V. *Observations on the Respiratory Movements of Insects. By the late* William Frederick Barlow, *F.R.C.S. Arranged and communicated by* James Paget, *F.R.S.*

Received August 20,—Read November 16, 1854.

THE following essay contains the greater part of a series of observations, made between 1845 and 1850, by one whose recent death deprived physiology of one of its most earnest truth-loving students. The papers, as left by their author, and committed to me by his father, contained little more than a record of the observations. I have arranged them to illustrate certain general facts, and have added some of the conclusions which they plainly indicate. I have felt the more justified in making these additions, by the belief that my intimate friendship with Mr. Barlow would enable me to write what he would have written, had his life been spared. And in communicating his researches to the Royal Society, I believe I am fulfilling the design with which, not long before his death, he was preparing them for publication.—J. P.

Natural respiratory movements of the Dragon-fly (Libellula).

From nearly all the following observations it may be gathered that these movements constantly vary, in both rate and force. Volition and emotions, changes of temperature and of light, account for many of these differences; and it might have been inferred that, on these disturbing causes being removed, there would be a great uniformity in the mode of breathing, if care were taken that observations should be made with strict regard to sameness of circumstances. It is not so, however; the respiratory movements become much more equal, but they are very far from maintaining true equality of rate and force, even within a short given period. They have times of acceleration and of decrease, which it is hard to account for. Within three or four minutes, even, their speed and strength will vary, although the insect be kept in unbroken quiet. And if different individuals be compared, it does not appear that the vigour of each insect, or the probable length of its life, can be calculated by the force of the respiratory movements.

One of many similar observations may illustrate these statements.

Experiment i. May 19, 1848.—I watched a dragon-fly (*Libellula depressa*) which had been caught the day before. Just before its capture it was pursuing its prey, and flying very swiftly, in all directions, in the sunshine. The temperature was moderate, and there was a slight breeze stirring. The respiratory movements corresponded with the activity of the insect, and were very quick and vigorous. I placed it under a glass, and noted its state on the following morning. The insect had

been free from any source of disturbance; the room was but faintly lighted; the temperature of the air was 52° FAHR.; circumstances which would have led me to anticipate that it would be in a very sluggish condition. I found it completely quiet, and making no respiratory movements which were visible on my first noting it. A touch aroused it somewhat, and it began to respire visibly, and to move voluntarily for a time or two; but it soon seemed like a thing half torpid, and ceased to move. I continued to observe it:—at one time it made plain respiratory movements; then, the force of these diminished, and they appeared to cease; and this train of circumstances was repeated several times, although great care was taken to maintain unchanged all the external conditions in which the insect was placed.

I afterwards proceeded to try the effects of mechanical irritation of the insect. On touching it with a feather between the points where the wings are attached, the wings moved rapidly several times;—I think in an involuntary manner, for I have produced precisely such movements, by similar means, in the decapitated dragon-fly. At this time the respiratory movements were lively and powerful; but they remained so for only a few seconds. I counted eleven in a quarter of a minute, but only three or four very feeble ones in the immediately following half-minute; then they became a little accelerated, but were very soon again impaired, and could not be perceived any more for some time.

An hour later I again watched the insect, which had been kept covered with a glass basin. Sometimes the respiratory movements were unseen; sometimes they were very slow and feeble; sometimes they were quick and strong; though, all the while, the insect did not stir.

The influence of excitement and mental emotion, mentioned in this observation, was again noted in many of the following. In all cases, voluntary efforts and agitation, of whatever kind, provoke the respiratory movements when they are too faint to be observed, and accelerate and strengthen them when they are already evident. But that variations of the movements are not wholly due to those of the mental state, will appear from the experiments that show similar variations in decapitated insects.

In like manner, the variations in the respiratory movements, according to the temperature of the insect, the accelerations with the rise, and the retardations with the fall of temperature, may be observed, in some measure, in those that are decapitated.

Influence of Decapitation on the Respiratory Movements.

The effects of decapitation, involving the removal of the supra- and sub-œsophageal ganglia (the analogues of the brain and medulla oblongata) of the insect, vary accordingly as the head is removed by a sharp instrument, or is suddenly crushed. In the latter case, the influence of 'shock' is added to that of the removal of the ganglia. In the following observations the head was severed with as little violence as possible:—

Exp. ii. Sept. 1, 1845.—I took a recently caught dragon-fly, and twice counted

its respiratory movements; they were at the rate of sixty-four in a minute. I then separated the head of the insect with a sharp knife. There ensued convulsive movements of the body, and gaspings of the head: the respirations were fifty in the minute; but after the lapse of four minutes, they were reduced to thirty-eight, and after four more minutes to thirty-five; the respiration was performed more feebly than just after the head's removal; and in ten minutes it was reduced to thirty-one times in the minute. During all this time the insect was still, unless it was touched; then movements of the wings ensued. Fæces were spontaneously passed.

