initial state in the ascending series. The result of the observation is given in the following table (Table 4).

Table 4

Pressure change (mm. Hg)	Required time (min. sec.)
759	0.00
660	3.21
550	8.26
500	11.24
450	14.55
400	19.12
350	24.35
300	31.35
250	41.25
230	46.33
200	55.53
180	63 48
160	73.40
150	80.00
Remained for 10 min.	
150	90.00
200	92.05
300	96.06
400	100.13
500	104.26
550	106.42
600	109.09
650	111.53
700	115.24
730	118.14
759	125.00

Pulse number per min.	Pressure (mm.) at the measurement
47	759
51	640
57	580
59	530
61	460
62	430
58	400
63	370
65	340
64	320
63	300
62	280
61	240
58	220
55	200
56	180
55	155
53	150

Pulse number per min.	Pressure (mm.) at the measurement
54 after 3 min.	150 mm.
56 ,, 5 ,,	
55 ,, 8 ,,	
54 ,, 10 ,,	
56	190
61	270
60	310
60	370
57	430
58	460
59	510
57	560
55	610
53	670
52	710
51	759
48 after 3 min.	759 mm.
50 ,, 5 ,,	
48 ,, 8 ,,	
48 ,, 10 ,,	

Temperature, 20.1–20.5°C

It may be seen that there occurs rather an early influence of the low pressure on the frequency of the pulse even at the beginning of the experiment at the 370 mm. Hg pressure in which the number becomes 63. This number decreases a little, on the contrary, at the lower pressure and becomes 53 at the final stage. Curiously it increases again in the ascending series at around 370 mm. Hg and then decreases to the initial number at the end of the experiment. The occurrence of the maximum frequency around 370 mm. Hg but not at the lowest pressure may surely be ascribed to the individual character.

The above relation is clearly seen in the graph as given below (Fig. 5).

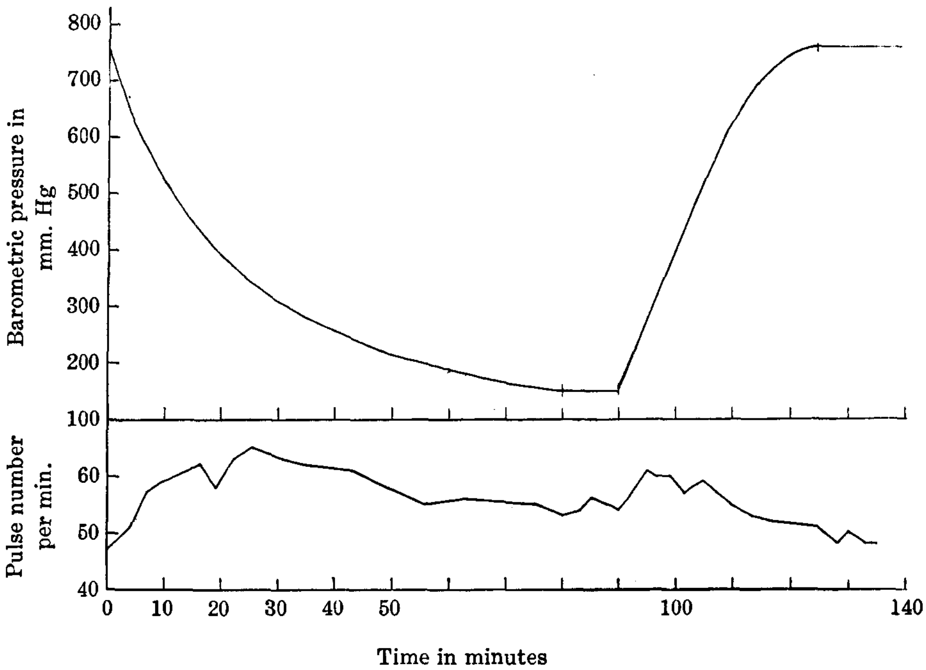

Fig. 5.

Experiment 5. A male salamander of 5.4 grams body weight was employed as the material. The initial pulse rate in this case was 44 in number per minute at 757 mm. Hg. From this stage it took 82½ minutes to attain 150 mm. Hg and then the restoring period lasted for 34½ minutes. The pulse rate at the different pressures is shown as follows (Table 5).

In the series of lowering pressure the number of the pulse increased steadily until it became 62 per minute at the lowest pressure where the animal remained maintaining the state of the irritated condition of the heart for 10 minutes. A gradual recovery to the original stage was brought about in the ascending series just as seen in the foregoing experiments. The relation may be seen clearly in the diagram (Fig. 6).