I now left the insect, and on returning in an hour, found the respirations in number as before, and quite as powerful. It lay in a tranquillity in which no motions but those of its breathing could be seen, and to one unobservant of the removal of the head, it would have seemed as if sleeping. Fæces were occasionally passed. Four hours later the breathing was feebler, its number being the same: the gaspings of the separated head, when it was touched, had less vigour; on my drawing a feather lightly over the surface, the legs retracted; slight movements of the wings also could be thus occasioned.

Fourteen hours elapsed before I renewed my observations. The insect was now respiring at the rate of twenty-six in the minute. Reflex movements could be yet excited in the body, but the head was quiet in spite of stimulus. In six hours more, the respiratory movements were still twenty-six, and regular. Eighteen hours later, they were still discernible, though very faint.

Exp. iii. Oct. 2.—I counted the respirations of a dragon-fly when it was tranquil, and found them 108 in the minute. I removed the head, and found them forty. Ten minutes afterwards they were fourteen: they were quite equable, and continued at this rate for some time longer.

Exp. iv.—The respiratory movements of another insect were sixty. On the head being removed they were twenty-five, and most regular. Ten minutes passed, and they were fifteen. Half an hour later they were seventeen, and feebler. In another instance they were reduced, on decapitation, from sixty-six to twenty-nine.

The foregoing experiments show that the effect of decapitation is always to diminish the frequency of the respiratory movements of the insect. They are confirmed by those which follow; but these prove other facts also; and first, that the irregularities in the mode and rate of breathing, which are noted in the natural respiration of the insect, are equally observed after decapitation, and are therefore not to be assigned to the will, or any mental state.

Exp. v.—On a day when the temperature was 59° Fahr., I counted the respirations of a cricket, in several minutes, with intervals of a quarter of a minute between each two. They were 84, 106, 79, 64, 59, 90. On the head being removed, they were 19, 27, 28, 20, 19, 14; and were less vigorous.

Exp. vi.—In a temperature of 52° Fahr., the respirations of another were counted like those of the last, and were 90, 70, 73, 72, 50, 62, and unequal in force as well as

in rate. The head was removed, and they became 29, 20, 14, 11, 11, 14, and were considerably reduced in force. In another insect they were reduced from 56, 37, 46, 40, 37, 36, to 20, 14, 12, 11, 9, 6.

Exp. vii.—I counted the respirations of a dragon-fly eleven times, in as many minutes, with intervals of a quarter of a minute between each two. They were 100, 101, 98, 100, 110, 106, 108, 108, 108, 108, 106. I then removed the head, and numbered the respirations in the same manner again, and found them 55, 61, 70, 70, 66, 70, 68, 67, 70, 70, 62.

The evidence of all the foregoing observations, proving the diminution, in both rate and force, of the respiratory movements when the head is removed, may serve to illustrate the admitted correspondence of the supra-œsophageal and sub-œsophageal ganglia of the insect, with the brain and medulla oblongata of the vertebrate animal. But that these movements should be only diminished, and should not cease, as they do when, in a vertebrate animal, the medulla oblongata is destroyed,—this may be regarded as indicating that there is, in the insect, a multiplication and diffusion of the nervous centres for the respiratory movements, corresponding with the plan of multiplicity in the respiratory organs. The same conclusion may be derived from experiments, which will be related, of the effects of dividing the body into segments.

Influence of Shock *on the Respiratory Movements.*

Exp. viii. May 11, 1848.—Wishing to ascertain the effects of shock upon the respiratory movements, I took a dragon-fly (*Libellula depressa*) which had been caught the day before, and was breathing pretty vigorously, between forty and forty-five times in the minute, and crushed its head completely and suddenly. There followed perfect stillness; the respiratory movements were quite indiscernible, until between three and four minutes had passed; then, they could be just seen; but they soon ceased again. After about four minutes more had elapsed, the respiratory movements were marked with rather more power, and persisted; but they were as yet very faint and unequal. In two hours, though they continued, they were still without vigour; and so they remained twenty-four hours later.

Exp. ix. May 13, 1848. Temperature 64°.—I took a dragon-fly, which was breathing at the rate of thirty-six, and crushed the head and upper part of the thorax. The respiratory movements ceased, but in less than a minute were resumed; they were, however, very feeble and so remained. In about eight minutes from the infliction of the shock, the movements were at the rate of thirty-nine, but their power was exceedingly diminished, and they required minute watching to observe them properly.

Exp. x.—I crushed the head and thorax of a dragon-fly; the respiratory movements ceased for two minutes. At the same time, another, while in full activity, was struck a sharp blow which inflicted a like injury. The respiratory movements stopped instantly, were suspended for many minutes, and never recovered any degree of power.

Exp. xi. May 22.—To another dragon-fly whose respiratory movements were similarly feeble, after recovering from the shock of crushing the head, I applied stimulus by holding it over water of the temperature of 185° FAHR., and the strength and frequency of the movements were greatly increased.

Exp. xii.—In a dragon-fly, which had been decapitated and was breathing distinctly at the rate of sixty-three, I crushed the last two abdominal segments. For a minute and a half the respiratory movements were but dimly visible; then they revived gradually. This shows the retrograde influence of shock.

These experiments, while they confirm those which illustrate the influence of mere decapitation, prove also that the influence of shock, *i. e.* of sudden violent destruction of a part, is essentially the same in the insect as in the vertebrate animal. They show that the separation and evident distinctness of nervous centres do not so dissociate the parts, with which they are severally connected, as to place any of them beyond the influence of the injuries inflicted on the rest. And yet, while these effects of shock may prove the mutual relations of the several ganglia, the following experiments on the division of the body into segments may show how each ganglion is the centre for the respiratory movements of its own segments.

Respiration in the separate segments of the Insect.

Exp. xiii. Sept. 7, 1845.—I decapitated a dragon-fly, which was breathing vigorously at the rate of fifty-five in a minute. In five minutes the respiratory movements were forty-two, and considerably less forcible than before the decapitation. Eight minutes later they were thirty-nine. I now divided the abdomen of the insect into three segments, with care to produce as little shock as possible. At first I could discern respiratory contractions in that division alone which was attached to the thorax, and I waited as long as seven minutes before I could distinguish them in the remaining segments; and now, in all, they were very weak in comparison with those in the thorax, and still more so in comparison with what had been noted in the perfect insect. Had this been owing to shock, they would probably have been restored; but twenty minutes later they were still indistinct, and at times imperceptible. The superior division continued to respire by far the most strongly. On placing the middle segment in my hand, the movements became, in about a minute, very distinct, and increased to the rate of 100 in the minute; but, on replacing it on the table, they became again obscure, and soon imperceptible. Three hours after the operation no respiratory movements were observable, nor could any be excited, though the legs of the insect could be excited to retraction.

Exp. xiv. Oct. 14, 1845.—I took a small dragon-fly, which was breathing powerfully at the rate of 116 per minute, the movements being possibly quickened by emotion. On removing the head, they were diminished, in one minute, to fifty-eight (just half the former frequency), and were much weaker. I divided the abdomen into two equal parts. The respiratory actions ceased awhile; but the effects of the

shock beginning to subside, they became apparent. In ten minutes they were more feeble but plain, and could be observed in both divisions. I could not succeed in counting those in the upper half; but fifteen minutes later they were fifty in the lower half. Two hours and a half after the segmentation, the respiratory movements were still visible.

Exp. xv. Oct. 14.—I counted the respiratory movements of a dragon-fly, of the same kind and size as the last. They were only sixty; and the difference is curious; for the two insects were caught together, and examined in the same manner, and in the same hour. On removing the head, the respirations were reduced to forty, and became much less distinct. The abdomen was bisected, and the respiratory movements ceased in it. In ten minutes they were renewed, but most faintly and slowly, and in the lower half alone. On breathing on the upper half, it contracted languidly for a few moments and then became motionless again.

Exp. xvi. June 29, 1846.—At a quarter before 2 P.M. I ascertained the respirations of a dragon-fly, while it was calm and at rest, to be thirty-two. Then I removed the head, and involuntary movements of the body, wings, and legs were noticed, which in a little while ceased, but were renewed, at pleasure, by excitation. In five minutes the respirations were reduced to twenty-eight, and were less powerful. The abdomen was now divided into three equal parts, two complete segments being in each. The respiratory movements were well-marked in both the upper divisions, most strongly in the uppermost; in the lowest, or caudal division, they were not observable. In the uppermost division of the abdomen, the respirations were at the rate of thirty-two; in the middle division, at the rate of forty-eight in the minute; in the caudal division, they were not excited even by breathing on it.