Pressure change (mm. Hg)	Required time (min. sec.)
757	0.00
650	3.47
550	8.24
500	11.23
450	14.58
400	19.22
350	24.52
300	32.02
250	42.11
225	49.06
200	57.24
180	65.49
160	76.07
150	82.30
Remained for 10 min.	
150	92.30
200	94.33
300	98.38
400	102.44
500	106.59
550	109.15
600	111.45
650	114.38
700	118.15
740	122.45
757	127.00

Table 5

Pulse number per min.	Pressure (mm.) at the measurement	Pulse number per min.	Pressure (mm.) at the measurement
44	757	59 after 3 min.	150 mm.
44	670	59 ,, 5 ,,	
44	630	61 ,, 8 ,,	
45	585	60 ,, 10 ,,	
47	540	58	215
48	490	60	265
47	440	61	315
46	390	58	365
48	340	55	415
48	320	51	470
50	300	50	520
51	270	47	570
52	250	46	615
55	225	45	665
58	200	44	710
62	185	43	730
60	180	41	757
60	170	42 after 3 min.	757 mm.
62	160	43 ,, 5 ,,	
62	150	42 ,, 8 ,,	
		42 ,, 10 ,,	

Temperature, 22.2–22.6°C

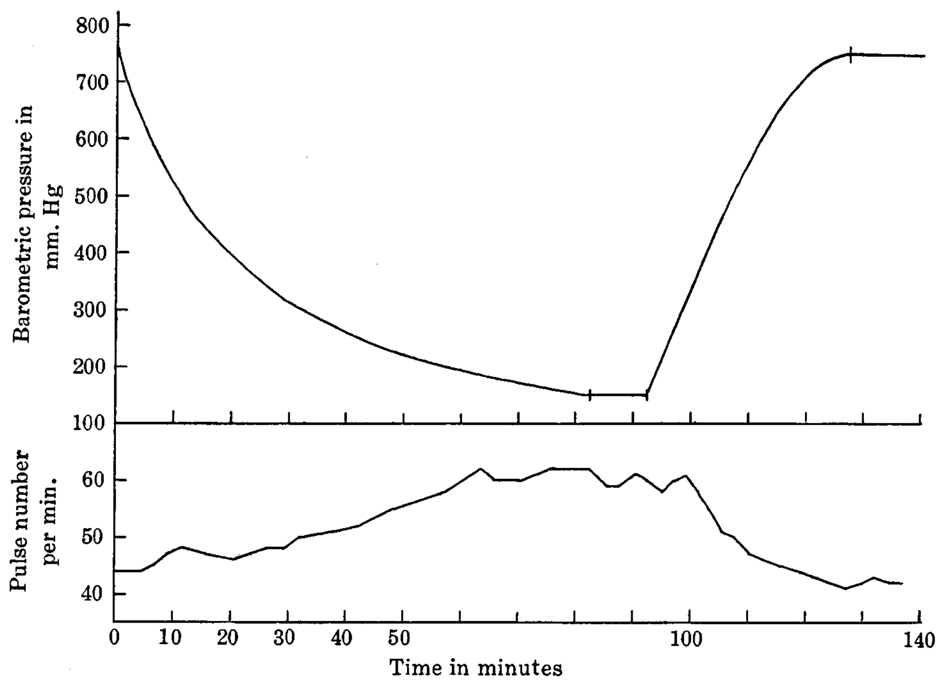

Fig. 6.

Experiment 6. A female of 7.3 grams body weight was used. The rate of the pulse at normal atmospheric pressure was 47 per minute. In the course of 80 minutes the pressure was lowered to 150 mm. Hg as before, but in this case a rapid restoration of the pressure was made. The pulse number at the various pressures is to be seen in the following table (Table 6).

Table 6

Pressure change (mm. Hg)	Required time (min. sec.)
754	0.00
700	1.46
600	5.55
500	11.27
450	15.01
400	19.20
350	24.48
300	31.50
275	36.16
250	41.40
225	48.27
200	56.15
185	62.05
165	71.27
150	80.00
Remained for 10 min.	
150 ↓ 754	90.00 ↓ 90.00

Temperature, 21.2–21.4°C

Pulse number per min.	Pressure (mm.) at the measurement
47	754
48	665
47	620
47	580
50	520
52	485
51	430
53	385
52	325
52	290
51	270
51	245
52	225
53	200
56	185
55	165
57	150
57 after 4 min.	150 mm.
59 ,, 6 ,,	150 mm.
57 ,, 8 ,,	150 mm.
57 ,, 10 ,,	150 mm.
59 after 0 min.	754 mm.
52 ,, 4 ,,	754 mm.
52 ,, 6 ,,	754 mm.
51 ,, 8 ,,	754 mm.
51 ,, 10 ,,	754 mm.
50 ,, 12 ,,	754 mm.
48 ,, 15 ,,	754 mm.

A gradual increase of the pulse frequency resulted, as before, from the lowering of the pressure. At 150 mm. Hg pressure the pulse became almost constant showing 57 in number per minute, which is an increase of 10 as compared with the initial. At the ascending pressure a rapid recovery of the pulse frequency was obtained with the sudden rise of the pressure. The graph shows the relation clearly (Fig. 7).