At half-past two the respiratory movements in the parts of the abdomen were feebler; in the thoracic division, they were still twenty-eight; in the middle division, fifty-two. At half-past three, the only respiratory movements discernible were those of the upper division; but they were much weaker and only twenty-four. Powerful respiratory contractions were excited by very lightly drawing a sharp point down the dark mesial line of the abdomen; and an incurvation of the body, and a peculiar movement of the legs towards the part irritated, were observed. At a quarter past seven the respiratory movements had ceased, but were renewed, though faintly, by breathing on the upper divisions of the abdomen. It was not easy to say why the caudal division did not respire, for its excito-motory power was not extinguished; it could be excited to motion, and fæces were expelled by it.

Exp. xvii.—The subject of this experiment was a lively dragon-fly, which breathed at the rate of thirty-five. The head was removed, and the respirations, which did not pause perceptibly, were forty-two. In five minutes, the respirations being at the same frequency, the abdomen was divided into three nearly equal parts. The caudal division breathed powerfully; the thoracic feebly; the middle one not at all. I placed this motionless part in my hand; in ten minutes it revived, and breathed at

the rate of forty-eight. It was laid on the table, and in ten minutes it ceased to respire. In the other segments the breathing went on languidly, and soon ceased entirely.

The foregoing experiments, on the effects of dividing the abdomen of the insect, are confirmed in their evidence of the several ganglia being the centres, each in its own segment, of the respiratory, as well as of other involuntary movements, by some that show the influence of chloroform and ether.

Having ascertained that the complete immersion of insects in the vapour of chloroform or sulphuric ether quickly suspends the power of voluntary, and then of the respiratory and other involuntary movements, I wished to learn the influence of these liquids applied in a more limited manner.

Exp. xviii.—In a dragon-fly (*Libellula vulgata*), which was respiring vigorously, I completely suspended the respiratory movements by moistening the under surface of the abdomen with a camel's-hair brush dipped in chloroform. The insect remained quite lively; and though so much of its respiratory movement was thus checked, yet no difference could be observed in the strength or activity of its voluntary actions.

In another, I suspended the abdominal respiratory movements by a similar application of chloroform, but it was so little affected in its general motor power that it took flight on being released from the hand.

In another, I suspended the respiratory motion of the two upper segments of the abdomen, by applying chloroform to them alone. The other segments remained in action, till, by similarly moistening them, segment after segment, I gradually stayed the action of them all.

These effects were not due to the tracheæ being filled with liquid. None like them were produced by immersing dragon-flies in water; for in this liquid the respiratory movements continue vigorous, and are accelerated when the water is of high temperature. On the other hand, the same suspension of respiratory motion ensues when only the vapour of chloroform is locally applied. I put about five drops of chloroform into a glass bottle, and tied a piece of white leather tightly over it; and then, through a small hole in the leather, I passed only the abdomen of the insect into the bottle. When, in a minute, I withdrew it, the respiratory movements had altogether ceased; but the insect remained conscious, and could be readily excited, presenting then the curious spectacle of the legs and wings quickly moving, while not a breathing movement could be seen. In a few minutes very slight respiratory actions became visible; and they were gradually restored to nearly their former rate and power. I then repeated the experiment, with the same result.

It might be certainly anticipated, from these experiments, that destruction of all the ganglia would abolish all respiratory movements; but it seemed right to determine the point by experiment.

Exp. xix.—I decapitated a dragon-fly (*Libellula vulgata*); there were still vigorous respiratory movements, thirty in the minute; and the most lively reflex actions were

produced by mechanical irritation, especially by irritating the last segment of the abdomen. I cut off this segment, and then introduced a long pin, which I moved up and down cautiously, with the view of destroying the ganglia, taking care not to injure the abdominal walls. The respiratory movements ceased entirely, and were not renewed; it became impossible, also, to occasion reflex actions by irritating the abdomen.

This experiment I have twice repeated with the same results.

Influence of Temperature and Galvanism on the Respiratory Movements.

The respirations of the dragon-fly present the same variations in vigour, as do the other movements, and the whole apparent life, according to the temperature of the medium in which it is placed. A kind of sleep overcomes the insect in the cold nights of autumn, after which it is found numb and motionless upon hedges, appearing as if dead, but easily revived by the sun's heat, or by artificial warmth. At these times its breathing is probably often suspended for a long period; and were it not that (as the following among many experiments show) the movements can be renewed after long suspension, the insect would be much more short-lived, and would perish at any considerable fall of temperature.

Exp. xx.—I put a dragon-fly (*Libellula depressa*), which was breathing at the rate of about forty-five in the minute, into water of the temperature of 100° F. The respiratory movements increased to 110. On removing the insect, and exposing it to the air, they were reduced to fifty. On replacing it in water of the same heat, the respiration again became greatly accelerated, but very quickly ceased, and was not renewed for a long time.

Another dragon-fly, breathing at the rate of thirty-five, was put into water at 90°, and its respiratory movements were raised instantly to seventy.

Exp. xxi.—I put a dragon-fly into a freezing mixture at 33°, and kept it in for thirty seconds. When taken out it was not respiring, but in less than a minute began to respire at the rate of thirty-five in the minute. I again immersed it for nearly three minutes. The respiratory movements this time ceased much longer and were more gradually renewed. The general activity of the insect was also more deeply affected. At first it seemed nearly insensible, and its voluntary movements were few and sluggish; but by degrees it became active. When it was breathing faintly and irregularly, in consequence of its exposure to the cold, I put it into water of the temperature of 98°. The respirations rose to 108, but they were still feeble, and the insect showed considerable excitement.

Exp. xxii.—The temperature of the air being 70° F., I put a dragon-fly, which was breathing vigorously, into water at 34°. After two minutes I removed it, and all movement had entirely ceased; but in a few minutes the respiratory movements were renewed, and it quickly recovered. I immersed it again with the same result. Afterwards, having let it remain for half an hour, I galvanized it while it was perfectly

motionless and insensible, and produced both respiratory motions, and movements of the legs and wings*.

The dragon-fly is very susceptible of galvanism; but if the wires be applied to the outer surface of the insect they produce little effect, because it is so bad a conductor. In all the experiments, therefore, from which I have drawn any conclusions, I first removed the head of the insect, and then, placing its under surface uppermost, passed a pin through the centre of the most anterior part of the thorax, and another through the last segment of the abdomen, and then fixed the insect to a table or flat piece of wood. I thus obtained a ready conduction for the galvanic current, when the heads of the pins were touched with the wires of the battery, and had the insect in a convenient position for observing its movements.

In regard to the influence of galvanism on the respiratory motions (to which alone, as in the former observations, I shall here refer), its almost constant effect is to accelerate them. I have, by its influence, increased the respirations from thirty to 150 in the minute, but a less increase (*e. g.* from thirty to fifty) was more usual. Sometimes, while galvanising in the method described above, I have observed an almost persistent respiratory contraction, so long as the current was continued; and on breaking the current, the respiratory relaxations and contractions alternated as before.

The effects of galvanism on the respiratory movements are well seen when the insect has been influenced by chloroform. For example, I exposed a recently caught dragon-fly to chloroform vapour. Soon, sensibility and all motions ceased, including the respiratory. I tried many plates of a trough excited first by water, and then by acid, but equally without effect; but having waited till the respiratory movements were resumed, I again employed the same power, and excited the contractions as often as I chose, making them much more powerful than they were when not thus stimulated.

The following chief conclusions may be drawn from the series of observations that have been related:—

1. The respiratory movements of dragon-flies (and probably of other insects) are naturally subject to considerable and frequent variations in force and rate, the causes of many of these variations being as yet unknown.

2. The respirations are always quickened by exercise, emotion, rise of temperature, galvanism, and mechanical irritation; and the last three agents quicken them in the decapitated, as well as in the perfect insect.

3. The respiratory movements of each segment of the trunk are, in some measure,

* In these experiments the changes of temperature were produced by submersion in water; but many others showed that submersion in water of the same temperature as the air produced no similar effects, and that those here described were equally produced in air of similarly varied temperature.

independent of the rest: they may be performed in separate segments, provided their nervous ganglia and cords are entire, and not paralysed by such influence as that of chloroform or ether.

4. The removal of the head, including the supra- and sub-œsophageal ganglia, does not, like the removal of the medulla oblongata of the vertebrate animal, put a stop to the respiratory movements, but diminishes their frequency and force, and deprives them of all influence of the will and of mental emotions.

5. The shock inflicted in the sudden destruction of the head, or of the terminal part of the abdomen, generally stops all the respiratory movements for a time, and greatly enfeebles them during the remainder of the insect's life.

6. The general tendency of the observations is to corroborate the opinion of the self-sufficiency of the several ganglia for the movements of their appropriate segments, and, thus far, of their essential independence; at the same time, their mutual relation and influence are proved by the co-ordinate similar movements of the segments, and by the diffused influence of shocks.