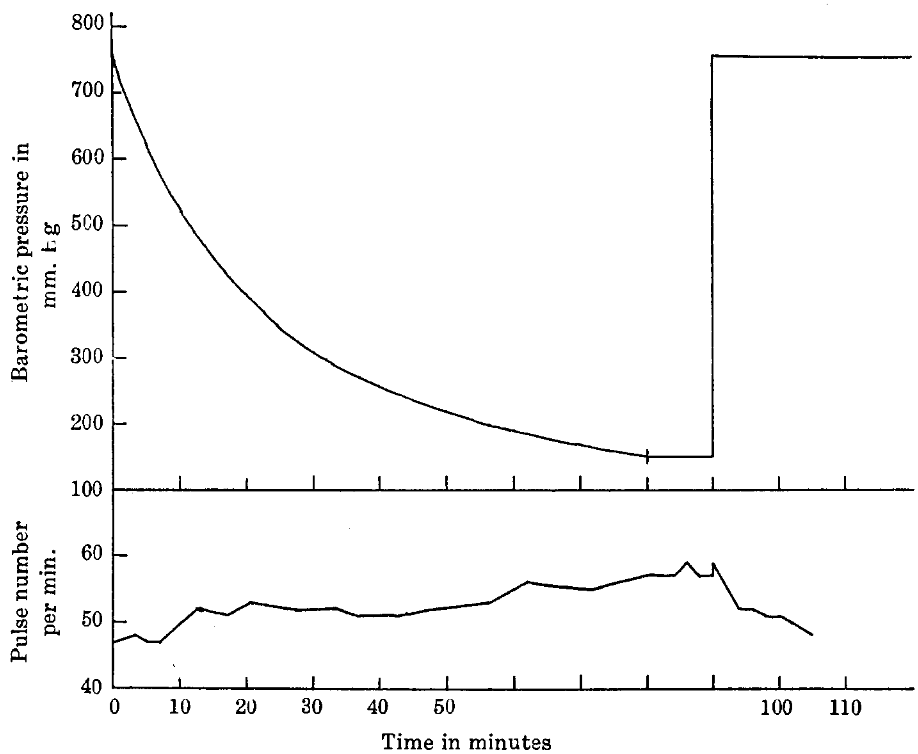

Fig. 7.

Conclusion

The oscillatory movement should be important only inasmuch as it may have significance in relation to the respiration of the buccal cavity. Apart from the report of MARCACCI (1894), that of BETHGE (1896) and that of BARROWS (1900) who attach great importance to a supposed buccal respiration, there has been no exact investigation which supports the opinion, though the subject has become the topic of discussion at times. On the other hand, it is generally accepted that induced dyspnea is associated with the acceleration of the respiratory movement. This was the case in the above experiment insofar as it was concerned with the pulmonary respiration. As to the oscillatory movement it has been shown, on the contrary, that it is depressed at low atmospheric pressures. Therefore, the oscillatory movement seems to come under the influence of some centre of irritation other than that of the respiratory movement of the lung. It is highly probable that the oscillatory movement is not of vital importance in relation to the respiration of the salamander.

BERT (1878) showed for the first time by exact observations that the pulse rate increases at the low atmospheric pressure in association with some physiological abnormalities, but oxygen administrated during the decompressed experiment overcomes at once the abnormal symptoms. There followed a dozen or more investigators, such as ZUNTZ and SCHUMBURG (1896), LOEWY A., J. LOEWY and ZUNTZ (1897), SCHRÖTTER and ZUNTZ (1902), COHNHEIM (1903, 1912), LOEWY (1932) TOZUKA, YAMAGUCHI and HATANAKA (1936) etc. who have ascertained that the pulse frequency increases with the decrease of the atmospheric pressure. The acceleration of the pulse rate under low barometric pressure is, on the other hand, closely associated with the depressed condition of the respiration (in cats and dogs, BAINBRIDGE 1920; and in man, BERT 1878). In this respect BAINBRIDGE's experiment on cats and dogs is considered fundamental in interpreting the phenomenon. According to him the tone of the cardio-inhibitory centre is modified by changes in the reaction of blood whose pH value is decreased by a fall of respiration and thus the respiratory movement possibly influences the pulse rate. Insofar as an animal such as the cat is concerned in which the cutaneous respiration has almost no bearing upon the case, the relation between the respiration and the pulse rate is somewhat complicated. However, it is clear that dyspnea at low atmospheric pressure causes the irritation of the circulatory system which in turn brings about the acceleration of the pulse rate.

This is a little different in the case of the salamander. As mentioned before GOTO (1934) laid stress on the cutaneous respiration of the animal which should be effected mainly by the subcutaneous blood vessels. Therefore the writers of this pâper are not convinced at present that the changes in the circulation caused by the depressed lung respiration under the influence of low atmospheric pressure directly regulate the pulse rate. In short, in the case of the animal of great cutaneous respiration the acceleration of the pulse rate may be brought about by the direct influence of low pressure through the skin, as does occur through the lung in the case of the animal with almost exclusively pulmonary respiration.

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